

DETOUR EXPERIMENTS WITH SPLIT-BRAIN OCTOPUSES

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INTRODUCTION

Octopuses will make detours down an opaque corridor in order to reach crabs initially visible but not directly accessible to them (Wells, 1964). The situation can be used to investigate the function of parts of the brain in short-term learning and in interocular transfer. In a previous account the effects of removing the vertical lobe were considered. If this lobe is removed from the visual learning system, the proportion of errors (the octopus makes an error if it turns the wrong way at the end of the corridor—see Fig. 1) is increased. The effect is negligible if the octopus completes the detour within about 30 s, but rises sharply if runs take longer as a result of self-imposed or operator-imposed delays (see method below). Runs taking up to 2 min were usually made correctly by controls, while the operated animals made chance scores in detours taking longer than 1 min (Wells, 1967).

The present account is of a further series of experiments extending the work on the visual system by using animals in which one side of the supraoesophageal brain was partly or wholly separated from the other by a longitudinal vertical cut. This technique allows one to draw conclusions about the function of the optic commissures and other structures in learning and in interocular transfer.

METHODS

Octopus vulgaris Lamarck was used, the experiments being made at the Stazione Zoologica, Naples, in the summers of 1965 (M series) and 1967 (N series). Individual octopuses weighed from 250 g to about 450 g. The animals were kept in separate aquaria and fed upon crabs until needed, any that failed to attack crabs regularly being discarded.

The apparatus used is shown in Fig. 1. In the M series of experiments the outer tank was of grey 'Eternit', a pressed asbestos substance. For the N series the outer tank was of white plastic. In both cases the dimensions were *c.* 100 × 50 × 30 cm deep. The internal maze was made of black and of transparent Perspex, as in the experiments reported in Wells (1967), with the addition of pairs of photoelectric cells and lights set to give beams of white light across the entrance and exit to the corridor and across the entrances to the feeding compartments. The light beams were set out 3 cm above the tank floor, too low to shine into the eyes of the animal but high enough to be interrupted by the passage of the arms even if, as sometimes occurred, an octopus actually swam along the corridor instead of crawling along the bottom. The photocells were wired to a four-channel event recorder that left a trace on cardiograph paper whenever a light beam was interrupted. Transparent shutters at each end of the corri-

dor could be operated remotely by lines running over pulleys to the end of the tank. During trials that included an enforced delay, the shutters were lowered as soon as the octopus had moved into the corridor, and kept closed until 30 or 60 s had elapsed. Between trials the animals were confined to the 'home' compartment, which included a trio of bricks, arranged to form a cave into which the octopus could retire; animals typically spent most of their time sitting at the entrance to this home, watching down the corridor and into the feeding compartments.

