Visual impairments in macaques following inferior temporal lesions are exacerbated selectively by additional damage to superior temporal sulcus

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The present study examined the behavioural effects of removing the inferior temporal cortex (area TE) either on its own or in combination with the adjacent fundus and upper bank of the superior temporal sulcus (area STP). Comparisons with preoperative behaviour showed that the addition of superior temporal sulcal damage led to an increase in visual components of the Klüver–Bucy syndrome, i.e. an increased tendency to touch and examine objects coupled with a decrease in emotional reactivity, but no excessive orality, changes in food preference, or coprophagia. No group differences were found in the learning of 3 pattern discriminations, but the animals with additional superior temporal sulcal lesions were more impaired than the others on 3 colour discriminations, successive reversals of an object discrimination, and a learning-set task. These findings indicate that STP provides an important route, independent of the route via TE, by which visual information can reach limbic structures to evoke affective responses and contribute to visual learning.

INTRODUCTION

Although the Klüver–Bucy syndrome was successfully fractionated over 30 years ago, the findings also created a puzzle that still remains unsolved. The main features of the ‘visual agnosia’ found after bilateral temporal lobectomy, i.e. the absence of emotional reactions to aversive visual stimuli and the apparent compulsion to manipulate and mouth objects, are now known to follow amygdalec tomy alone3,38,40; yet removal of the inferior temporal cortex (area TE), through which visual information reaches the amygdala, yields only minimal signs of the visual agnosia12,22. The finding that these signs do follow complete disconnection of the amygdala from the visual modality13,14 indicates that visual inputs must reach this structure through tissue outside area TE. Confirming this conclusion are the reports that very extensive temporal cortical ablations that include not only inferior temporal but also superior and polar temporal cortex will reproduce the agnosic symptoms4,18.

A prime temporal cortical candidate for conveying visual information to the amygdala independently of area TE is the tissue immediately dorsal to it in the fundus and upper bank of the rostral superior temporal sulcus. This region,
which comprises area IPa and the rostral portions of areas PGa, TPO, and TAa, receives an array of information from different sensory modalities and has accordingly been called the 'superior temporal polysensory area' or STP. Evidence that this STP region receives prominent visual inputs is indicated by electrophysiological, anatomical and metabolic studies. It has been shown that there are many neurons within this rostral STP region that, like those in area TE, have large bilateral receptive visual fields. Many of these rostral STP units respond to stimulus movement while others are selective for particular complex forms, including faces. Anatomical studies have shown that at least some of the visual inputs to rostral STP are independent of area TE, in particular those arising from the various visual regions in the caudal portions of the superior temporal sulcus. Finally, like area TE, the STP region projects directly to the amygdala. Indeed, these projections are, if anything, even more dense than those from area TE itself.

These same anatomical considerations may also help explain another related paradoxical consequence of selective temporal lobe lesions, namely, that ablation of area TE sometimes produces a lesser impairment in visual learning than does removal of those limbic structures to which it conveys visual information. Although in this case the limbic structures include not only the amygdala but also the hippocampal formation, the anatomical evidence indicates that, for this structure also, the depths and upper bank of the superior temporal sulcus provide an alternate source of visual information.

The aim of the present study was to compare the behavioural effects of removing area TE alone with the effects of removing both area TE and STP. It was hypothesized that the latter lesion, which should produce the more complete visuo-limbic disconnection, would yield both an explicit Klüver–Bucy syndrome and more impaired visual learning. A lesion restricted to STP was deemed unnecessary since: (1) there is no evidence that such lesions alone produce signs of the Klüver–Bucy syndrome; and (2) the visual learning that was examined here is known to be either unaffected by superior temporal sulcal lesions or considerably less affected by sulcal lesions than by removal of area TE.

MATERIALS AND METHODS

Subjects

The subjects were 6 male, young adult cynomolgus monkeys (Macaca fascicularis) ranging in weight from 3.4 to 5.9 kg at the time of surgery. All of the animals were housed individually and were fed a diet of monkey chow supplemented with fruit. Water was available ad libitum.

Apparatus

Testing was conducted in a Wisconsin General Testing Apparatus (WGTA) inside a darkened, sound-shielded room with background white noise. The test compartment was 66 cm wide, 32 cm deep and 70 cm high. The monkey sat in a testing cage within an illuminated compartment, which was separated from the testing apparatus by an opaque, sliding screen.

Assessment of the Klüver–Bucy syndrome

Food board test. The monkeys were allowed a free choice from a variety of edible and inedible objects displayed on a wooden board at the front of the WGTA. The board, which was tilted towards the animal at an angle of 15° from the horizontal, measured 66 cm by 22.5 cm. The board contained 10 wells (diameter, 2.5 cm) distributed over 3 rows, the furthest row being 20 cm from the front of the cage. Three of the wells chosen at random contained a single food item, a raisin, a peanut or a banana pellet (P.J. Noyes Co., 300 mg), with all of which the animals were familiar. The remaining 7 wells held different inedible objects which were comparable in size to the food items. A pool of 12 inedible objects was used, with the particular set of objects and their distribution being changed after every trial.

