

## THE MEDIAN INFERIOR FRONTAL LOBE AND TOUCH LEARNING IN THE OCTOPUS

BY M. J. WELLS AND J. Z. YOUNG

*Department of Zoology, University of Cambridge, and  
Department of Anatomy, University College London*

(Received 6 July 1971)

### INTRODUCTION

Touch learning in the octopus is dependent upon the integrity of a small (*c.* 1 mm<sup>3</sup>) region near the front end of the supraoesophageal lobes of the brain. This region includes the posterior buccal lobe, the subfrontal lobe, and the lateral and median inferior frontal lobes, which lie round the other two laterally and on top (Fig. 1; Young, 1971). Animals cannot be trained to discriminate between objects by touch, or to reject a single object repeatedly presented, if these parts are removed entirely (Wells, 1959*a*). Attempts to narrow down the critical area have indicated that, for touch learning to occur at all, a minimal number of cells must remain at the base of the subfrontal lobe, where this merges into the medial walls of the posterior buccal lobe (Wells, 1959*a*; Wells & Young, 1965, 1966). The function of the median inferior frontal lobe has remained unclear. This region is composed of many interweaving tracts; it is the main tactile input linking the brachial nerves with the subfrontal lobe. Its approximately one million cells send their axons only to the subfrontal lobes, which have five million cells (Young, 1971). Preliminary experiments have suggested that removal of the median inferior frontal lobe makes little difference to touch learning (Wells, 1959*a*; Wells & Young, 1965). There is, however, some doubt about the interpretation of these experiments, because it was not known at the time that damage to the inferior frontal system reverses a normal untrained preference for smooth rather than rough objects (Wells & Young, 1968). A re-examination of the data reveals that the animals that showed a significant improvement in performance during training after removal of the median inferior frontal were all trained in the direction of their probable untrained preference.

A preliminary re-investigation confirmed that animals without the median inferior frontal perform better when trained with the rough object positive than with rough negative, but the experiments were otherwise equivocal (Wells & Young, 1969). Four out of the six animals trained S<sup>+</sup>/R<sup>-</sup> actually became more *indiscriminate* as training proceeded. The only conclusion that could be reached at that time was that damage to the median inferior frontal interferes with touch learning; it was not clear whether it actually prevented it.

The present account reports more extensive experiments on the function of the median inferior frontal lobe. It is mainly concerned with the effect of three classes of lesion: (1) removal of the median inferior frontal only, leaving the rest of the brain intact; (2) removal of parts from the rest of the supraoesophageal brain; and (3)

removal of the median inferior frontal as well as these parts of the supraoesophageal lobes. It will be shown that removal of the median inferior frontal considerably slows, but does not completely prevent, touch learning.

#### MATERIAL AND METHODS

*Octopus vulgaris*, from the Bay of Naples, was used in the experiments, carried out at the Naples Zoological Station during the summers of 1969 and 1970. The animals were kept in individual plastic tanks and fed on crabs or pieces of sardine. Operations

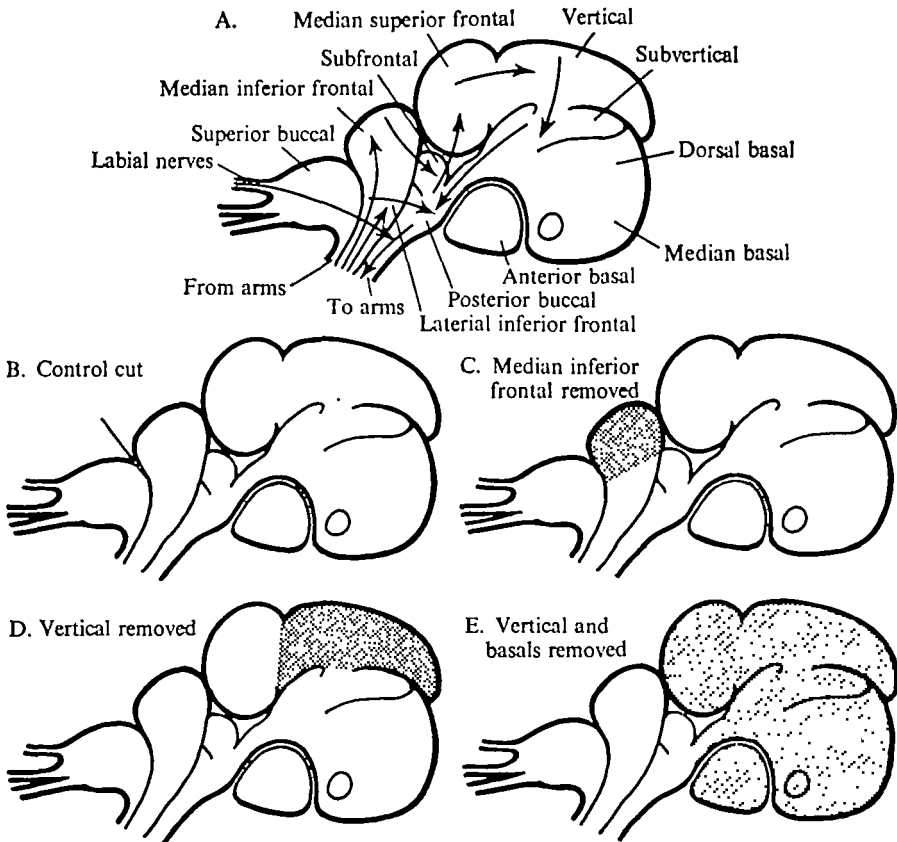


Fig. 1. A, Diagram of the supraoesophageal lobes of *Octopus*. B-E, The lesions made in the experiments.

were carried out under urethane anaesthesia, and usually involved section of the optic nerves and removal of a part of the central supraoesophageal brain. Details of the lesions in individual animals are given in the results sections below. Fig. 1 shows the relative position of the parts concerned and the nature of the main classes of lesion considered. The results from any animals that died or ceased to feed regularly were discarded.

Animals were trained to discriminate between two Perspex spheres 25 mm in diameter presented successively. One of the spheres (13R, the 'rough' sphere) had 13 latitudinal grooves, each 0.8 mm wide and 1 mm deep, cut into its surface, 14°

apart; the other (OR) had a smooth surface. These were presented to the animal, one at a time, by lowering the sphere on the end of a Nylon line to touch against one of the arms. The animal was rewarded for grasping one of the spheres with the suckers and passing it under the interbrachial web towards the mouth, and punished for taking the

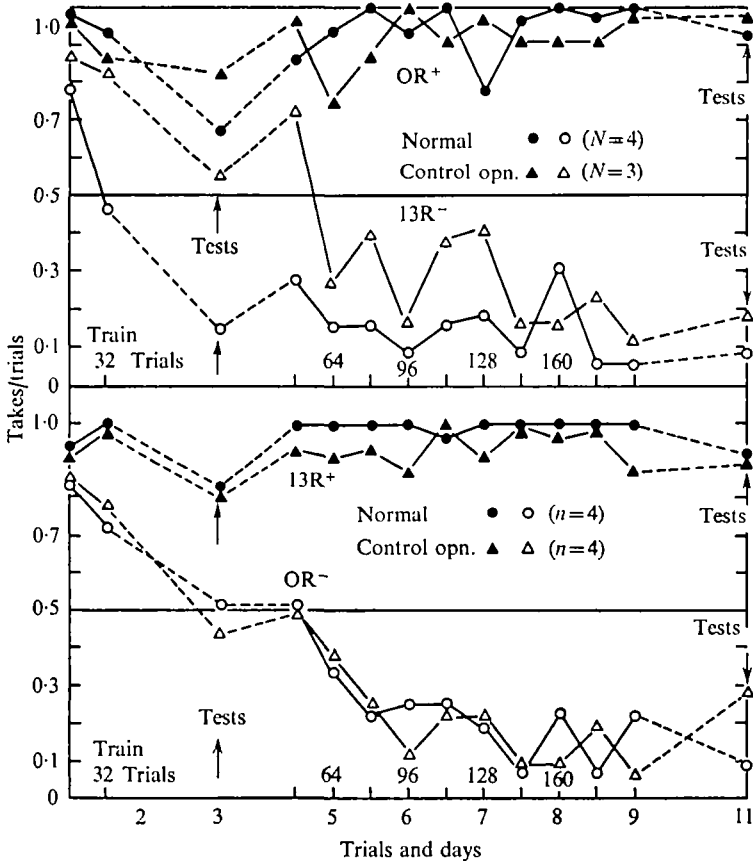


Fig. 2. Learning by control animals. Filled and open circles show the proportion of takes to trials of the positive and negative objects by blinded but otherwise unoperated (= normal) animals. Filled and open triangles show the performance of blinded animals with a cut between the median inferior frontal and superior buccal lobes (control operation). After the first 32 trials, given in a single session, the animals had 60 unrewarded tests before training was continued. There was a similar test at the end of training.

other. Rewards were small pieces of fish, given on the end of a thin wire probe. Punishments were 8–12 V a.c. shocks, given by touching the animals with a pair of electrodes. After the reward or punishment was given the training sphere was pulled away. The animal could reject the test object by pushing it away, or simply by letting go of it after examination with the suckers. Occasions when the animal grasped a sphere and hung on without starting to take or reject it were scored as rejections (and the sphere was removed) after 20 sec. The animals were neither rewarded nor punished for rejections. The animals had no pre-training experience in the laboratory of the test objects or of others like them and there was normally no pre-training to take the positive object or correction procedure for incorrect rejection in the course of discrimination

training. The only exception to this was in the experiments described on p. 390 below where animals having lesions of the median inferior frontal lobe were given training to take the smooth sphere as a preliminary to discrimination training with OR *vs.* 13R.