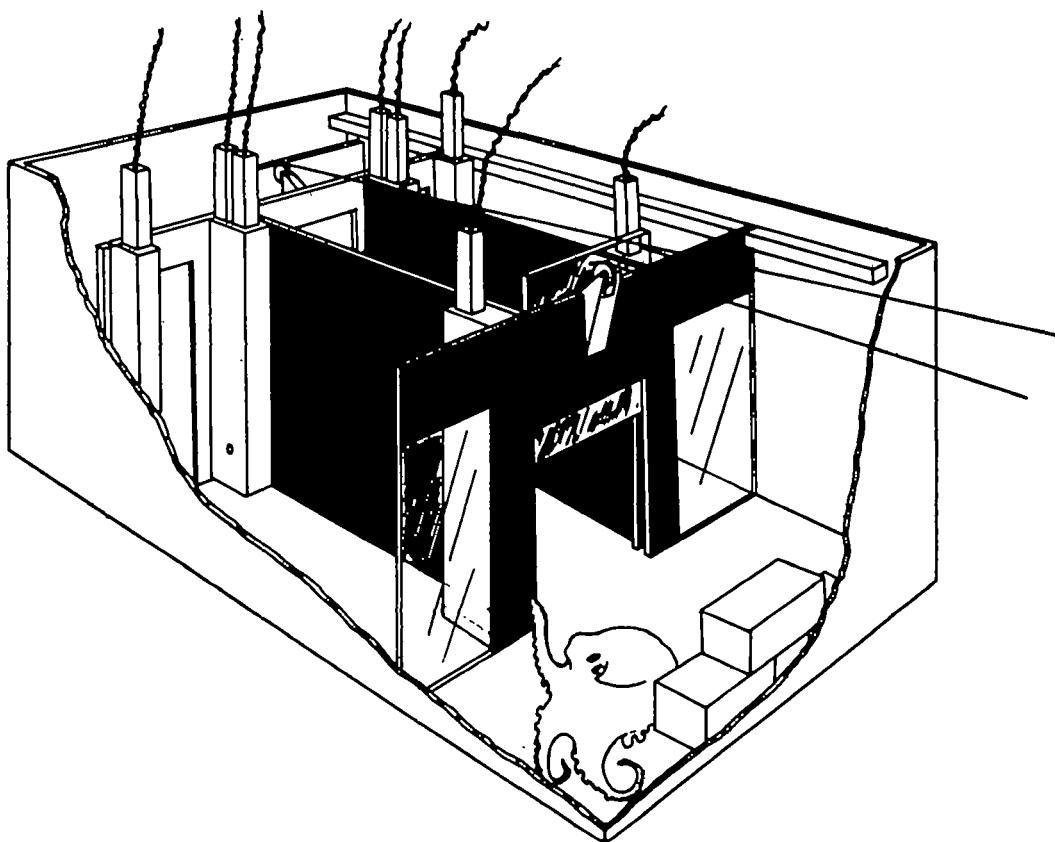


Fig. 1. Detour apparatus used. In order to get crabs shown in one or other of the two lateral 'feeding' compartments, an octopus starting from the 'home' compartment as shown, had to make a detour down an opaque corridor, turn right or left at the end and continue into the feeding compartment. Movement through the apparatus could be monitored by photocells set at either end of the corridor and across the entrances to the feeding compartments. Remotely controlled shutters at each end of the corridor could be lowered to enforce delays.

There were about six trials/day. At each trial a crab was shown in one of the feeding compartments. The crab was removed as soon as the octopus entered the corridor and was replaced only if and when the detour had been completed successfully. Octopuses that had successfully or erroneously arrived in one of the feeding compartments were allowed to return home directly by raising the maze. Trials lasted for a maximum of 5 min, during which the animal might make several attacks from the home and one or more abortive entries into the corridor. Normally, however, an attack was made and

a detour completed, rightly or wrongly, within 60 s of the start of a trial. In nearly all cases trials were alternately to the left and right sides. It will be shown below that octopuses do not learn to alternate in this situation.

Brain lesions were made under urethane anaesthesia (3% in sea water) and were limited to a single vertical cut, made with a scalpel along the mid-line of the supraoesophageal lobes. The brains of the operated animals were preserved and sectioned, so that the extent of each lesion could be examined. The cuts made fall into three groups: (1) those involving only the superior frontal and vertical lobes, that is, limited to parts known to be concerned in visual learning (Young, 1964) but leaving the optic commissures intact ($n = 4$). (2) Those in which the split was extended to divide parts of

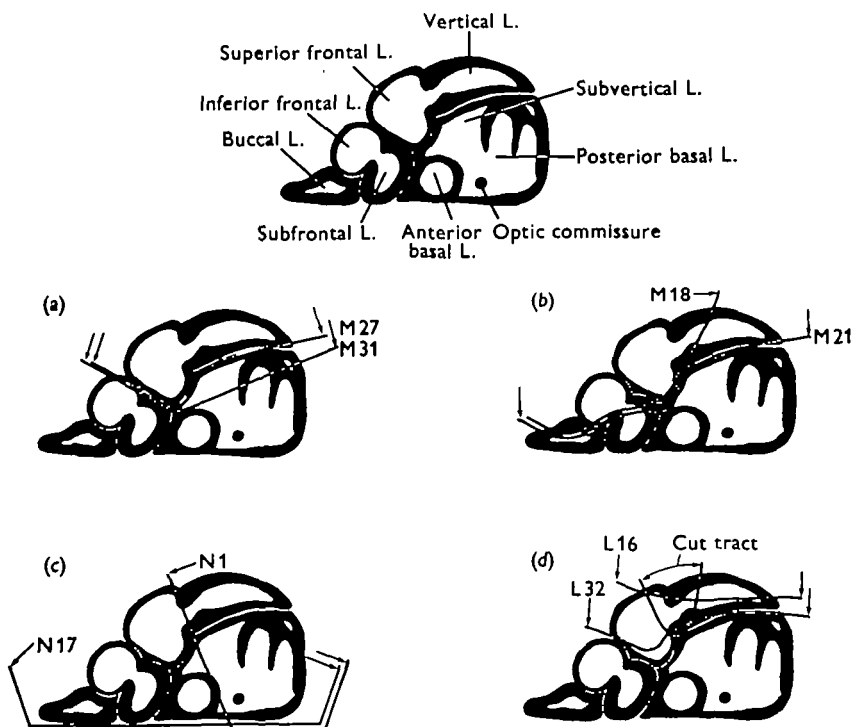


Fig. 2. Lesions made. The diagrams represent median longitudinal sections through the supra-oesophageal lobes, with the maximum extent of median longitudinal vertical cuts shown for the largest and the smallest lesions, (a) from animals classified as 'type 1' lesions (M series), (b) from those classed as 'type 2' lesions (M series) and (c) from those classed as 'type 3' (M, N series); (d) shows the maximum and minimum extent of the regions removed from animals in the L series of experiments quoted from Wells (1967) and ('cut tract') the minimal extent of longitudinal vertical cuts that Muntz (1961b) found would prevent interocular transfer in long-term visual discrimination experiments.

the tactile learning machinery in the inferior frontal system (Wells, 1966) again without damage to the optic commissures ($n = 3$). (3) Splits extending to the gut, cutting the optic commissures and dividing the basal lobes ($n = 8$). There were, in addition, 4 animals, intended to have type 3 splits, where the success of the operation was uncertain; subsequent histological examination indicated that some commissural fibres might remain intact.

