1-26-1951

Influence of Handedness of the Application of Acetylcholine and Glutamic Acid to the Motor Cortex of the Albino Rat

Donald G. Doehring

INFLUENCE ON HANDEDNESS OF THE APPLICATION OF ACETYLCHOLINE AND GLUTAMIC ACID TO THE MOTOR CORTEX OF THE ALBINO RAT

By

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A Thesis

In partial fulfillment of the

Requirements for the Degree of

Master of Arts in Psychology

The University of New Mexico
1951

This thesis, directed and approved by the candidate's committee, has been accepted by the Graduate Committee of the University of New Mexico in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

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January 24, 1951

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Introduction and Statement of the Problem. Neurophysiologists have devoted much time to the study of the method of transmission of the nerve impulse. After the development of adequate electrical measuring instruments the best explanation of transmission seemed to be in terms of electrical changes. The impingement of a stimulus results in a depolarization of the cell membrane at the region of impingement. This depolarization in turn depolarizes the adjacent region of the neuron and so on, resulting in a difference in electrical potential which travels to an appropriate region of the nervous system. Later investigators found evidence of chemical transmission of impulses in certain parts of the organism. Further investigation revealed that the chemical involved could be found in other parts of the nervous system and a theory of chemical transmission of nerve impulses throughout the entire nervous system was formulated. The mode of chemical transmission which was discovered involves acetylcholine (Ach). The Ach theory did not supplant the electrical theory, but was used in conjunction with it. It was postulated that Ach aids in the electrical transmission of nerve impulses by acting as the agent which depolarizes the neuron membrane.

In explaining learning some psychologists make use of the nervous system and some do not. Those who do not

make use of the nervous system consider that it is best to postulate an "empty organism" and build up learning theories based on observation of the overt behavior of the organism. Despite the influence of such theories investigations of the neurology of learning have been carried on for many years. The immense structural complexity of the cerebral cortex possesses a great attraction for theorists who would like to explain learning in terms of the establishment of fixed patterns of cortical connections. The repeated passage of impulses through a certain part of the motor cortex, for instance, would lay down a neural "trace," which would make it easier for impulses to pass through that part of the cortex again. Since the motor cortex controls movements, the laying down of a trace or path in a certain area should make it easier for the organism to make the movements which are controlled by that area. Thus practice would result in the formation of more or less fixed neural pathways for impulses in the motor cortex.

Peterson thought that it would be worth while to investigate practice in terms of the establishment of neural connections. Since Ach facilitates the passage of nerve impulses, he thought that application of Ach to a specific area of the motor cortex might result in spontaneous firing of the neurons of the region. Practice is assumed to consist

in part of neural action in a specific cortical area; therefore the application of Ach to a specific area might act as practice for the movements controlled by that area. Preferential handedness is a relatively simple and clear-cut movement pattern. Peterson had located the cortical handedness area of the rat and had shown that handedness preference can be influenced by forced practice in the food situation.[1,2] Therefore he thought that if application of Ach to the handedness area of a rat's cortex resulted in a swing over to the use of the contra lateral (non-preferred) limb it would provide evidence for a neural explanation of practice.

The first investigation carried out by Peterson consisted of the application of Ach to that motor cortex which controlled the non-preferred hand.[3] Both ambidextrous and single-handed rats were used and a certain amount of change in preferential handedness was noted in some of the rats. No control rats were used. Later investigations made use of

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[1]G. M. Peterson, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, 1934, 9, 1-67.

[2]G. M. Peterson, "Transfers of Handedness in the Rat from Forced Practice," Journal of Comparative Psychology, In Print.

[3]G. M. Peterson, "Changes in Handedness in the Rat by Local Application of Acetylcholine to the Cerebral Cortex," Journal of Comparative and Physiological Psychology, 1949, 42, 404-412.

Ach by itself and in combination with other chemical substances which had been found to prevent the breaking-up of Ach for a certain period of time.[4, 5] As yet none of these studies have produced consistently positive results.

The Problem. The purpose of this study was to repeat the experimental design used in Suess' study, i. e., to attempt to influence the handedness of ambidextrous rats by application of Ach and glutamic acid to the motor cortex.[6] This study was a slight departure from that of Suess in that more post-operational reaches were taken.

Importance of the Study. If Ach or glutamic acid or a combination of the drugs would cause a statistically significant transfer in preferential handedness it would give some indication of the role of the motor cortex in practice and justify further investigation along the same lines. Such investigations, if successful, would throw some light on the physiological processes involved in

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[4]G. M. Peterson and J. W. Rigney, "Influence on Handedness of Acetylcholine Locally Applied with other Chemicals to the Cerebral Cortex of the Rat," Journal of Comparative and Physiological Psychology, 1950, 43, 264-272.

[5]E. R. Suess, "Influence on Handedness of Local Application of Acetylcholine with Glutamic Acid to Cerebral Cortex of the Rat," (unpublished Master's thesis, The University of New Mexico, Albuquerque, 1949).

[6]Ibid.

learning.

Review of the Literature. I. Acetylcholine. As stated previously, an electrical theory was the first theory which seemed to fit the observed manifestations of neural activity. Chemical theories, however, had already been propounded for special cases of neural transmission. In 1905 T. R. Elliott suggested that an adrenalin-like substance might be liberated at sympathetic nerve endings which acted upon the effector cells.[7] Loewi, in 1921, found that when the vagus nerve leading to the heart of a frog was stimulated a substance could be found in the Ringer solution in the heart which would cause an effect similar to vagus stimulation, when applied to another heart. He called the substance "Vagusstoff," thinking that it was released from the vagus nerve. He also found that the effect of the Vagusstoff was heightened when it was used in conjunction with eserine.[8]

Vagusstoff has been identified as acetylcholine (Ach), an unstable ester of choline. It is formed from acetic acid and choline. Its structural formula is:

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[7]D. Nachmansohn, "The Role of Acetylcholine in the Mechanisms of Nerve Activity," Vitamins and Hormones, 1945, 3, p. 338.

[8]Ibid., pp. 338-339.

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[7]H. Beckmann, "The Role of Acetylcholine in the Mechanisms of Nerve Activity," Vitamins and Hormones, 1945, 3, p. 338.

[8]Ibid., pp. 338-339.

$$(CH_3)_3 = \underset{OH}{N} -CH_2-CH_2-O-COCH_3.$$

It is hygroscopic, very soluble in water and alcohol, and is easily decomposed by heat and alkali.[9] Ach is broken down by an enzyme, cholinesterase. The action of cholinesterase is impeded by eserine, explaining Loewi's results.

Dale and Kibjakow suggested that Act acted as a transmitter across ganglionic synapses and neuromuscular junctions, using as evidence the same type of experiments as those performed by Loewi. In all of these experiments Ach was considered to function in bridging the gap at synaptic junctions. The evidence used was the presence of Ach in perfusion fluid after neural stimulation.[10]

Nachmansohn approached the study of Ach from a different angle.[11] He reasoned that since cholinesterase hydrolized Ach, the presence of Ach in neural tissue could be inferred from the presence of cholinesterase, and the rate of removal of Ach could be inferred from the degree of concentration of cholinesterase in a given tissue. This method was used because of the difficulty of obtaining Ach from

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[9]Goodman and Gilman, The Pharmacological Basis of Therapeutics. New York: The MacMillan Company, 1941, p. 351.