Discrimination training was given in groups of 16 trials (8<sup>+</sup>, 8<sup>-</sup>, given alternately with the positive first), individual trials being 5 min apart. There were two such groups per day, one in the morning, the other 6–8 h later. In some experiments there was a preliminary training session of 8, 32 or 60 trials (half positive and half negative) given

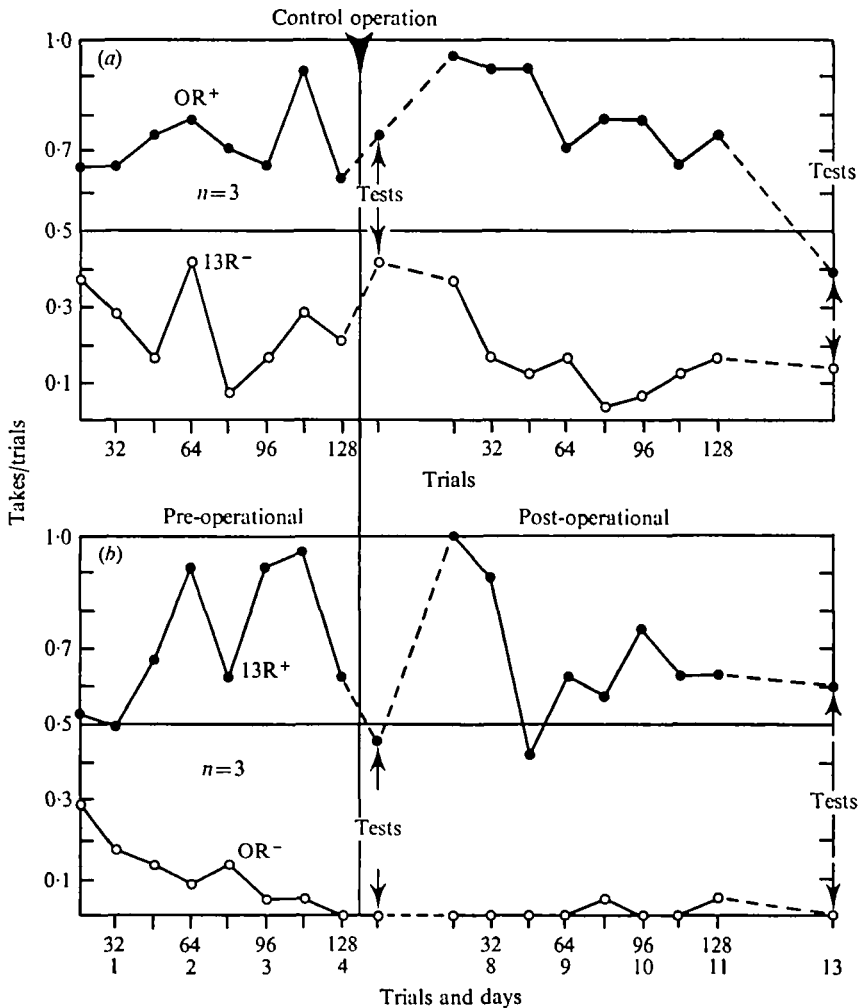


Fig. 3. For legend see facing page.

in a single group at 5 min intervals. In these instances the single group of trials was followed by a 2-day break in training and then by a session in which the objects used in training were presented alternately 60 times in a series of unrewarded tests. The results of these single-session learning experiments have been published elsewhere (Wells & Young, 1970). They show that the performance of normal (blinded but otherwise unoperated animals) can be altered significantly by as few as 8 (4<sup>+</sup>, 4<sup>-</sup>) training trials. Animals with damage to the vertical and inferior frontal lobe systems also learn, but

accumulate less in the memory for a given number of trials. The 60-tests method of assessing discrimination has the advantage that it largely eliminates problems of the level of reponse; as a result of certain lesions the proportion of takes in training experiments may be raised to the point where discrimination is masked. A long series of extinction tests reduces the level of take progressively and reveals any latent capacity for discrimination.

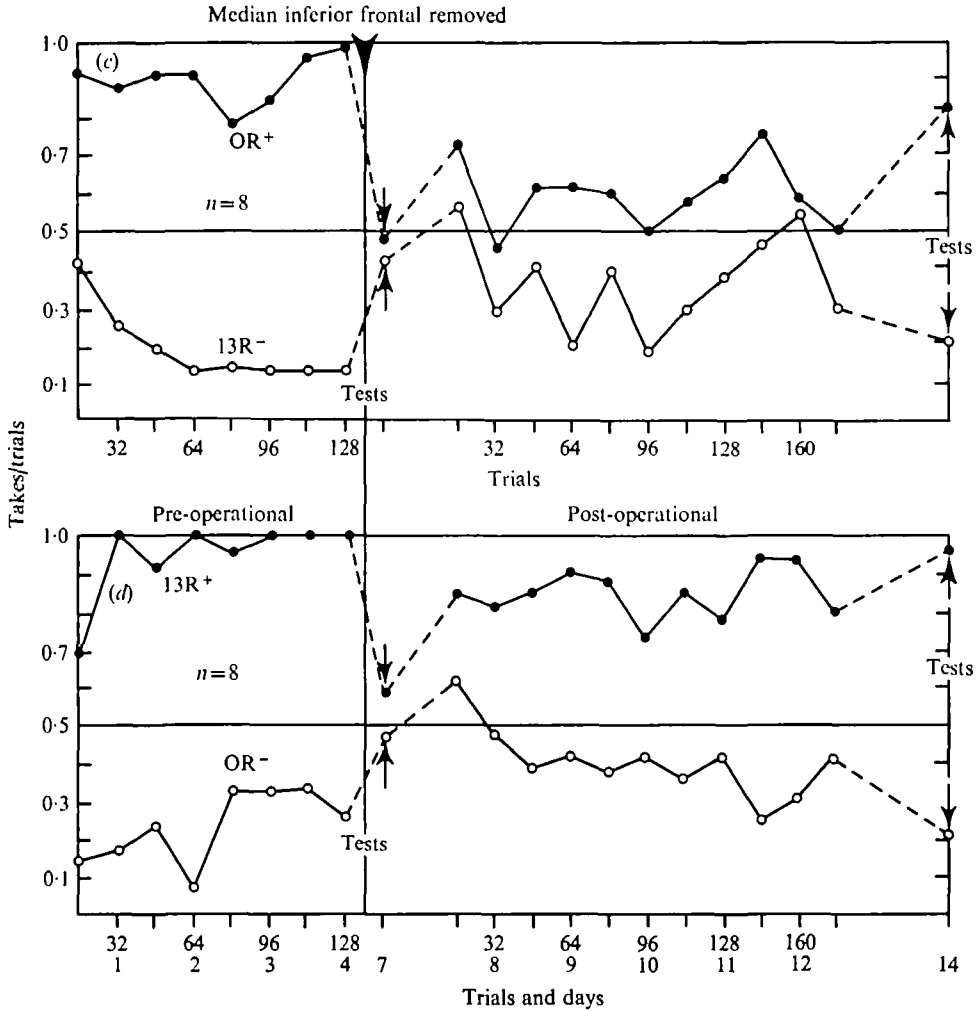


Fig. 3. Removal of median interior frontal. Train-operate-train experiments. These animals had some experience of the test objects before the beginning of the experiment shown here. Control operations (a, b) have little effect on performance, but removal of the median inferior frontal lobe (c, d) produces an abrupt decline in performance, which is particularly marked for those trained OR<sup>+</sup>/13R<sup>-</sup>.