It will be shown below that operations of types (1) and (2) above produce animals that behave essentially like controls in detour experiments though they make a somewhat higher proportion of errors; and that although octopuses with operations of type (3) will sometimes make detours rapidly and successfully, they are characteristically reluctant to run and tend to abandon detours and return home after entering the corridor at a far higher proportion of trials than octopuses with the other types of lesion. Maps of the lesions are given in Fig. 2.

In all 30 animals were used. Thirteen of these were tested both before and after operation.

RESULTS

(1) *Learning in the detour situation*

Most octopuses make successful detours at their first trial in the apparatus; their subsequent performance changes little with practice.

Fig. 3 *a* and *b* summarizes aspects of the performance of the 20 unoperated animals that were tested in unbroken series of 20 undelayed trials. Thereafter pairs of trials including an enforced delay in the corridor alternated with pairs (one detour to the left, one to the right) of undelayed trials. Fig. 3 *c* and *d* also shows the performance of three animals subjected to a longer series of tests including delayed runs; only their performance in undelayed trials is plotted. In the first ten trials of the experiments summarized in Fig. 3 *a* 20 octopuses made a total of 30 errors in 200 trials; in their second ten trials they made 45 errors. In the longer experiment summarized in Fig. 3 *c*, three of the same octopuses totalled 12 errors in their first 60 trials and nine in their last 60. Neither of these changes in performance is significant at the $P = < 0.05$ level.

Other measures that might indicate whether the performance of the octopuses improves with practice are: (1) the time spent attacking through windows of the feeding compartments before going into the corridor; (2) the number of occasions on which abortive entries into the corridor are made, the octopus returning to the home compartment without completing a detour; (3) the time spent running through the maze once a detour has begun.

Two of these three measures reveal significant changes in behaviour with practice in the maze situation. The number of trials including an abortive entry declined from 37 in the first ten trials of the experiment summarized in Fig. 3 *a* to 17 in the second ten. This difference is significant at the $P = < 0.01$ level ($\chi^2 = 7.3$). The number of runs completed in less than 30 s (approximately the mean time for all undelayed runs—see Table 1) increased from 111 to 125 over the same period, a difference that is not significant at the $P = < 0.05$ level (Fig. 3 *b*). In the longer series of trials shown in Fig. 3 *c* and *d* the same trends are apparent. Abortive entries fell from eight in the first 20 trials to zero in the last 20, while fast runs lasting less than 30 s rose from 22 to 41 ($\chi^2 = 11.0$ $P = < 0.001$). The third measure of performance adopted (time spent attacking before entering the corridor—Fig. 3 *b*, *d*) revealed no significant changes in performance. In the first ten trials attacks lasted 30 s or less on 150 occasions; in the second ten the number increased to 154. Thirty-one attacks lasted less than 30 s in the first 20 trials and 42 in the last 20 trials of the longer experiment shown in Fig. 3 *d*. These trends are not significant at the $P = < 0.05$ level.

Various conclusions may be drawn from this analysis. It is obvious that the animals are not learning to run alternately to left and to right or to recognize a sequence of intermediate cues that will carry them into the correct feeding compartment once they

