

## LATERAL INTERACTION AND TRANSFER IN THE TACTILE MEMORY OF THE OCTOPUS

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### INTRODUCTION

Blinded octopuses can be trained to discriminate between rough and smooth objects by touch (Wells & Wells, 1956, 1957). This capacity is not eliminated by removal of the greater part of the supraoesophageal brain, including all the parts known to be concerned in visual learning (Wells, 1961). Provided the posterior buccal, inferior frontal and subfrontal lobes remain, learning can proceed; with these parts removed the animals cannot be trained to discriminate by touch, although they can carry out all the of movements required to take or reject objects that they grasp (Wells, 1959).

Recently a split-brain technique has been evolved to investigate touch learning in the inferior frontal system more thoroughly. A median longitudinal cut dividing the supraoesophageal brain does not prevent touch learning. It does, however, prevent the side-to-side transfer of the effects of experience, so that, if the objects that the animal must learn to distinguish are presented to the arms on one side of the body only, that side alone will learn to respond correctly. In the intact animal the arms on both sides respond correctly following training restricted to either side. With the split-brain animal the two sides can thus be trained independently, with the convenience that the performance of one side can be used as a control for the effects of a brain lesion in the other. Using this split preparation it has been possible to show that learning depends upon structures in the posterior buccal/subfrontal region (Pl. 1, fig. 1). The median inferior frontal lobe and large parts of the subfrontal lobe can be removed without preventing touch-learning; discrimination breaks down only when the last few thousand of the five million-odd small cells in the subfrontal are eliminated (Wells & Young, 1965).

There is, at the present time, no way of knowing whether the small cells of the posterior buccal/subfrontal region are actually concerned in the changes that must accompany the establishment of a memory trace. They could, for example, constitute an essential component of some 'printing in' or 'reading out' device, necessary for the establishment or interpretation of a memory trace elsewhere. It seems, however, unlikely that the engram is located in the suboesophageal brain (if only on anatomical grounds, see Young, 1966) and for the present it is reasonable to operate on the assumption that the posterior buccal/subfrontal region is the actual seat of the changes concerned in learning.

Assuming this, it becomes important to know how widespread these changes are.

Is the nervous tissue on both sides used to compute the responses carried out by the arms on any one side? Is the trace bilateral? Does side-to-side transfer depend upon the establishment of a trace in the 'inexperienced' part of the brain, or does this side merely 'read out' from stores established in the 'experienced side'?

The present account deals with experiments carried out in attempts to solve some of these problems.

#### MATERIAL AND METHOD

*Octopus vulgaris* Lamarck from the Bay of Naples was used throughout. The animals weighed from 300 to 600 g. Individuals were kept separately and used for experiments as soon as they were observed to be feeding regularly and apparently undamaged.

The octopuses were all blinded by cutting the optic nerves. In some of them the supraoesophageal brain was split by a longitudinal vertical cut (Pl. 1, fig. 4). In some, parts were removed from one or from both sides of the brain. The operations were carried out under anæsthesia with 3% urethane. They produced no gross motor defects and the animals were able to grasp, take and reject objects in an apparently normal manner. At the end of the experiments all the brain legions were checked from serial sections.

Table 1. *Exp. 1 a. Animals blinded, no other operation*

Trained one side only (RHS) with the smooth sphere positive, the rough negative. Four positive and four negative trials per session. Two sessions per day for 5 days.

Animal	Takes		Proportion of correct responses (%)	$\frac{x-y}{x+y} = I$
	Of the positive object (x)	Of the negative object (y)		
NSB	39	24	69	0.24
NSD	40	18	78	0.38
NSE	38	12	83	0.52
NSF	38	11	84	0.55
NSN	40	12	85	0.54
NSO	31	8	79	0.59
NSP	39	8	89	0.66
NTH	36	14	78	0.44
NTI	38	7	89	0.69
NTL	37	9	85	0.61
NXS	40	17	79	0.40
NXT	36	10	83	0.57
NWL	39	18	76	0.37
NYA	40	17	79	0.40
Totals	531	185	81	0.50

The operated animals were trained to distinguish between Perspex spheres 2 cm. in diameter (Text-fig. 1) one sphere being smooth, the other roughened by grooves cut into its otherwise smooth surface. Presented with either of these objects, an untrained octopus will typically respond by grasping the sphere and passing it under the inter-brachial web towards the mouth. If the animal is rewarded with a piece of fish for taking one object in this way, and punished with a small electric shock (here generally 8-10 V. a.c.) for taking the other, it soon learns to reject the 'negative' sphere, while

continuing to take the 'positive'. This training technique has been described elsewhere (Wells & Wells, 1956, 1957) and has formed the basis of many tactile experiments (Wells, 1964, 1965). For the present experiments a slight modification to the original method was introduced, in that the test objects, presented on the end of a Nylon line, were snatched away at the moment of passing beneath the interbrachial web instead of letting the animal pass them all the way to the mouth. This was done to prevent contamination of the 'untrained' side; it seems to make no detectable difference to performance, which is as good as when the animals are allowed to retain the test objects until immediately after the delivery of punishment or reward (Wells & Young, 1965).

Previous experiments with split-brain octopuses having revealed a marginal untrained preference for the rough object in the majority of animals (Wells & Young, 1965), training for the present series was always in the more 'difficult' direction, with the smooth positive and the rough negative. The animals were trained at sixteen trials per day, in two sessions of eight trials. Individual trials were at 5 minute intervals with a period of at least 6 hr. between sessions. Positive and negative trials (four of each in each session) alternated; there is no evidence that octopuses can learn to respond at every other trial. Training was generally limited to one side of the animal. Transfer tests, in which the spheres were presented to the arms on the untrained side, were always given in addition to continued training on the trained side, and were inserted into the training sequence as follows:

$$+(+) - (-) + (-) - (+) + (+) - (-) + (-) - (+)$$

unrewarded transfer tests being indicated by brackets.

