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Amygdalectomy and Disconnection in Visual Learning for Auditory Secondary Reinforcement by Monkeys

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Nine monkeys in 3 groups took part in an experiment on visual discrimination learning set in an automatic apparatus. Each new visual discrimination problem was solved using auditory secondary reinforcers. Primary food reinforcement was delivered only after a new problem had been solved to a criterion, and the problem was then replaced by a new one; thus, within-problem learning relied purely on secondary and not on primary reinforcement, but the secondary reinforcers were associated with primary reinforcement. Bilateral amygdalectomy severely retarded within-problem learning. Disconnection of the amygdala from auditory input, by crossed unilateral lesions of amygdala and of auditory cortex combined with forebrain commissurotomy, had a similar effect to that of bilateral amygdalectomy. Disconnection of the amygdala from visual association cortex left learning unimpaired. Thus, for normal performance in this task, interaction of the amygdala with the sensory modality of the secondary reinforcer was essential, but interaction of the amygdala with the sensory modality of the discriminative stimuli was not necessary. It was concluded that the amygdala is involved in associating stimuli with the primary reinforcing attributes of food reward, and not with its other attributes.

There is good evidence that the amygdala is involved in some aspect of monkeys' visual discrimination learning for food reward. Schwartzbaum and Poulos (1965) trained their monkeys in a series of object discriminations ("object discrimination learning set") and showed, in 2 experiments with slight variations of procedure, a substantial impairment in amygdalectomized animals. The same animals were also impaired in visual reversal learning (Schwartzbaum and Poulos, 1965, Experiment 2). The impairment in reversal learning has been replicated in a number of studies, and these experiments on reversal learning have also shown impairments in the first, nonreversal, visual discrimination problem (Barrett, 1969; Mahut, 1971; Jones and Mishkin, 1972; Aggleton and Passingham, 1981). A modified visual learning-set procedure was adopted by Spiegler and Mishkin (1981), and they found that amygdalectomy produced an impairment as severe as that observed by Schwartzbaum and Poulos (1965). Learning scores in the acquisition of single visual discrimination problems have also sometimes shown mild or severe impairments in amygdalectomized animals (Figure 1 in Douglas and Pribram, 1966; Schwartzbaum and Pribram, 1960; Mahut, 1971). Similar impairments in visual discrimination learning have been reported to follow bilateral amygdalectomy combined with hippocampectomy (Correll and Scoville, 1965, 1970; Malamut et al., 1984; Zola-Morgan and Squire, 1985).

In some experiments, a small number of discrimination problems have been learned without apparent impairment by monkeys with amygdalectomy (Schwartzbaum, 1965) or with amygdalectomy plus hippocampectomy (Orbach et al., 1960). Discussing Orbach et al.'s (1960) result, Correll and Scoville (1970) suggested that their own procedure, in which several problems were learned concurrently, might be more sensitive to lesion effects than the earlier group's procedure of single problem learning. The most important determinant of sensitivity, however, may simply be the total number of problems presented, whether serially or concurrently; acquisition of a single discrimination without impairment by a lesioned group might arise by chance, since variation of learning scores between problems within monkeys can be very large (E. A. Gaffan et al., 1986). A further complicating factor, however, in relation to the number of discrimination problems, is the possibility that, at least in some experiments, the magnitude of the impairment may decrease with practice in new discrimination problems. This is suggested in the results of Malamut et al. (1984); and Douglas et al. (1969) observed unimpaired learning of several pattern discriminations by amygdalectomized animals that were described as highly sophisticated in discrimination learning. But, as the results of Schwartzbaum and Poulos' experiments (1965) show, practice does not always abolish the deficit. So although there is good evidence for the visual learning impairment, there are some unexplained inconsistencies in the severity of the impairments in the existing reports. The size of the lesion, and the method of producing it, certainly vary from experiment to experiment; but those variations cannot readily explain the variations in severity of impairment, since, for example, the amygdala ablations in Schwartzbaum and Poulos' (1965) experiments, illustrated by Schwartzbaum (1964), were quite small. In what follows, we argue that a more careful and detailed psychological analysis of visual discrimination learning for food reward may clarify the amygdala's specific contribution to it, and to other tasks as well.

In a learning task in the standard Wisconsin General Test Apparatus, food reward for a correct choice is delivered in the following way: a piece of food is placed in a well under the correct visual stimulus, the monkey displaces the stimulus, sees the piece of food, and takes it. This complex event possesses 3 broad types of attribute (Gaffan, 1979, pp. 442–443). First, there