Each animal received two trials per day for 7 days, the trials occurring at the beginning and end of every food preference test (see below). Once the food items had been removed, the animals were allowed an additional 30 s period of access to the inedible objects. It was noted whether any of the
inedible objects were touched or mouthed, and whether any of these manipulations occurred before or after all of the food items had been taken. If the animal did not pick up the food items within 120 s, the trial was terminated, although this happened to no animal more than once out of the 14 trials before surgery. Testing started between 2 and 7 weeks preoperatively and followed acquisition of two visual discriminations (see below). Starting 14–21 days after surgery the same procedure was repeated, except that the animals were allowed up to 10 min per trial to pick up all 3 food items.

**Food preference.** Food preferences were examined during the same sessions that food/non-food selection was measured and with the same apparatus. For this test, an item was placed in each of the two most distant food wells, 33 cm apart, and the monkey was allowed up to 60 s to choose one of them. Instances when the animal touched an item but did not consume it were also recorded. Five different items were used: half a peanut, a banana pellet (P.J. Noyes Co., 300 mg), a piece of Puffed Wheat (Quaker, breakfast cereal), a small ball of raw minced beef and a metal clip. Each animal received 40 trials per session during which each of the 10 possible pairings of items occurred 4 times in a balanced sequence.

**Reactions to aversive objects.** The animals' defensive responses to 4 different aversive objects were assessed in the WGTA both before and after surgery. The objects, each positioned between 20 and 25 cm from the cage front, were: (1) a stuffed snake suspended 8 cm above the floor of the WGTA; (2) the stuffed head of a rhesus monkey; (3) a leather glove of the type used to handle monkeys; and (4) a large bottle brush (30 cm long) suspended 25 cm above the floor of the WGTA. The glove (object 3) held a banana pellet, which, if removed, was replaced before the next exposure. The brush (object 4) was set swinging from side to side just before every exposure. In every session the animal was exposed to one object only. Each object was shown for four 15-s periods, with a 45-s interval between exposures during which the opaque screen was lowered. The occurrence or absence of emotional gestures or responses during these 15-s exposure periods was noted. The particular gestures and responses scored were those examined in previous studies of emotionality in macaques¹,⁵,¹¹, and comprised: head or body lunge, open mouth (threat or 'scandalized'), shake cage, vocalize (type noted), grind teeth, yawn, lip smack, head/eye avert, grimace, jump back, cower, sit hunched, and 'present'.

Beginning 7–13 days preoperatively, the 4 objects were shown over a period of 6 days in the sequence listed. Beginning 17–23 days postoperatively (30 days after the first preoperative session) the objects were repeated in the same sequence, except that, to reduce habituation, intervals of 1–2 weeks separated presentations of the different objects.

In a second test of responses to aversive objects, conducted approximately 7 months postoperatively, a measure was taken of the latency to take a food item (banana pellet) placed 18 cm from the front of the cage and touching one of a new set of objects. These were a plastic glove, a rubber snake, the skull of a monkey, and a lifesize, white polystyrene model of a human head. The animals received 4 sessions, one per object, distributed over 6 days, each session consisting of 10 trials separated by 30-s intertrial intervals. Each trial lasted 60 s whether the food item was taken or not.

**Assessment of visual learning**

**Simultaneous visual discriminations.** A pair of visual stimuli, each affixed to an 8 cm square cardboard plaque, were placed over two food wells spaced 36 cm apart and 17 cm from the cage front. The left/right positions of the stimuli were

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*Fig. 1. Reconstruction of TE and TE + STP lesions on a series of standard coronal sections. The cases show the largest (TE3, TE + STP1) and smallest (TE1, TE + STP3) lesions in each group. The lesions are shown in black. The sections at AP ~1 also show, in black, the extent of degeneration and gliosis in the medial pulvinar. The central drawing of a lateral view of a brain shows the intended extent of the TE (black) and TE + STP (black and grey combined) lesions and the level of each cross-section. The AP stereotaxic coordinates are for reference only. cs, central sulcus; ios, inferior occipital sulcus; sf, sylvian fissure; sts, superior temporal sulcus.*
determined by a pseudorandom sequence, and displacement of the correct stimulus revealed the reward (a 300 mg banana pellet, P.J. Noyes Co.).

Preoperatively, the animals received a colour discrimination, red (+) vs green (−), followed by a pattern discrimination, a plus sign (+) vs an outline square (−). Each of the two colour stimuli covered the entire plaque, and each of the two patterns consisted of white bars set on dark grey backgrounds. The animals were trained on each task at the rate of 40 trials per session until they reached a criterion of 90 correct responses in 100 consecutive trials. Training was completed approximately 6 weeks before surgery.