#### EXPERIMENTAL RESULTS

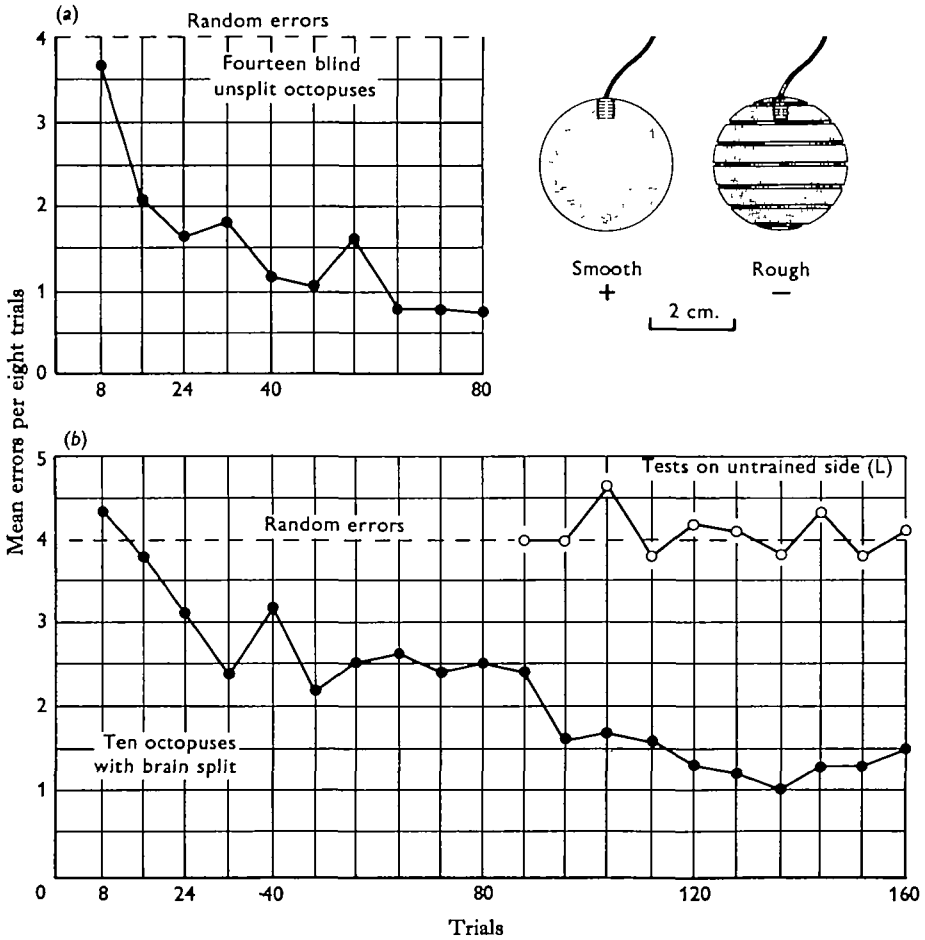
In all thirty-five octopuses were trained during the months of July, August and September 1965. The results obtained are considered below as a series of experiments, although they were in fact done simultaneously, individual octopuses being brought into training as their condition and the availability of tanks permitted. The overlap of training times produced in this way has the advantage that it irons out any fluctuations in performance produced by minor changes in the temperature or oxygenation of the circulating sea water; the only disadvantage is that it makes for a complicated training programme on the part of the experimenter. At any one time, about one third of the animals under training were controls, with the optic nerves cut but no other operations.

##### *Exp. 1. Comparison of the performance of split and unsplit animals trained on one side only*

Fourteen blinded animals were trained without splitting for eighty trials at sixteen trials per day. The test objects were presented to the arms on the right side of the body only. The performance of the animals is summarized in Text-fig. 1. The two best octopuses (NSP and NTI in Table 1) each made 89% correct responses, the worst (NSB) 69% correct. The mean was 81%. Individual scores, showing the range of performance, are given in Table 1.

It is convenient for present purposes to consider two measures of response, both of which are included in Table 1. The percentage of correct responses shows the level of performance in a conventional manner. The index of correct response (*I*, hereafter),

computed as the difference in the number of takes of the positive and negative objects divided by the total number of takes, gives a second measure of discrimination, which is not so dependent upon the overall level of response. An octopus that takes only a small proportion of the total number of objects presented will inevitably make a low percentage error score, but may nevertheless achieve a relatively high index figure, because this measures only the difference between the number of positive responses



Text-fig. 1. Comparison of learning during training of one side by animals (a) with brain intact, and (b) with brain split. In (b) the open circles show tests on the untrained left side.

to the positive and negative objects. An index approaching unity together with a low percentage score indicates an animal that is 'cautious' (or sick) but accurate. The implication is that the octopus would yield a better percentage score if its level of response was not so depressed.

In Text-fig. 1 the performance of the fourteen control animals is compared with the performance of ten split-brain octopuses trained under exactly the same conditions. The scores of the split octopuses were substantially worse than those of intact animals subjected to the same number of trials at the same rate of training. Thus the fourteen

unsplit octopuses averaged 81% correct responses in their first eighty trials, while the ten split brain animals scored only 64% correct. The indices for the split animals were also low, compared with the unsplit animals, the mean indices being, respectively, 0.23 and 0.50 (individual scores are given in Table 2a).

These results cannot be attributed to side-effects of the operation. The ten split animals were not visibly sick, they fed well, and they took the same proportion of the test objects presented to them as controls (62% as against 63% of all objects presented during the first eighty trials). Their failure is, in short, a failure to discriminate. They did not learn to distinguish between the rough and smooth spheres as effectively as controls.

Table 2a. *Exp. 1b. Supraoesophageal lobes completely split before training*

Train right side. Test left side. Conditions otherwise as for Exp. 1a. Brackets enclose scores in a 3rd set of eighty trials and transfer tests made during this period. These are not included in the totals.

	RHS 1st 80 trials			RHS 2nd 80 trials				LHS 80 transfer tests				
	Takes		Proportion correct (%)	<i>I</i>	Takes		Proportion correct (%)	<i>I</i>	Takes		Proportion correct (%)	<i>I</i>
	+	-			+	-			+	-		
	+	-			+	-			+	-		
A. Octopuses with no damage to the trained side of the brain												
NSS	24	7	71	0.55	25	3	78	0.79	14	26	35	-0.30
NST	40	26	68	0.21	40	3	96	0.86	18	32	33	-0.28
NSU	28	15	66	0.30	36	10	83	0.57	15	15	50	0
NTM	18	14	55	0.13	39	11	85	0.56	40	39	51	0.01
					32	0	90	1.0	32	32	50	0
NTN	40	24	70	0.25	40	26	68	0.21	40	40	50	0
					(40)	22	73	0.29	37	27	63	-0.16
Totals A	150	86	66	0.29	180	53	82	0.55	127	152	44	-0.09
B. Octopuses with some damage to the trained side												
NSQ	31	18	66	0.27	32	10	78	0.52	23	9	68	0.43
NSR	32	14	73	0.39	39	12	84	0.53	35	31	55	0.06
NSW	24	30	43	-0.11	35	8	84	0.63	10	21	36	-0.36
NSX	34	22	65	0.21	33	7	83	0.65	31	37	43	-0.09
NTK	32	21	64	0.21	39	14	81	0.47	39	27	65	0.18
					(39)	12	84	0.53	35	27	60	0.13
Totals B	153	105	62	0.19	178	51	82	0.56	138	125	53	0.06
Totals both groups	303	191	64	0.23	358	104	82	0.55	265	277	49	-0.02

Further details of the lesions in these animals are given in Table 2b.