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is the intrinsic incentive value of the reward, presumably some function of its taste. Second, there are the accidental properties of the reward: sensory features that are of no intrinsic value, such as its visual appearance. Third, since this is a food reward that is familiar to the animal, there are the autonomic and motor responses that its accidental features elicit because they are associated in memory with its intrinsic incentive value. All 3 types of attribute may be associated with the displaced visual stimulus in the discrimination learning task. The ultimate motivation for performance of the task is the intrinsic incentive value of the reward, but this does not imply that the only way for the animal to solve the problem is by relying on the associations of the displaced visual stimulus with that intrinsic value. Instead, the animal may learn to obtain the intrinsic value of the reward by displacing the stimulus that is associated in memory with the second and third types of attribute. Monkeys are adept at learning such memory-dependent performance rules (Gaffan, 1985), and they can readily learn visual–visual associations between a stimulus object and the visual properties of the contents of the well under the object (Gaffan and Bolton, 1983). Experiments by Riopelle et al. (1954) and by Riopelle and Francisco (1955) have been cited (Medin, 1977, p. 39; Macphail, 1982, pp. 207–208) as evidence that sophisticated monkeys learn as much from a marble as from a food reward on the first trial of a new visual discrimination. The experiments cited do not quite show this, since marbles had a different effect from food rewards, and the tasks on the second trial were more akin to delayed matching and nonmatching than to discrimination learning. But experiments designed for the purpose can show that monkeys do possess the ability in question, to learn to get food reward by selecting visual stimuli that are associated in memory with some event that has no intrinsic incentive value (Experiment 4, Gaffan et al., 1984; Gaffan, 1985).

There is a similar associative multiplicity in visual discrimination learning for food reward in an automated apparatus. Here, choice of the correct stimulus is followed by some intrinsically neutral accidental properties of the food reward event, such as the noise of a food dispenser operating; such events, comparable to the sight of the peanut in the Wisconsin General Test Apparatus, evoke learned responses because they signal the imminence of an event with intrinsic incentive value. In this type of apparatus, therefore, a new discrimination problem may also be solved by associating the visual stimuli with any of the 3 types of attribute of the food reward event. The associability of the visual stimuli with each of these 3 types of attribute will vary with the details of the experimental arrangement. In particular we assume, from the wide range of evidence to this effect presented by Rescorla (1980, 1985), that associations of the visual discriminative stimuli with the intrinsically neutral sensory properties of the reward event will be strong when (as in the Wisconsin General Test Apparatus) those sensory properties are in the same modality as the discriminative stimulus and are spatially contiguous with it, but will be weak when (as in the experiment described below) they are spatially discontiguous from the discriminative stimuli and are not in the same modality.

The aim of the present experiment was to isolate from each other, so far as possible, the associative learning about each of 2 of the types of attribute of food reward: its intrinsic incentive value, and the responses that its accidental attributes evoke by virtue of their association with this value. The third type of associative learning, association of the discriminative stimuli with the accidental attributes themselves, was minimized by putting the accidental attributes in a different sensory modality from that of the discriminative stimuli, as well as in a separate spatial location. In the present task, visual discrimination problems were solved without the visual stimuli becoming associated with the intrinsic incentive value at all. Instead, the visual stimuli in each new problem were, in the course of solution, associated with an auditory secondary reinforcer (an accidental sensory attribute of the reward event) that was itself associated with the intrinsic incentive value. For some animals in the experiment, white noise was associated with food and became a secondary reinforcer, and a train of clicks was associated with no food and became a secondary nonreinforcer; for the remaining animals, the roles of these 2 auditory stimuli were the opposite, clicks being the secondary reinforcer and white noise the secondary nonreinforcer. The effects of bilateral amygdalectomy in this task (see below) showed that the amygdala is important for its normal performance; disconnection of the amygdala from either the visual or the auditory modality shows whether the amygdala is important for associating stimuli with the intrinsic incentive value of food, or with the responses evoked by the accidental properties of a food reward.

A number of experiments have shown that the effects of bilateral amygdalectomy on visually controlled behavior and visual learning for food reward can also be produced by disconnection of the amygdala from the visual modality (Downer, 1961; Barrett, 1969; Horel and Keating, 1969, 1972; Doty et al., 1973). In the present experiment, we disconnected the amygdala from visual association cortex, in one group of monkeys, by crossed unilateral lesions of the amygdala and of that cortex. We know that bilateral lesions of visual association cortex would produce a severe impairment in the present task, since, in previous experiments, we showed that bilateral ablation of the inferotemporal area, a lesion within the area of the present ablation of visual association cortex, produced a severe and permanent deficit of simultaneous visual discrimination learning with the present stimulus materials and response requirements (D. Gaffan et al., 1986; E. A. Gaffan et al., 1986). Furthermore, in unpublished experiments we have confirmed that crossed unilateral lesions of amygdala and of visual association cortex impair visual discrimination learning for immediate food reward in the present apparatus. In a second group of monkeys, we made crossed unilateral lesions of amygdala and of auditory cortex. The third surgical group, as mentioned, was one with bilateral amygdalectomy. All groups were trained in the task preoperatively.

Following crossed unilateral lesions, the disconnection groups were subjected to forebrain commissurotomy in order to disconnect the hemisphere with the intact amygdala from any heterotopic projections from the opposite intact sensory cortex (Pandya et al., 1969). Because, in sectioning the anterior commissure, it is not always possible to avoid slightly damaging the fornix unilaterally, and because we expected the auditory disconnection to produce a greater deficit than the visual disconnection did, we purposely sectioned the fornix unilaterally in the visual disconnection, but not in the auditory disconnection group; thus any greater deficit in the auditory than in the visual group cannot be explained by the degree of damage to the fornix.

Materials and Methods

Subjects. We used 9 male cynomolgus monkeys (*Macaca fascicularis*). All were experimentally sophisticated; they had been trained in visual discrimination learning for immediate food reward in the apparatus described below. For some animals, white noise was the secondary reinforcer and clicks were the secondary nonreinforcer, while for others the roles of the 2 noises were the opposite; the values of the 2 noises remained identical throughout any individual animal's training and pretraining, as described below. At the time of first surgery, the animals weighed, on average, 4.2 kg.