RESULTS

(1) *The performance of control animals*

Fig. 2 shows the progress of learning to discriminate between OR and 13R for two classes of control animal: blinded but otherwise unoperated animals ( $n = 8$ , 4 trained OR<sup>+</sup> and 4 13R<sup>+</sup>) and blinded animals with a 'dummy' operation ( $n = 7$ , 3 trained

OR<sup>+</sup> and 4 13R<sup>+</sup>). In the dummy operations the central supraoesophageal part of the brain was exposed and a cut was made between the superior buccal and median inferior frontal lobes. This cut (see Fig. 1B) constitutes a routine part of the operation of median inferior frontal removal. It produces some damage to the blood vessels at the back of the superior buccal lobe, killing some of the neurones that innervate the posterior salivary glands.

The animals were trained as follows. On day 1 they were given a 'double' session of 32 trials (16<sup>+</sup>, 16<sup>-</sup>) in a group. This has been plotted in Fig. 2 as if done in two sessions of 16 trials, so that the scores are comparable with those obtained in the rest of the experiment. After this initial session the animals were given a 36 h rest and on day 3 were subjected to 60 unrewarded tests, 30 with each of the objects used in training, presented alternately. In Fig. 2 the scores made in the tests are summarized and scaled to be comparable with the scores made in later training. After a further day without training or tests, training was resumed at the standard rate of 16 trials per session, two sessions per day and continued for 5 days. After this there was a further day's break before a final session of 60 unrewarded tests.

Both classes of control animals learned rapidly (Fig. 2). The animals with a control lesion were slightly slower to learn the OR<sup>+</sup>/13R<sup>-</sup> discrimination than normal blinded but otherwise unoperated controls. This somewhat greater tendency to take the rough agrees with other observations that any interference with the central nervous system produces a swing towards rough preference. Despite this initial disadvantage in the OR<sup>+</sup>/13R<sup>-</sup> discrimination, the animals with a control cut attained the same standards as the controls without lesions, with either direction of training. It may be concluded that the operational technique does not *per se* produce a decline in the capacity to learn to discriminate.

## (2) *Removal of the median inferior frontal*

### A. *Train-operate-train experiments*

Twenty-two animals were first thoroughly trained, half of them with OR<sup>+</sup>/13R<sup>-</sup> and half with 13R<sup>+</sup>/OR<sup>-</sup> (Fig. 3). The animals had 8, 16 or 32 trials followed after 36 h by 60 unrewarded tests, 30 with each of the objects used in training. This part of the experiment, carried out in the course of single-session learning experiments (Wells & Young, 1970), is not shown in Fig. 3. The animals were then given 128 further training trials at the usual rate of 16 trials per session, two sessions per day. After this the median inferior frontal lobe was removed from sixteen of the animals, and in six a control incision was made between the median inferior frontal and the superior buccal lobe. They were left for 2 days to recover and during the second day were fed with pieces of fish. On the third day after the operation the animals were given 60 unrewarded tests, 30 with each of the objects used in the pre-operational training. Training was continued next day.

The control group (three animals were trained with OR<sup>+</sup> and three with 13R<sup>+</sup>) showed somewhat less accuracy in tests immediately after operation than at the end of pre-operational training. With resumption of training performance very quickly returned to pre-operational levels (Figs. 3a, b). The animals without median inferior frontals (all 100% removals) showed less retention of the capacity to discriminate in the post-operative tests.

Performance, however, improved during post-operative training, and in the final tests without reward discrimination was very good in both directions and much better than immediately after operation (Fig. 3*c, d*). The level of discrimination achieved by the animals trained OR<sup>+</sup>/13R<sup>-</sup> was better than that of animals with similar lesions not trained before operation but given the same amount of training afterwards (Fig. 4*a, c*). There is thus good evidence of retention over the operation, as well as of a capacity to learn afterwards. It should be noted that the increased proportion of errors arising as a result of the lesions included extra errors in both directions. The negative sphere was taken more than before and the positive less, even when this was 13R, the object 'preferred' by untrained animals with their median inferior frontal lobes removed. The effect was apparent both in the unrewarded tests carried out immediately after operation and during the subsequent re-training of the animals. One must conclude that removal of this part of the brain interferes with both retention and relearning and that the median inferior frontal is involved in both positive and negative learning.

*B. Animals trained only after removal of the median inferior frontal*

*Bilateral removals.* Eight animals were trained 13R<sup>+</sup> and eight OR<sup>+</sup> for 160 trials given in 10 sessions of 16 trials. From every animal at least 85% of the median inferior frontal lobe had been removed, and in 10 out of 16 (6 on OR<sup>+</sup>, 4 on 13R<sup>+</sup>) this lobe had been destroyed altogether. After operation the animals were left for several days to recover, until they were taking fish and crabs regularly. The results of training are summarized in Fig. 4*a* and *b*. There was no detectable difference in performance between the animals with 100% lesions, and those with 85% of the median inferior frontal removed; the results from all the animals with lesions have been combined in plotting Fig. 4.

The eight animals trained with 13R<sup>+</sup> and OR<sup>-</sup> together made 988 correct responses in 1280 trials, 77% correct (Fig. 4*b*). The eight trained with OR<sup>+</sup> did less well, with 694 correct in the same number of trials, 54% correct responses (Fig. 4*a*). The overall level of take was considerably and progressively depressed in the latter group, only 46% of all the objects presented being accepted against 59% by the eight animals trained 13R<sup>+</sup>/OR<sup>-</sup>. This difference in response level seems to have arisen because the animals trained with OR<sup>+</sup> tended to err in the direction of their untrained preference for 13R. In the early sessions of training they got repeated shocks for taking 13R and, compared with animals trained 13R<sup>+</sup>/OR<sup>-</sup>, relatively few rewards for accepting the positive object. The proportion of takes fell off, particularly towards the end of each training session.

In an attempt to minimize this difficulty eight further animals were trained at a slower rate of eight trials (4<sup>+</sup>, 4<sup>-</sup>) per session, four animals in each direction. Each animal had 10 such training sessions. All had 80% or more of the median inferior frontal removed. The four trained OR<sup>+</sup> included three animals with 100% lesions; the 13R<sup>+</sup> group one such. There were no consistent differences between animals with 100% lesions and animals with 80%+ lesions. The results are shown in Fig. 4*c* and *d*. Reducing the number of trials per session increased the proportion of spheres taken by the OR<sup>+</sup> group. Despite this, only one of the four animals trained smooth<sup>+</sup>/rough<sup>-</sup> showed clear signs of an increasing capacity to discriminate in the trained direction; this individual had the whole of the median inferior frontal removed.

Clearly the performance of animals trained after removal of the median inferior frontal is not readily altered by training; the untrained preference for rough objects is difficult to eliminate. It is certain, however, that training had some effect on discrimination, since the performance of animals trained with  $13R^+$  was consistently different

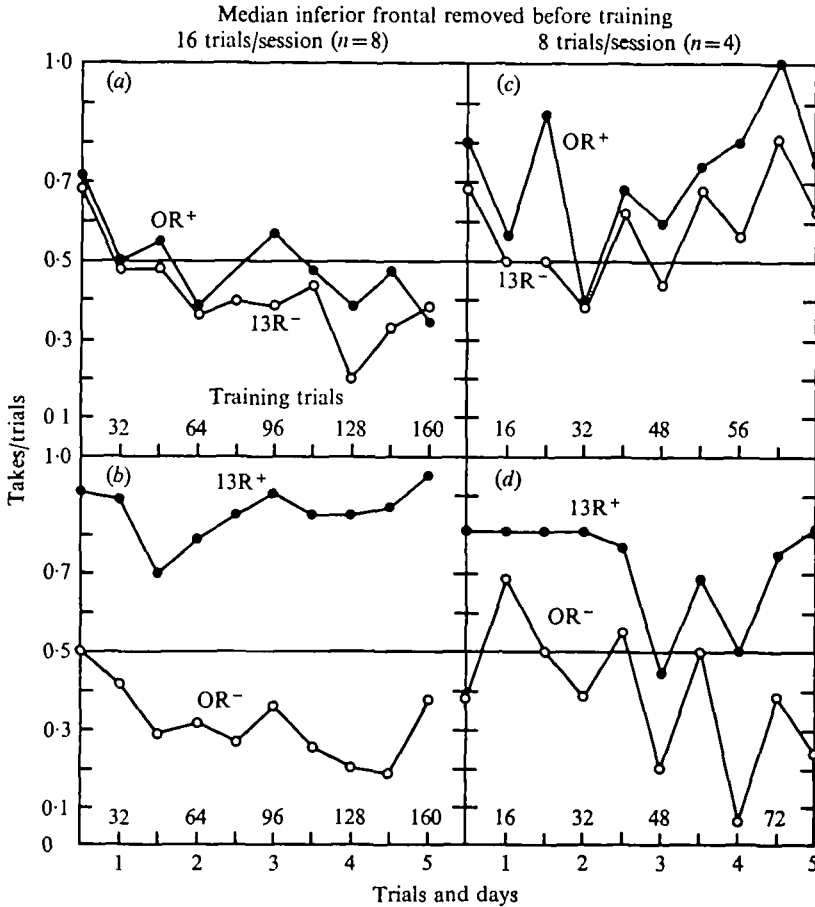


Fig. 4. Training after median inferior frontal removal, plotted as in Fig. 3. (a) and (b) show the result of training at 16 trials per session, (c) and (d) at eight trials per session.

from that of animals trained with  $OR^+$ . Animals trained in the direction  $13R^+/OR^-$  took  $13R^+$  about twice as often as  $OR^-$ . Those trained in the  $OR^+/13R^-$  direction took the two spheres about equally often. As Fig. 4 shows, this difference is not simply attributable to the differences in level of take. One must conclude that both groups of animals learned to discriminate even though the performance of those trained in the  $OR^+/13R^-$  direction never reached levels where the effects of their training consistently outweighed the unlearned preference for the rougher of the two objects.