Training for a further eighty trials produced some improvement in the performance of the split-brain octopuses, and by the end of 160 trials the ten animals had attained standards of accuracy comparable with those reached by the fourteen controls after eighty trials. The mean score of the ten split animals in their second eighty trials was 82% ( $I = 0.55$ ), a figure comparable with the 81% (and  $I = 0.48$ ) achieved by the controls in their *first* eighty trials. The proportion of takes during the second eighty trials by the experimentals (58%) was close to that of the controls in their first eighty trials (63%).

There seems, then, to be little doubt that after splitting the brain touch-learning is slowed. This could be due to disruption of the normal functioning of the trained

side by the operation. Alternatively, it may indicate that both sides of the brain normally take part in computing the response made by the arms on the trained side. It will be argued in the discussion of these results that the latter is the more probable explanation.

Table 2b. *Split then train, Exp. 1b*

This table gives details of the lesions in the animals split before training, rated on a three point scale, where 0 = no damage, 1 = slight damage, 2 = serious damage. In no case was a lobe wholly destroyed as a result of the cut dividing the brain. Figures in brackets show the scores in a 3rd set of trials and transfer tests made during this period.

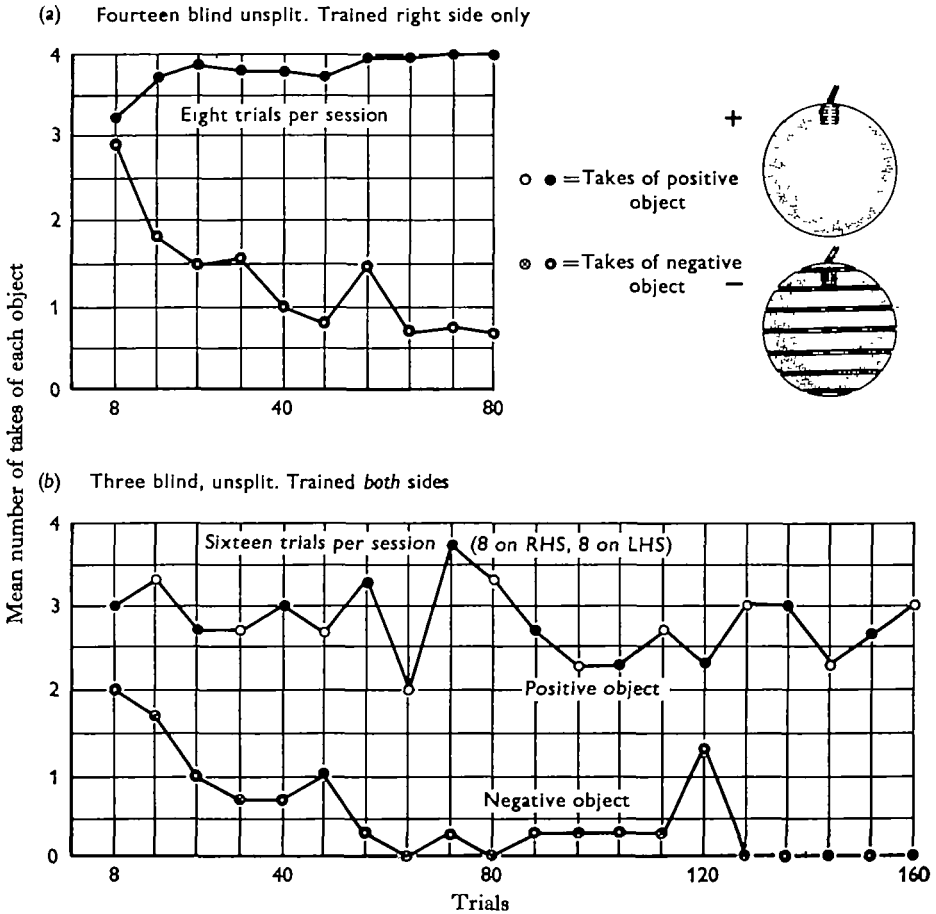
Animal	Trained side (RHS)				Untrained side (LHS)			
	Lesion		Performance in training (2nd 80 trials)		Lesion		Performance in tests	
	Subfrontal	Posterior buccal	Proportion of correct responses (%)	<i>I</i>	Subfrontal	Posterior buccal	Proportion of correct responses (%)	<i>I</i>
<b>A. Animals with no damage to the trained side of the brain</b>								
NSS	0	0	78	0.79	0	0	35	-0.30
NST	0 (+some LHS tissue)	0	96	0.86	1	1	33	-0.28
NSU	0	0	83	0.57	1	0	50	0
NTM	0	0	85	0.56	1	0	51	0.01
NTN	0 (+some LHS tissue)	0 (+some LHS tissue)	68	0.21	2	2	50	0
<b>B. Animals with damage to the trained side of the brain</b>								
NSQ	1	1	78	0.52	0 (+some RHS tissue)	0	68	0.43
NSR	0	1	84	0.52	0	0	55	0.06
NSW	0	1	84	0.63	0	0	36	-0.36
NSX	1	1	83	0.65	1	0	43	-0.09
NTK	1	0	82	0.47	0	0	65	0.18
			(84)	0.60			60	0.13

Two further facts emerge from the split-brain experiments. One is that the precise position of the split is unimportant, so far as the trained side is concerned. In Table 2a the animals are grouped into two sets, those in which the split damaged the inferior frontal system on the side to be trained (i.e. was to the right side of the mid-line) and those in which it did not (Pl. 1, fig. 2). Details of the lesions in these animals are given in Table 2b. The performance of the two groups was so closely alike that it is not possible to separate them on this basis.

Table 2a also shows the results of transfer tests, carried out on the untrained side of the body. The mean score in these tests was 49% correct, the index -0.02. There was therefore no transfer, that is no evidence of capacity to perform correctly the task learned on the opposite side. This was an expected result, earlier experiments of a similar type (Wells & Young, 1965) having shown that operations of this kind, carried out before training, provide an effective block to the spread of information from one side to the other.