[10]Nachmansohn, op. cit., p. 339.

[11]Ibid., p. 341.

neural tissue.

It was believed that a major objection to a chemical theory of transmission was that Ach could not be removed fast enough to account for the very rapid rate of conduction in certain parts of the nervous system. Nachmansohn showed in several experiments that the concentration of cholinesterase was high enough to account for a sufficiently rapid removal of Ach.[12]

Besides showing that Ach could be removed rapidly enough to account for rapid neural conduction, Nachmansohn suggested a new role for Ach.[13] Instead of acting as a synaptic transmitter he said that it acted along the membrane of the neuron in conjunction with the transmission of electrical current along the neuron. The increase in end arborizations at the synapse would create sufficient current to bridge the synaptic gap without postulating a special substance of transmission. The action of Ach along the neural membrane, then, was to increase the permeability of the membrane. In the resting state of the neuron the membrane is selectively permeable to potassium ions. When the

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[12] Ibid., pp. 341-346.

[13] Ibid., pp. 358-360.

neural tissue.

permeability is increased a free flow of ions occurs, resulting in depolarization of that portion of the membrane. This depolarization induces a depolarization of the adjacent portions of the neuron, where the Ach has successively increased the permeability of the membrane. This process continues along the neuron and across the synapse to its eventual destination, and the total result is a nerve impulse. Ach, then, at all times acts in conjunction with the flow of current and thus this theory is in accordance with an electrical theory of transmission.

One of the proofs advanced for the theory was Nachmansohn's experiment on electric eels.[14] He found that voltage in the electric organ of Electrophorus electricus varies in an S-shaped curve from head to tail. The quantity of cholinesterase was found to vary in exactly the same manner. This indicates that the strength of electrical charges is positively correlated with the amount of Ach present.

Nachmansohn explains the common discovery of Ach at synaptic junctions in two ways:

(1) Since there are a multitude of end arborizations

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[14] Ibid., pp. 351-358.

at the synapse Ach leaks out into the perfusion fluid, being originally contained within the cell membrane.[15]

(2) The reason that Ach is not found at the surface of the neuron is that axonal surface membranes are impervious to Ach, probably because Ach is lipoid insoluble and there is a lipoid membrane surrounding all axons. The end arborizations do not have this lipoid coating, allowing the Ach to escape into the perfusion fluid.[16]

As to the generality of Ach action, Nachmansohn and others showed by experiments with cholinesterase inhibitors that it is "highly probable that the Ach system plays an identical role in the conducting mechanism of all types of nerve and of muscle."[17]

Electrocorticogram changes resulting from the application of Ach to the cortex have been found. For example, Miller, Stravraky and Woonton found that the application of esserine to the cortex of cats and rabbits depressed

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[15] Ibid., pp. 370-371.

[16] Rothenberg, Sprinson and Nachmansohn, "Site of Action of Acetylcholine," Journal of Neurophysiology, 1948, 11, 111-116.

[17] T. H. Bullock, H. Grundfest, D. Nachmansohn, and M. A. Rothenberg, "Generality of the Role of Acetylcholine in Nerve and Muscle Conduction," Journal of Neurophysiology, 1947, 10, 11-22.

slow and fast waves of the electrocorticogram.[18] When Ach was applied to the eserinized cortex large rapid waves consisting of diphasic spikes appeared. These spikes were similar to those produced by strychninization of the cortex. Chatfield and Dempsey, using cats, applied Ach to the cortex, which had previously been treated with prostigmine, and found that fast large waves were produced in the somesthetic, motor, and auditory areas, but not in the association area.[19]

II. Glutamic Acid. Glutamic acid is officially classified as a "non-essential" amino acid, but it seems to be the only amino acid which is metabolized by brain tissue.[20] There are two forms of glutamic acid, the l ( ) and d (-) forms. The l ( ) form is the natural glutamic acid but Kogl states that glutamic acid obtained from the proteins of cancerous tissues contains the d (-) form.[21] According to Krebs, glutamic acid is of special importance

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[18]F. R. Miller, G. W. Stravraky, and G. A. Woonton, "Effects of Eserine, Acetyloholine and Atropine on the Electroencephalocorticogram," Journal of Neurophysiology, 1940, 3, 131-138.

[19]Chatfield and Dempsey, American Journal of Physiology, 1941, 135, 663.

[20]B. Harrow, Textbook of Biochemistry, Philadelphia and London: W. B. Saunders Company, 1947.

[21]Ibid., p. 52.

in the metabolism of nervous tissue.[22]

The petit mal form of epilepsy has been successfully treated with glutamic acid, the number of attacks sometimes being reduced by as much as eighty-five per cent. Rats which were fed the l form of glutamic acid showed a statistically significant increase in learning ability, according to an experiment reported by Harrow.[23] The use of glutamic acid on human subjects has failed to confirm the results reported by Harrow.[24]

Of more importance to this study is an experiment of Nachmansohn where it is shown that l glutamic acid increases the rate of formation of Ach in dialyzed brain tissues. The d form had only a small effect.[25] On the basis of such evidence Harrow believed that glutamic acid may be a coenzyme of choline acetylase, the substance which synthesizes Ach.[26]

III. Handedness. In 1934 Peterson published a comprehensive report on handedness in rats, including the

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[22]Ibid., p. 373.

[23]Ibid., p. 537.

[24]D. G. Ellison, P. R. Fuller, and R. Urmston, "The Influence of Glutamic Acid on Test Performance," Science, 1950, 112, 248-250.

[25]Nachmansohn, op. cit., pp. 366-367.

[26]Harrow, op. cit., p. 539.

results of a number of experiments which he had conducted.[27] He found that right handedness and left handedness probably occur with equal frequency in rats, and ambidexterity occurs much less frequently. Handedness is stable in a given situation, but may be different in different situations. The portion of the cerebrum which is primarily involved in controlling handedness seems to be somewhere in the frontal part of the contralateral hemisphere; the approximate area can be determined by electrical stimulation of the cortex. Small destructions in this area result in apparently permanent transfer of handedness, but re-education of the formerly preferred limb is possible. Large destructions not involving the area do not effect preferential handedness, indicating a relatively high localization of function for this trait.

Peterson and Carter found that the application of strychnine, alcohol, potassium cyanide, atropine sulphate and caffeine sulfate to either the homolateral or contralateral area had no influence on preferential handedness.[28]

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[27]G. M. Peterson, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, 1934, 9, 1-67.

[28]G. M. Peterson and G. W. Carter, "The Local Application of Drugs to the Motor Cortex of the Rat," Journal of Comparative Psychology, 1936, 22, 123-129.

Peterson and Fracarol performed a number of operations in various cortical locales in 1938, using ambidextrous rats.[29] From the results they concluded that the cortical region for the control of handedness can be specifically localized in a region 250 microns posterior to the genu of the corpus callosum, directly over the dorsal convexity of the caudate nucleus, and lies below layer III of the cortex, probably in level V.