### (3) Unilateral removals in split-brain animals

The supraoesophageal brain of 12 untrained animals was split completely by a longitudinal vertical cut and the median inferior frontal lobe was removed on the right side only.



Octopuses with their brains split are known to 'prefer' rough to smooth objects when tested before training (Wells & Young, 1968). In order to discover whether this preference is accentuated by removal of the median inferior frontal lobe, the 12 animals were tested 2 days after operation by presenting 13R and OR alternately, first to the

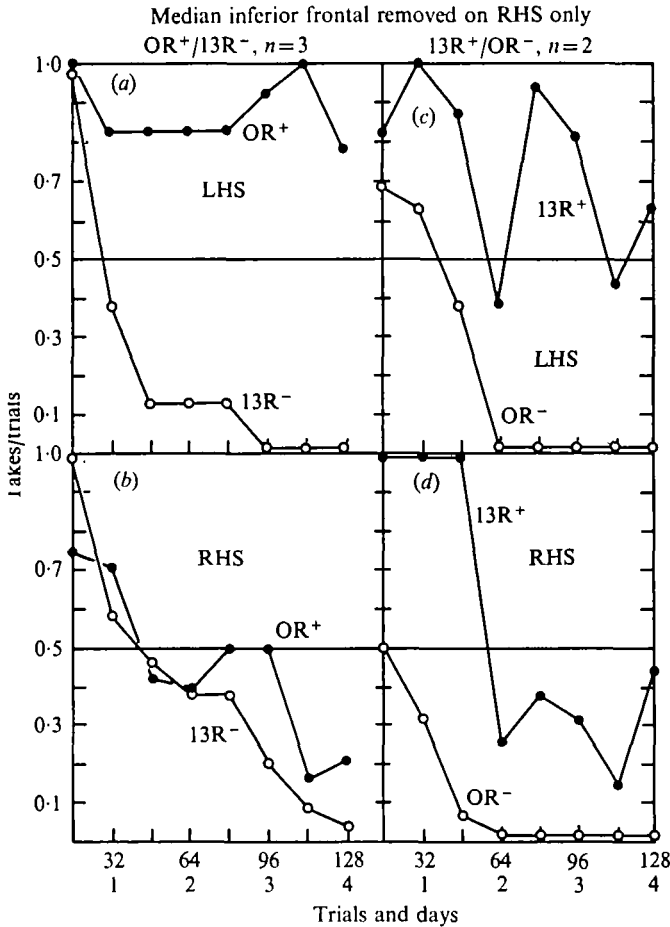


Fig. 5. The performance of split-brain animals with the median inferior frontal lobe removed on the right side. (a) and (b) show the result of training three animals with OR<sup>+</sup>/13R<sup>-</sup>, (c) and (d) two animals with 13R<sup>+</sup>/OR<sup>-</sup>. Both sides were trained and the performance of the arms on each side is shown separately.

right and then to the left side of each animal. Each object was presented 15 times to each side. 13R was taken 142 times by the arms on the right-hand side (RHS) and 124 times by those on the left (LHS). The corresponding figures for OR were 104 and 102. One must conclude that removal of the median inferior frontal lobe has no significant effect on the rough preference or on the level of take of split-brain octopuses.

Five of the animals were then trained to discriminate in the normal manner but on both sides, so that sessions of training lasted for 32 instead of 16 trials. The order of presentation was as follows: R+ L+, R- L-, R+ L+, R- L-, then L+ R+, L- R-, L+ R+, L- R-, then R+ L+ and so on to give eight presentations of each object to each side.

Training was continued for eight sessions. The results are shown in Fig. 5. The intact left sides of all five animals learned, with scores ranging from 74 to 90% correct. The right sides of the same animals performed reasonably well when the rough object was positive (scores of 64 and 81% correct) but were less satisfactory with OR+; of the three such animals one scored 58% correct, one 52% and the third remained perverse with a score of 49% (compared with 85% by the intact LHS of the same animal). In part the very low scores made by the side with the lesion are due to a much reduced level of take. The animals tended to start by taking objects on both sides, but while the LHS continued to take, positive responses by the RHS showed a progressive reduction as training continued (Fig. 5).

(4) *Median inferior frontal lesions and learning to take smooth objects*

In an effort to eliminate the bias imposed by the untrained preference for rough objects, 11 animals with lesions to their median inferior frontal lobes were given intensive training to take the smooth sphere as a preliminary to the usual rough/smooth discrimination training. Run in parallel with these there were seven controls with cuts made between the inferior frontal and superior buccal lobes.

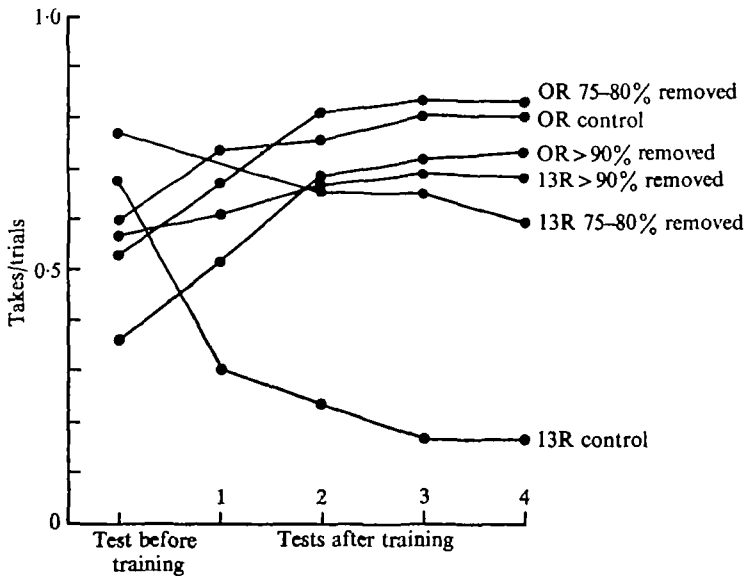


Fig. 6. The results of positive training alone. The animals were given OR together with fish 16 times per day, in two sessions of eight training trials. The points show the take of OR and 13R objects in unrewarded-test sessions (30 presentations of each object) given every fourth day. The lines show separately the results from animals with more than 90% median inferior frontal removed and 75-80% removed.

On the first day the animals were subjected to the standard 60 unrewarded tests (30 with the rough object, 30 with the smooth) to establish their untrained preference. For the next 3 days the animals were given two 8-trial training sessions per day. At each trial the smooth sphere was presented and the animal was rewarded if it took it, which it usually did on every occasion, after the first two or three sessions. If the animal failed to take the sphere, this was presented again, together with a piece of fish.

After 3 days (48 trials) of this training the animals were given a further 60 unrewarded tests with OR and 13R. This cycle of training and testing was repeated 4 times.

Fig. 6 shows the scores made in the tests. The animals all learned to take OR+, the effect of the training being similar in the animals with their median inferior frontal lobes removed completely, in the animals with 75-80% lesions and in the controls.