*Exp. 2. The additive effect of training both sides and the effects of increasing the rate of training*

Exp. 1, above, shows that animals with the two sides of the brain connected perform better than animals in which only one side is available to determine the responses. A possible explanation is that both sides are normally used to compute the responses



Text-fig. 2. Comparison of learning by animals trained on one side only (a) and on both sides (b). The animals in (a) are those of Text-fig. 1 a. Note that those in (b) receive twice as many trials per session as in (a). They make more errors with the positive and less with the negative object.

of the arms on either side. An attempt was made to confirm this by training unsplit animals on both sides at once. Each side had the usual sixteen trials per day, trials on the two sides being given in the following order:

$$+ - (+)(-) - + (-)(+) + - (+)(-) - + (-)(+)$$

where the symbols in brackets show training on the right side, so that there was a total of sixteen trials per session and thirty-two trials per day.

It was reasoned that, if the two sides of the brain are independent with respect to

touch learning, then the performance of any one side should remain at the level of the controls in Exp. 1, which were trained on one side only. If, on the other hand, both sides combine to compute a response by either, then one might expect an improvement in the performance of both sides, since each can draw upon the experience of the contralateral half of the animal as well as on its own direct experience.

Three animals were trained. Their performance (Text-fig. 2) differed in various ways from that of octopuses trained on one side only. Thus the indices of correct response for the first eighty trials with each side were 0.75 (LHS) and 0.64 (RHS), both indicating substantially better discrimination than the score of  $I = 0.48$  for the first eighty trials with the RHS of animals trained only on that side. Considered, however, in terms of the proportion of correct responses, the difference is less impressive. The bilaterally trained animals averaged 79% (LHS) and 78% (RHS) correct responses, figures comparable with the 81% correct attained by the octopuses trained on one side only. Taken together, the indices and percentage correct scores indicate a shift in the pattern of errors. The higher total rate of training (thirty-two trials per day instead of sixteen, counting both sides) was associated with a much lower proportion of takes to trials (47% as against 64%) and with a rise in the proportion of errors due to refusal to accept the positive object (57%, compared with 14% when trained on one side only at half the total number of trials per day).

There is thus no doubt whatever that events affecting one side of the body alter the performance of the other. But the experiment does not show the exact nature of the interaction. The fact that the animals trained at thirty-two trials per day discriminated better than those trained at sixteen trials per day could be attributed to the effect of a drop in the proportion of takes from 64 to 47%. Even assuming that it was indiscriminate such a drop would cause an improvement in performance, since at sixteen trials per day the great majority of errors are due to the octopuses taking the negative object. As the proportion of takes and the proportion of negative errors fall towards 50%, performance is bound to improve. The experiment was therefore inconclusive, since it did not include controls for the effect of increasing the rate of training. The observed improvement in discrimination could have been due to unspecific effects of the extra shocks and rewards received at the higher rate of training, since both would tend to raise the threshold for positive responses.

#### *Exp. 3a. Results with animals split in mid-training*

Text-fig. 3 and Table 3a show the results of training eight animals for eighty trials on the right side at sixteen trials per day and then splitting. Training was continued for a further eighty trials on the right, while tests were given on the left.

The operations were followed by an abrupt decline in the animals' performance on the trained side (right), a decline that was only partly compensated by further training. Thus the score of the eight octopuses in their first eighty, preoperational, trials was 83% correct ( $I = 0.55$ ). In the eighty trials immediately after the operations the proportion of correct responses fell to 65% ( $I = 0.30$ ).

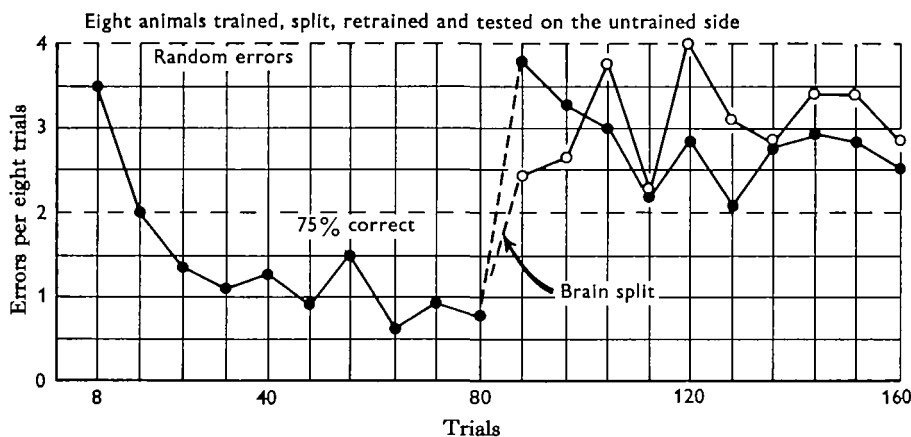
The operations produced a negligible decline in the proportion of takes (from 53 to 50%), and only a small rise in the proportion of positive errors (from 43 to 50%). The relatively poor post-operational performance cannot therefore be attributed to gross changes in the proportion of takes or in the pattern of errors; such small changes as



Table 3a. Exp. 3a. Train-split-train results

Conditions as in Exp. 1a, for the first eighty trials, after which the brain was divided by a longitudinal cut and training continued. Lesions, arising because the cut dividing the brain was off-centre are described on a three point scale; 0 = no damage to the trained side, 1 = slight damage, 2 = severe damage. In no case was the whole of any lobe destroyed. The animals are arranged in an order determined by their performance in transfer tests with the untrained side (Table 3b); NTH made 80% correct responses in these tests and NSP 45% correct. A score of 61% correct responses in eighty trials is significant at the 5% level ( $\chi^2$ ). Figures in brackets show the results of a 3rd set of eighty trials.