Peterson and Chaplin concluded on the basis of results of cerebellar and cortical operations that the pyramidal systems of the cortex predominate in controlling handedness of the rat.[30]

In view of the evidence for the role of Ach in neural conduction Peterson applied it to the handedness area which controlled the non-preferred limb in order to ascertain whether it would facilitate transfer of handedness.[31] 108

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[29]G. M. Peterson, and L. C. Fracarol, "The Relative Influence of Locus and Mass of Destruction Upon the Control of Handedness by the Cerebral Cortex," Journal of Comparative Neurology, 1938, 68, 173-190.

[30]G. M. Peterson and J. P. Chaplin, "Extrapyramidal Mechanisms in Handedness in the Rat," Journal of Comparative Psychology, 1942, 33, 343-361.

[31]G. M. Peterson, "Changes in Handedness in the Rat by Local Application of Acetylcholine to the Cerebral Cortex," Journal of Comparative and Physiological Psychology, 1949, 42, 404-412.

single handed rats and forty-two ambidexters were used. Transfer occurred in two of the single handed rats and fifteen of the ambidexters. This indicated that not only did the drug seem effective, but ambidextrous rats were more sensitive to the influence. Clonic contractions of the contralateral fore-limb after application of the drug showed that the drug was affecting the proper cortical area.

Peterson and Rigney used a combination of drugs along with Ach in a factorial design.[32] They found that Ach had a barely significant positive effect in influencing handedness, glycine had no effect and di-isopropylfluorophosphate tended to have a negative effect. In a preliminary study not employing a factorial design they found that in one of two cases an application of Ach and glutamic acid to the handedness area controlling the non-preferred limb produced transfer, and in a single case where Ach, glutamic acid and eserine were applied transfer occurred.[33]

Peterson and Suess employed a factorial design to test the effects of Ach and the two forms of glutamic acid

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[32]G. M. Peterson and J. W. Rigney, "Influence on Handedness of Acetylcholine Locally Applied with Other Chemicals to the Cerebral Cortex of the Rat," Journal of Comparative and Physiological Psychology, 1950, 43, 264-272.

[33]Ibid., pp. 264-265.

upon ambidextrous rats.[34] No significant results were obtained for any of the combinations used. Ten of the ambidexters used by Suess were artificial, being created by subjecting them to forced reaching with the non-preferred hand. Many of the rats used in the design were "poor" ambidexters in that they showed considerable inconsistency in day-to-day reaching with the non-preferred hand. Only the fifty reaches immediately preceding and following the operation were taken into consideration in statistical treatment of the data. For these reasons it was decided that the study should be repeated with the addition of several improvements to the design.

Procedure. Age, sex, and the previous amount of reaching in the food situation of the rats used in the study were not controlled. It was felt that none of these factors would affect the performance of the rats, since the criterion for ambidexterity was solely based upon the reaches taken during pre-operational observations.

I. Recording of Reaches. The method for obtaining information on handedness was that developed by Peterson.[35]

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[34]Suess, op. cit., pp. 1-41.

[35]G. M. Peterson, "Mechanisms on Handedness in the Rat," Comparative Psychology Monographs, 1934, 9, 1-67.

The rat was placed in a small cage to which a canary-type feeding dish was attached. Part of the dish extended inside the cage and contained grain mash. The rat might eat by mouth feeding at first, but when the food reached a certain level the rat was forced to obtain food by grasping with the fore-paw. When the rat reached into the dish, brought back a handful of food to its mouth and ate, a reach was recorded.

The rats were kept in a state of food deprivation which was sufficient to produce the required number of reaches per day. 350 pre-operation and 550 or more post-operational reaches were recorded for each rat used in the factorial design, with the exception of the records of the animals which were utilized from Suess' study. As has been stated previously, a limited number of post-operational reaches were taken on these rats. The reaches of the rats in this study were recorded according to the following plan:

Day 1. 100 reaches were taken in two consecutive periods of fifty reaches each.

Day 2. Same as Day 1.

Day 3. Same as Days 1 and 2.

Day 4. Fifty reaches were taken and the rat was immediately operated upon. After the rat had recovered enough to eat 150 more reaches were taken.

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Day 2. Same as Day 1.

Day 3. Same as Days 1 and 2.

Day 4. Fifty reaches were taken and the rat was immediately operated upon. After the rat had recovered enough to eat 150 more reaches were taken.

Day 5. 100 reaches were taken in two consecutive periods of fifty reaches each.

Day 6. Same as Day 5.

One week after Day 6, 100 reaches were taken in two periods of fifty. One week after that 100 more reaches were taken in the same way.

The above was the standard procedure used, but there were several exceptions to the post-operational procedure. Some rats were re-operated upon after Day 6 and some were re-operated upon after the entire procedure had been completed. These variations are shown in the records of reaching.

After all reaching had been completed the brain was removed and examined for damage in the handedness area upon which the drugs had been placed. Those rats which had damage in that area are indicated in the records of reaching (Table IX). Only cases in which the cortex was found to be undamaged were placed in the experimental design.

II. Operational Procedure. After having finished fifty reaches on Day 4 the rat was immediately etherized. The hair covering the top of the skull was then clipped and an incision was made which exposed the skull. A trephine one eighth inch in diameter was used to drill a hole in the skull tangent to the frontal and midline sutures, directly

over the handedness area. This exposed the dura mater of the cerebrum. The openings were always made over the handedness area contralateral to the non-preferred limb. A small cotton bolus saturated with the desired liquid was placed over the hole and the skin was closed with wound clips. The rat was placed in the reaching cage during the period of recovery.

In re-operations the wound clips were removed and the cotton bolus was replaced with another saturated with the same liquid. The wound was then closed with wound clips.

III. Drugs. In accordance with the requirements of the experimental design the following drugs were applied:

(1) Ach-A five per cent solution of the drug in tap water was used on all original operations. A ten per cent solution was used in re-operation.

(2) Glutamic Acid-Equal parts of a saturated solution of either l or d glutamic acid at room temperature and a ten per cent solution of Ach were combined to make the five per cent Ach solutions with glutamic acid, when this treatment was called for. Otherwise, equal parts of tap water and a saturated solution of glutamic acid (d or l) were prepared where the treatment called for omission of Ach.

(3) Tap water was used on the control rats of the

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design.

IV. Factorial Design. Following the procedures of Rigney and Suess a factorial design was used which could be statistically treated by analysis of variance.[36, 37, 38] The following symbols were used to denote the application or non-application of drugs:

A - Ach

a - no Ach

B - l-glutamic acid

B'- d-glutamic acid

b - no glutamic acid

The symbol "R" denoted that the right side of the cortex had been operated upon and "r" denoted that the left side had been operated upon.

The factorial design was as follows:

ABR Ach and l-glutamic on the right cortex

ABr Ach and l-glutamic on the left cortex

AB'R Ach and d-glutamic on the right cortex

AB'r Ach and d-glutamic on the left cortex

AbR Ach on the right cortex

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[36]Peterson and Rigney, op. cit., p. 266.

[37]Suess, op. cit., p. 21.

[38]R. A. Fisher, The Design of Experiments, New York: Hafner Publishing Company, 1949.

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The symbol "B" denoted that the right side of the cortex had been operated upon and "x" denoted that the left side had been operated upon.

The factorial design was as follows:

ABB	Ach and l-glutamic on the right cortex
ABx	Ach and l-glutamic on the left cortex
AB'B	Ach and d-glutamic on the right cortex
AB'x	Ach and d-glutamic on the left cortex
AbB	Ach on the right cortex

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[36] Peterson and Rigney, op. cit., p. 266.

