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LATERAL PREFERENCES IN MONKEYS

by

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(Rec. 20-X-1960)

INTRODUCTION

As a result of the recent investigations of "hand" preferences in monkeys by COLE (1957) and WARREN (1958) two factors have been isolated that influence the degree of preference shown. The first factor relates to practice or learning: the number of animals showing significant lateral preferences and also each individual animal's consistency (throughout a given test and also between different tests) increases with the amount of testing given under constant conditions. The second factor relates to the complexity of the task or test for handedness: both the degree and consistency of lateral preferences increase with more complex test conditions. This finding confirmed the earlier work of KOUNIN (1938). WARREN (1958) has also summarised the results obtained from rats, cats, monkeys, chimpanzees and man, and suggests "the possibility that the importance of environmental determinants, relative to anatomical factors, increases with phyletic status within the mammalian series".

It is the aim of the present paper to present further information about the factors concerned in the manifestation of hand preferences in monkeys. The practice effect has been observed in 16 animals over a period of 9-12 months and in another 16 animals for at least 6 months. In all the tests except one (the least complex) it was possible to observe both the hand used to manipulate an inedible object (such as the lid of a food container) and also the hand used to bring the food to the mouth. Thus an indication has

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been obtained of the consistency of preference on a single test. An analysis of the effect of various neuro-surgical procedures upon the hand preferences of a group of 30 animals has also been made.

METHODS

Subjects. Lateral preferences were routinely observed in animals that have at the same time served as subjects for other behavioural investigations during the years 1956-60. Thus the weights and training histories of 46 of the present group of 48 animals have already been reported elsewhere (8 animals by ETTLINGER & WEGENER, 1958; 12 animals by ETTLINGER, 1959a; 3 animals by ETTLINGER, 1959b; 11 animals by BURTON & ETTLINGER, 1960; 12 animals by BATES & ETTLINGER, 1960). One additional animal was given the adapting test of ETTLINGER & WEGENER (1958) and the remaining animal was given the first two tests of those described by BURTON & ETTLINGER (1960). This last animal, together with the 11 subjects of BURTON & ETTLINGER (1960) were subsequently used in a futher study, involving one new test, which is to be reported (BURTON & ETTLINGER, 1961).

Apparatus. All animals were tested in the Wisconsin General Testing Apparatus.

Tests. These have been described in detail in previous reports. The visual tests fall into three main groups, according to the kind of manual manipulation required: first, the large majority of visual tests, in which the animal was required to learn simultaneous two- (or rarely five-) choice discriminations based on differences in shape, hue, size, or multiple dimensions between the cues, and in which the manipulation involved pushing a sliding lid off a food container and grasping a peanut; secondly, those tests in which the animal was required to draw towards itself, by pulling on a cord, one of two sliding boxes and then to lift a hinged lid and take hold of the nut, when learning visual temporal discriminations as described by BURTON & ETTLINGER (1960); and thirdly, the test described by ETTLINGER (1959a) in which the animal was confronted with a row of 11 peanuts and allowed to take three on each of six trials. The somatosensory tests in every instance involved the pushing of alternative sliding lids in the dark, with the presence of reward being indicated by differences in shape, size, roughness or spatial position between the cues. In the auditory tests the animal was required to draw in, by pulling on a cord, one of two boxes running on rails and then to lift open a hinged lid

and remove a nut, exactly as in the visual temporal discrimination tests. A peanut served as the food reward for correct choice in all the tests.

Procedure. The general training procedures have been described in previous reports. Except in the field test of ETTLINGER (1959a) training was routinely continued until each animal achieved a standard level of performance of 10 or less errors in 100 consecutive trials on any test. A record was then taken of the hand used to manipulate the lids and also of that used to grasp the food during a block of 30 trials forming part of the final 100 trials. (As a rule the block of 30 trials was taken from the last 50 or so trials, in which none or only very few of the 10 permissible errors occur.) Occasionally training was abandoned when an animal had received a large number of trials without achieving the standard level of performance. Under those circumstances the hand preferences were recorded during a block of 30 successful trials forming part of the final 100 test trials. In the field test of ETTLINGER (1959a) the hand used by each animal to take hold of the nut was recorded on all 18 trials.

Categories of Preference. Whenever an animal used one hand (either to move a lid or to grasp food) in at least 27 of 30 (90%) trials a strong preference is recorded, and indicated as a "Right" or "Left" preference. Use of a hand on 16-26 trials is indicated by "R > L" or "L > R". Occasionally one hand, say the left, was used on 14-15 trials with the box to the animal's left side, and the other hand on at least 14 trials with the right box. This kind of preference is recorded as "Left for left side, Right for right side". Similarly some animals used the right hand on 14 or 15 trials with the left box, and *vice versa*. Such a preference is referred to as "Right for left side, Left for right side".

RESULTS

PREFERENCES ON THE FIRST TEST (UNOPERATED ANIMALS)

Strength of preference. The hand preferences shown by 48 animals on their first test are presented in Table I (visual testing) and II (somatosensory testing). The categories of preference have been fully described in the section on Methods. "Right" and "Left" preferences are strong tendencies (the same hand used in 90% or more of trials). The other categories imply some degree of ambiguity in the handedness. Ambiguity (or more strictly, inconsistency) is also present when the same hand is not strongly preferred for both manipulation of the box lids and also for grasping the nut.

TABLE I

Hand preferences on their first test, if visual, in 39 unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts	Field Test
Right	A	C, E, F	6	3
Left	B, C	A, D	14	0
Right > Left	D	B	4	0
Left > Right			3	3
Right for left side / Left for right side	E, F		0	0
TOTALS		6	27	6

The letters A-F refer to six individual animals. The figures refer to the total number of animals in each group. The headings of the columns and of the rows are explained in the text.