In contrast, there were large differences in the treatment of 13R by controls and by

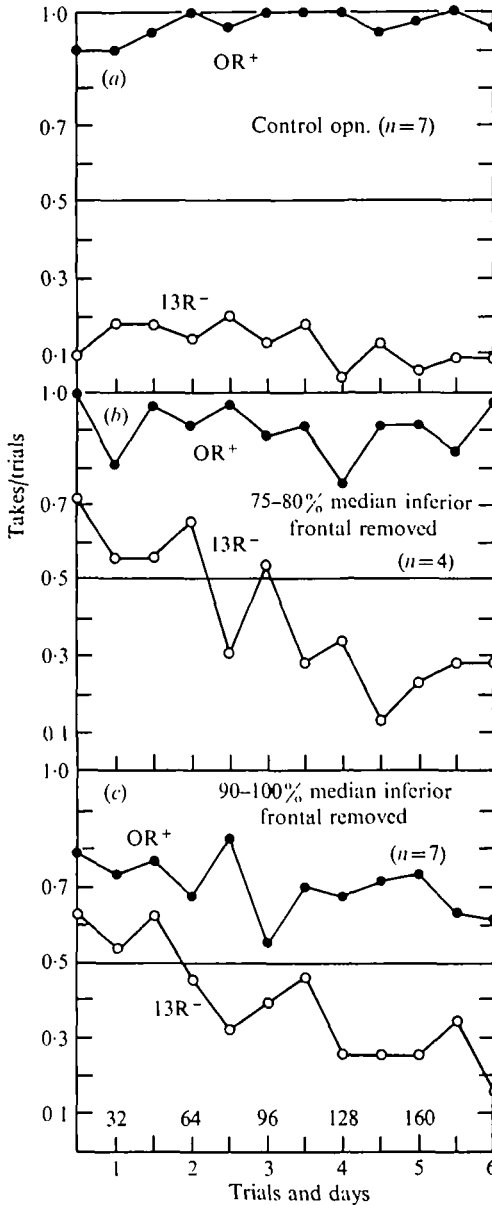


Fig. 7. Training to discriminate between OR+ and 13R- following positive training to take OR (see Fig. 6). (a) Shows the performance of seven control animals with a cut between median inferior frontal and superior buccal lobes, (b) the performance of four animals with 75-80%, and (c) the performance of seven with 90-100% of their median inferior frontal lobes removed.

experimental animals. Controls rapidly learned to leave this object alone, although it appeared only in the tests. The animals with 75–80% lesions to the median inferior frontal lobe showed the same trend as controls, but to a much smaller extent. The animals with 90–100% lesions took 13R *more* often as training and tests continued, though the proportionate increase was small (from 119 to 143 out of 210 such objects presented at any one test series) compared with the increase in the takes of OR, which doubled in the same period.

The animals were then trained to discriminate between the rough and the smooth sphere, with smooth positive. All of them discriminated successfully. The result with the operated animals was, however, significantly worse than that of the controls and was associated with a much higher level of positive responses towards the negative rough object (Fig. 7). The predilection for rough objects can be overlaid by smooth positive training, but is difficult to eliminate altogether. There is, however, no longer any room for doubt about the ability to learn in the OR<sup>+</sup>/13R<sup>-</sup> direction. Removal of the median inferior frontal does *not* prevent touch learning; the rough preference *can* be reversed and performance *does* improve progressively, though more slowly than normally, in the course of training with reward and punishment. Again, a small amount of the lobe (20–25%) appreciably assists the process.

#### (5) *Lateral transfer and the median inferior frontal lobe*

The poor discrimination of animals with the median inferior frontal lobe removed could be due to the elimination of channels through which one part of the touch-learning system can communicate with others. We know that intact animals learn more rapidly than split-brain animals even when the training is restricted to one side of the animal, and there is evidence from train-operate-test experiments that a record is laid down in both sides of the brain in these circumstances (Wells & Young, 1966). The bulk of the median inferior frontal lobe is made up of interweaving tracts of incoming fibres from the brachial nerves. The cells of the lobe presumably come under the influence of impulses from several arms and in turn pass such influence on to the subfrontal lobe. Removal of the median inferior frontal might eliminate cross-reference and produce an inferior performance because each side of the body (or each arm, since there is evidence that the record associated with each arm is to some degree separate – see Wells, 1959*b*) is then dependent upon its individually acquired experience.

To test this hypothesis the animals trained for the experiment shown in Fig. 7 had their smooth<sup>+</sup>/rough<sup>-</sup> training continued on the LHS only while the RHS was trained in the opposite (reversed) direction. The only difference in technique was that in order to limit further experience to one side, the training spheres were pulled away just before rather than just after they had been passed under the interbrachial web. Positive and negative left and right trials were arranged as follows:

- a.m. L+R+, L-R-, L+R+, L-R+, L+R-, L-R-, L+R+, L-R-;  
 p.m. L+R-, L-R+, L+R-, L-R-, L+R+, L-R+, L+R-, L-R+.

Thus there were 16 trials, eight on each side (4<sup>+</sup>, 4<sup>-</sup>) in each session. This treatment should lead to confusion if connexions remain between the two sides. If removal of the median inferior frontal lobe eliminates or impairs lateral transfer, one would expect animals so operated upon to learn to discriminate in different directions on the two sides more readily than controls.

In the event, surprisingly, it proved to be quite possible to train normal animals (with intact inferior frontals) to discriminate in opposite directions on the two sides of the body. All seven of the controls began by behaving perversely on the right (reversal to rough<sup>+</sup>/smooth<sup>-</sup>) side, and all of them showed at least elimination of this response

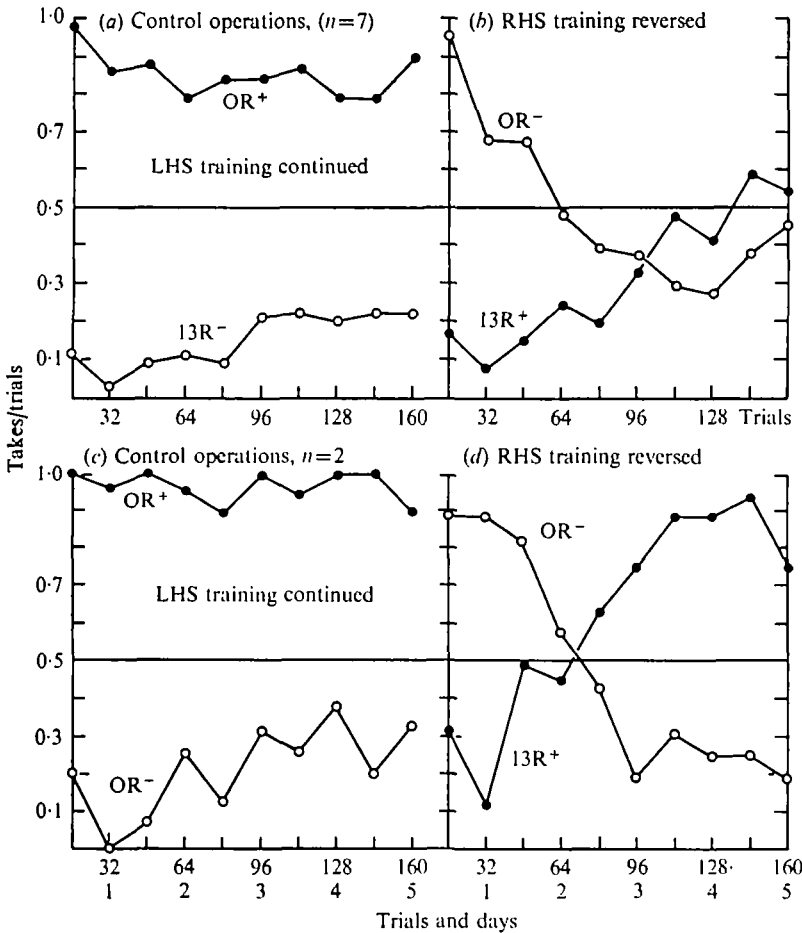


Fig. 8. Training the two sides of control animals in opposite directions. Plots on the LHS (a) and (c) show a continuation of the training (OR<sup>+</sup>/13R<sup>-</sup>) summarized in Fig. 7, now restricted to the arms on the LHS of the body. Plots (b), (d) show the results of reversed training (13R<sup>+</sup>/OR<sup>-</sup>) limited to the RHS of the body, carried out at the same time. The RHS begins by performing perversely, but reverses with at most a small influence on the performance of the LHS. (a) and (b) show the performance of all the animals ( $n = 7$ ). (c) and (d) show the performance of the two best individuals.

during the next 160 trials (Fig. 8a, b). The two 'best' animals (Fig. 8c, d) came to perform equally well on the two sides by the end of the experiment. In all the animals there were signs of a slight but progressive increase in the tendency for the non-reversal side to take the negative object and reject the positive. This shows that the two sides were not acting independently; what the reversal side was learning was affecting the performance of the side already trained.

Ten of the original 11 animals without median inferior frontal lobes were used in this phase of the experiment. Of these, the four animals with the smallest lesions (75-80%

of the median inferior frontal lobe removed) behaved substantially like controls. The LHS continued to discriminate in the direction  $OR^+/13R^-$ , the RHS (reversal to  $13R^+/OR^-$ ) came to perform equally well in the opposite direction after an initial period of perverse responses (Fig. 9*a, b*). As in controls the accuracy of discrimination by the trained LHS declined during reversal training of the RHS (controls, compare Figs. 7*a* and 8*a*, experimentals Figs. 7*b* and 9*a*).