[37] Goess, op. cit., p. 21.

[38] A. A. Rigney, The Design of Experiments, New York: Rigney Publishing Company, 1949.

Abr Ach on the left cortex

aBR l-glutamic on the right cortex

aBr l-glutamic on the left cortex

aB'R d-glutamic on the right cortex

aB'r d-glutamic on the left cortex

abR tap water on the right cortex

abr tap water on the left cortex

It was intended that one replication of the design should be made, resulting in two rats for each combination of drugs, or twenty-four rats in all.

V. Criterion of Ambidexterity. It was decided that a good measure of ambidexterity would be the number of non-preferred reaches taken in the 350 pre-operational reaches. Merely deciding which rat seemed to be the best ambidexter on examination of the reaching record might bring in the bias of the selector, since the rats for the design were not selected until the post-operational records of many of them were known. Suess had obtained 350 pre-operational reaches for each of his rats; therefore the same method of selection was used in deciding which of his cases to include in the design. The twenty-four rats of the factorial design were selected on this basis, with a few exceptions. The exceptions were cases where Suess' rat took only a few more non-preferred reaches than the rat of this investigator in

Abr	Ach on the left cortex
aBR	l-glutamic on the right cortex
aBr	l-glutamic on the left cortex
aB'R	d-glutamic on the right cortex
aB'r	d-glutamic on the left cortex
abR	tap water on the right cortex
abr	tap water on the left cortex

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a certain category of the design. In such a case Suess' rat was not used, since it is not known which of his rats were the "artificial" ambidexters previously mentioned. In the modified design using only twelve rats the same criterion of ambidexterity was used in the selection of cases.

Results. Approximately 300 rats were observed for ambidexterity in the period of one year. From these rats fifty-four were selected for further observation of possible ambidexterity. Seventeen of the fifty-four rats were discarded, having lost their ambidexterity quickly. The thirty-seven remaining rats were operated upon. Their records of reaching are shown in Table IX. Examination of the reaching records will show that many of the rats took very few ambidextrous reaches, some averaging less than one-non-preferred reach per fifty reaches. The original intention of the study was to find twenty-four good ambidexters to repeat the design used by Suess, since the animals used by Suess displayed poor ambidexterity. Over a two semester period, however, the required twenty-four "good" ambidexters were not obtained. It was decided, therefore, to utilize the best ambidexters found in both studies to complete the design. Such a design could make use of only the fifty pre-operational and post-operational reaches of the rats, for reasons mentioned previously. The animals were selected

according to the criterion of ambidexterity stated previously. Table I gives the numbers of the rats selected and the fifty pre-operational and fifty post-operational reaches taken by each rat.

As stated previously, only those rats which evidenced no cortical damages were used in the factorial design. It was assumed that there had been no cortical damage in any of the cases taken from Suess, since these rats had been utilized in his factorial design.

Table II shows the results of an analysis of variance of the data given in Table I. None of the results is significant, indicating no influence resulting from any of the combinations of drugs used.

In order to make use of a greater number of pre-operational and post-operational reaches in the statistical analysis, twelve of the best ambidexters found in this study were selected. Since the rats had already been operated upon it was necessary to select the best ambidexter which had been operated on in each category of the design. Three analyses of variance of the non-preferred reaches of these rats were run. The comparisons made were fifty pre-operational reaches to fifty post-operational, 150 pre-operational to 150 post-operational and 350 pre-operational to 350 post-operational reaches. The rats selected and reaches

according to the criterion of ambidexterity stated previously. Table I gives the numbers of the rats selected and the fifty pre-operational and fifty post-operational reaches taken by each rat.

As stated previously, only those rats which evidenced no cortical damages were used in the factorial design. It was assumed that there had been no cortical damage in any of the cases taken from cases, since these rats had been utilized in his factorial design.

Table II shows the results of an analysis of variance of the data given in Table I. None of the results is significant, indicating no influence resulting from any of the combinations of drugs used.

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taken are shown in Tables III, IV, and V. Analysis of variance of the data is shown in Tables VI, VII, and VIII. The results of the analysis show no significance for any of the meaningful combinations of drugs. In one case no variability resulted from operating on different cortical hemispheres with Ach. This merely indicates that the side of the cortex that is operated on by itself does not have any influence on a change of handedness.

Since reoperations were not done in all cases, there is no statistical treatment of reoperation results. It will be remembered that the same solutions were applied in reoperation as in the original operations, except that where Ach was required it was used in a ten per cent solution. An examination of equal periods of pre-operational and post-operational reaches in reoperations gives little evidence of strong influence of the drugs. Only animals whose brains were found intact were considered in this comparison. In seven cases, more post-operational non-preferred reaches were taken. In four of the cases the differences were marked. An ABR rat showed 119 more non-preferred post-operational reaches in eight periods and an AbR rat showed 61 more reaches. These were more than balanced, however, by two control rats, which showed 190 and 147 more non-preferred reaches, respectively, in eight post-operational periods.

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Discussion. As shown in Tables I, III, V, and VII post-operational non-preferred reaches were in general fewer than pre-operational reaches. This does not necessarily indicate that the drugs had a negative effect. If the Ach and glutamic acid cases took significantly more non-preferred reaches than the control rats after the operation, it would indicate a positive influence even though the results were negative as a whole. The general negative influence could then be attributed to the affects of the operation. As stated previously, however, no significance was found.

The purpose of this study was to repeat Suess' experimental design with better ambidexters. This was done on the assumption that the more non-preferred reaches are taken the easier it will be to influence a change of handedness.

Twenty-four good ambidexters were not found, but with the use of the data for eight of Suess' best ambidexters the design was completed. The fact that it was necessary to use only his best rats shows that the rats used in this design were a better group as a whole in regard to ambidexterity. Unfortunately even though the group was undoubtedly better an examination of the reaching records shows that many of the rats used were unsatisfactory in ambidexterity. There are three possible

reasons for this:

(1) Suess did not designate which of his rats had been given forced reaching. Some of his rats included in this study may have been from the forced-reaching group. Suess says that these rats are for all intents and purposes as good as natural ambidexters. This is not necessarily the case, however. It has not been proven that the ambidexterity of single-handed rats given forced reaching is equivalent to that of natural ambidexters. Thus those rats which had been given forced reaching by Suess would tend to take fewer non-preferred reaches in the post-operational situation than true ambidexters.

(2) The only factorial analysis which could be made on all twenty-four rats was in terms of fifty pre-operational reaches compared to fifty post-operational reaches. If the influence of the drugs did not begin until after fifty post-operational reaches had been taken it would not be shown in this design. More post-operational reaches were treated in the modified design, using only twelve rats. In these analyses, however, because of the few cases involved, the degrees of freedom were greatly reduced and the remainder term vanished, leaving only the interactions to test the influence of treatments.

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(3) Only a few of the rats used in the design show

consistent reaching with the non-preferred hand. Some took many non-preferred reaches in the first few periods and then reverted to virtual single-handedness before the operation. Some rats switched their handedness preference after the first few periods of observation and continued until they took practically all of their reaches with the previously non-preferred hand.

