area of the cortex, and in the medial brain stem, the physiological correlate of waking with respect to neuronal discharge is a change in pattern rather than an increase in total amount of activity.

The change in pattern of unit discharge supports the concept of Bremer (*11*) that "wakefulness should also permit the differentiation of cortical receptions which is necessary for perceptual integration."

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28 September 1961

Spatial Discontiguity in Monkeys with Lesions of the Frontal Cortex

Abstract. In learning a black-white discrimination response, the efficiency of rhesus monkeys with lesions of the anterior frontal cortex varies inversely with the spatial separation of the discriminative stimuli from the places of response and reward. Though there is a similar relationship in intact animals, impairment of learning due to discontiguity is greater in the animals with brain lesions.

Contiguity in space and time among elements to be associated has long been regarded as an effective condition for learning. This principle had recently been demonstrated experimentally for spatial contiguity in discriminative learning (*1*). Moreover, McClearn and Harlow (*2*) have shown that for normal rhesus monkeys, the probability of correct reaction decreases as the distance between relevant visual cues and the loci of reactions and of their outcomes increases.

Monkeys with anterior frontal lobe lesions are deficient in delayed-reaction responses (*3*) required by tasks in which critical cues are *temporally* separated from reactions and outcomes. Mishkin and Weiskrantz (*4*) have reported that the discriminative learning of monkeys with frontal lesions is also impaired (relative to that of control animals) by temporal discontiguities. The experiment reported here tested the effect of *spatial* separations on monkeys with frontal brain lesions. The testing procedure of the McClearn and Harlow experiment was replicated.

The four monkeys used in the present study and McClearn and Harlow's four monkeys had very similar histories. Both groups consisted of adult animals that had been tested continually for over 3 years. Both had had extensive training on discrimination learning set, delayed reaction, and a variety of other problems. Thus, both groups were well adapted to the general test situation. The surgery for the animals in this study (*5*) involved bilateral removal of the cortex rostral to the premotor area and frontal eye fields, similar to that described by French (*6*) for "Area 9" monkeys, but it also included the removal of cortex along the dorsal margin of the longitudinal fissure. One month after the operations, the monkeys were tested on 5-second direct, spatial delayed reactions, and they performed no better than would be expected by chance. This was in marked contrast with their nearly perfect preoperative scores on identical problems. Immediately after these preliminary tests, the monkeys were tested as described below.

The upright spatial contiguity board (*2*, Fig. 1) was mounted on the movable carriage of a Wisconsin General Test Apparatus. Two vertical channels, 2 inches wide, were symmetrically located on the board, 15 inches from center to center. At the bottom of each channel a wooden block with a 2- by 2-inch face could be pushed back by a subject to expose an underlying foodwell. The discriminanda (discriminative stimuli), also blocks with 2- by 2-inch faces, could be fixed in the channels at varying distances above the manipulanda (response blocks). The face of one discriminandum was painted black and the other white, while the rest of the display was a uniform gray.

Raisins were given as rewards for reactions to the manipulandum below the positive discriminandum; reactions to the other manipulandum produced no reward. Within a series of four noncorrection trials, the bottom edges of the two discriminanda were kept at the same distance (0, 1, 2, or 4 inches) above the top edges of the manipulanda. From series to series, the vertical separations were changed, with the restriction that each condition should appear once in each group of four consecutive series. The lateral position of the positive discriminandum was varied independently according to a Gellerman

Table 1. Total correct responses of four monkeys with frontal brain lesions during 20 days of discrimination testing. Each monkey was given a total of 320 trials for each condition.

Condition	Monkey			
	C	G	S	Z
0 inch	272	295	273	304
1 inch	245	275	218	274
2 inches	226	264	183	256
4 inches	194	263	179	214

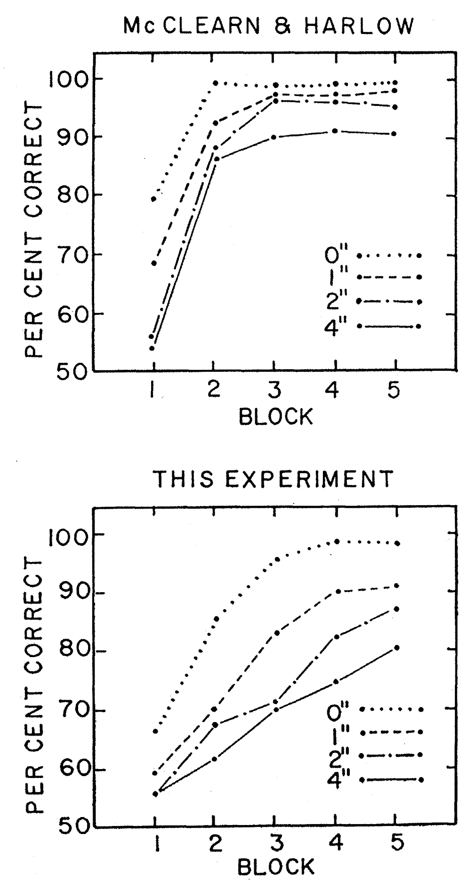

Fig. 1. Percentage of correct reactions by all animals as a function of successive 4-day periods (blocks) of testing during which each animal was given 64 trials for each condition. In both experiments four monkeys were used.

sequence (*7*). For 20 days each monkey was given 16 trials per day for each of the four conditions (a total of 64 trials per day).