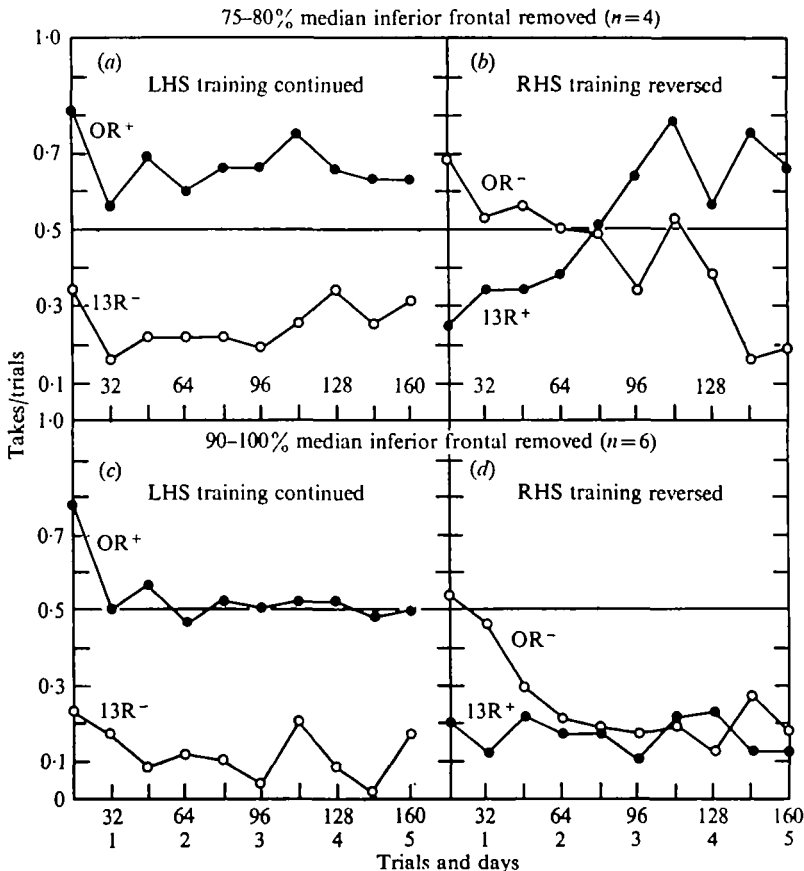


Fig. 9. Training the two sides of the same animals in opposite directions; animals with lesions to the median inferior frontal lobe. (a) and (b) show the performance of the LHS and RHS of four animals with 75-80% of their median inferior frontal lobes removed. (c) and (d) show the left and right sides of the six animals with the median inferior frontal removed completely.

The remaining six animals (90-100% lesions) continued to discriminate successfully, though with some reduction of positive takes, on the LHS (Fig. 9*c*). On the RHS responses to the smooth decreased, but positive responses to the rough did not show a corresponding increase (Fig. 9*d*). It should be noted that although the total number of takes of the LHS declined, discrimination remained as good as or better than before (compare Figs. 7*c* and 9*c*).

The experiments show that there is some lateral transfer in controls and in animals with 75-80% of their median inferior frontal lobes removed but very probably none in octopuses with 100% lesions. Also that these cannot readily learn a reversal.

(6) Removal of the vertical or median superior frontal lobes

Removal of the vertical and/or median superior frontal lobes affects touch learning; after these operations animals learned more slowly than usual (Wells & Wells, 1957; Wells, 1965). This finding was confirmed in the present series of experiments. In Fig. 10a and b the performance of eight animals, four trained on OR<sup>+</sup>/13R<sup>-</sup> and four on 13R<sup>+</sup>/OR<sup>-</sup>, is shown and may be compared with the performance of the dummy-operated controls summarized in Fig. 2. The animals with damage to the vertical

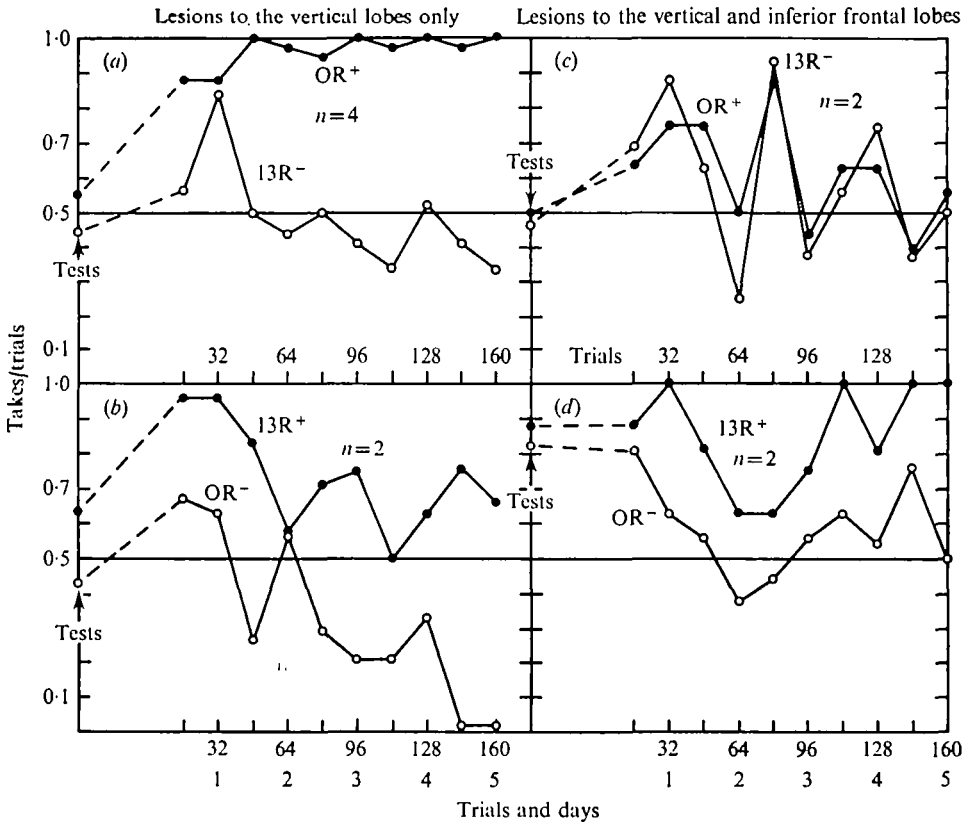


Fig. 10. Training of animals after removal of the vertical lobes. This was done without damage to the inferior frontal system in (a) and (b), but with damage to the median inferior frontal lobe in (c) and (d). These animals had an initial set of 60 training trials, given in a single session 36 h before the tests shown at the start of these experiments. There was a further break of 24 h before the resumption of training at the standard rate of 16 trials/session.

and/or superior frontal lobes learned to discriminate, but more slowly than the controls and to a lower level of accuracy. There was no obvious correlation between the amount or type of tissue left and the scores made. The animals trained with smooth positive learned better than the reverse; this operation may reduce the preference, but does not reverse it (Wells & Young, 1968). The errors made were largely in the direction of taking the negative object too often. With 13R<sup>+</sup> there were also more errors due to failure to take the positive than with controls.

In a further four animals (two on  $OR^+/13R^-$ , two on  $13R^+/OR^-$ ) the lesions extended into the inferior frontal system (Fig. 10*c, d*). These animals produced a much poorer set of scores and the two trained with the smooth object positive failed to discriminate altogether.

(7) *Removal of the basal lobes*

The anterior basal, posterior basal and dorsal basal lobes lie below the vertical and subvertical lobes, behind the inferior frontal system (Fig. 1). If they are removed, together (inevitably) with the vertical lobe, octopuses show an untrained preference for rough rather than smooth objects (Wells & Young, 1968). This does not, however, make them unable to learn when a smooth object is positive. In one animal with this lesion very effective discrimination was achieved (Fig. 11).

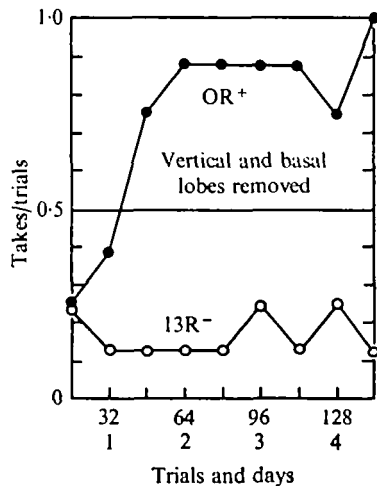


Fig. 11. Learning by an animal with removal of the whole supraoesophageal lobe behind the inferior frontal system, which was intact.