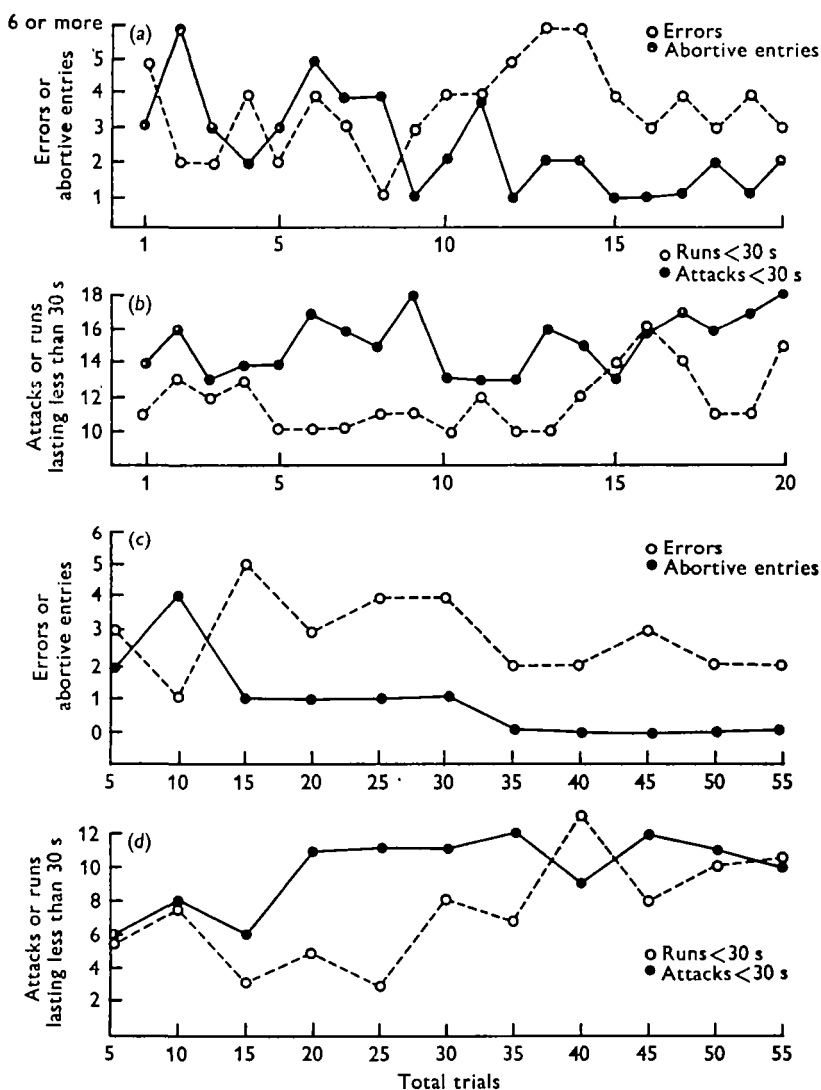


Fig. 3. The performance of 20 unoperated octopuses (11 from the M series, nine from the N) summarized for their first 20 undelayed trials in the detour apparatus; (a) shows the number of errors made (○) and the number of trials at which there were abortive entries into the corridor (●); (b) shows the number of runs taking less than 30 s (○) and the number of attacks that lasted for less than 30 s before a run down the corridor (●)—trials including abortive entries were excluded from this count; (c), (d) shows similar plots of the results of extending the period of training with three of the animals.

have seen a crab. They cannot be learning to carry out a specific series of movements as a means of maintaining a correct orientation with respect to the crab. In any of these events the proportion of errors made would decline with practice. Nor, it seems, are

they learning that the sight of a crab should be followed by a move into the corridor; the time spent attacking through the glass did not decline significantly with practice. What they *are* apparently learning is to proceed along the corridor once they are in it; the proportion of abortive entries and the total running time both decline significantly as trials continue.

The most economical explanation of these results is that the octopus learns to persevere in running through the maze, but learns nothing about how to orient itself within the maze in order to reach the crab. Since the animal is predominantly successful in its detours (and since, anyway, most individuals make a successful detour first time) it seems reasonable to suppose that the octopus is doing something that comes naturally to it.

Making detours around obstacles must be part of the animal's normal behavioural repertoire.

This is not a very surprising conclusion. *O. vulgaris* is an inshore species, living mainly on crabs which it catches among the rocks and weedbanks where both live. Situations analogous to that facing it in the detour apparatus must be routine. The animal must frequently lose visual contact with its prey, if the crab that it is stalking runs behind a rock or into a weed-thicket. On these occasions the octopus must search around the obstacle visually and with its arms, exactly as it does when its own movements carry it out of sight of the crab in the detour situation. At least one other cephalopod is known to behave in a similar manner—*Sepia* continues to follow around the edges of partitions as if hunting for prawns that it has seen pass behind a barrier and out of its sight, a response that can be eliminated by removal of the vertical lobe, a part of the brain known to be concerned in learning from training experiments (Sanders & Young, 1940).

(2) *Watched and automatically recorded trials*

In order to record eye movements and other details of the detouring response, one must stand over the apparatus and watch the octopus. *Octopus* is a highly visual animal. There was a possibility that it might gain clues about which way to turn from the attitude of the observer, quite apart from any possible distraction from the task in hand if he moved, and a preliminary series of experiments was carried out to discover whether the presence of an observer affected performance. In Fig. 4 the proportion of errors made in 357 watched undelayed runs from the M series is compared with the proportion of errors made in 351 machine-recorded undelayed trials made with the same animals. In both cases the proportion of errors rose with total running time, that is, with the number of seconds elapsed between entry into the corridor and exit from the choice compartment into one or other of the feeding bays. At machine-recorded trials the observer withdrew as soon as the octopus had entered the corridor and started towards the exit door at the far end. From then on the movements of the animal were monitored by the event-recorder alone. As Fig. 4 shows, there would appear to be no grounds for making a distinction between observations made with and without the recording device, and throughout the rest of this account no such distinction is drawn. Automatic recording was in fact used for all trials including an enforced delay and for about half of all undelayed runs in the M series of experiments. The N series (controls, and animals with severed optic commissures) were all watched.