TABLE II

Hand preferences on their first test, if somato-sensory, in nine unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts
Right			0
Left	A		3
Right > Left			2
Left > Right		A	2
Left for right side / Right for left side			1
TOTALS		1	8

The letters, figures and headings have the same meanings as in Table I.

TABLE III

Summary of Tables I and II, showing hand preferences on their first test (irrespective of sensory modality) in 42 unoperated monkeys.

Hand Preference	
Right	6
Left	17
Ambiguous	19
	42

Animals tested only on the field test of Table I have been omitted. Animals using their right or left hand in 27 of 30 trials for both lids and nuts are said to have a right or left preference; all other categories of preference from Tables I and II are classified as ambiguous.

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Taking first the least complex visual test, the field test in which the animal merely picked peanuts off a board, it is seen from Table I that a strong preference was shown by only three of the six animals (50%). The proportion of animals showing a strong and consistent preference rises to 61% (20 out of 33) when the results for more complex [1]) visual tests are considered. In these tests the animals were required to push open a sliding lid in order to gain a nut. If moreover the measure of hand preference is restricted to just one kind of response, namely to the use of the hand for grasping food (as in the field test, and in the tests of WARREN, 1958), then an additional five animals (animals A, C, D, E and F of Table I) show strong preferences on the complex tests, raising the proportion to 76%. Unexpectedly the proportion of animals showing strong and consistent preferences on their first test falls to 33% when the nine animals first trained in the dark on a complex tactile discrimination test are considered (Table II). If now the six animals that were first tested on the field test (no lids) are excluded and the sensory modality of testing is disregarded, then it is seen from Table III that 23 of 42 animals (55%) showed a strong and consistent preference (the same hand used in 90% of trials for manipulation of both the lids and nuts) on their first test.

Distribution of preferences. It is clear from the present results that more animals in this sample of 42 showed a strong preference for the left hand than for the right hand on their first test. This finding applies equally to the complex visual and somatosensory tests (Tables I and II) but is reversed or absent in two groups of animals, namely in the six animals tested first on the field test, and in the six animals showing inconsistent preferences for lids and nuts on the complex visual tests. The difference between the actual and expected incidence of strong right handedness (Table III) reaches statistical significance ($p = .034$, two-tailed binomial test).

Inspection of the results for the six inconsistent animals of Table I and the one similar animal of Table II fails to reveal any obvious trend in the distribution of the preferences. It is surprising however, that all of the seven animals that showed different (inconsistent) preferences for manipulation of lids and nuts at the same time gave evidence of a strong preference (right

1) The preferences on the field test were recorded on the first two days of training, on the more complex tests during the final 100 trials of training, perhaps as much as 1-5 weeks after training began, depending on the difficulty of the first test. Thus some additional practice was given at the same time as more complex tests were used.

or left) for either manipulation of the lids or of the nuts or of both (with the opposite hands).

PREFERENCES ON THE LAST TEST (UNOPERATED ANIMALS)

Strength of preferences. Gross differences in the complexity of the tests do not exist when lateral preferences on the last test are considered. For in all last tests the animals were required to manipulate both a lid and a food reward. However, in the case of the 12 animals tested last on an auditory test (Table V) manipulation of the lids and nuts was preceded and accompanied by manipulation of a cord (see section on Tests).

The interval between testing on the first and last tests varied considerably. In eight animals it ranged from two to seven weeks; in 16 animals from six to nine months; in the remaining 16 animals from nine to 12 months. Results are available for only 40 animals since two of the original group of 42 animals (Table III) were trained on only one test.

It is seen from Table IV that the proportion of animals showing a strong and consistent preference on complex visual tests has actually fallen from 61% on the first test to 57% (8 out of 14 animals) on the last test. However the eight animals with less than two months' interval between the first and last tests fall into this group of 14 animals. In the case of the somatosensory tests the proportion has risen from 33% on the first test to 79% (11 out of 14 animals) on the last test (Table V). Moreover all (100%) of the 12 animals tested last on an auditory discrimination test showed strong and consistent preferences (Table V). So that combining all the sensory modalities of testing (Table VI) 31 out of 40 animals (78%) gave evidence of strong and consistent preferences on their last test, as against 55% on the first test. The difference between these proportions on the first and last tests is significant ($\chi^2 = 4.71$, $p = <0.05$).

Distribution of preferences. Although the proportion of animals showing a strong preference changed only slightly as between the first and last visual tests (Tables I and IV) the relative distributions of right and left preference changed to a marked extent. 30% of the 20 animals showing strong and consistent preferences on the first visual test preferred the right hand. This value has risen to 63% on the last visual test. Similarly, disregarding sensory modality, only six out of 23 animals (26%) showing a strong and consistent preference on the first test (Table III) preferred the right hand. On the last test this proportion has risen to 13 out of 31 animals (42%). The difference between the actual and expected

TABLE IV

Hand preferences on their last test, if visual, in 14 unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts
Right	A		5
Left	B, C		3
Right > Left			1
Left > Right		B, C	1
Right for left side / Left for right side			1
Right for right side / Left for left side		A	0
TOTALS		3	11

The letters, figures and headings have the same meanings as in Table I.

TABLE V

Hand preferences in their last test, if somatosensory or auditory, in 26 unoperated monkeys.

	Somatosensory test	Auditory test
Hand Preference	Lids + Nuts	Lids + Nuts
Right	5	3
Left	6	9
Right for left side / Left for right side	3	0
TOTALS	14	12

The figures and headings have the same meanings as in Table I. All animals showed the same preference for both lids and nuts.

TABLE VI

Summary of Tables IV and V, showing hand preferences on their last test (irrespective of sensory modality) in 40 unoperated monkeys.