Animal	80 pre-operational trials				Lesion to the trained side		80 post-operational trials			
	Takes		Proportion of correct responses (%)	I	Sub-frontal	Posterior buccal	Takes		Proportion of correct responses (%)	I
	+	-					+	-		
NTH	36	14	78	0.44	2	2	34	15	74	0.39
NSD	40	18	78	0.38	1	1	9	9	50	0
							(6	4	53	0.20)
NSE	38	12	83	0.52	1	1	31	20	64	0.22
							(35	12	79	0.49)
NTI	38	7	89	0.69	0	0	39	9	88	0.63
NTL	37	9	85	0.61	0	0	40	17	79	0.40
NSO	31	8	79	0.59	1	2	29	30	49	-0.02
							(30	22	60	0.15)
NSN	40	12	85	0.54	0	0	9	5	55	0.29
							(26	5	76	0.68)
NSP	39	8	89	0.66	0	0	17	7	63	0.42
							(20	5	69	0.60)
Totals	299	88	83	0.55			208	112	65	0.30

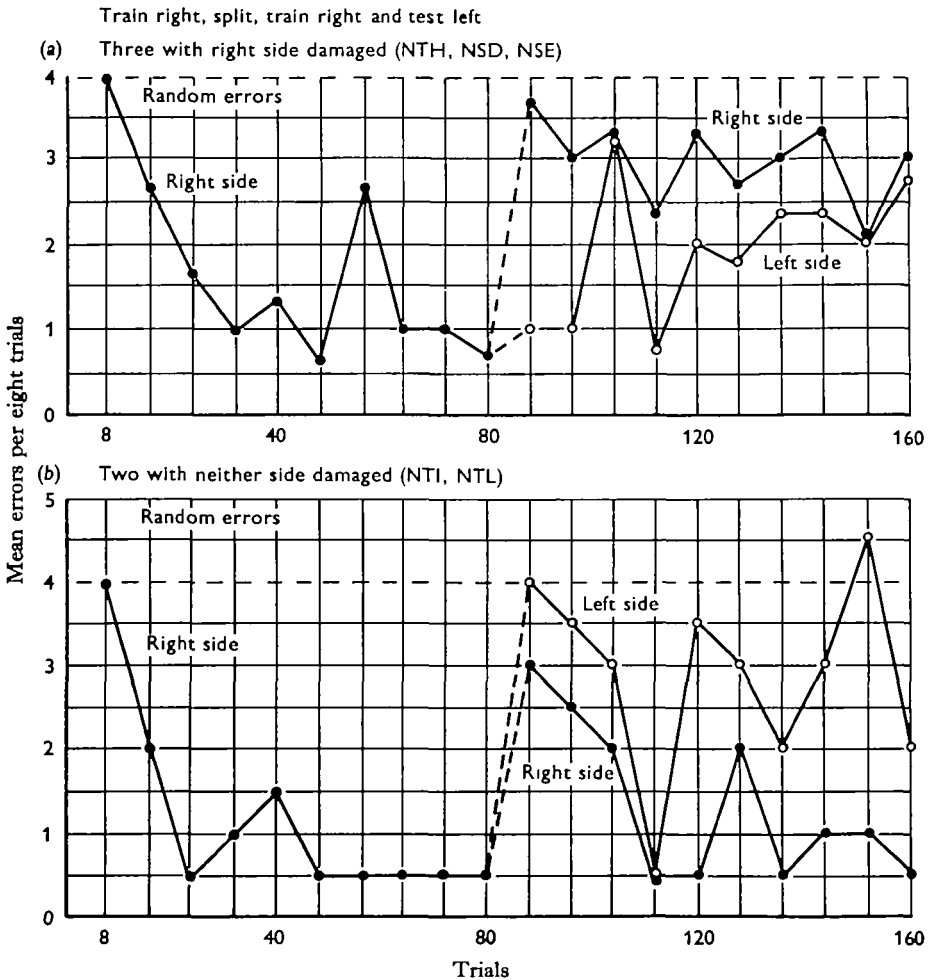


Text-fig. 3. Learning by octopuses trained on one side (R) for eighty trials, then split and re-trained on right and tested on left (open circles).

there were would have tended, if anything, to improve performance rather than otherwise. The decline was due to a failure to discriminate.

Further analysis of the results shows that performance in general correlates with the severity of any damage to the trained side (Table 3a). The four octopuses with damage to the subfrontal and posterior buccal lobes on the trained side together made 59% correct responses, the other four averaged 71% correct. Within the damaged group,

however, octopus NTH, with the largest lesion, made 74% correct responses, a considerably better score than the 64% (NSE) and 50% (NSD) attained by the two octopuses showing least damage. NSO was badly damaged, and made only 49% correct responses in the eighty trials following the operation. It should be noticed that two of the undamaged octopuses, NSN and NSP, also scored badly (55 and 63%) in



Text-fig. 4. Performance of the octopuses of Text-fig. 3 in relation to extent of injury (a) right side damaged, (b) cut central, neither damaged, (c) left side slightly damaged, (d) left side severely damaged. In each case the brain was split after eighty trials. Open circles show scores in tests with the untrained left side.

the trials immediately following the operation. These animals (like NSD) took very few objects in the first eighty post-operational trials. Further training, however, led to an increased number of takes and scores of 75 and 69%. There was no similar improvement when training was continued with the damaged NSD.

It will be noticed that in all instances there was an abrupt decline in performance following the operation. Even the least-damaged animals, with the posterior buccal

and subfrontal lobes on the trained side untouched by the cut, showed a marked deterioration in the quality of their performance. This cannot be attributed to any direct effect of the operation on the trained side and must imply, as Exp. 1 b (Text-fig.