(3) *The effect of lesions of types (1) and (2)*

Splitting parts of the brain known to be concerned in visual and tactile discrimination learning (see Wells, 1966; Young, 1964) has little effect on the ability to make detours. In Table 1 the performance of control and operated animals is compared for all trials, including runs with enforced delays during which the animal was shut

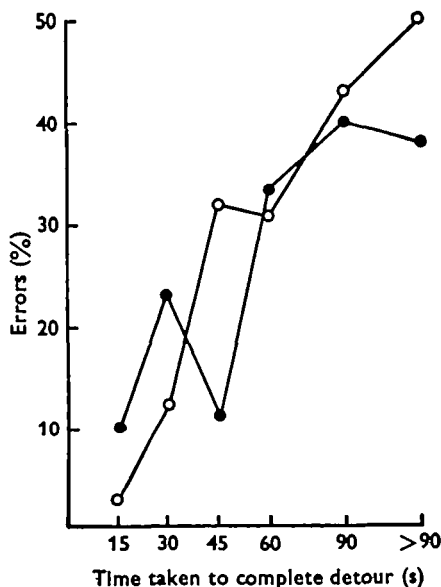


Fig. 4. A comparison of the results obtained in observed and automatically recorded trials, M Series. The proportion of errors made by turning into the wrong feeding compartment is plotted against the time spent running through the maze. Results from 357 observed trials are shown, O; those from 351 automatically recorded runs, ●. They show that there is no grounds for supposing that the presence of an observer influences the performance of the octopus. In subsequent figures and tables no distinction is made between results recorded by machine or by direct observation.

in the corridor. Clearly the presence of lesions of types (1) and (2) made little difference to the performance of the animals. The performance of controls and of operated animals differed only in the fastest runs, completed within 30 s of entering the corridor. This is significant at the $P = < 0.05$ level ($\chi^2 = 5.6$) but only provided that all the control results are summed and compared with all the experimentals. If one considers only those animals used both before and after operation the difference ceases to be significant. The seven such octopuses made a total of 66 undelayed runs before operation and of these eight were errors, i.e. 12%. After operation the same animals made 114 detours and of these 20 were errors, i.e. 18%. The remaining sample of nine controls, that were not subsequently operated upon performed somewhat better, making 133 runs of which only ten (< 8%) were errors. In runs taking longer than 30 s the animals with partially divided brains performed as well as controls.

Table 1

(Each column shows the number of errors made over the total number of trials completed within the stated time, M series. The performance of the experimental animals differs from that of controls only for the fastest (< 30 s) runs (see text).)

	Time in seconds					
	0-15	16-30	31-45	46-60	61-90	> 90
Controls						
Undelayed	2/99	16/102	13/63	14/48	24/57	22/49
30 s delay	—	—	6/23	7/17	10/17	5/16
1 min delay	—	—	—	—	10/22	16/33
Total	2/99	16/102	19/86	21/65	44/96	43/98
Errors % of total	2	16	22	32	46	44
Errors % of total*	9 ± 2		27 ± 4		45 ± 4	
Operated type 1 lesions.						
Visual system split						
Undelayed	3/38	11/44	7/31	8/25	11/27	11/27
30 s delay	—	—	1/2	2/8	2/9	4/12
1 min delay	—	—	—	—	2/8	8/16
Total	3/38	11/44	8/33	10/33	15/44	23/55
Errors % of total	8	25	24	30	34	42
Errors % of total*	17 ± 4		27 ± 5		39 ± 5	
Operated Type 2 lesions.						
Split extends into tactile system						
Undelayed	4/19	2/13	2/16	4/12	6/16	8/20
30 s delay	—	—	1/1	2/4	2/5	4/8
1 min delay	—	—	—	—	6/9	6/11
Total	4/19	2/13	3/17	6/16	14/30	18/39
Errors % of total	21	15	18	37	47	46
Errors % of total*	19 ± 7		27 ± 7		46 ± 6	

* Mean and standard deviation of percentage (all figures to nearest 1 %).

Table 2

(Each column shows the number of errors made over the total number of trials completed within the stated time, N series. As with the M series, the performance of controls and experimental animals differs only for the fastest runs.)

	Time in seconds				
	0-15	16-30	31-60	61-90	> 90
Controls					
n = 9	7/114	5/24	6/21	2/11	4/11
Errors % of total*	9 ± 2		25 ± 8		—
Operated type 3† lesions					
n = 8	5/52	13/45	14/63	12/48	13/47
Errors % of total	19 ± 4		24 ± 4		—

* Mean and standard deviation of percentage (all figures to nearest 1 %).

† Includes 2 M series animals.

(4) *The effect of cutting the optic commissures: lesions type 3*

A total of 255 completed runs was made by eight animals (two from the M series and six from N) in which the optic commissures were cut. The performance of controls from the M series has already been described (Table 1). A further group of nine unoperated animals made 181 runs during the N (1967) series of experiments; five of these octopuses were subsequently tested as operated animals after their commissures had been cut.