Surgery. Upon completing preoperative training (see below), the animals were assigned to 3 operative groups. For all groups, general surgical and anesthetic methods were as previously described (Gaffan et al., 1984). The animals were housed singly following surgery. Apart from behavioral changes (see below), postoperative recovery was uneventful in all cases. The surgical procedures described below are labeled with abbreviations. Note that 2 of the 3 surgical groups were subjected to a series of operations, with behavioral testing after each stage.

The *bilateral amygdalectomy group* was subjected to a single surgical procedure, as follows ("BA"). A craniotomy was opened over each frontal lobe and was extended with rongeurs anteriorly to the brow, medially within 2–3 mm of the midline, posteriorly to the level of the arcuate sulcus, and laterally and inferiorly into the lateral wall of the temporal fossa to the level of the superior temporal sulcus. The dura was cut along the superior, posterior, and inferior margins of the craniotomy, and turned back in a flap over the orbit and brow. The frontal lobe was gently retracted with a brain spoon to expose the medial surface of the anterior part of the temporal lobe. Pia mater over the amygdala on the medial surface was cauterized with a metal sucker that was insulated except at the tip. The amygdala was ablated by aspiration with the same sucker. The lateral ventricle and the anterior surface of the hippocampus were visible posterior limits of the lesion. Laterally, gray matter of the amygdala was removed until white matter of the temporal stalk and uncinate fascicle appeared. Inferiorly and anteriorly the intention was to leave perirhinal and polar cortex intact, as far as possible. The ablation was performed in both hemispheres in one surgery. The dura was sewn and the wound was closed in layers.

The *visual disconnection group* was subjected first to crossed unilateral ablations of visual association cortex and of amygdala, as follows ("XVA"). An amygdalectomy was carried out just as described above, but in one hemisphere only. For some animals, this was the right hemisphere and for others the left (see Histology, below); the amygdalectomy was in the hemisphere contralateral to the preferred hand of each animal. In the opposite hemisphere, visual association cortex was ablated as follows. Part of the ablation was an inferotemporal removal, as previously described (D. Gaffan et al., 1986), involving the inferior bank of the superior temporal sulcus, the lateral bank of the occipitotemporal sulcus, and all the cortex between those 2 limits; this ablation was continued anteriorly beyond the tip of the superior temporal sulcus. Posteriorly, however, the ablation was extended beyond the inferotemporal area into the inferior part of prestriate cortex. The ablation was carried into the anterior bank of the lunate sulcus posteriorly, and was extended to the level of the posterior tip of the lateral sulcus superiorly, although the ablation did not include the lateral sulcus, being bounded still by the inferior bank of the superior temporal sulcus. Inferiorly, the lesion was extended, as in its anterior part, to the lateral bank of the occipitotemporal sulcus. Both banks of the ascending tip of the inferior occipital sulcus were included in the ablation.

The animals in the visual disconnection group were subjected to 2 further surgeries to transect the forebrain commissures in 2 stages. In the first, the rostrum, genu, and anterior body of the corpus callosum were sectioned. In the second, the anterior commissure and the splenium and posterior body of the corpus callosum we sectioned.

For the first stage of forebrain commissurotomy ("FC1"), a bone flap was opened over the midline and the dura was cut in a flap over the hemisphere opposite to the existing amygdalectomy. Veins draining into the superior sagittal sinus were cauterized and cut, and the hemisphere was gently retracted with a brain spoon. The anterior body of the corpus callosum and the rostrum and genu were sectioned with a glass sucker. This callosal section extended posteriorly to the level of the descending columns of the fornix.

For the final operation ("FC2") on the visual disconnection group, a similar bone flap was opened again, but it was posterior to the first flap and over the opposite hemisphere, that is, the hemisphere of the amygdalectomy. This hemisphere was retracted in the same fashion as the other had been. The splenium of the corpus callosum was sectioned with a glass sucker and the section was carried forward to meet the posterior limit of the previous corpus callosum section, thus sectioning the corpus callosum completely. The interventricular foramen was then entered with a narrow brain spoon and the anterior commissure (which was shrunken in appearance, owing to the previous ablation in inferotemporal cortex) was sectioned in the midline with cautery applied by a metal sucker insulated except at the tip. In addition, the fornix was sectioned unilaterally in the same hemisphere as the amygdalectomy. The unilateral fornix transection was carried out at a posterior level, where the fimbria-fornix ascends in the lateral ventricle.

The *auditory disconnection group* was first subjected to crossed unilateral ablations of the amygdala and of the superior temporal gyrus ("XAA"). The unilateral amygdalectomy was carried out as described above. As in the visual group, the amygdalectomy was in the hemisphere contralateral to an animal's preferred hand. To ablate the superior temporal gyrus, the general method was similar to that for inferior temporal ablation, involving a craniotomy with rongeurs, a dural flap, pial cauterization, subpial aspiration, and subsequent closing of the wound in layers; it was not necessary to remove the zygoma. The gray matter of the gyrus was ablated and the white matter was left intact. The ablation extended from the upper bank of the superior temporal sulcus inferiorly to the temporal plane superiorly. The whole of the temporal plane, including the lateral bank of the circular sulcus, was included in the ablation. The posterior limit was the tip of the lateral sulcus, and the anterior limit was the tip of the superior temporal sulcus.