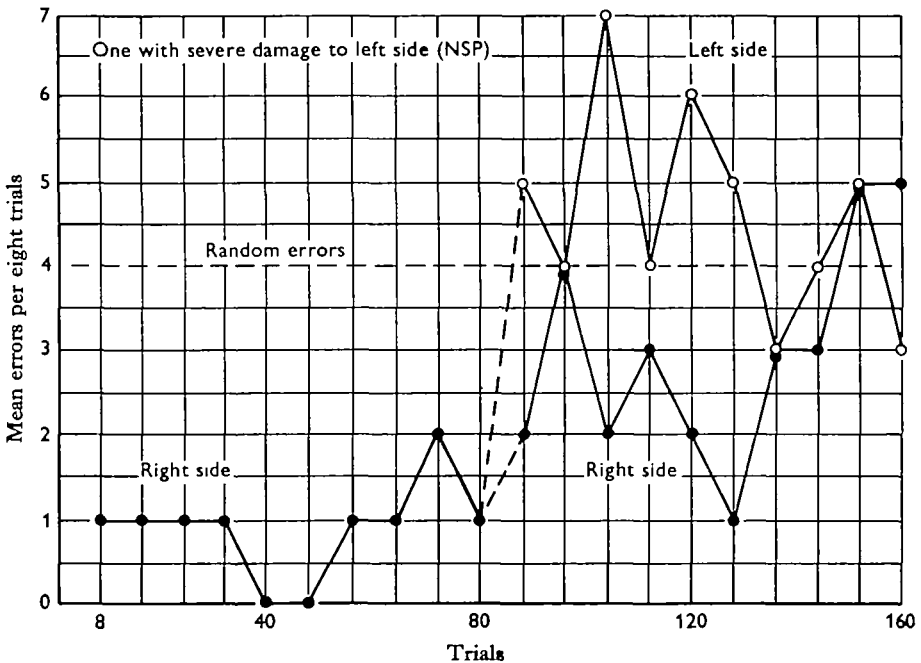
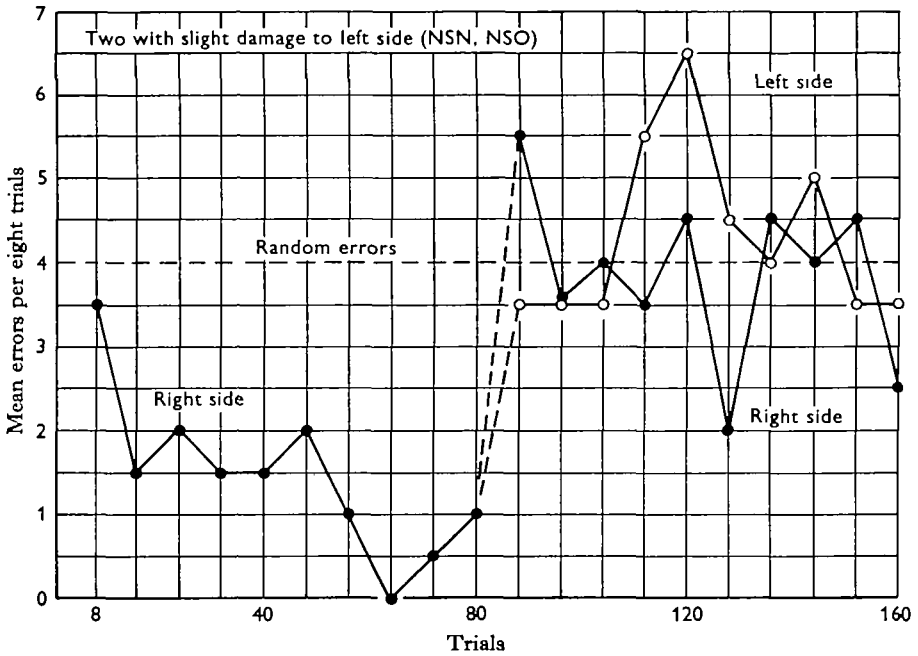


Fig. 4c and d. For legends see facing page.

1) does, that both sides of the brain are concerned in some way in computing discriminatory responses by the trained arms.

*Exp. 3b. Transfer tests with these animals*

During the post-operational training of the eight animals concerned in Exp. 3a above, transfer tests were carried out on the untrained side. The results are summarized in Table 3b and Text-fig. 3. Taken collectively they show transfer of the capacity to discriminate to the untrained side. The untrained left sides of the split animals together made 62% correct responses ( $I = 0.26$ ) in the 640 transfer tests.

Table 3b. *Exp. 3b. The results of tests on the untrained (LH) side of the octopuses trained for Exp. 3a (see Table 3a)*

The extent of damage to the subfrontal and/or posterior buccal lobes is rated on a three-point scale; 0 = no damage, 1 = slight damage, 2 = severe damage. Scores of more than 60% or less than 40% correct in eighty trials are significant at the 5% level ( $\chi^2$ ). Figures in brackets show the results of a further set of eighty tests.

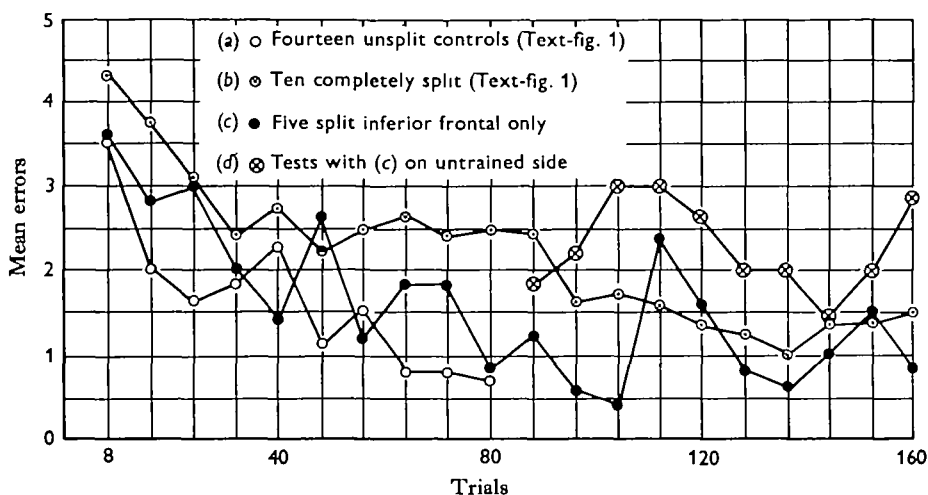
Animal	Lesion on the untrained side		Post-operational performance in tests with the untrained side			
	Subfrontal	Posterior Buccal	Takes		Proportion of correct responses (%)	I
			+	-		
NTH	0 (+much RHS tissue)	0	34	10	80	0.55
NSD	0 (+some RHS tissue)	0	25 (15)	5 11	75 55	0.67 0.15
NSE	0 (+some RHS tissue)	0	25 (17)	6 8	74 61	0.61 0.36
NTI	1 } Splits almost exactly 0 } central	0	32	19	66	0.25
NTL			0	36	27	61
NSO	1	1	25 (6)	27 8	48 48	-0.04 -0.14
NSN	0	1	14 (5)	18 5	45 50	-0.13 0
NSP	2	1	19 (18)	23 21	45 46	-0.10 -0.08
Totals			210	135	62	0.22

Averaging the data in this manner, however, conceals a considerable range in performance, which correlates rather closely with the exact position of the cut dividing the two sides (Text-fig. 4). Details of individual performances and lesions are given in Table 3b. This shows that in the three highest scoring animals (NSD, NSE, NTH) the cut dividing the brain lay to the right of centre, so that the left, transfer, side was not only intact but also had some of the trained-side tissue attached to it. (Pl. 1, figs. 3, 4). The two next scores (NTI 66% correct, NTL 61% correct—both are significant at the 5% level) had the cut very nearly central, with slight damage to the subfrontal lobe on the test side in the case of NTI. Of the remaining three animals two (NSN, NSO), with cuts to the test side of centre, did not discriminate at all, while a third (NSP) with the most extensive damage of any octopus in this series, made only 45% correct responses (Text-fig. 4d). A tendency for animals with very large lesions to prefer the rough object in discrimination experiments has already been noted elsewhere (Wells & Young, 1965).