As with lesions affecting only the vertical and superior frontal lobes, any extension of the damaged area into the inferior frontal system produced a much lower capacity to discriminate. Fig. 12 compares the performance of animals with more and less damage to the median inferior frontal and/or the subfrontal lobes. In five of the animals (all trained  $OR^+/13R^-$ ) the cell layers at the back of the median and lateral inferior frontal lobes were damaged; the performance of these five is summarized in Fig. 12*a*. In four further animals the whole of the median inferior frontal lobe had been removed. When two of these were trained  $OR^+/13R^-$ ,  $13R$  was taken nearly twice as often as  $OR$  (Fig. 12*b*). The two remaining animals, trained with  $13R^+$ , showed some discrimination (Fig. 12*c*).

The result from the single animal with no basal lobes and an intact inferior frontal system shows that octopuses can learn to discriminate after removal of the basal lobes. The performance of the five animals with slight damage to the inferior frontal system shows that the untrained preference for rough can be overcome; these animals took the test spheres about equally often and although the scores made in their initial and final tests are not significantly different at the  $P = 0.05$  level ( $\chi^2 = 3.3$ ) there



was clearly some tendency for the ratio of takes of OR to 13R to increase as training proceeded. The remaining animals show effects of inferior frontal damage comparable with those already discussed for animals with their vertical lobes removed (Fig. 10c, d). On the basis of this small sample it would appear that removal of the basal lobes

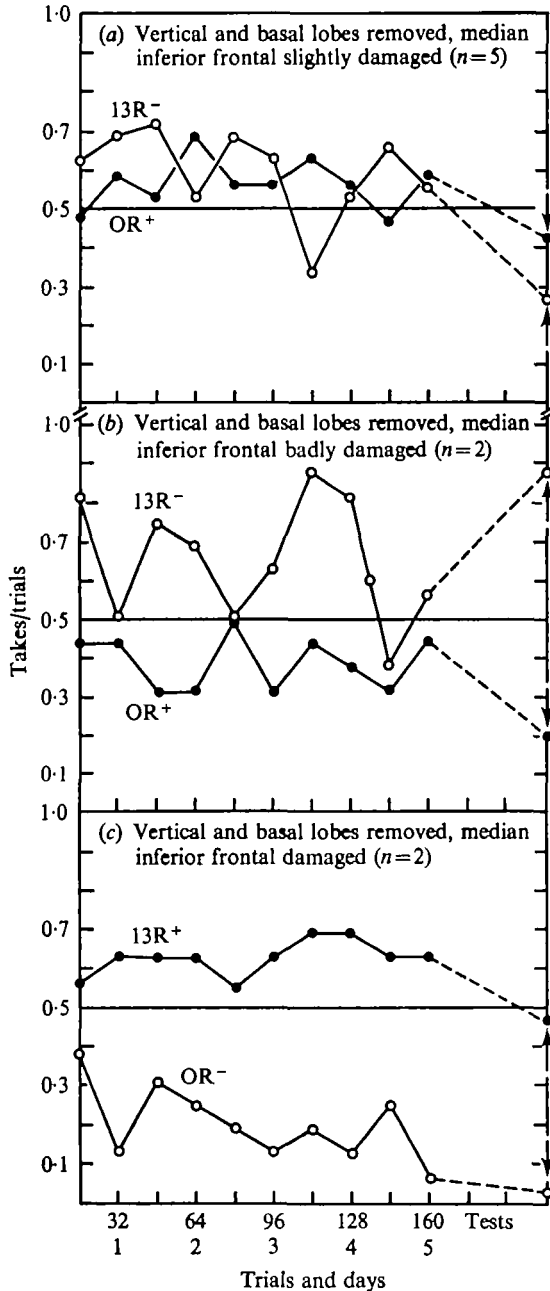


Fig. 12. Learning after removal of the vertical and basal lobes with various amounts of damage to the inferior frontal system. In (a) the damage was injury to the layers of cells over the surface of the back of the median and lateral inferior frontal lobes. In (b) and (c) the whole median inferior frontal and subfrontal lobes were badly damaged.

does not increase the defect caused by removal of the overlying vertical and subvertical lobes; what matters is the extent of any damage to the inferior frontal system.

The same conclusion was reached as a result of an earlier and more extensive series of experiments that have been summarized in Wells (1959*a*). However, those experiments were made before it was realized that removal of large parts from the brain has an effect on untrained preferences. Six out of the eight animals concerned were trained to discriminate with a rough cylinder as positive. Two animals were trained smooth<sup>+</sup>/rough<sup>-</sup>, however, and reached a standard of 85% or more correct responses (Wells, 1959*a*).

#### DISCUSSION

##### *Phenomena associated with lesions to the inferior frontal system*

###### (1) *Reversal of preference*

Blinded but otherwise unoperated animals generally show an untrained preference for smooth over rough objects. In 1600 unrewarded tests at which equal numbers of rough and smooth objects were presented, a sample group of 10 control animals took the smooth at 44% and the rough at 29% of the occasions on which they were presented (Wells & Young, 1968). This preference for smooth is reduced or reversed by operations involving removal of parts from the brain. It is reversed by splitting the supra-oesophageal brain without removal of tissue (Wells & Young, 1968, 1969) and, as the present series of experiments has shown, it is also reduced by comparatively minor cuts separating the superior buccal and median inferior frontal lobes (the 'control' operation, the effects of which are summarized in Figs. 2 and 3). The strongest swing towards a preference for rough is produced by lesions involving the median inferior frontal lobe.

It is possible that the swing towards rough preference arises from operational trauma. The fact that operations having little or no effect on the capacity to learn to discriminate (basal lobes removal, control cuts) produce a swing to rough would tend to support this interpretation. It may well be that rough objects are inherently more stimulating than smooth and that the signals from the latter are lost in nervous chatter in animals with brain damage. If this is the correct explanation there might be a progressive reversion to the unoperated condition with time. There are as yet no data on this; one would need to keep animals for a period of weeks without training after operation and then test them, and this has not been done.

An alternative type of explanation is that the change in preference brought about by the operations is due to interference with some specific function of the touch-learning system. This possibility is considered below.

###### (2) *Failure of lateral transfer*

A surprising finding from the experiments described above was that it is possible to train octopuses to discriminate in opposite directions with the arms on the two sides of the body. In controls, which learned to do this well, there was, however, clearly some interference between the two sides, since the performance of the non-reversed LHS was more erratic after the introduction of reversed training on the RHS; compare figs. 7 and 8. This is in keeping with what we already know about lateral

transfer in *Octopus*; the untrained side of a normal animal will discriminate as reliably as the trained side (Wells, 1959*b*; Wells & Young, 1965).

We also know that octopuses trained on one side after removal of the median inferior frontal lobe fail to discriminate when tested on the untrained side (Wells & Young, 1969). From this result one would expect it to be easier than usual to train octopuses to discriminate in different directions on the two sides after inferior frontal removal.

In the event animals with 75–80% of the median inferior frontal removed performed very much as controls; the RHS of these animals reversed successfully and the LHS, although continuing to discriminate in the same direction as before, was adversely affected (Figs. 7*b*, 9*a*, *b*). The performance of the six animals with 90–100% lesions was more interesting. The reversal side of these animals failed to learn; there was a decline in the proportion of takes of OR that was not accompanied by a corresponding rise in the proportion of takes of 13R (Fig. 9*d*). This very considerable change had little or no effect upon the performance of the LHS of the same animals, which continued to discriminate (in, note, the 'difficult' direction OR + / 13R –) as well as before. There was a slight drop in the overall proportion of takes by the LHS, continuing a trend already shown before the start of reversal training (Figs. 7*c*, 9*c*). It would seem that there is little or no communication between left and right halves of the tactile learning system if the inferior frontal lobe is removed.

### (3) *Inaccuracy in discrimination training*

After removal of the median inferior frontal lobe the performance of octopuses in discrimination experiments is very much worse than that of controls. It is particularly poor when the animals are trained smooth + / rough –. The failure is not, however, attributable to rough preference; the increased number of errors made includes a substantial proportion of failures to take rough when this is positive. One must conclude that the median inferior frontal lobe is involved in both positive and negative learning.

It would also seem to be characteristic of these animals that their rate of response drops unusually rapidly when discrimination is unsuccessful. They begin to err by rejection of positives rather than by excess takes of the negative object (Figs. 5*b*, *d*, 9*d* – an exception is shown in 4*c* where, however, the rate of training was half that adopted elsewhere). In this they differ, for example, from animals with their vertical lobes removed, where a poor performance is characteristically associated with a high rate of response and a greatly increased proportion of negative errors. Removal of the median inferior frontal seems to produce a condition where food has a relatively slight effect on the overall response rate compared with shocks.