Finally, the animals in the auditory disconnection group were subjected to forebrain commissurotomy ("FC") as follows [only 2 of the animals were operated on, since the third (No. 22891) showed such a severe impairment following XAA alone (see Results) that the impairment could not have been exacerbated by commissurotomy]: The corpus callosum and the anterior commissure were sectioned in one surgery, the methods being similar to those already described. The hemisphere contralateral to the amygdalectomy was exposed for the commissurotomy. The fornix was left intact, so far as possible, in this group.

Histology. Each animal was given a lethal dose of anesthetic and then perfused through the heart with saline, followed by formol–saline solution. The brains were blocked in the coronal stereotaxic plane posterior to the lunate sulcus and were then removed from the head, photographed, and allowed to sink in a sucrose–formalin solution. The brains were cut in 50 μm sections on a freezing microtome. Every fifth section was retained and stained with cresyl violet, and extra sections were retained from the vicinity of the anterior commissure.

Figure 1 shows stained sections from one typical brain. (This animal had the best behavioral performance in the visual-amygdala disconnection group.) The large ablations in the present experiment caused considerable distortion of the remaining intact tissue. In the hemisphere with amygdalectomy in the brain illustrated, the lateral parts of the temporal lobe have moved anteriorly and medially. The anterior part of the intact superior temporal sulcus is visible at an unusually anterior level in this hemisphere (top left, Fig. 1). A level of the hippocampal system that would normally be posterior to the amygdala has moved superiorly and anteriorly into the space left by the amygdala ablation (bottom right, Fig. 1). Conversely, in the hemisphere with ablation of visual association cortex, the intact cortex medial to the ablated anterior middle temporal sulcus is visible in an unusually lateral position (bottom left and right, Fig. 1). To determine the extent of the ablation in such material, each brain was examined microscopically in order to identify the remaining intact tissue. The amygdalectomy varied in detail from case to case, but there was no systematic difference between the amygdalectomies in the 3 surgical groups. The extent of the ablation is shown for each animal in Figure 2, in which the tissue that was ablated is indicated on drawings of a normal brain. Damage to the hippocampus, as illustrated in Nos. 308, 22891, and 22842, was restricted to the most anterior part (1–2 mm) of the hippocampus.

For the ablations of auditory and visual cortex, the extent of the ablated areas is drawn on the surface of a normal brain in Figure 3. Within each group, the 3 animals were very similar to one another. The ablation at the more posterior levels extended in all cases into the depths of the lateral or superior temporal sulcus, as intended, and as illustrated for the more anterior levels in Figure 2.

In the 5 brains with forebrain commissurotomy, section of the corpus callosum and anterior commissure was complete in all cases. The fornix was transected unilaterally, as intended, in the 3 animals in the visual disconnection group (see above). The fornix was not sectioned in the 2 animals with forebrain commissurotomy in the auditory disconnection group (see above), but the fornix had sustained some damage during the corpus callosum section.