The results of learning under the four conditions are shown in Fig. 1, where they may be compared directly with those obtained by McClearn and Harlow (*2*). Performance improved under all conditions in both studies. In the experiment reported here, the number of correct reactions increased significantly from the first to the last 4-day period (block) of training with each amount of separation (*8*).

Another parallel with the McClearn and Harlow data is the increase of correct reactions as the amount of separation decreases. Table 1 presents the overall performance of the animals under each condition. The exact probability that the rank order of difficulty should be the same for every subject is $(1/24)^4$ for my experiment (*9*). If results from the two experiments are pooled, this probability becomes $(1/24)^8$.

The only major disparity between the findings of the two studies lies in the relatively depressed performance of the monkeys with frontal brain lesions at each separation, differences which are statistically reliable (*10*). Thus, while the general findings of McClearn and Harlow are confirmed for monkeys with frontal brain lesions, the data are also in harmony with the previously noted deficiencies of these animals in learning situations with temporal discontiguities.

For monkeys with frontal brain lesions, the ability to learn is apparently impaired in those contexts in which contiguity relations, either temporal or spatial, are less than optimal. Their improved responses after practice suggest that the loss may not be permanent. Training procedures that would allow animals to achieve mastery of the easier conditions before the more difficult are attempted might well facilitate recovery from the effects of spatial separation just as they do from the effects of temporal separation (*4, 11*).

Riopelle and Churukian (*12*) report that when differential color is confined to areas at the centers of visual forms, both normal monkeys and those with frontal brain lesions discriminate less effectively than when only the borders of the forms are colored. The performance is least efficient among monkeys with brain lesions when only the center of a form is colored. The results may be explained in terms of the spatial relationships involved. Since the forms consist of plaques that the monkeys must move away from food-wells to obtain a reward, there is a relative lack of contiguity when colors are present at the center rather than at the edges of the forms.

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9. Since there are $4! = 24$ possible permutations of order, the likelihood that N subjects would show the same order is $(1/24)^N$.
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Tonic Immobility: Differences in Susceptibility of Experimental and Normal Sheep and Goats

Abstract. Tonic immobility ("animal hypnosis" or catatonic trance) could not be induced in 1-year-old foster lambs and kids. Control animals, conforming to a characteristic of their species, could be readily immobilized. The suggested explanation for this difference in behavior is that the foster animals did not develop a normal flight distance because of the ambivalent behavior of the "stepmother," who alternately permitted and refused nursing.

"Tonic immobility refers to negative or quiescent behavior even in the presence of disturbing stimulation" (*1*). While it is in effect, an organism makes no attempt to change position or struggle for freedom. Theories have associated the phenomenon with sleep (*2*), spacial disorientation (*3*), death feigning (*4*), and the paralysis of fear (*5–7*). Birjukov and Karmanova (*8*) consider tonic immobility to be a special form of internal inhibition, and Lobashey *et al.* (*9*) agree with Pavlov that the phenomenon is based on a process of inhibition in the motor analyzer related to unconditioned self-protective reflexes. Fear plus the physical prevention of flight, as in the capture situation, seem to bring on the response, which appears suddenly. This response has been described by such names as animal hypnosis, catatonic trance, akenesis, action inhibition, thanatosis, and death feigning (*10*).

A number of different animals, including cockroaches, lizards, fish, snakes, geese, ducks, chickens, pigs, horses, sheep, goats, foxes, hares, mice, guinea pigs, opossums, lions, and monkeys, are subject to tonic immobility (*11*). Animals too young to show the fear-flight response when approached are not susceptible (*7*), and adult animals tend to lose the response as familiarity with the human being increases (*6, 12*). If a food signal is coupled with a strong fear stimulus (loud rattle), chickens become less susceptible to tonic immobility, whereas increased periods of wakefulness increase the duration of the response (*9*).

In the experiment reported here (*13*), when nine kids and ten lambs reached physical maturity (1 year of age), they were subjected to the immobilizing procedure by the experimenter (M.S.A.), who had never seen them before and did not know which were control and which were experimental animals. Four of the kids and five of the lambs had been raised by foster ("step") mothers who had born young of their own which were removed at birth (*14*). None of the "stepmothers" immediately accepted the substitutes as if they were their own young, so there was a period varying from 3 to 30 days during which the new mother at times allowed the young to nurse but at times butted it. The young formed watchful, tense attachments to the mothers, and their persistent nursing attempts were only partially fulfilled. During the period of butting the mothers were confined by stanchions in rooms away from the rest of the flock or herd, but they were released daily long enough to find out if they still butted the young when free to do so. The foster mothers were released permanently as soon as acceptance was reasonably well established (that is, when it was certain that they would not injure the young by butting them), and by this time the young were adept at