Hand Preference	
Right	13
Left	18
Ambiguous	9
	40

Animals using their right or left hand in 27 of 30 trials for both lids and nuts are said to have a right or left preference; all other categories of preference from Tables IV and V are classified as ambiguous.

incidence of strong right hand preferences on the last test is no longer statistically significant ($p = >0.1$).

Seven out of 42 animals (17%) were inconsistent in their preferences (for lids and nuts) on the first test. Only three out of 40 animals (8%) were similarly inconsistent on their last test.

SUMMARY OF DIFFERENCES BETWEEN PREFERENCES ON FIRST AND LAST TEST

55% of animals gave evidence of strong and consistent preferences on their first test, as against 78% on the last test. 26% of animals showing strong and consistent preferences were right handed on the first test, as against 42% on the last test. 17% of animals were inconsistent in their preferences for the hand used in moving a lid and grasping a nut on the first test, as against 8% on the last test.

Patterns of change in preferences.

In Table VII are shown the changes in hand preference of 40 animals during testing on up to ten separate tests. Eight animals from the original group of 48 (Tables I and II) have been excluded: the six animals tested first on the field test (Table I) and one further animal each from Tables I and II that received training on only one test.

The first finding relates to the large number of animals changing their preference between the first and second tests compared with the smaller number changing between subsequent tests. For 18 animals (45% of 40) showed a different preference on test 2 than they had shown on test 1, whereas only eight (25% of 32) changed their preferences between tests 2 and 3, and four (13% of 32) changed between tests 3 and 4. Nevertheless, on occasion an animal changed its preference even after prolonged training. Thus an animal which preferred the left hand strongly on the first test (and is identified by the letter G in Table VII) continued this preference on test 2, showed weak left handedness ($L > R$) on test 3, a strong right preference on tests 4-6, again a weak left preference on test 7 and a strong right preference on test 8. Such changes are atypical and cannot readily be related to variations in the conditions (*e.g.* sensory modality) of successive tests.

Another finding concerns the greater frequency of a full reversal of a strong preference than of change to a weaker one. Thus of the animals with a strong right preference on the first test, one showed a strong left preference on the second whereas there was none with a weak right preference. This trend is continued, so that on test 3-6 two of the animals were

TABLE VII

Changes in the hand preferences of 40 unoperated monkeys during testing for periods of up to one year.

1		2	3	4	5	6	7	8	9	10
		Serial Number of Test (irrespective of sensory modality)								
Right Pref.	R:	3, (D)		D	D	(D)		D		
A, B, C,	L:	F	E, F	E, F	E, F	E,F	E	E	E	
D, F, (E)	R > L:		(D)				D			
	L > R:	(E)								
Left Pref.	R:	2, (3)	3, (A)	5	4	A, G, N	(A)	A, G	(A)	A
	L:	8, (6)	11, (2)	11, (3)	9, (3)	9, (3)	6, (2)	7, (2)	B, C, D	B, C, D
17, (3)	L > R:		G				G, (H)			
	R for l. / L for r.	(Q)	Q, R	R	R					
Right > Left	R:	2, (B)	C, D	C, D	C, D	C				
	L:	E	E	E						
A, B, C,	L > R:	D								
D, E										
Left > Right	R:	2, (B)	E	E	E	E	E			
	L:	C	C, D, F	C, D, F	C, D	C, D	C	B		
6, (B)	L > R:	A, (F)		(B)	(B)					
	R for l. / L for r.	G	G, (B)	G	F	(B)	(B)			

Right for l. side
Left for r. side
A, B

R > L: A
R for l. / L for r. B

The figures at the head of columns indicate the serial number of successive tests (irrespective of modality). The headings of rows refer to hand preferences (given in full, or in abbreviated form in the sub-rows). The capital letters refer to individual animals and the figures to total numbers of animals. Letters or figures in brackets indicate animals that showed the given preference only in respect of lids of food containers.

strongly left-handed and none weakly right-handed. Similarly, of the animals showing a strong left preference on the first test four or five showed strong right preferences on tests 2-5 as against none or one with a weak left preference. If, however, the animal showed a weak preference (R > L or L > R) on the first test it was ultimately more likely to show a strong preference with the same hand than to reverse its handedness. Thus three of five animals showing a weak right preference on the first test are strongly right-handed on the second.

Finally, there is only a very slight trend for animals (indicated by brackets in Table VII) that showed inconsistent preferences (as between lids and nuts) on any one test also to be more likely to change in their preferences from test to test than other animals. Thus if changes in preference only on tests 3-10 are considered, it can be seen from Table VII that three inconsistent animals changed their preferences, whereas only two fully consistent animals (G of the Left group for test 1, and F of the L > R group on test 1) changed their preferences in the same way. However animal A of the Left group on test 1 affords an example of an unchanged right preference (tests 2-10) despite the occasional inconsistency in the use of the hands for lids and nuts on any one test. It also appears that if an animal is inconsistent in its preference for lids and nuts on any one test it is likely to continue to be inconsistent on subsequent tests. Therefore inconsistency, although reduced by practice, appears repeatedly in some animals and never in others.

EFFECT OF NEUROSURGICAL PROCEDURES

Table VIII tabulates the results of this analysis. As hand preferences continue to change even in some unoperated animals despite prolonged

TABLE VIII

Effect of brain surgery on hand preferences for lid-opening in 30 monkeys.

Type of Ablation	No Change	Change	Totals
Bil. Anterior Frontal	7	L to: R for r. side; L for l. side	8
Bil. Inferior Temporal	9	0	9
Unil. Inferior Temporal	2	R > L to: R	3
Bil. Posterior Parietal	5	L to: R L to: R	7
Left Optic Tract Section	0	R to: L L > R to: L R for l. side; L for r. side: to: L	3
Totals	23	7	30

The figures represent numbers of monkeys in each category. Each animal has been included in this table only once, in respect of its preferences on the last test (irrespective of sensory modality) before surgery and on the same test (not necessarily the first) after surgery. Where an animal was operated upon more than once it has been included in the table only in respect of its first operation.

training (Table VII) a certain frequency of change associated with testing before and after surgery is likely to result from factors not directly related to the surgery. However it can be seen from Table VIII that every one of three animals that had the left optic tract cut (giving rise to blindness of the right half-field of vision in both eyes) changed their preferences to become strongly left-handed.