These results strongly suggest the presence of memory traces in the untrained side as well as the trained side. On the evidence of the scores of octopuses NTI and NTL, the only animals with truly central cuts, the trace established on the untrained side is somewhat less effective as a determinant of correct responses than the trace in the untrained side. These animals scored, respectively, 88 and 79% correct when training was continued with the right side, but only 66 and 61% when tested on the left. The figures are not, of course, strictly comparable, because the trained side performance was being reinforced during this time.

#### *Exp. 4. Pathways for side-to-side transfer*

When one side of an intact animal is trained, the other side will respond correctly. It seems likely from Exp. 3*b* that this involves the establishment of a record in the untrained side of the brain. The most obvious pathways for this side-to-side transfer are within the inferior frontal system. We know that lateral transfer can occur there



Text-fig. 5. Comparison of performance of five octopuses with the inferior frontal system split and the rest of the brain intact with that of the unsplit and completely split animals of Text-fig. 1.

because animals with only the inferior frontal system remaining perform correctly on both sides after unilateral training (Wells & Young, 1965). Transfer could, however, also occur through other parts of the supra-oesophageal brain, and it may depend upon specific tracts within the inferior frontal system. In some preliminary experiments the following results were obtained:

(a) Splitting the median inferior frontal lobe did not prevent side-to-side transfer. Two animals were operated in this way, with some damage to the top of the subfrontal; the rest of the brain was left intact. The results of subsequent training and testing are included in Table 4. The operation had no detectable effect on training or transfer.

(b) Splitting the whole of the inferior frontal system did not prevent transfer, provided that the rest of the brain was left intact. Five animals were split and then trained. The results are summarized in Table 4. These animals learned, but a little more slowly than unsplit controls. The standard achieved after eighty trials (72% correct,

$I = 0.38$ ) was, in fact, between that of the unsplit controls (81%) and the completely split octopuses (64%) of Exp. 1, above (Text-fig. 5). However, after 160 trials the partly split animals reached a high level (88%,  $I = 0.67$ ).

The performance of the partly split octopuses in transfer tests is particularly interesting since it shows that side-to-side transfer can take place through parts of the supra-oesophageal brain outside the inferior frontal system. In transfer tests these five animals averaged 73% correct responses ( $I = 0.48$ ). In all of them the inferior frontal system was completely divided.

Table 4. *Animals with partly split brains*

Train right side, test left. Sixteen trials per day as Expt. 1, Table 1. Brackets enclose scores in a 3rd set of eighty trials and tests, not included in totals.

	RHS 1st 80 trials				RHS 2nd 80 trials				LHS 80 transfer tests				
	Takes		proportion correct (%)	$I$	Takes		Proportion correct (%)	$I$	Takes		Proportion correct (%)	$I$	
	+	-			+	-			+	-			
<i>A. Animals with the median inferior frontal lobe split, rest intact</i>													
NWN	36	10	83	0.57	37	8	86	0.64	40	14	83	0.48	
NWQ	29	6	79	0.66	35	7	85	0.67	27	2	81	0.86	
Totals for A	65	16	81	0.60	72	15	86	0.66	67	16	82	0.67	
<i>B. Animals with the inferior frontal system split, rest intact</i>													
NUU	38	13	82	0.49	40	3	96	0.86	22	10	65	0.38	
NUZ	30	20	63	0.20	38	10	85	0.58	23	8	69	0.48	
					(36	8	85	0.64	14	4	63	0.56)	
NWI	35	16	74	0.37	36	9	84	0.60	36	17	74	0.36	
					(vertical lobe removed, then	40	25	69	0.23	38	24	68	0.23)
NWM	21	9	65	0.40	37	11	83	0.54	26	10	70	0.44	
NUQ	33	12	76	0.47	39	5	93	0.77	35	5	88	0.75	
Totals for B	157	70	72	0.38	190	38	88	0.67	142	50	73	0.48	
<i>C. Animals with complete splits, from Table 2 (mean scores)</i>													
	303	191	64	0.23	358	104	82	0.55	265	277	49	-0.02	
<i>D. A single unsplit animal trained and tested as A, B, C</i>													
NYA	40	17	79	0.40	40	0	100	1.0	40	2	98	0.91	

One of the animals (NWI) was subjected to a second operation at the end of the experiment. In this the vertical lobe was removed. When training and transfer tests were continued, the octopus took a higher proportion of the test objects than before, and discrimination declined in consequence, since it was already taking all of the positives before the second operation. However, the score following vertical lobe removal showed continued discrimination and transfer, at a reduced level of accuracy. The result of this part of the experiment is, therefore, a further indication that memory traces are indeed established within the untrained side of the inferior frontal system.

## DISCUSSION

The experiments show that octopuses trained to make tactile discriminations using the arms on one side of the body learn better when both sides of the brain are present. The relatively poor performance of split-brain animals, trained in the same way, is not attributable to a lower proportion of takes or to a change in the pattern of errors; they simply make more errors, indiscriminately.

This leaves two possibilities. One must suppose *either* that both sides of the brain normally play a part in computing the responses of the arms on any one side, *or* that the operation has other, unspecified, deleterious effects upon the trained side of the brain.

There are several reasons for believing that the former is the more likely explanation. These are:

1. The lack of effect of 'control operations'. Splitting the median inferior frontal, for example, has no effect upon the performance of animals trained on one side (Expt. 4 above). Extension of the lesion slightly deeper into the brain, so that it divides the subfrontal, abruptly doubles the proportion of mistakes made in training (Exp. 1). Extensive lesions to the basal lobes, including removal of the parts immediately behind the subfrontal region, are without effect on touch learning (Wells, 1959; Wells & Young, 1965).

2. The absence of visible damage to the sides separated by the split (Pl. I, fig. 2). If splitting the subfrontal produces the decline in performance that it does by upsetting, say, the blood supply to the training side or by exposing the brain tissue to other less beneficial body fluids, one might expect degeneration of the wounded cells within 5 or 10 days of operation. The animals were kept for at least this long. Apart from physical disruption of cell masses occasionally caused by the cut itself there was no sign of secondary damage. Splits produced a decline in the capacity to discriminate even in animals where the trained side appeared to be quite untouched.