For the reasons given above any influence that the drugs had might have been masked by the inconsistencies in the day to day reaching of the rats used in the design. These were the best ambidexters that could be found in a two semester period, not counting the time spent by Suess in collecting his ambidexters. With the facilities available it is likely that it would take a period of years to find enough good ambidexters to fill out an experimental design. Since Peterson found that only two out of 108 single-handed rats were influenced by the application of Ach the possible success in using such rats seems remote, unless more effective combinations of drugs can be found. Baker used a method of forced reaching in investigating the influence of Ach.[39] An Ach and a control group (using

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water) were given equal amounts of forced reaching with the non-preferred hand and then the drugs were applied. Any differences in post-operation non-preferred reaching in a free-reaching situation could then be attributed to the influence of the cortical applications. However, he selected an unfortunate amount of forced practice and very few animals in either group were influenced. The same difficulty is encountered to a degree in this approach as is encountered in the use of ambidexters. The amount of transfer of handedness resulting from a given number of forced reaches varies considerably from rat to rat.

Further investigation by this method at a more critical level of forced practice, however, may prove more fruitful than the investigations already done with ambidextrous rats.

Summary and Conclusions. Twenty-four ambidextrous rats were used in a factorial design to ascertain the influence of acetylcholine and the two forms of glutamic acid on handedness. The combinations of drugs were applied to the handedness area of the motor cortex which controlled the non-preferred hand. Twelve rats were used in a modification of the factorial design which had the same purposes and utilized the same methods as the first design. Statistical analysis of the data by means of analysis of variance

showed no significant influence for any of the combinations of drugs. It was felt that the inconsistency of the non-preferred reaching of the rats involved negated any influence which the drugs might actually have had. It was suggested that further attack of the problem might be done by using a method of forced reaching already employed by Baker.

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TABLE I

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN THE LAST PRE-OPERATIONAL PERIOD AND THE FIRST POST-OPERATIONAL PERIOD

Combinations	Rats	Reaches with Non-preferred Hand Pre-operation	Post-operation	D
ABR	1F	24	11	-13
	3M*	34	3	-31
ABr	2F	1	3	2
	1M*	4	0	-4
AB'R	3F	13	7	-6
	4M*	20	10	-10
AB'r	4M	14	0	-14
	5M	22	15	-7
AbR	6F	26	20	-6
	18F*	9	0	-9
Abr	7F	0	0	0
	17M*	3	0	-3
aBR	8M	0	0	0
	21F*	26	9	-17
aBr	9F	4	2	-2
	10M	32	27	-5
aB'R	11F	11	7	-4
	22M*	25	4	-21
aB'r	12M	14	9	-5
	13F	10	6	-4
abR	14F	3	1	-2
	24M*	9	0	-9
abr	15F	5	19	14
	16F	2	0	-2

* Cases taken from Suess

** In all of the tables "F" indicates a female rat and "M" indicates a male rat.

TABLE I

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN THE LAST PRE-OPERATIONAL PERIOD AND THE FIRST POST-OPERATIONAL PERIOD

Combinations	Rats	Reaches with non-preferred hand before operation		Reaches with non-preferred hand after operation	
ABR	1F	24	11		-13
	3M*	3*		3	-31
ABr	2F	1		3	2
	1M*	4		0	-4
AB'R	3F	13		7	-6
	4M*	20		10	-10
AB'r	4F	14		0	-14
	5M	22		15	-7
AbR	6F	26		20	-6
	18F*	9		0	-9
Abr	7F	0		0	0
	17M*	3		0	-3
aBR	8M	0		0	0
	21F*	26		9	-17
aBr	9F	4		2	-2
	10M	32		27	-5
aB'R	11F	11		7	-4
	22M*	25		4	-21
aB'r	12M	14		9	-5
	13F	10		6	-4
abR	14F	3		1	-2
	24M*	9		0	-9
abr	15F	5		19	14
	16F	2		0	-2

* Cases taken from Buggs

** In all of the tables "F" indicates a female rat and "M" indicates a male rat.

TABLE II

ANALYSIS OF VARIANCE OF THE REACHING DIFFERENCES SHOWN IN TABLE I

Treatments	Degrees of Freedom	Sum of Squares	Mean Squares
Total	23	1718	
Acetylcholine (A)	1	81	81
Glutamic Acid (B)	2	239	119.5
Hemispheres (R)	1	400	400
(Interactions)			
AxB	2	25.5	12.75
AxR	1	0	0
BxR	2	106	53
AxBxR	2	198.5	99.25
Estimate of Error	12	1901.5	158.46

Treatments	Degrees of Freedom	Sum of Squares	Mean Square
Total	83	1272	
Acetylcholine (A)	1	81	81
Glutamic Acid (B)	2	239	119.5
Hemispheres (H)	1	400	400
(Interactions)			
AxB	2	25.5	12.75
AxH	1	0	0
BxH	2	104	52
AxBxH	2	180.5	90.25
Estimate of Error	72	1920.5	158.96

TABLE III

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN THE LAST PRE-OPERATIONAL PERIOD AND THE FIRST POST-OPERATIONAL PERIOD WITH THE DESIGN INCLUDING ONLY TWELVE RATS

Combi-nations	Rats	Reaches with Non-preferred Hand Pre-operation	Post-operation	D
ABR	1F	24	11	-13
ABr	2F	1	3	2
AB'R	3F	13	7	-6
AB'r	4M	14	0	-14
AbR	6F	26	20	-6
Abr	7F	0	0	0
aBR	8M	0	0	0
aBr	10M	32	27	-5
AB'R	11F	11	7	-4
AB'r	12M	14	9	-5
abR	14F	3	1	-2
abr	16F	2	0	-2

TABLE IV

ANALYSIS OF VARIANCE OF THE REACHING DIFFERENCES SHOWN IN TABLE III

Treatments	Degrees of Freedom	Sum of Squares	Mean Squares
Total	11	265	
Acetylcholine (A)	1	32	32
Glutamic Acid (B)	2	49	24.5
Hemisphere (R)	1	6	6
(Interactions)			
AxB	2	9	4.5
AxR	1	28	28
BxR	2	59	29.5
AxBxR	2	82	41

TABLE IV

ANALYSIS OF VARIANCE OF THE REACTION TIME MEASURES
SHOWN IN TABLE III

Treatments	Degrees of Freedom	Sum of Squares	Mean Square
Total	11	265	
Acetylcholine (A)	1	32	32
Glutamic Acid (B)	2	49	24.5
Hemisphere (H)	1	6	6
(Interactions)			
AxB	2	9	4.5
AxH	1	28	28
BxH	2	59	29.5
AxBxH	2	82	41

TABLE V

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN THE LAST THREE PRE-OPERATIONAL PERIODS AND THE FIRST THREE POST-OPERATIONAL PERIODS

Combinations	Rats	Reaches with Non-preferred Hand Pre-operation	Post-operation	D
ABR	1F	72	12	-60
ABr	2F	10	19	9
AB'R	3F	58	30	-28
AB'r	4M	56	4	-52
AbR	6F	30	52	22
Abr	7F	3	0	-3
aBR	8M	9	0	-9
aBr	10M	60	77	17
aB'R	11F	41	40	-1
aB'r	12M	50	23	-27
abR	14F	14	1	-13
abr	16F	29	0	-29