### (4) *The function of the median inferior frontal lobe*

Experiments made some years ago had indicated that octopuses can learn to discriminate by touch in the absence of the median inferior frontal. Provided that the posterior buccal lobe and a few of the small cells of the ventral subfrontal region were present on the side concerned, animals appeared to be able to learn (Wells, 1959*a*). The matter appeared to be settled until the discovery of preference changes following operations (Wells & Young, 1968) which threw into doubt findings based on learning

in the rough positive/smooth negative direction. The present series of experiments shows that the early conclusions were, however, essentially correct. It is now certain that octopuses can learn tactile discriminations without their median inferior frontal lobes.

If this is the case, how can one specify the function of this region? When it is removed, the amount of experience that is needed to produce a given change in discriminatory behaviour is increased; learning is less efficient. This could be accounted for in terms of the distributive function of the median inferior frontal. When it is removed lateral transfer fails and split-brain experiments show that two sides of a brain learn more efficiently than one (Wells & Young, 1966). Failure of distribution of information cannot, however, explain the swing to rough preference.

In this context it is useful to compare the effects of inferior frontal removal with the effects on visual memory of removing the vertical lobe. In both cases there is a reduction of accuracy of discrimination immediately after operation, but some capacity for further storage survives. The errors made are liable to be in either direction, by failure to take the positive object or figure as well as by taking or attacking the negative (Young, 1960). After removal of either lobe there is a reversal of some preferences (Young, 1968). There is, moreover, a parallel in the matter of lateral transfer; after removal of the median inferior frontal the two sides of the tactile learning system appear to be disconnected; after removal of the vertical lobe interocular transfer of the effect of visual experience is prevented (Muntz, 1961).

The inferior frontal-subfrontal and the superior frontal-vertical lobe systems are very much alike in structure; in both there is a region containing several millions of small cells, many of them amacrines, fed from a region of interweaving tracts (the frontal lobe of each set). It seems probable that the two systems operate in a similar manner in adjusting the level of responses to objects touched (by the inferior frontal system) or seen (by the vertical lobe system). In each case the system seems to act as a whole so that interference anywhere along the circuit produces essentially similar results. Removal of the median superior frontal has very much the same effect on visual or tactile learning as removal of the vertical lobe (Bradley, Wells & Young, 1972; Wells, 1965; but see Young, 1964). The median inferior frontal is the structural analogue of the median superior frontal, not the vertical lobe, yet removal of the two has fully comparable consequences on learning in their respective modalities. In this situation the phenomenon of untrained reversal of preference is particularly interesting. It suggests that one function of the intact systems must be to impose a bias so as to compensate for variations in the intensity of stimuli. After removal of the vertical lobe octopuses 'prefer' white to black figures seen in their tanks and are difficult to train in the Black+ direction (Young, 1968). After removal of the inferior frontal, blinded octopuses prefer rough to smooth objects. In the wild state either stimulus is likely to yield food or to prove it to be inedible, and it is important that the responses of the animal shall be based on experience rather than on the degree to which objects seen or touched excite the primary receptors. It is likely that white shapes and rough objects are more stimulating to the receptors than black or grey shapes and smooth objects. It is important that the animals do not pay undue attention to these classes of stimuli as a result.

The median inferior frontal/subfrontal complex thus emerges as a system that com-

compensates for variations in sensory excitation so that the animal pays attention to and learns to recognize all physically different tactile stimuli about equally readily. When this part is removed, two things go wrong; the compensating system fails, and there is a reduction in storage capacity because the distribution of input through the tactile learning system is impaired. The inferior frontal may itself be a memory store, but there is no need to suppose this, and the subfrontal lobe with its millions of small cells (and which has alone been shown to be vital for touch learning) would seem to be the more likely site for the changes ultimately responsible for the regulation of learned tactile behaviour.

#### SUMMARY

1. After removal of the median inferior frontal lobe, blinded octopuses already trained to discriminate by touch between rough and smooth spheres continued to do so, but at a lower level of accuracy.

2. Animals without pre-training showed a strong tendency to take rough objects after this operation and learned to discriminate well only when trained to take rough and reject smooth.

3. When animals with intact inferior frontal lobes were given food in the presence of a smooth sphere they learned to take the smooth; in subsequent extinction tests they continued to take the smooth but soon ceased to take rough objects.

4. Animals without median inferior frontal lobes also increased their tendency to take a smooth object associated with food. But they did not behave in the same way as controls in extinction tests; they continued to take the rough objects even if they had not been rewarded for doing so.

5. Operated animals thoroughly pre-trained to take smooth objects showed some capacity to discriminate these from rough objects in subsequent successive training with food and shock, though continuing to take the rough far more than control animals.

6. Animals without brain damage could be taught to take smooth rather than rough objects on one side, and continued to do so when trained in the reverse direction on the other. There was, however, some lateral interference; performance on the unreversed side was worse after the introduction of reversed training.

7. Animals with lesions to the median inferior frontal lobe failed to learn on the reversal (rough<sup>+</sup>/smooth<sup>-</sup>) side, responses to both objects declining progressively as training continued. At the same time as this discrimination by the non-reversal (smooth<sup>+</sup>/rough<sup>-</sup>) side continued to develop. There was thus no evidence of lateral transfer in these animals.

8. It was confirmed that tactile learning is still possible after removal of the vertical and basal lobes, but with some decrease in the normal preference for smooth objects.

9. The median inferior frontal is thus not essential for tactile learning, but greatly facilitates it, making some contribution to the acquisition of both positive and negative responses, perhaps by spreading information through both sides of the touch-learning system. The effect of its removal in touch learning can be compared with the effect of vertical lobe removal on visual learning. It is concluded that one function of these parts is to compensate for the intensity of stimulation so that animals do not pay undue attention to brightly reflective or texturally rough objects.

Our thanks are due to the Director and Staff of the Stazione Zoologica at Naples for continued assistance. The work was partly supported by grants from the Science Research Council of Great Britain and the United States Air Force. We are grateful to Miss E. Bradley and Miss Stephanie Buckley for help in preparation of the manuscript and to Miss P. Stephens for skilled histological assistance.

## REFERENCES

- BRADLEY, E., WELLS, M. J. & YOUNG, J. Z. (1972). Comparison of visual and tactile learning in *Octopus* after lesions to the two memory systems. (In preparation.)
- MUNTZ, W. R. A. (1961). The function of the vertical lobe of *Octopus* in interocular transfer. *J. comp. Physiol. Psychol.* **54**, 186-91.
- WELLS, M. J. (1959a). A touch-learning centre in *Octopus*. *J. exp. Biol.* **36**, 590-612.
- WELLS, M. J. (1959b). Functional evidence for neurone fields representing the individual arms within the central nervous system of *Octopus*. *J. exp. Biol.* **36**, 501-11.
- WELLS, M. J. (1965). The vertical lobe and touch learning in the *Octopus*. *J. exp. Biol.* **42**, 233-55.
- WELLS, M. J. & WELLS, J. (1957). The effect of lesions to the vertical and optic lobes on tactile discrimination in *Octopus*. *J. exp. Biol.* **34**, 378-93.
- WELLS, M. J. & YOUNG, J. Z. (1965). Split-brain preparations and touch learning in the *Octopus*. *J. exp. Biol.* **43**, 565-79.
- WELLS, M. J. & YOUNG, J. Z. (1966). Lateral interaction and transfer in the tactile memory of the *Octopus*. *J. exp. Biol.* **45**, 383-400.
- WELLS, M. J. & YOUNG, J. Z. (1968). Changes in textural preferences in *Octopus* after lesions. *J. exp. Biol.* **49**, 410-12.
- WELLS, M. J. & YOUNG, J. Z. (1969). The effect of splitting part of the brain or removal of the median inferior frontal lobe on touch learning in *Octopus*. *J. exp. Biol.* **50**, 515-26.
- WELLS, M. J. & YOUNG, J. Z. (1970). Single-session learning by octopuses. *J. exp. Biol.* **53**, 779-88.
- YOUNG, J. Z. (1960). The failures of discrimination learning following the removal of the vertical lobes in *Octopus*. *Proc. R. Soc. Lond. B* **153**, 18-46.
- YOUNG, J. Z. (1964). Paired centres for the control of attack by *Octopus*. *Proc. R. Soc. Lond. B* **159**, 565-88.
- YOUNG, J. Z. (1968). Reversal of a visual preference in *Octopus* after removal of the vertical lobe. *J. exp. Biol.* **49**, 413-19.
- YOUNG, J. Z. 1971. *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford: Clarendon Press.