DISCUSSION

WARREN (1958) using 17 monkeys in his careful study was able to demonstrate statistically that practice increases the strength, consistency (between preferences on the first and second halves of a single test) and generality (between different tests) of lateral preferences in the monkey. His animals were tested three times over the course of about 11 months on the same three tests. Other training intervened between successive cycles of testing for hand preferences. In the present study all three of WARREN's findings have received indirect confirmation. However different measures of strength and consistency have been used, and the generality of preferences has in this investigation been followed not by correlations between different tests but by noting frequencies of change in preference between successive tests (Table VII). Moreover in WARREN's study the effect of practice was assessed by comparison of preferences on three repetitions of the same tests, whereas in the present work it was generally assessed by comparison of preferences on successive and different tests.

One new finding is the small proportion (33%) of animals with strong and consistent preferences on the first somatosensory test given in the dark. The manipulations involved in this test (described in detail by ETTLINGER & WEGENER, 1958) are the same as for the complex visual tests, except that pushing the lids is preceded by palpation, in the dark, of one or both of the dissimilar tactile cues. Previous quantitative reports on lateral preferences during somatosensory testing in the dark are not known. However WARREN (1958) found only 30% of animals with a greater than 80% preference on the first administration of a simple visual test. Therefore the value of 33% of animals with a greater than 90% preference would not be exceptionally low for a simple test. In fact the test was not simple, so that no satisfactory explanation can be offered, more particularly since the trend is reversed in the last somatosensory test (Table V).

Also unexpected was the low proportion (26%) of strongly right-handed, as against 74% of strongly left-handed, animals on the first test. This difference had virtually disappeared on the last test. WARREN (1953) has reported on the preferences of 84 monkeys on a single test. He found no

asymmetry. However the animals were not required to push lids in his test so that preference was observed in respect of the hand taking food. Also WARREN (1958) refers to the animals in his earlier study as "experimentally sophisticated". Therefore further observations are needed of the lateral preferences on a complex test in untrained monkeys. Inspection of Table VII indicates that the asymmetry is already greatly reduced on the second test (nine animals with strong and consistent right preferences, 11 with left preferences) although more marked again on some subsequent tests.

Finally it has been found that hand preferences are changed to the left in animals rendered blind in the right halves of the two fields of vision. This confirms the earlier reports of KLÜVER (1937) and of SETTLAGE (1939). In all investigations handedness was assessed on visual tests. Further animals, showing the same change in hand preference but when the left optic tract was cut subsequent to other surgical procedures, have been described by ETTLINGER (1959a). It would seem that the preferred hand is likely to be on the side of the body that receives the sensory information guiding its movements (that is, the preferred hand is opposite to the cerebral hemisphere receiving the relevant sensory inflow). Thus the nature of the sensory control of a manual manipulation would appear to be another major determinant of hand preference.

SUMMARY

Hand preferences have been observed in a group of 48 monkeys. It is found that practice in manipulation increases the proportion of animals showing strong and consistent preferences and reduces the initial predominance of left preferences in this sample of animals to near equality with right. The proportion of animals showing strong and consistent preferences is low during initial somatosensory discrimination testing in the dark. The various kinds of change in preference observed on up to ten consecutive tests are analysed in some detail. Thus a full reversal is common in animals changing from a strong preference, whereas a strengthening of the same preference is common in animals changing from a weak preference. 45% of animals change their preference between the first and second test, but this proportion is progressively reduced, for example to 13% changing between tests 3 and 4. Finally the effects of various neurosurgical procedures on the preferences in 30 animals are tabulated. These comprise frontal, temporal or parietal cortical ablations and also section of one optic tract. Only the latter procedure gives rise to changes in hand preferences. It is concluded that the nature of the sensory control (whether visual or somatosensory, or if visual, whether confined to one half visual field) of a manual manipulation is another major determinant of hand preference.

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ZUSAMMENFASSUNG

Bei 48 Affen wurde Links- bzw. Rechtshändigkeit beobachtet. Durch Übung liess sich der Anteil der Tiere mit starker und anhaltender Bevorzugung der rechten bzw. der linken Hand steigern; während bei diesen Tieren ursprünglich die Linkshänder überwogen, waren hinterdrein beide Gruppen nahezu gleichgross. In anfänglichen Tastversuchen im Dunkeln waren ausgesprochene und anhaltende Bevorzugungen einer Hand selten. Die verschiedenen Arten des Bevorzugungswechsels wurden in bis zu 10 aufeinanderfolgenden Versuchen in Einzelheiten untersucht. Bei ausgesprochenen Einhändern ist der Umschlag ins Gegenteil häufig, während Tiere mit anfangs nur schwacher Bevorzugung einer Hand diese gewöhnlich verstärken. 45% der Tiere wechseln ihre Bevorzugung zwischen dem ersten und zweiten Versuch; weiterhin wechseln immer weniger Tiere, z.B. 13 % zwischen dem dritten und vierten.

Endlich wurden die Auswirkungen verschiedener neurochirurgischer Operationen auf die Händigkeit von 30 Tieren festgehalten. Es handelte sich um Eingriffe in die Stirn-, Schläfen- und Scheitelrinde sowie Zertrennung eines *tractus opticus*. Nur der letztgenannte Eingriff führte zu einem Wechsel der Händigkeit. So ergibt sich der Schluss, dass die Art der Sinneskontrolle der tätigen Hand, taktil oder optisch im ganzen oder nur im halben Gesichtsfeld, ein wesentlicher Mitbestimmer für die Händigkeit ist.