TABLE V

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN TWO LAWS

THERE PRE-OPERATIONAL PERIODS AND THE FIRST TWO PRE-

OPERATIONAL PERIODS

Combinations	Rats	Reactions with pre-operation	Non-preferred lead post-operation	D
ABR	1F	72	1C	-60
ABr	2F	10	1P	9
AB'R	3F	58	30	-28
AB'r	4M	54	4	-50
AbR	6F	30	52	22
Abr	7F	3	0	-3
aBR	8M	9	0	-9
aBr	10M	60	77	17
aB'R	11F	43	40	-3
aB'r	12M	50	23	-27
abR	14F	14	1	-13
abr	16F	29	0	-29

TABLE VI

ANALYSIS OF VARIANCE OF THE REACHING DIFFERENCES SHOWN IN TABLE V

Treatments	Degrees of Freedom	Sum of Squares	Mean Squares
Total	11	7249	
Acetylcholine (A)	1	208	208
Glutamic Acid (B)	2	988	494
Hemispheres (R)	1	1	1
(Interactions)			
AxB	2	2268	1134
AxR	1	109	109
BxR	2	3300	1650
AxBxR	2	375	187.5

TABLE VII

FACTORIAL DESIGN AND THE DIFFERENCE BETWEEN THE SEVEN PRE-OPERATIONAL PERIODS AND THE SEVEN POST-OPERATIONAL PERIODS

Combi-nations	Rats	Reaches with Non-preferred Hand Pre-operation	Post-operation	D
ABR	1F	191	58	-133
ABr	2F	42	27	-15
AB'R	3F	179	30	-149
AB'r	4M	140	55	-85
AbR	6F	74	105	31
Abr	7F	79	0	-79
aBR	8M	47	0	-47
aBr	10M	125	159	34
aB'R	11F	59	201	142
aB'r	12M	133	105	-25
abR	14F	42	6	-36
abr	16F	97	37	-60

Combinations	Rats	Beaches with Pre-operation	Non-preferred Band Post-operation	D
ABR	12	121	58	-133
ABr	28	42	37	-15
AB'R	37	179	30	-149
AB'r	44	180	55	-89
ABR	67	74	105	31
Abr	72	79	0	-79
aBR	88	47	0	-47
aBr	10M	125	159	34
aB'R	11F	59	201	142
aB'r	12M	133	105	-25
abR	14F	42	6	-36
abr	16F	97	37	-60

TABLE VIII

ANALYSIS OF VARIANCE OF THE REACHING DIFFERENCES SHOWN IN TABLE VII

Treatments	Degrees of Freedom	Sum of Squares	Mean Squares
Total	11	68752	
Acetylcholine (A)	1	15987	15987
Glutamic Acid (B)	2	246.5	123.25
Hemispheres (R)	1	121	121
(Interactions)			
AxB	2	19945.5	9972.75
AxR	1	10027	10027
BxR	2	16921.5	8460.75
AxBxR	2	5504.5	2752.25

ANALYSIS OF VARIANCE OF THE MEASURED DATA

Treatments	Degrees of Freedom	Sum of Squares	Mean Square
Total	11	69752	
Acetylcholine (A)	1	15987	15937
Glutamic Acid (B)	2	246.5	123.25
Hemisphere (H)	1	321	321
(Interactions)			
AxB	2	1595.5	797.75
AxH	1	13027	13027
BxH	2	1691.5	845.75
AxBxH	2	550.5	275.25

TABLE IX

RECORDS OF REACHING OF ALL RATS OPERATED UPON, INCLUDING EIGHT CASES FROM SUESS

Rats and Treatments																					
1F-ABR			3F*-ABR			17M**-ABR			18M-ABR			2F-ABr			1M*-ABr		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	14	36	1	26	24	1	47	3	1	46	4	1	11	39	1	20	30
	11	39		11	39		48	2		47	3		7	43		26	24
2	37	13	2	21	29	2	15	35	2	50	0	2	5	45	2	27	23
	19	31		32	18		28	22		49	1		9	41		13	37
3	26	24	3	33	17	3	37	13	3	50	0	3	3	47	3	24	26
	26	24		22	28		20	30		49	1		6	44		25	25
4	26	24	4	16	34	4	46	4	4	50	0	4	1	49	4	4	46
operation			operation			operation			operation			operation			operation		
	39	11		47	3		47	3		50	0		3	47		0	50
	49	1		46	4		50	0		50	0		11	39		0	50
	50	0		50	0		50	0		50	0		5	45		0	10
5	50	0		45	5	5	50	0	5	50	0	5	1	49	5	0	50
	48	2		reop.			49	1		50	0		0	50		0	50
6	30	20	5	26	24	6	48	2	6	50	0	6	0	50			
	28	22		28	22		42	8		50	0		0	50			
7	31	19				***one week			one week			7	7	43			
	reop.					7	32	18	7	50	0		reop.				
	35	15					45	5		50	0		0	50			
	38	12				one week			one week				0	50			
	30	20				8	50	0	8	50	0		0	50			
8	24	26					50	0		50	0	8	15	35			
	22	28				9	49	1	9	50	0		16	34			
9	22	28					46	4		50	0	9	6	44			
	24	26				10	50	0	10	50	0		16	34			
one week							50	0		50	0	one week					
10	20	30				11	45	5	11	50	0	10	0	50			
	21	29					reop.			reop.			0	50			
one week							50	0		50	0	one week					
11	43	7					50	0		50	0	11	0	50			
	38	12					50	0		50	0		0	50			
						12	50	0	12	50	0						
							50	0		50	0						
						13	50	0	13	50	0						
							50	0		50	0						
						one week			one week								
						14	50	0	14	50	0						
							50	0		50	0						

* cases taken from Suess

** examination after brain removal revealed destruction in handedness area

*** All reaching was taken on consecutive days, except where "one week" indicates a one week interval between reaching periods.

Day	R	L	R	L	R	L	R	L	R	L	R	L
1	14	36	26	24	1	47	3	1	46	4	1	11
	11	39	11	29		48	2		47	3		7
2	37	13	2	21	29	2	12	38	2	50	0	2
	10	21		32	18		28	22		46	1	6
3	26	24	3	33	17	3	27	13	3	20	0	3
	26	24		22	28		20	30		46	1	4
4	26	24	4	16	24	4	46	4	4	30	0	4
operation			operation			operation			operation			operation
	39	11		46	3		47	3		50	0	
	46	1		46	4		50	0		50	0	
5	50	0		50	0		20	0		50	0	
	50	0		46	4		50	0		48	2	
6	48	2		resp.			48	1		50	0	
	30	20	5	26	24	5	48	2		50	0	
7	28	22		28	22		42	8		50	0	
	31	19										
resp.												
	37	13										
	38	12										
	30	20										
8	24	26										
	22	28										
9	22	28										
	24	26										
one week												
10	20	30										
	21	29										
one week												
11	14	7										
	38	12										

Day	R	L	R	L	R	L	R	L	R	L	R	L
1	14	36	26	24	1	47	3	1	46	4	1	11
	11	39	11	29		48	2		47	3		7
2	37	13	2	21	29	2	12	38	2	50	0	2
	10	21		32	18		28	22		46	1	6
3	26	24	3	33	17	3	27	13	3	20	0	3
	26	24		22	28		20	30		46	1	4
4	26	24	4	16	24	4	46	4	4	30	0	4
operation			operation			operation			operation			operation
	39	11		46	3		47	3		50	0	
	46	1		46	4		50	0		50	0	
5	50	0		50	0		20	0		50	0	
	50	0		46	4		50	0		48	2	
6	48	2		resp.			48	1		50	0	
	30	20	5	26	24	5	48	2		50	0	
7	28	22		28	22		42	8		50	0	
	31	19										
resp.												
	37	13										
	38	12										
	30	20										
8	24	26										
	22	28										
9	22	28										
	24	26										
one week												
10	20	30										
	21	29										
one week												
11	14	7										
	38	12										

* cases taken from those

** examination after brain removal revealed destruction in hippocampus area

*** All rescling was taken on consecutive days, except those "one week" indicates a one week interval between rescling periods.