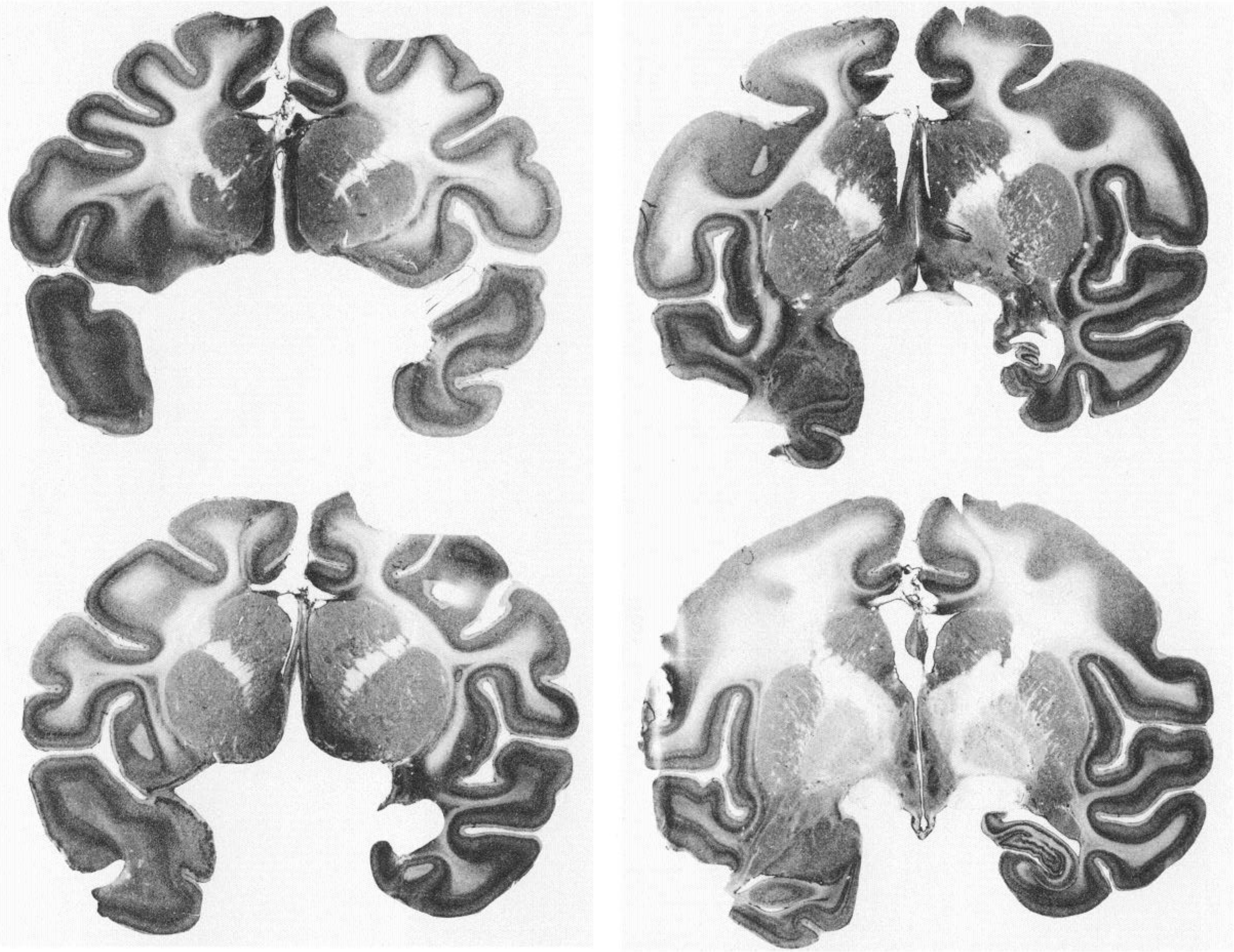

Figure 1. Four sections, 2.5 mm apart, from the brain of monkey No. 308. From anterior to posterior, the order of the sections is: top left, bottom left, top right, bottom right. See the text for a discussion of the temporal lobe ablations. The forebrain commissures have been sectioned. In the fornix, which has been sectioned unilaterally, degenerative changes can be seen in the right half at this level (*bottom right*). On the superior surface of the right hemisphere, in the *top and bottom right sections,* there is a cut, made postmortem, to mark one hemisphere and thus prevent the hemispheres from being inadvertently reversed during histological processing. Also on the superior surface of this hemisphere, in the *top and bottom left sections,* there is damage, produced postmortem in removing the brain from the skull, in the region of the unsewn dural flap for commissurotomy where the pial surface became attached to the dura and skull.