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INTRODUCTION

As a result of the recent investigations of "hand" preferences in monkeys by COLE (1957) and WARREN (1958) two factors have been isolated that influence the degree of preference shown. The first factor relates to practice or learning: the number of animals showing significant lateral preferences and also each individual animal's consistency (throughout a given test and also between different tests) increases with the amount of testing given under constant conditions. The second factor relates to the complexity of the task or test for handedness: both the degree and consistency of lateral preferences increase with more complex test conditions. This finding confirmed the earlier work of KOUNIN (1938). WARREN (1958) has also summarised the results obtained from rats, cats, monkeys, chimpanzees and man, and suggests "the possibility that the importance of environmental determinants, relative to anatomical factors, increases with phyletic status within the mammalian series".

It is the aim of the present paper to present further information about the factors concerned in the manifestation of hand preferences in monkeys. The practice effect has been observed in 16 animals over a period of 9-12 months and in another 16 animals for at least 6 months. In all the tests except one (the least complex) it was possible to observe both the hand used to manipulate an inedible object (such as the lid of a food container) and also the hand used to bring the food to the mouth. Thus an indication has

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been obtained of the consistency of preference on a single test. An analysis of the effect of various neuro-surgical procedures upon the hand preferences of a group of 30 animals has also been made.

METHODS

Subjects. Lateral preferences were routinely observed in animals that have at the same time served as subjects for other behavioural investigations during the years 1956-60. Thus the weights and training histories of 46 of the present group of 48 animals have already been reported elsewhere (8 animals by ETTLINGER & WEGENER, 1958; 12 animals by ETTLINGER, 1959a; 3 animals by ETTLINGER, 1959b; 11 animals by BURTON & ETTLINGER, 1960; 12 animals by BATES & ETTLINGER, 1960). One additional animal was given the adapting test of ETTLINGER & WEGENER (1958) and the remaining animal was given the first two tests of those described by BURTON & ETTLINGER (1960). This last animal, together with the 11 subjects of BURTON & ETTLINGER (1960) were subsequently used in a futher study, involving one new test, which is to be reported (BURTON & ETTLINGER, 1961).

Apparatus. All animals were tested in the Wisconsin General Testing Apparatus.

Tests. These have been described in detail in previous reports. The visual tests fall into three main groups, according to the kind of manual manipulation required: first, the large majority of visual tests, in which the animal was required to learn simultaneous two- (or rarely five-) choice discriminations based on differences in shape, hue, size, or multiple dimensions between the cues, and in which the manipulation involved pushing a sliding lid off a food container and grasping a peanut; secondly, the tests in which the animal was required to draw towards itself, by pulling on a cord, one of two sliding boxes and then to lift a hinged lid and take hold of the nut, when learning visual temporal discriminations as described by BURTON & ETTLINGER (1960); and thirdly, the test described by Ettlinger (1959a) in which the animal was confronted with a row of 11 peanuts and allowed to take three on each of six trials. The somatosensory tests in every instance involved the pushing of alternative sliding lids in the dark, with the presence of reward being indicated by difference in shape, size, roughness or spatial position between the cues. In auditory tests the animal was required to draw in, by pulling on a cord, one of two boxes running on rails and then to lift open a hinged

and remove a nut, exactly as in the visual temporal discrimination tests. A peanut served as the food reward for correct choice in all the tests.

Procedure. The general training procedures have been described in previous reports. Except in the field test of ETTLINGER (1959a) training was routinely continued until each animal achieved a standard level of performance of 10 or less errors in 100 consecutive trials on any test. A record was then taken of the hand used to manipulate the lids and also of that used to grasp the food during a block of 30 trials forming part of the final 100 trials. (As a rule the block of 30 trials was taken from the last 50 or so trials, in which none or only very few of the 10 permissible errors occur.) Occasionally training was abandoned when an animal had received a large number of trials without achieving the standard level of performance. Under those circumstances the hand preferences were recorded during a block of 30 successful trials forming part of the final 100 test trials. In the field test of ETTLINGER (1959a) the hand used by each animal to take hold of the nut was recorded on all 18 trials.

Categories of Preference. Whenever an animal used one hand (either to move a lid or to grasp food) in at least 27 of 30 (90%) trials a strong preference is recorded, and indicated as a "Right" or "Left" preference. Use of a hand on 16-26 trials is indicated by "R > L" or "L > R". Occasionally one hand, say the left, was used on 14-15 trials with the box to the animal's left side, and the other hand on at least 14 trials with the right box. This kind of preference is recorded as "Left for left side, Right for right side". Similarly some animals used the right hand on 14 or 15 trials with the left box, and *vice versa*. Such a preference is referred to as "Right for left side, Left for right side".

RESULTS

PREFERENCES ON THE FIRST TEST (UNOPERATED ANIMALS)

Strength of preference. The hand preferences shown by 48 animals on their first test are presented in Table I (visual testing) and II (somatosensory testing). The categories of preference have been fully described in the section on Methods. "Right" and "Left" preferences are strong tendencies (the same hand used in 90% or more of trials). The other categories imply some degree of ambiguity in the handedness. Ambiguity (or more strictly, inconsistency) is also present when the same hand is not strongly preferred for both manipulation of the box lids and also for grasping the nut.

TABLE I

Hand preferences on their first test, if visual, in 39 unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts	Field Test
Right	A	C, E, F	6	3
Left	B, C	A, D	14	0
Right > Left	D	B	4	0
Left > Right			3	3
Right for left side / Left for right side	E, F		0	0
TOTALS		6	27	6

The letters A-F refer to six individual animals. The figures refer to the total number of animals in each group. The headings of the columns and of the rows are explained in the text.