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																					
19M-ABr			3F-AB'R			4M*-AB'R			21M**-AB'R			22M-AB*R			20M**AB'R		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	7	43	1	22	28	1	31	19	1	50	0	1	50	0	1	44	6
	2	48		15	35		26	24		50	0		50	0		45	5
2	3	47	2	19	31	2	32	18	2	47	3	2	50	0	2	41	9
	0	50		23	27		30	20		47	3		50	0		31	19
3	1	49	3	25	25	3	29	21	3	49	1	3	49	1	3	33	17
	0	50		30	20		23	27		50	0		47	3		44	6
4	0	50	4	37	13	4	30	20	4	50	0	4	49	1	4	42	8
operation			operation			operation			operation			operation			operation		
	0	50		43	7		40	10		47	3		49	1		50	0
	0	50		41	9		34	16		50	0		50	0		50	0
	0	50		36	14		43	7		50	0		50	0		50	0
5	0	50	5	50	0		37	13	5	50	0	5	50	0	5	50	0
	0	50		50	0		reop.			50	0		50	0		50	0
6	0	50	6	50	0	5	47	3	6	50	0	6	50	0	6	50	0
	0	50		50	0		50	0		50	0		50	0		50	0
one week			7	50	0				one week			one week			one week		
7	0	50		reop.					7	50	0	7	50	0	7	50	0
	0	50		50	0					50	0		50	0		50	0
one week				50	0				one week			one week			one week		
8	0	50		50	0				8	50	0	8	50	0	8	50	0
	0	50	8	50	0					50	0		50	0		50	0
				50	0												
			9	36	14												
				40	10												
			one week														
			10	42	8												
				44	6												
			one week														
			11	50	0												
				50	0												

* cases taken from Suess

** examination after brain removal revealed destruction in handedness area

| | | |

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																								
4M-AB'r			5M-AB'r			23M**AB'r			24F-AB'r			25F-AB'r			26M-AB'r		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	21	29	1	25	25	1	0	50	1	2	48	1	24	26	1	26	24
	8	42		17	33		0	50		1	49		48	2		17	33
2	39	11	2	14	36	2	8	42	2	1	49	2	45	5	2	2	48
	16	34		10	40		0	40		0	50		48	2		0	50
3	19	31	3	18	32	3	1	49	3	0	50	3	40	10	3	0	50
	21	29		20	30		0	50		0	50		20	30		1	49
4	14	36	4	22	28	4	0	50	4	0	50	4	2	48	4	0	50
operation			operation			operation			operation			operation			operation		
	0	50		15	35		0	50		0	50		0	50		0	50
	0	50		9	41		0	50		0	50		1	49		0	50
	4	46		7	43		0	50		0	50		2	48		0	50
5	13	37	5	0	50	5	0	50	5	0	50	5	0	50	5	0	50
	13	37		0	50		0	50		0	50		1	49		0	50
6	9	41	6	0	50	6	0	50	6	0	50	6	0	50	6	0	50
	16	34		1	49		0	50		0	50		0	50		0	50
one week			one week			one week				reop.		one week			one week		
7	18	32	7	9	41	7	0	50		0	50	7	0	50	7	0	50
	13	37		4	46		0	50		0	50		0	50		0	50
one week						one week				0	50	one week					
8	14	36	8	7	43	8	0	50	7	0	50	8	0	50	8	0	50
	19	31		2	48		0	50		0	50		0	50		0	50
9	10	40				9	0	50	8	0	50						
	24	26					0	50		0	50						
10	18	32				10	0	50	one week								
	19	31					0	50	9	0	50						
11	14	36				11	0	50		0	50						
	reop.						reop.		one week								
	10	40					0	50	10	0	50						
	22	28					0	50		0	50						
	32	18					0	50									
12	13	37				12	0	50									
	18	32					0	50									
13	16	34				13	0	50									
	20	30					0	50									
one week						one week											
14	24	26				14	0	50									
	19	31					0	50									

** examination after brain removal revealed destruction in handedness area

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																								
6F-AbR			18F*-AbR			27M-AbR			7F-Abr			17M*-Abr			28M**Abr		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	34	16	1	0	50	1	49	1	1	30	20	1	40	10	1	21	29
	34	16		2	48		48	2		35	15		32	18		16	34
2	42	8	2	0	50	2	30	20	2	7	43	2	32	18	2	10	40
	46	4		27	23		41	9		4	46		27	23		5	45
3	49	1	3	30	20	3	36	14	3	2	48	3	20	30	3	5	45
	47	3		37	13		30	20		1	49		4	46		3	47
4	24	26	4	41	9	4	16	34	4	0	50	4	3	47	4	0	50
operation			operation			operation			operation			operation			operation		
	30	20		50	0		23	27		0	10		0	50		1	49
	37	13	5	10	0		21	29	5	0	50		0	50		0	50
	31	19		reop.			8	42		0	50		0	50		3	47
5	33	17	6	50	0	5	0	50		0	50		0	50	5	0	50
	36	14					0	50	6	0	50		reop			0	50
6	44	6				6	3	47		0	50	5	1	49	6	0	50
	47	3					0	50		0	40		0	50		0	50
	reop.					one	week		7	reop.					one	week	
	17	33				7	1	49		0	50				7	0	50
	6	44					6	44		0	50					0	50
	12	38				one	week			1	49				one	week	
7	39	11				8	1	49	8	0	50				8	0	50
	49	1					1	49		0	50					0	50
8	46	4				9	3	47	9	0	50				9	0	50
	30	20					0	50		0	50					0	50
one	week					10	0	50	one	week					10	0	50
9	35	15					2	48	10	0	50					0	50
	36	14				11	3	47		0	50				11	0	50
one	week						reop.		one	week						reop.	
10	12	38					2	3	11	0	50					0	50
	17	33				12	0	50		0	50					0	50
							0	50								0	50
						13	1	49							12	0	50
							0	50								0	50
						14	2	48							13	0	50
							1	49								0	50
						one	week								one	week	
						15	0	50							14	0	50
							0	50								0	50