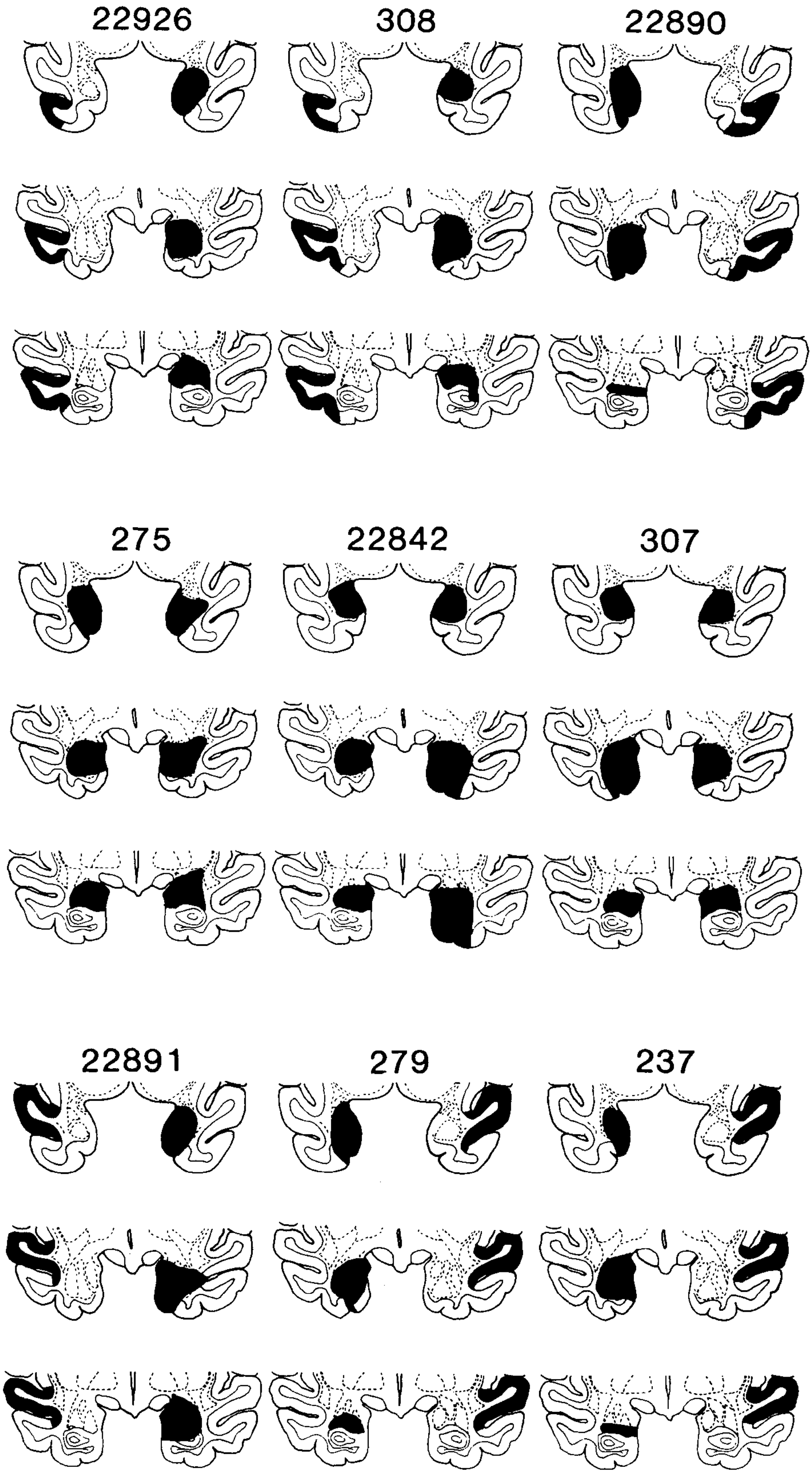

Figure 2. The extent of the lesion in the anterior temporal lobe, drawn for 3 levels (2.5 mm apart) of each animal of the visual–amygdala disconnection group (*top*), the bilateral amygdalectomy group (*middle*), and the auditory–amygdala disconnection group (*bottom*). The *number above each column* of 3 sections identifies the individual animal within the group.

Apparatus. The same computer-controlled apparatus was used as was previously described in detail (Gaffan et al., 1984). In brief, the monkey touched a large, immobile glass screen to choose between colored visual stimuli that were displayed on a television monitor immediately behind the screen. The 2 visual stimuli were displayed on the left and on the right, 180 mm from each other. The locus of the animal's response in choosing a stimulus was directly at the center of that stimulus; the response was detected by infrared beams traveling along the surface of the glass. Food rewards were dispensed to a hopper that was centrally placed under the stimulus display. Each reward consisted of 2 pieces of food. The pieces were either a peanut or a sugar-coated puffed rice grain, and both were delivered in roughly equal numbers in an unsystematic order. Visual stimuli were created by an algorithm described previously (Gaffan et al., 1984), which generated a very large set of different stimuli, each consisting of 2 colored shapes superimposed on each other: for example, a pair of discriminative stimuli for one particular discrimination "problem" (as defined below) might consist of a small brown square-root sign superimposed on a large white upper-case "P" for the positive stimulus, and a small pink lower-case "q" superimposed on a large blue numeral "7" for the negative stimulus of the pair. The stimuli were 40 mm in height and were viewed by the monkey at arm's length, since the apparatus was outside the cage that held the animal during training, and the animal had to reach out through the horizontal bars of the cage to operate the apparatus. The auditory stimuli were played through a loudspeaker that was above and behind the stimulus display. Two noises were used: broadband white noise and a 6 Hz click train, each lasting 1.5 sec. The loudness of the white noise was set to 78 dB and that of the clicks was adjusted to give a human listener an impression of loudness that was subjectively similar to that of the white noise. The only visible light in the cubicle holding the apparatus was from the stimuli and the constant gray background of the stimulus display, which was blacked out only when 10 sec of darkness was required by the schedule described below. Infrared sources and an infrared-sensitive closed-circuit television camera enabled the monkey to be observed by experimenters in a separate laboratory.

The task. Each daily session had 30 new visual discrimination problems, presented consecutively, with an interval between problems of 10 sec. For each new problem, a positive and a negative discriminative stimulus was chosen at random from the large population available (see Apparatus, above). For each trial within a problem, the 2 stimuli were presented side by side, occupying the left or right position at random, and the animal chose one stimulus by touching it. The chosen stimulus, when touched, jumped to a higher position on the stimulus display; at the same time the nonchosen stimulus disappeared, and also the appropriate auditory stimulus was delivered. The auditory stimulus lasted 1.5 sec; after the first 0.5 sec of the auditory stimulus, the chosen visual stimulus disappeared. If the chosen stimulus was the positive, the auditory stimulus was the secondary reinforcer; but if the chosen stimulus was the negative, the auditory stimulus was the secondary nonreinforcer. For some animals the reinforcer was clicks and the nonreinforcer was white noise; for others, vice versa. Trials continued, with an intertrial interval of 7 sec, until either the positive or the negative stimulus had been chosen 4 times consecutively. After 4 correct choices in a row, a food reward was delivered; after 4 wrong choices in a row, 10 sec darkness was enforced. These 2 events, the primary reinforcer and the primary nonreinforcer, were delivered immediately after the end of the 1.5 sec auditory stimulus which was the fourth of its kind in 4 trials. Either of the 2 primary events terminated the current problem. The number of trials per problem was therefore not fixed but was always at least 4, enabling learning curves to be drawn for trials 1–4.

Preoperative training. As was noted above, all the monkeys, before entering the present experiment, were sophisticated in visual discrimination learning for immediate food reward. Upon entering the experiment they were pretrained as follows: They were given a series of visual discrimination problems in which any choice of the negative stimulus produced the secondary nonreinforcer and no food reward, and any choice of the positive stimulus produced the secondary reinforcer, which was followed by food reward half of the time, at random. The amount of pretraining administered to individual monkeys varied from 15 to 30 sessions.