TABLE II

Hand preferences on their first test, if somato-sensory, in nine unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts
Right			0
Left	A		3
Right > Left			2
Left > Right		A	2
Left for right side / Right for left side			1
TOTALS		1	8

The letters, figures and headings have the same meanings as in Table I.

TABLE III

Summary of Tables I and II, showing hand preferences on their first test (irrespective of sensory modality) in 42 unoperated monkeys.

Hand Preference	
Right	6
Left	17
Ambiguous	19
	42

Animals tested only on the field test of Table I have been omitted. Animals using their right or left hand in 27 of 30 trials for both lids and nuts are said to have a right or left preference; all other categories of preference from Tables I and II are classified as ambiguous.

Taking first the least complex visual test, the field test in which the animal merely picked peanuts off a board, it is seen from Table I that a strong preference was shown by only three of the six animals (50%). The proportion of animals showing a strong and consistent preference rises to 61% (20 out of 33) when the results for more complex [1]) visual tests are considered. In these tests the animals were required to push open a sliding lid in order to gain a nut. If moreover the measure of hand preference is restricted to just one kind of response, namely to the use of the hand for grasping food (as in the field test, and in the tests of WARREN, 1958), then an additional five animals (animals A, C, D, E and F of Table I) show strong preferences on the complex tests, raising the proportion to 76%. Unexpectedly the proportion of animals showing strong and consistent preferences on their first test falls to 33% when the nine animals first trained in the dark on a complex tactile discrimination test are considered (Table II). If now the six animals that were first tested on the field test (no lids) are excluded and the sensory modality of testing is disregarded, then it is seen from Table III that 23 of 42 animals (55%) showed a strong and consistent preference (the same hand used in 90% of trials for manipulation of both the lids and nuts) on their first test.

Distribution of preferences. It is clear from the present results that more animals in this sample of 42 showed a strong preference for the left hand than for the right hand on their first test. This finding applies equally to the complex visual and somatosensory tests (Tables I and II) but is reversed or absent in two groups of animals, namely in the six animals tested first on the field test, and in the six animals showing inconsistent preferences for lids and nuts on the complex visual tests. The difference between the actual and expected incidence of strong right handedness (Table III) reaches statistical significance ($p = .034$, two-tailed binomial test).

Inspection of the results for the six inconsistent animals of Table I and the one similar animal of Table II fails to reveal any obvious trend in the distribution of the preferences. It is surprising however, that all of the seven animals that showed different (inconsistent) preferences for manipulation of lids and nuts at the same time gave evidence of a strong preference (right

1) The preferences on the field test were recorded on the first two days of training, on the more complex tests during the final *100* trials of training, perhaps as much as 1-5 weeks after training began, depending on the difficulty of the first test. Thus some additional practice was given at the same time as more complex tests were used.

or left) for either manipulation of the lids or of the nuts or of both (with the opposite hands).

PREFERENCES ON THE LAST TEST (UNOPERATED ANIMALS)

Strength of preferences. Gross differences in the complexity of the tests do not exist when lateral preferences on the last test are considered. For in all last tests the animals were required to manipulate both a lid and a food reward. However, in the case of the 12 animals tested last on an auditory test (Table V) manipulation of the lids and nuts was preceded and accompanied by manipulation of a cord (see section on Tests).

The interval between testing on the first and last tests varied considerably. In eight animals it ranged from two to seven weeks; in 16 animals from six to nine months; in the remaining 16 animals from nine to 12 months. Results are available for only 40 animals since two of the original group of 42 animals (Table III) were trained on only one test.

It is seen from Table IV that the proportion of animals showing a strong and consistent preference on complex visual tests has actually fallen from 61% on the first test to 57% (8 out of 14 animals) on the last test. However the eight animals with less than two months' interval between the first and last tests fall into this group of 14 animals. In the case of the somatosensory tests the proportion has risen from 33% on the first test to 79% (11 out of 14 animals) on the last test (Table V). Moreover all (100%) of the 12 animals tested last on an auditory discrimination test showed strong and consistent preferences (Table V). So that combining all the sensory modalities of testing (Table VI) 31 out of 40 animals (78%) gave evidence of strong and consistent preferences on their last test, as against 55% on the first test. The difference between these proportions on the first and last tests is significant ($\chi^2 = 4.71$, $p = <0.05$).

Distribution of preferences. Although the proportion of animals showing a strong preference changed only slightly as between the first and last visual tests (Tables I and IV) the relative distributions of right and left preference changed to a marked extent. 30% of the 20 animals showing strong and consistent preferences on the first visual test preferred the right hand. This value has risen to 63% on the last visual test. Similarly, disregarding sensory modality, only six out of 23 animals (26%) showing a strong and consistent preference on the first test (Table III) preferred the right hand. On the last test this proportion has risen to 13 out of 31 animals (42%). The difference between the actual and expected

TABLE IV

Hand preferences on their last test, if visual, in 14 unoperated monkeys.

Hand Preference	Lids	Nuts	Lids + Nuts
Right	A		5
Left	B, C		3
Right > Left			1
Left > Right		B, C	1
Right for left side	{		1
Left for right side	{		
Right for right side	{	A	0
Left for left side	{		
TOTALS		3	11

The letters, figures and headings have the same meanings as in Table I.

TABLE V

Hand preferences in their last test, if somatosensory or auditory, in 26 unoperated monkeys.

	Somatosensory test	Auditory test
Hand Preference	Lids + Nuts	Lids + Nuts
Right	5	3
Left	6	9
Right for left side	{ 3	0
Left for right side	{	
TOTALS	14	12

The figures and headings have the same meanings as in Table I. All animals showed the same preference for both lids and nuts.

TABLE VI

Summary of Tables IV and V, showing hand preferences on their last test (irrespective of sensory modality) in 40 unoperated monkeys.