* cases taken from Suess

** examination after brain removal revealed destruction in handedness area

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																					
29F-Abr			8M-aBr			21F*-aBR			30M-aBR			31M-aBR			9F-aBr		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	10	40	1	20	30	1	38	12	1	48	2	1	44	6	1	30	20
	1	49		46	4		36	14		49	1		45	5		39	11
2	9	41	2	46	4	2	44	6	2	50	0	2	47	3	2	21	29
	0	50		50	0		48	2		50	0		47	3		14	36
3	5	45	3	46	4	3	48	2	3	43	7	3	46	4	3	9	41
	7	43		45	5		41	9		48	2		48	2		6	44
4	8	42	4	50	0	4	24	26	4	50	0	4	49	1	4	4	46
operation			operation			operation			operation			operation			operation		
	4	46		50	0		32	9		0	0	wouldn't				2	48
	6	44		50	0	5	8	0	5	50	0	reach				0	50
	6	44		50	0	6	46	4		50	0					0	50
5	0	50	5	50	0	7	49	1	6	50	0				5	3	47
	1	49		50	0					50	0					0	50
6	4	46	6	50	0				one week						6	2	48
	4	46		50	0				7	50	0					2	48
7	0	50	7	50	0					50	0				one week		
	reop.		one week						one week						7	1	49
	0	50	8	50	0				8	50	0					0	50
	0	50		50	0					50	0				one week		
	0	50													8	0	50
8	0	50														0	50
	0	50															
9	0	50															
	0	50															
one week																	
10	0	50															
	0	50															
one week																	
11	0	50															
	0	50															

* cases taken from Suess

* cases taken from Spree

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																					
10M-aBr			32M-aBr			33F**aBr			34M-aBr			35M-aBr			11F-aB'R		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	3	47	1	0	50	1	35	15	1	10	40	1	5	45	1	49	1
	17	33		1	49		24	26		7	43		6	44		45	5
2	23	27	2	0	50	2	33	17	2	8	42	2	0	50	2	46	4
	23	28		0	50		6	44		3	47		1	49		42	8
3	12	38	3	0	50	3	21	29	3	4	46	3	2	48	3	43	7
	16	34		2	48		15	35		2	48		2	48		27	23
4	32	18	4	0	50	4	6	44	4	1	49	4	1	49	4	39	11
operation			operation			operation			operation			operation			operation		
	27	23		0	50		0	50		0	50		1	49		43	7
	21	29		0	50		3	47		0	50		1	49		40	10
	29	21		0	50		0	50		0	50		0	50		27	23
5	35	15	5	0	50	5	6	44	5	0	50	5	0	50	5	23	27
	24	26		0	50		1	49		0	50		0	50		7	43
6	5	45	6	0	50	6	2	48	6	0	50	6	0	50	6	7	43
	18	32		0	50		1	49		0	50		0	50		2	48
one week			one week				reop.		one week			one week			one week		
7	30	20	7	1	49		0	50	7	4	46	7	0	50	7	14	36
	31	19		0	50		0	50		0	50		0	50		7	43
one week			one week				0	50	one week			one week			one week		
8	27	23	8	0	50	7	2	48	8	0	50	8	0	50	8	10	40
	33	17		0	50		4	46		0	50		0	50		4	46
						8	1	49									
							0	50									
						one week											
						9	0	50									
							0	50									
						one week											
						10	0	50									
							0	50									

** examination after removal of brain revealed destruction in handedness area

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments																					
22M*-aB'R			36M**aB'R			37M-aB'R			13F-aB'r			12M-aB'r			14F-abR		
Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L	Day	R	L
1	1	49	1	49	1	1	42	8	1	50	0	1	29	21	1	45	5
	47	3		48	2		44	6		31	19		20	30		38	12
2	37	13	2	50	0	2	49	1	2	10	40	2	17	33	2	49	1
	38	12		50	0		50	0		2	48		17	33		40	10
3	43	7	3	49	1	3	50	0	3	4	46	3	25	25	3	47	3
	27	23		50	0		50	0		3	47		11	39		42	8
4	25	25	4	50	0	4	50	0	4	10	40	4	14	36	4	47	3
operation			operation			operation			operation			operation			operation		
	18	1		50	0		50	0		6	44		9	41		49	1
	28	3		50	0		50	0		2	48		7	43		50	0
	43	0		50	0		50	0		1	49		7	43		50	0
5	42	8	5	50	0	5	50	0	5	2	48	5	21	29	5	50	0
	49	1		50	0		50	0		0	50		28	22		48	2
			6	50	0	6	50	0	6	0	50	6	19	31	6	50	0
				50	0		50	0		0	50		14	36		47	3
			one week			one week			7	2	48	one week			7	50	0
			7	50	0	7	50	0		reop.		7	1	49		reop.	
				50	0		50	0		2	48		13	37		41	9
			one week			one week				1	49	one week				16	34
			8	50	0	8	50	0		0	50	8	8	42		24	26
				50	0		50	0	8	0	50		2	48	8	47	2
										0	50	9	7	43		31	19
									9	0	50		6	44	9	15	35
										0	50	10	1	49		0	50
									one week				reop.		one week		
									10	0	50		0	50	10	30	20
										0	50		0	50		35	15
									one week				0	50	one week		
									11	0	50	11	1	49	11	44	6
										0	50		0	50		13	37
												12	1	49			
													6	34			
												one week					
												13	1	49			
													3	47			

* cases taken from Suess

** examination after brain removal revealed destruction in handedness area.

TABLE IX

RECORDS OF REACHING (cont.)

Rats and Treatments								
24M*-abR			15F-abr			16F-abr		
Day	R	L	Day	R	L	Day	R	L
1	5	45	1	18	32	1	21	29
	29	21		34	16		17	33
2	32	18	2	16	34	2	15	35
	40	10		21	29		29	21
3	46	4	3	5	45	3	9	41
	48	2		8	42		11	39
4	41	9	4	5	45	4	2	48
operation			operation			operation		
	50	0		19	31		0	50
	50	0		5	45		0	50
5	20	30		7	43		0	50
	43	7	5	0	50	5	0	50
	30	20		0	50		1	49
	21	29	6	1	49	6	0	50
				2	48		0	50
			7	3	47	7	0	50
			reop.			reop.		
				12	38		0	50
				45	5		0	50
				42	8		0	50
			8	11	39	8	0	50
				13	37		0	50
			9	7	43	9	1	49
				22	28		0	50
			one week			one week		
			10	32	18	10	0	50
				44	6		0	50
			one week			one week		
			11	44	6	11	0	50
				50	0		0	50

* cases taken from Suess

Day	K	L	Day	K	L	Day	K	L
1	5	45	1	18	22	1	21	29
	29	21		44	16		47	33
2	32	18	2	16	34	2	15	38
	40	10		21	29		20	21
3	46	4	3	5	48	3	9	41
	48	2		3	42		11	39
4	41	9	4	5	43	4	2	48
operation operation operation								
	50	0		19	31		0	50
	50	0		5	45		0	50
5	20	30		2	43		0	50
	43	7	5	0	50	5	0	50
	30	20		0	50		1	49
	31	29	6	1	49	6	0	50
				2	48		0	50
			7	3	47	7	0	50
				Prod.			Prod.	
				12	38		0	50
				45	5		0	50
				42	8		0	50
			8	31	39	8	0	50
				13	37		0	50
			9	7	43	9	1	49
				22	28		0	50
				one week		one week		
			10	32	18	10	0	50
				18	6		0	50
				one week		one week		
			11	44	6	11	0	50
				50	0		0	50

* cases taken from those

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