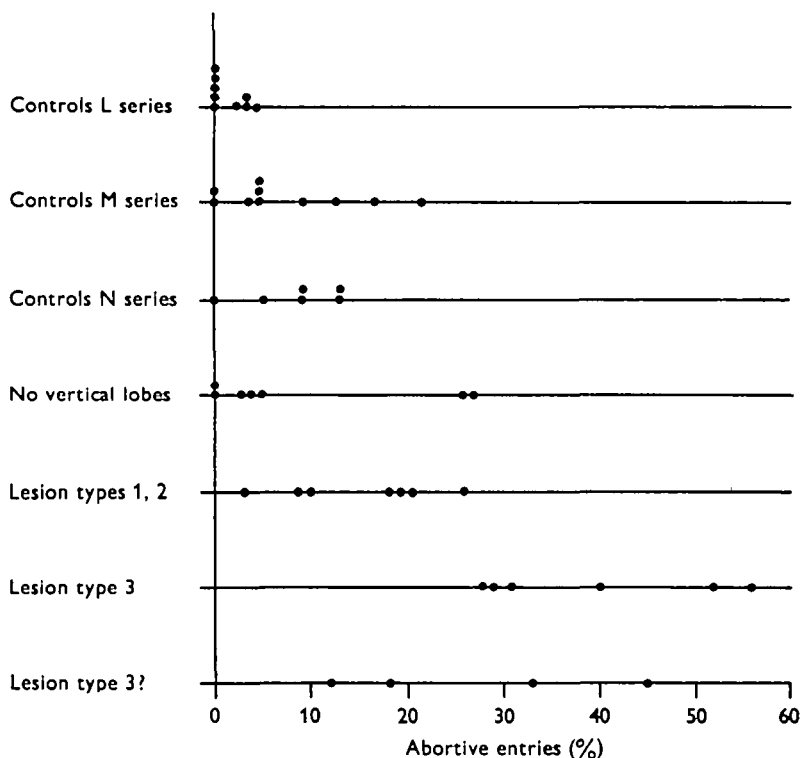


Fig. 5. Showing the proportion of trials at which only abortive entries were made by animals with various lesions (for which see Fig. 2). Each point shows the result obtained with a single individual having the stated type of lesion. The lowest line ('lesions type 3?') shows the performance of animals in which section of the optic commissures was intended but subsequently found to be uncertain.

The results obtained are summarized in Table 2. The proportion of errors made by controls and experimentals was significantly different (experimental animals made more mistakes) only for trials lasting less than 30 s.

A comparison of the performance of animals with and without the commissures cut, based on completed runs, is however, only part of the story. To get a better assessment of the effect of this operation one must also take into account occasions when the animals attacked a crab through the window of a feeding compartment, set off into the corridor, and then failed to complete a detour at all.

In Fig. 5 the performance of octopuses after various operations is compared in terms of the proportion of trials at which only abortive runs were made; that is, the

proportion of trials including one or more entries into the corridor but no subsequent run through to a feeding compartment. Generally, on these occasions, the animals returned home between attacks and forays into the corridor; occasionally they remained in the corridor until the end of the 5 min maximum duration of a trial. Results with 21 operated and 29 control animals are included in Fig. 5, which summarizes data from all the animals in the M and N series that completed 20 or more runs, together with 16 animals from a further (L) series of experiments made in 1964 and already reported in Wells (1967); the L series experimental animals had their vertical and/or superior frontal lobes removed.

The proportion of abortive runs made by the six individuals that completed 20 or more detours after section of the optic commissures ('lesions type 3' in Fig. 5) was in every single case outside the range shown by other octopuses.

(5) *A possible explanation of the effect of type 3 lesions*

Lesions of type 3, made to sever the optic commissures, also separate the two halves of the basal lobes, which are known to be higher motor centres (Boycott, 1961; Young, 1964). This has surprisingly little effect on locomotion. The animals are still able to move about their tanks in a well-integrated manner and, as Table 2 shows, they can, and often do, complete the complicated series of movements necessary to effect a detour just as rapidly as unsplit controls. The implication is that the activities of the motor control regions in both sides of the suboesophageal brain can be organized from the basal lobes on one side of the supraoesophageal brain.

In the intact octopus one must assume arrangements to ensure that visual inputs to the two sides of the supraoesophageal brain do not lead to contradictory orders to the muscle system of the animal. In principle dominance by one side at a time might be arranged at a supraoesophageal or at a suboesophageal level. If the former were the case, one would expect some sign of competition for control after operations dividing large parts of the supraoesophageal brain.

Observations of the detailed behaviour of animals after section of the optic commissures indicates that such competition does indeed occur. The animals vacillate. In detour experiments, where a crab was shown at a distance from the home, there was an unusually high proportion of trials at which the animals emerged from the home but never got as far as the transparent wall of the feeding compartment. There were, moreover, a number of trials at which split-brain octopuses did come forward but appeared to be hampered by the adhesion of their unstimulated side, even to the extent of dragging bricks from the home with them as they approached the glass. Since the same individuals were, on other occasions, seen to make successful detours by means of rapid well-integrated movements, adhesion cannot be attributed to uncontrolled reflex action of the suckers. The simplest explanation of these phenomena is competition; input to the two eyes (from the crab, and the home, both desirable objectives) can result in incompatible orders to the two sides of the motor system. Such an explanation is clearly consistent with the observation that split-basal octopuses frequently give up and go home after having attacked and passed into the corridor. *Ex hypothesi*, these animals attack, run into the corridor, and are then unable to suppress rival commands arising as a result of input from the eye that has not seen the crab, but has observed that home is being left behind.