Hand Preference	
Right	13
Left	18
Ambiguous	9
	40

Animals using their right or left hand in 27 of 30 trials for both lids and nuts are said to have a right or left preference; all other categories of preference from Tables IV and V are classified as ambiguous.

incidence of strong right hand preferences on the last test is no longer statistically significant ($p = > 0.1$).

Seven out of 42 animals (17%) were inconsistent in their preferences (for lids and nuts) on the first test. Only three out of 40 animals (8%) were similarly inconsistent on their last test.

SUMMARY OF DIFFERENCES BETWEEN PREFERENCES ON FIRST AND LAST TEST

55% of animals gave evidence of strong and consistent preferences on their first test, as against 78% on the last test. 26% of animals showing strong and consistent preferences were right handed on the first test, as against 42% on the last test. 17% of animals were inconsistent in their preferences for the hand used in moving a lid and grasping a nut on the first test, as against 8% on the last test.

Patterns of change in preferences.

In Table VII are shown the changes in hand preference of 40 animals during testing on up to ten separate tests. Eight animals from the original group of 48 (Tables I and II) have been excluded: the six animals tested first on the field test (Table I) and one further animal each from Tables I and II that received training on only one test.

The first finding relates to the large number of animals changing their preference between the first and second tests compared with the smaller number changing between subsequent tests. For 18 animals (45% of 40) showed a different preference on test 2 than they had shown on test 1, whereas only eight (25% of 32) changed their preferences between tests 2 and 3, and four (13% of 32) changed between tests 3 and 4. Nevertheless, on occasion an animal changed its preference even after prolonged training. Thus an animal which preferred the left hand strongly on the first test (and is identified by the letter G in Table VII) continued this preference on test 2, showed weak left handedness ($L > R$) on test 3, a strong right preference on tests 4-6, again a weak left preference on test 7 and a strong right preference on test 8. Such changes are atypical and cannot readily be related to variations in the conditions (*e.g.* sensory modality) of successive tests.

Another finding concerns the greater frequency of a full reversal of a strong preference than of change to a weaker one. Thus of the animals with a strong right preference on the first test, one showed a strong left preference on the second whereas there was none with a weak right preference. This trend is continued, so that on test 3-6 two of the animals were

TABLE VII

Changes in the hand preferences of 40 unoperated monkeys during testing for periods of up to one year.

1	2	Serial Number of Test (irrespective of sensory modality) 3	4	5	6	7	8	9	10
Right Pref. A, B, C, D, F, (E)	R: 3, (D) L: F R > L: (E)	E, F (D)	D E, F	D E, F	(D) E,F	E D	D E	E	
Left Pref. 17, (3)	R: 2, (3) L: 8, (6) L > R: R for l. / L for r. (Q)	3, (A) 11, (2) G Q, R	5 11, (3) R	4 9, (3) R	A, G, N 9, (3)	(A) 6, (2) G, (H)	A, G 7, (2)	(A) B, C, D	A B, C, D
Right > Left A, B, C, D, E	R: 2, (B) L: E L > R: D	C, D E	C, D E	C, D	C				
Left > Right 6, (B)	R: L: C L > R: A, (F) R for l. / L for r. G	E C, D, F G, (B)	E C, D, F (B) G	E C, D (B) F	E C, D (B)	E C (B)	B		
Right for l. side *Left for r. side* A, B	R > L: A R for l. / L for r. B								

The figures at the head of columns indicate the serial number of successive tests (irrespective of modality). The headings of rows refer to hand preferences (given in full, or in abbreviated form in the sub-rows). The capital letters refer to individual animals and the figures to total numbers of animals. Letters or figures in brackets indicate animals that showed the given preference only in respect of lids of food containers.

strongly left-handed and none weakly right-handed. Similarly, of the animals showing a strong left preference on the first test four or five showed strong right preferences on tests 2-5 as against none or one with a weak left preference. If, however, the animal showed a weak preference (R > L or L > R) on the first test it was ultimately more likely to show a strong preference with the same hand than to reverse its handedness. Thus three of five animals showing a weak right preference on the first test are strongly right-handed on the second.

Finally, there is only a very slight trend for animals (indicated by brackets in Table VII) that showed inconsistent preferences (as between lids and nuts) on any one test also to be more likely to change in their preferences from test to test than other animals. Thus if changes in preference only on tests 3-10 are considered, it can be seen from Table VII that three inconsistent animals changed their preferences, whereas only two fully consistent animals (G of the Left group for test 1, and F of the L > R group on test 1) changed their preferences in the same way. However animal A of the Left group on test 1 affords an example of an unchanged right preference (tests 2-10) despite the occasional inconsistency in the use of the hands for lids and nuts on any one test. It also appears that if an animal is inconsistent in its preference for lids and nuts on any one test it is likely to continue to be inconsistent on subsequent tests. Therefore inconsistency, although reduced by practice, appears repeatedly in some animals and never in others.

EFFECT OF NEUROSURGICAL PROCEDURES

Table VIII tabulates the results of this analysis. As hand preferences continue to change even in some unoperated animals despite prolonged

TABLE VIII

Effect of brain surgery on hand preferences for lid-opening in 30 monkeys.

Type of Ablation	No Change	Change	Totals
Bil. Anterior Frontal	7	L to: R for r. side; L for l. side	8
Bil. Inferior Temporal	9	0	9
Unil. Inferior Temporal	2	R > L to: R	3
Bil. Posterior Parietal	5	L to: R L to: R	7
Left Optic Tract Section	0	R to: L L > R to: L R for l. side } to: L L for r. side }	3
Totals	23	7	30

The figures represent numbers of monkeys in each category. Each animal has been included in this table only once, in respect of its preferences on the last test (irrespective of sensory modality) before surgery and on the same test (not necessarily the first) after surgery. Where an animal was operated upon more than once it has been included in the table only in respect of its first operation.

training (Table VII) a certain frequency of change associated with testing before and after surgery is likely to result from factors not directly related to the surgery. However it can be seen from Table VIII that every one of three animals that had the left optic tract cut (giving rise to blindness of the right half-field of vision in both eyes) changed their preferences to become strongly left-handed.