The experimental task was then administered in 5 d blocks of daily sessions. Each animal continued to work at it until at least 80% of the problems presented in each of 2 successive 5 d blocks ended with food reward, i.e., with 4 consecutive choices of the positive rather than the negative stimulus.

Postoperative training. Following each surgery the animals worked at the task for 20 daily sessions.

Informal observations of behavioral changes outside the task. These were noted postoperatively and are described below.

Results

Preoperative training

Criterion was reached after 12.8 sessions on average, excluding the criterial sessions. Final preoperative within-problem learning rates differed markedly among animals. In the last 5 preoperative sessions, a total of 150 new problems, the error rate on trial 4 of new problems ranged from 7.3 to 30.7% across individual monkeys. Monkeys were assigned to operative groups to balance the groups' preoperative abilities, as assessed by their trial 4 scores, and the resulting final preoperative group learning curves are shown in Figure 4.

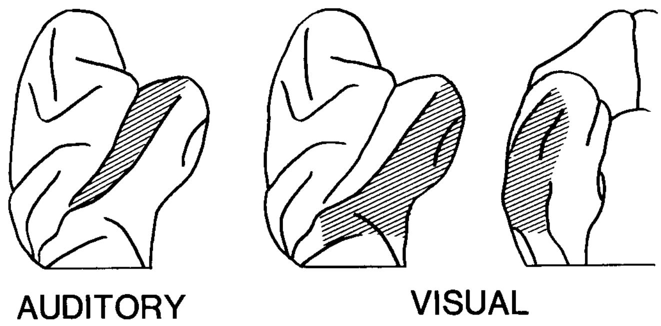

Figure 3. The externally visible extent of the ablations of association cortex in the auditory disconnection group (*left*) and in the visual disconnection group (*middle and right*).

Postoperative training

As a measure of the learning ability of individual animals, we took their error rates on trial 4 for the last 150 problems following each stage of surgery, and as a measure of postoperative deficit we took the difference between that error rate and the individual's comparable preoperative rate (see above). This measure of deficit following each stage of each surgery is shown in Figure 5, which also indicates the range of animals in groups. Analysis of variance of the deficits after the final stage of surgery (as shown also in Fig. 4) revealed that the difference between preoperative and postoperative scores varied significantly among groups ($F = 8.294$, $df(2,6)$; $p < 0.05$); designed comparisons indicated that the postoperative deficit was significantly greater for the bilateral amygdalectomy group than for the visual disconnection group ($F = 15.657$, $df(1,6)$; $p < 0.01$) and was significantly greater for the auditory disconnection group than for the visual disconnection group ($F = 7.918$, $df(1,6)$; $p < 0.05$), but did not differ significantly between the bilateral amygdalectomy group and the auditory disconnection group ($F = 1.307$, $df(1,6)$).

Inspection of Figure 5 shows that the visual disconnection group performed equally well at all postoperative stages. In the auditory disconnection group, the effects of crossed unilateral ablations alone, prior to forebrain commissurotomy, varied widely among individuals within the group; one animal, No. 22891, was so severely impaired at this stage that, as noted above (Surgery), it was unnecessary to subject this animal to forebrain commissurotomy for the final postoperative stage. This animal, therefore, was trained at the "FC" stage with forebrain commissures intact, and continued to perform at a chance level, which is represented in Figure 4 as an increase in error rate of 24% over its preoperative score.

Informal observations of behavioral changes outside the task

Animals subjected to bilateral amygdalectomy all showed a hunched posture immediately after surgery, but recovered normal posture after 4–6 d. Throughout their subsequent life, however, certain changes remained evident. None of them withdrew

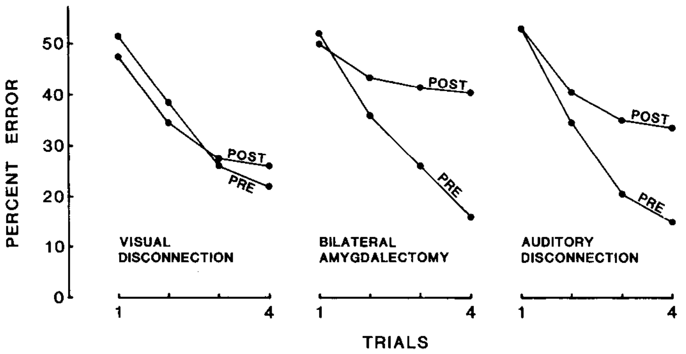

Figure 4. Within-problem learning curves before any surgery (*PRE*) and after all surgical procedures (*POST*) for the 3 surgical groups. Percent error is shown for the first 4 trials of new problems in the last 5 sessions of preoperative and postoperative performance for each group.