(5) *The effect of unilateral blinding on split-brain octopuses*

One means of testing the hypothesis that commands from the two sides of the brain compete for control of the lower motor centres in split-brain animals is to cut off the sensory input to one side. Performance should improve if the defect in performance is indeed the result of an internal conflict. Since the relevant sensory input in detour experiments is predominantly visual (Wells, 1964) it is easy to arrange this by cutting the optic nerves to the brain on one side. This experiment was carried out with three animals, N1 (already included in the data cited in Table 2 and in Fig. 5), N3 (which completed only seven runs before blinding) and N20, an animal with a similar (type 3) lesion, so far omitted from the present account (except as a component of 'lesion type 3?' in Fig. 5) since there was some doubt about the completeness of its operation; in some sections optic commissural fibres appeared to remain intact. N20, however, behaved like other split-brain octopuses in that it made a substantial proportion of abortive runs (18%, nine trials out of a total of 50).

Before unilateral blinding, split-brain octopus N1 made 39 detours. During the period of these tests there were in addition 15 trials at which only abortive entries into the corridor were made; the octopus thus ran into the corridor, but failed to complete a detour at 28% of all trials. Subsequent to the optic nerves being cut on one side the same animal failed to complete a run on only two occasions in 61 trials at which it entered the corridor—3% abortive runs, compared with 28% before its second operation.

The scores made by N20 were very similar. 18% abortive entries in 50 trials before blinding, only 3% in 31 trials after. The preblinding performance of N3 was the poorest of the three. This octopus made only abortive entries at 14 out of 21 pre-operational trials (67%), but again there was an improvement in performance as a result of cutting the optic nerves on one side; after the operation the animal made abortive entries at 15 out of 29 trials, i.e. 52% of all trials compared with a pre-operational 67%.

DISCUSSION

The following observations have been made in the course of the experiments described above:

1. Octopuses obliged to run through a maze in order to get a crab which is seen but is not directly accessible to them show very little improvement in performance with practice. The proportion of errors made does not fall with repeated runs through the apparatus.
2. Vertical division of parts of the brain known to be concerned in visual and tactile learning has little effect on the proportion of errors made in detour experiments.
3. Cutting the optic commissures in the basal lobes does not prevent octopuses from making successful detours, but they characteristically make a high proportion of abortive runs; the animals enter the corridor normally but then return home without completing a detour. They are apparently hampered by an inability to repress contradictory orders arising as a result of visual inputs to the two sides of the body.
4. Performance reverts to normal levels if such animals are blinded in one eye.

These results must be considered in relation to two previous findings:

1. That vertical lobe removal has a marked effect on the capacity to make detours; it is followed by an increase in errors in all but the fastest runs and substantially reduces the maximum duration of successful detours (Wells, 1967).
2. That longitudinal vertical division of the vertical lobe before unilateral visual discrimination training prevents the establishment of a long-lasting contralateral trace (Muntz 1961 *a-c*).

When an octopus sees a crab and then makes a detour through a maze to get it, it is only reasonable to assume that it carries some record of its observation. This representation evidently endures for a minute or two and is then lost; in the meantime it determines that the octopus continues to run through the maze rather than to go home.

If the vertical lobe is removed octopuses make as many errors as correct responses in completed runs lasting longer than about 1 min; unoperated animals continued to make better-than-chance scores in detours lasting up to twice as long (Wells, 1967). The present experiments show that longitudinal vertical section of the vertical lobe is *not* equivalent to vertical lobe removal; in this series the animals performed as well as controls in runs lasting longer than 1 min (Table 1).

The performance of octopuses after division of the vertical lobe is particularly interesting in relation to Muntz's (1961 *b, c*) observation that this operation prevents interocular transfer in visual discrimination experiments. Muntz trained octopuses over a period of days using one eye, and then tested the animals using the other. Unoperated octopuses performed well with the untrained eye, octopuses with their vertical lobes removed did not.

When an octopus attacks a crab, it generally does so with one eye clearly leading and the other facing away from the target. In the detour apparatus the attack is normally followed by a move into the corridor. The octopus may now lead along the corridor with the eye that it has used to view the crab or with the other eye. On the face of it continued progress in the latter instance implies interocular transfer; the performance of the animal is still being determined by its recent sight of the crab despite the fact that it is now guiding the details of its run down the corridor with the 'inexperienced' eye. If this interpretation is correct it is interesting because it shows that interocular transfer can occur in a short-term learning situation following an operation that precludes it under long-term conditions.

The case that interocular transfer occurs in the detour situation depends on the validity of the assertion that the octopus uses the leading eye to direct its passage through the maze. The evidence which this view is based on is as follows: (1) blinding by cutting the optic nerves to one eye produces systematic errors. The animals tend to make detours always to the same side regardless of the compartment in which the crab is shown. One would not expect this to happen were the detour guided otherwise than visually (Wells, 1964). (2) Split-brain (lesion type 3) animals rarely complete detours following an eye change. Unoperated animals and octopuses with lesions of types 1 and 2 (Fig. 2) changed the leading eye as they entered the corridor at about one-third of the runs that they subsequently completed (Table 3). Split-brain octopuses did so at only 12% of their completed runs; the difference is significant at the $P = < 0.001$ level ($\chi^2 = 39$).