DISCUSSION

WARREN (1958) using 17 monkeys in his careful study was able to demonstrate statistically that practice increases the strength, consistency (between preferences on the first and second halves of a single test) and generality (between different tests) of lateral preferences in the monkey. His animals were tested three times over the course of about 11 months on the same three tests. Other training intervened between successive cycles of testing for hand preferences. In the present study all three of WARREN's findings have received indirect confirmation. However different measures of strength and consistency have been used, and the generality of preferences has in this investigation been followed not by correlations between different tests but by noting frequencies of change in preference between successive tests (Table VII). Moreover in WARREN's study the effect of practice was assessed by comparison of preferences on three repetitions of the same tests, whereas in the present work it was generally assessed by comparison of preferences on successive and different tests.

One new finding is the small proportion (33%) of animals with strong and consistent preferences on the first somatosensory test given in the dark. The manipulations involved in this test (described in detail by ETTLINGER & WEGENER, 1958) are the same as for the complex visual tests, except that pushing the lids is preceded by palpation, in the dark, of one or both of the dissimilar tactile cues. Previous quantitative reports on lateral preferences during somatosensory testing in the dark are not known. However WARREN (1958) found only 30% of animals with a greater than 80% preference on the first administration of a simple visual test. Therefore the value of 33% of animals with a greater than 90% preference would not be exceptionally low for a simple test. In fact the test was not simple, so that no satisfactory explanation can be offered, more particularly since the trend is reversed in the last somatosensory test (Table V).

Also unexpected was the low proportion (26%) of strongly right-handed, as against 74% of strongly left-handed, animals on the first test. This difference had virtually disappeared on the last test. WARREN (1953) has reported on the preferences of 84 monkeys on a single test. He found no

asymmetry. However the animals were not required to push lids in his test so that preference was observed in respect of the hand taking food. Also WARREN (1958) refers to the animals in his earlier study as "experimentally sophisticated". Therefore further observations are needed of the lateral preferences on a complex test in untrained monkeys. Inspection of Table VII indicates that the asymmetry is already greatly reduced on the second test (nine animals with strong and consistent right preferences, 11 with left preferences) although more marked again on some subsequent tests.

Finally it has been found that hand preferences are changed to the left in animals rendered blind in the right halves of the two fields of vision. This confirms the earlier reports of KLÜVER (1937) and of SETTLAGE (1939). In all investigations handedness was assessed on visual tests. Further animals, showing the same change in hand preference but when the left optic tract was cut subsequent to other surgical procedures, have been described by ETTLINGER (1959a). It would seem that the preferred hand is likely to be on the side of the body that receives the sensory information guiding its movements (that is, the preferred hand is opposite to the cerebral hemisphere receiving the relevant sensory inflow). Thus the nature of the sensory control of a manual manipulation would appear to be another major determinant of hand preference.

SUMMARY

Hand preferences have been observed in a group of 48 monkeys. It is found that practice in manipulation increases the proportion of animals showing strong and consistent preferences and reduces the initial predominance of left preferences in this sample of animals to near equality with right. The proportion of animals showing strong and consistent preferences is low during initial somatosensory discrimination testing in the dark. The various kinds of change in preference observed on up to ten consecutive tests are analysed in some detail. Thus a full reversal is common in animals changing from a strong preference, whereas a strengthening of the same preference is common in animals changing from a weak preference. 45% of animals change their preference between the first and second test, but this proportion is progressively reduced, for example to 13% changing between tests 3 and 4. Finally the effects of various neurosurgical procedures on the preferences in 30 animals are tabulated. These comprise frontal, temporal or parietal cortical ablations and also section of one optic tract. Only the latter procedure gives rise to changes in hand preferences. It is concluded that the nature of the sensory control (whether visual or somatosensory, or if visual, whether confined to one half visual field) of a manual manipulation is another major determinant of hand preference.

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ZUSAMMENFASSUNG

Bei 48 Affen wurde Links- bzw. Rechtshändigkeit beobachtet. Durch Übung liess sich der Anteil der Tiere mit starker und anhaltender Bevorzugung der rechten bzw. der linken Hand steigern; während bei diesen Tieren ursprünglich die Linkshänder überwogen, waren hinterdrein beide Gruppen nahezu gleichgross. In anfänglichen Tastversuchen im Dunkeln waren ausgesprochene und anhaltende Bevorzugungen einer Hand selten. Die verschiedenen Arten des Bevorzugungswechsels wurden in bis zu 10 aufeinanderfolgenden Versuchen in Einzelheiten untersucht. Bei ausgesprochenen Einhändern ist der Umschlag ins Gegenteil häufig, während Tiere mit anfangs nur schwacher Bevorzugung einer Hand diese gewöhnlich verstärken. 45% der Tiere wechseln ihre Bevorzugung zwischen dem ersten und zweiten Versuch; weiterhin wechseln immer weniger Tiere, z.B. 13 % zwischen dem dritten und vierten.

Endlich wurden die Auswirkungen verschiedener neurochirurgischer Operationen auf die Händigkeit von 30 Tieren festgehalten. Es handelte sich um Eingriffe in die Stirn-, Schläfen- und Scheitelrinde sowie Zertrennung eines *tractus opticus*. Nur der letztgenannte Eingriff führte zu einem Wechsel der Händigkeit. So ergibt sich der Schluss, dass die Art der Sinneskontrolle der tätigen Hand, taktil oder optisch im ganzen oder nur im halben Gesichtsfeld, ein wesentlicher Mitbestimmer für die Händigkeit ist.