3. The results of analagous experiments on the visual system. Muntz (1961*b*) has shown that removal of one optic lobe produces an immediate decline in the performance of octopuses trained using only the eye on the other side. The two optic lobes project on stalks from opposite sides of the brain. It is difficult to imagine effects not dependent on nerve conduction that could operate under these conditions.

4. The results of previous work on the inferior frontal system. Symmetrical brain lesions made by removing the basal lobes and progressively larger amounts of the inferior frontal system have shown the critical importance of the small cells in the subfrontal and posterior buccal lobes; tactile discrimination continues when only a few thousand (out of an original  $5.2 \times 10^8$ ) of these cells remain, and fails when all are removed (Wells, 1959). The same result has been obtained using a quite different technique in which the brains were split and subfrontal tissue removed from one side (Wells & Young, 1965). The various experiments on the inferior frontal system all indicate that the post-operational performance of octopuses in touch-learning experiments depends largely upon the proportion of the small cells of the bilateral subfrontal lobe that remains. The relatively poor performance of the split-brain animals, which have half of the subfrontal disconnected, is clearly compatible with this. None of these lines of evidence proves that both halves of the brain combine to

compute the responses made by the arms on one side. They show only that this is the most economical assumption. It is difficult to imagine any other effect that would disturb discriminations to the degree that splitting does, without affecting the proportion of objects taken. The effect of splitting the inferior frontal system is very specific and persistent. It would seem most reasonable to suppose that the decline in tactile performance is a consequence of removing half of the tissue normally used to compute the responses.

The train-split-test experiments described above on pages 394 to 395 were designed to test the assumption that the memory traces governing learned tactile responses are bilateral. If this were so one might expect animals to perform correctly on both sides despite division of the brain, provided that the split is made *after* training. It was found that the animals did, indeed, continue to discriminate after division of the brain, provided that the cut caused no serious damage to the subfrontal and posterior buccal lobes on the untrained, test side. By far the best performances were by those animals with some cells of trained-side tissue left in contact with the untrained side. Two others with exactly central splits discriminated, though at a much lower level of accuracy; and two, with cuts to the test side of a centre, failed to discriminate at all. In addition to these, one octopus discriminated, but perversely, taking nearly twice as many negative as positive objects following the operation. This last result raises a problem already recognized and reported elsewhere (Wells & Young, 1965). It seems that animals with very large lesions tend to 'prefer' the rough objects in this sort of experiment. This preference phenomenon is difficult to investigate, since the preference is not apparent in intact octopuses or in animals suffering removal of the vertical lobe. In all untrained animals the effect is masked by the high proportion of takes. For present purposes the importance of this marginal preference is that octopuses that fail to discriminate in transfer tests cannot necessarily be held to contain no memory traces on that side. These may be present, but too weakly established to determine 'correct' discriminatory responses in the face of an apparently innate bias towards objects with irregular surfaces. The existence of the phenomenon slightly increases the weight of the evidence from those animals that *did* discriminate successfully on the untrained side. Muntz (1961 *a, b, c*) has shown that interocular transfer occurs in octopuses trained using one eye and tested using the other. Transfer is nearly perfect for easy discriminations, but becomes progressively less efficient with more difficult visual tasks. It is prevented by a median longitudinal cut through the superior frontal vertical lobe tract. If the cut is made after training the animal performs correctly using the untrained eye. If the optic lobe of the trained side is removed the same result is obtained. It has not yet been shown that there can be effective performance after removal of the optic lobe of the trained side *and* removal of the vertical lobe system, but the implication is clearly that memory traces relating to things seen are established within the optic lobe on the untrained side. Taken together with the effects of tactile training reviewed above, these results make it very unlikely that the records of tactile events are unilateral. On present evidence it must be concluded that tactile memory traces are bilateral in the octopus.



## SUMMARY AND CONCLUSIONS

1. Blinded octopuses were trained to discriminate by touch between rough and smooth spheres, using the arms on one side only.
2. Intact octopuses learned more rapidly than animals with the supraoesophageal brain split by a longitudinal cut.
3. With the brain split before training no side-to-side transfer occurred. Animals operated upon in this way did not discriminate when tested on the untrained side.
4. When intact octopuses were trained on both sides each side appeared to benefit from the experience gained by the other. The effect was difficult to evaluate because most of the errors in the experiments were due to taking the 'negative' object, with the result that raising the rate of training itself tends to improve performance by lowering the proportion of takes.
5. Animals trained on one side and then split continued to discriminate on the trained side, though at a reduced level of accuracy. When tested on the untrained side the performance of these animals was variable, depending upon the exact position of the split. The best scores were made by octopuses with some trained-side tissue left in contact with the test side. Animals with exactly medial cuts continued to discriminate, though at a reduced level of accuracy. Octopuses with the untrained side damaged did not discriminate at all.
6. Side-to-side transfer of the effects of tactile training can occur within the inferior frontal system. It can also be demonstrated to occur elsewhere in the supraoesophageal brain if the inferior frontal system has been split. Presumably this other pathway passes through the superior frontal/vertical lobe system.
7. These results are considered in relation to visual experiments on interocular transfer and it is concluded that memory traces are established on both sides of the brain as a result of unilateral training.

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#### EXPLANATION OF PLATE

Fig. 1. Horizontal section of normal octopus brain to show the lateral inferior frontal (*fr. i. l.*), posterior buccal (*buc. p.*) and lower part of the subfrontal lobes (*subfr.*). The superior buccal lobe (*buc. s.*) lies in front and the anterior basal lobe (*bas. a.*) behind.

Fig. 2. Horizontal section after operation. The cut has divided the superior and posterior buccals and passed between the subfrontals without damaging them. The trained side (R) learned well but there was no accurate response by the L side (Octopus NSS; Tables 2*a* and *b*). Note that the anterior and median basal lobes (*bas. a.* and *bas. m.*) were not divided. The vertical lobes, lying more dorsally, were divided.

Figs. 3, 4. The cut was made after training the right side and lies to the right of the mid-line. After operation the right showed no correct responses, but the left performed correctly (animal NSD; Tables 3*a* and *b*). The record has been transferred before the operation. Note that the whole supraoesophageal mass was divided. Fig. 3 lies more ventrally than Fig. 4. *fr. i. med.* = median inferior frontal, *subv.* = subvertical and *fr. s. l.* = lateral superior frontal lobe.