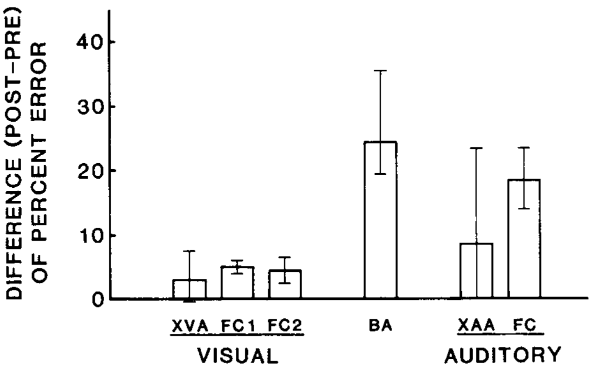

Figure 5. Postoperative deficits are shown as a difference between the error rate on trial 4 of new problems preoperatively and the error rate on trial 4 of new problems following each stage of surgery. Differences are shown with respect to individual animals' preoperative error rates. The histogram shows the group averages and the *error bars* show the ranges of individuals within groups. The error rates were taken from the last 5 sessions of training after each surgical stage.

from a human observer approaching them, even when touched, and none showed fear of other animals.

The animals in the visual disconnection group also showed changes as a result of their first surgery. When a human observer approached the home cage and opened the door, they did not withdraw from the front of the cage as normal animals do; even baring of the person's teeth and close approximation of the person's face to the monkey's produced no response. Unlike the animals with bilateral amygdalectomy, however, these animals immediately jumped backwards when lightly touched on the skin. When, out of sight of other monkeys, they were individually shown the net that is used regularly in the laboratory for catching naive animals, none showed any reaction. All normal animals, by contrast, reacted with alarm calls, withdrawal, and open-mouth threat grimaces.

No behavioral changes outside the task were evident in the animals of the auditory disconnection group.

Hand preference was not changed by surgery.

Discussion

Visual discrimination learning for auditory secondary reinforcement was severely impaired both by bilateral amygdalectomy and by disconnection of the amygdala from auditory cortex, while disconnection of the amygdala from visual cortex left learning unimpaired (Fig. 4). The results were clear and consistent within groups. The greatest within-group variation was in the auditory disconnection group at the stage before forebrain commissurotomy (Fig. 5, XAA). The fact that the animal with a severe impairment at this stage, No. 22891, had the unilateral auditory cortex ablation in the left hemisphere, while the others had it in the right, is possibly of significance, given the recent evidence of hemispheric asymmetry in the auditory cortex of macaques (Heffner and Heffner, 1984). But this animal also had a more complete ablation of the posterior and dorsal amygdala than did the other 2 animals in the auditory disconnection group (see Fig. 2). The individual differences in this group at this stage should therefore be interpreted with caution.

In the introduction, we noted the evidence that the amygdala is involved in the learning of visual discriminations for food reward, and argued that food rewards have 3 different types of attribute with which visual discriminanda can be associated. The task in the present experiment was designed to eliminate, as a source of within-problem visual discrimination learning, associations of the visual stimuli with the intrinsic incentive value of food. It was further designed to reduce as far as possible the associability of the visual stimuli with the intrinsically neutral sensory properties of the reward event. By incorporating these features in its design, the task put maximum emphasis on associations of the visual discriminanda with the third type of attribute of reward events, that is, with the responses that intrinsically neutral sensory properties of the reward event evoke because of their own association with the intrinsic incentive value of food. Visual disconnection of the amygdala had very little effect on visual discrimination learning rate in this task, showing that visual interaction with the amygdala is not important for associating visual stimuli with a reward event that does not possess intrinsic incentive value. The results from the auditory disconnection group show that it is necessary for the amygdala to receive input from the intrinsically neutral sensory properties of the secondary reinforcers in the present task in order to maintain their associability with visual discriminanda. Since the task was designed to maximize the role of associations of visual stimuli with the responses that intrinsically neutral sensory properties of the reward event evoke because of their own association with the intrinsic incentive value of food, this result suggests that the amygdala maintains the association of the auditory secondary reinforcers with the incentive value of food. Taken together with the evidence from previous experiments, which show the importance of the amygdala in associating visual stimuli with food rewards, these new results are consistent with the very simple hypothesis that the amygdala is important for associating sensory stimuli with the intrinsic incentive value of food, and not with its other attributes.

This hypothesis is also consistent with the observation (Weiskrantz, 1956) that following bilateral amygdalectomy, monkeys may at first be aphagic, and, on recovery from aphagia, will take into their mouths non-food objects. More generally, the amygdala may be important for associating stimuli with a wide range of intrinsically biologically important aspects of events, not just those of food reward (Weiskrantz, 1956). Our observations of altered behavior at the sight of a net in animals with bilateral amygdalectomy or with visual–amygdala disconnection, replicate many similar observations that are consistent with this broader hypothesis; in this instance, presumably, monkeys have learned an association between the sight of the net and the intrinsic disincentive value of confinement.

The present hypothesis may also have relevance to tasks other than visual discrimination learning. Mishkin (1978) showed that, in the absence of the hippocampus, the amygdala makes a substantial contribution to recognition memory for baited samples. This contribution may take the form of associative memory for the food reward (bait), which is presented with the sample at its acquisition trial: At the retention test in a recognition memory experiment with baited samples, the sample, but not the novel object, will evoke a memory of food reward, and this difference between the objects may help the animal determine which is the sample. Certainly this possibility should be considered in future recognition memory experiments. Malamut et al. (1984) emphasize that amygdalectomy plus hippocampectomy produces a more severe impairment in recognition memory than in the association of visual stimuli with food, but this difference may reflect the relative contribution of the hippocampus to these 2 tasks, and not that of the amygdala.

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