The result with split-brain animals could be attributed to division of the basal lobes. These are higher motor centres (Boycott, 1961) and their division might be expected to disrupt the capacity to make detours even if this were guided by touch. The series of observations cited in (1) above makes this explanation unlikely, however, since there is no reason why blinding in one eye should disrupt a detour guided by touch.

The fact that split-brain animals run at all after an eye change is evidence that the animals have learned something about the maze situation as such. Experience does not teach them to orient themselves correctly, but they do learn to run down the corridor once in it (see results section (1), pp. 378 to 380). The comparative rarity of eye-change runs by split-brain octopuses shows, however, that runs down the corridor are only partly determined by past experience of the maze. Animals are more likely to continue the run if the lead side is in connexion with the side that has recently seen the crab.

Table 3. *Eye changes*

(Columns show the number and proportion of completed runs at which octopuses changed the leading eye on entry into the corridor.)

	Total no. of completed runs	Runs including an eye change	% of total
All M and N controls	698	254	37
Lesions, types 1 and 2	345	106	31
Lesions, type 3	25	209	12

The total numbers of runs recorded here are less than those given in Tables 1 and 2, since the latter include runs for which a full record of eye movements is lacking.

One is left with the propositions (*a*) that the animal is somehow driven to continue its passage through the maze by its recent sight of the crab and (*b*) that the representation so established modifies responses arising as a result of visual input coming to the brain through the leading eye. In other words, that interocular transfer has occurred; information acquired through one eye is available to both sides of the body.

The interesting point here is that interocular transfer clearly occurs in animals with the vertical and superior frontal lobes split. This is the operation that Muntz (1961 *b*) showed stopped the establishment of a bilateral trace. After this operation a long-lasting representation is established on one side of the brain only (in the optic lobe of the side concerned—Muntz, 1961 *a*), and is not available to modify responses arising as a result of subsequent visual inputs to the untrained eye. This must mean that long term and short-term representations are different in kind and that the establishment of long-term traces involves extra structures that are not required to make short-term effects available bilaterally. This confirms previous results including vertical lobe removal (Wells, 1967) which again does not prevent interocular transfer in the present short-term situation. The optic commissures (or other structures close to these in the basal lobes) are adequate as a pathway via which one side can read out from, or receive a copy of, short-term representations established in the other. But they are not a pathway by which co-ordination of the two sides is achieved following long-term unilateral training. Long-term effects must be represented by a bilateral trace if the

two sides of the animal are to be co-ordinated as a result of visual experience limited to one side.

There is an interesting difference in the case of touch learning in *Octopus*. Here it has been shown that the effect of experience restricted to one side is *not* immediately available to the other. Any octopus can be trained to reject an object (such as a Perspex ball or cylinder) that is repeatedly presented to it. Given shocks for accepting the object, it learns in two or three trials. If this training is limited to one side of the body and if the 'untrained' side is tested at intervals, it is found that the effect of the experience takes about an hour to become effective in determining the response of the 'inexperienced' side. If this is tested sooner the octopus will take the object that the trained side has learned to reject (Wells, 1959). As a result of prolonged training a bilateral trace is set up in the inferior frontal system and both sides of this combine to determine the responses of either side of the body (Wells & Young, 1966). Here then, the 'short-term' mechanism, ensuring co-ordinated responses of the two sides of the body in response to stimuli recently analysed by one side seems to be lacking. It is perhaps less necessary than in the case of vision, where objects pass readily and rapidly from one visual field to another. In touch, any object of interest is likely to be trapped by the first arms to come into contact with it.

SUMMARY AND CONCLUSIONS

1. Octopuses will move out of sight of their prey and make detours through a maze to get crabs that are initially visible but not directly accessible to them.
2. Successful detours are made without training, and performance shows little change with practice.
3. Longitudinal division of the vertical and subvertical lobes and/or of the superior and inferior frontal lobes does not affect performance.
4. Extension of the cut downwards to include the optic commissures produces animals that sometimes perform quite normally, and at other times vacillate, apparently unable to prevent the onset of incompatible responses arising from visual inputs to the two sides of the body. If the optic nerves are cut on one side such animals perform normally. In the intact octopus conflict between the two sides must be avoided by exchange of information through the optic commissures, or through structures closely associated with these.
5. This situation is compared with that found in training experiments involving visual discrimination. In detours the information acquired through one eye modifies the behaviour of both sides of the body for a few minutes. Its availability is not changed by prior removal of the superior frontal and/or vertical lobes. Following unilateral training involving visual discrimination, responses arising as a result of visual inputs to either side of the body are modified for many weeks, but only provided that the superior frontal-vertical lobe system remains intact. If this system is split the untrained side remains naive.
6. It is concluded that the long and short-term storage of representations of objects seen must be different in kind and that the establishment of long-lasting bilateral traces involves structures that are not essential for the side-to-side distribution of information in the short-term situation.

7. This state of affairs is compared with the situation in touch learning, where there seems to be no functional equivalent of the optic commissures. Long-term bilateral traces are established as a result of unilateral training but the effect takes an hour or more to spread to the untrained side.

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