Postoperative testing started 4 weeks after surgery with retention tests on the red vs green discrimination and then the plus sign vs outline square discrimination. Testing continued until the animal had either reached the preoperative criterion or completed 1500 trials. These two discriminations were followed by a series of 4 additional simultaneous visual discriminations in the following sequence: orange (+) vs yellow (−); a white horizontal (+) vs a white vertical (−) bar; mauve (+) vs pink (−); and, finally, the white letters W (+) vs N (−). The animals were trained at the same rate and to the same criterion as before but now testing was stopped after a maximum of 1250 trials. The two stimuli in each of the 3 pattern discriminations contained equal areas of white set on a uniform dark grey background. The luminances of the colour stimuli were matched only roughly. In all cases multiple versions of the same stimulus were used. Although the first 3 of these discriminations followed one another in immediate succession, the last one (N vs W) was not given until 2 weeks after completion of the learning set task (see below).

Serial reversal learning. Approximately 18 months after surgery the animals were trained on a serial reversal problem. The stimuli were a white plastic box (10 cm long, 2 cm high and 6.5 cm wide) and an inverted cup painted gold (9 cm high, 5 cm diameter at top, and 6.5 cm diameter at base). The stimuli were placed over two food wells spaced 50 cm apart and 17 cm from the animals test cage. Selection of the cup was rewarded with a banana pellet, the positions of the two objects being determined by a pseudorandom sequence. The animals were trained for 30 trials per day to the criterion of 28 or more correct responses in one session followed by at least 26 correct responses in the next session. Following attainment of criterion, the reward contingencies were reversed, the animals now finding the reward under the white box. There were a total of 7 such reversals, each one following the attainment of criterion on the preceding one. In this and the following tasks the house lights were turned off in the animal’s compartment.

Learning set. This task, which followed 6 weeks after the Serial Reversal task, consisted of 80 problems, each involving a new pair of junk objects. A given pair, placed over the food wells used in the previous task, was presented for 10 choice trials preceded by a preference trial. On half of the problems, determined by a pseudorandom schedule, both objects were baited on the preference trial, and the object chosen was designated as correct. On the other half of the problems, neither object was baited on the preference trial, and the object chosen was designated as incorrect. Three problems were presented in turn within a single session until a total of 40 ‘baited’ and 40 ‘unbaited’ problems had been completed.

Surgical and histological procedures

Animals were immobilized with ketamine hydrochloride (10 mg/kg i.m.), anesthetized with Nembutal (35 mg/kg i.v.), and secured in a head holder. All surgeries were performed aseptically and bilateral removals were completed in one stage. The temporal muscle was incised and retracted to expose the zygoma, a portion of which was then removed. Following a craniotomy, the temporal cortex was exposed and, with the aid of a microscope, cortical tissue was removed by aspiration with a small gauge sucker.

Fig. 2. Extent of the TE and TE + STP lesions as shown on standard lateral and ventral diagrams. The dashed lines encapsulate the cortex in the banks of the rhinal sulcus, the occipitotemporal sulcus, and the superior temporal sulcus. The dotted lines represent the fundus of the superior temporal sulcus. Abbreviations as Fig. 1; ots, occipitotemporal sulcus; rs, rhinal sulcus.
For the TE removals (Figs. 1 and 2), the lesion was intended to extend from a line approximately 10 mm anterior and parallel to the inferior occipital sulcus rostrally to the anterior limit of the superior temporal sulcus. The ventromedial limit of the lesion was the fundus of the occipitotemporal sulcus and the lateral lip of the rhinal sulcus. Anteriorly, the lesion therefore included the posterior perirhinal cortex, which forms part of cytoarchitectonic area TG. The intended dorsal limit of the TE lesion was the bottom of the lower bank of the superior temporal sulcus, thereby sparing STP. The TE + STP lesion (Figs. 1 and 2) had the same rostral, caudal and ventromedial limits as those described above but extended dorsally to include all of the fundus and upper bank of the superior temporal sulcus at the same levels as the TE lesion.

At the completion of behavioural testing, each animal received a fatal dose of Nembutal and was perfused intracardially with a 10% solution of formol saline. The brains were then removed, blocked, embedded in celloidin, and cut at 25 μm in the coronal plane. Every twentieth section was stained with thionine.

Fig. 2 shows the TE and TE + STP lesions on standard lateral and ventral views. The superior temporal sulcus, the rhinal sulcus, and the occipitotemporal sulcus have all been opened diagrammatically in order to show the extent of the damage within these sulci. The lesions were as intended except that in every case there was bilateral damage to the lateral bank of the rhinal sulcus, which spared area 35 but often involved much of area 36. This rhinal damage was equivalent in the two surgical groups. In addition, in case TE3, the lesion in the right hemisphere extended caudally behind the intended limit to include part of area TEO (Fig. 2). In no case was there damage to either the amygdala or the hippocampus.

In all 3 TE cases the upper bank of the superior temporal sulcus was completely spared, although the fundus was invaded in some hemispheres (Figs. 1 and 2). By contrast, the 3 TE + STP cases also encroached onto the exposed surface of area TA, but none extended caudally into the visual areas MST and FST, which are located in the superior temporal sulcus immediately caudal to area IPa.

In all cases, there was gliosis in the most posterior portion of the medial pulvinar nucleus (Fig. 1), and this was somewhat more extensive in the group with the larger lesions. The lateral geniculate nucleus appeared normal in nearly all hemispheres, although restricted patches of degeneration were noted in layers IV and VI in the left hemisphere in case TE3.

A quantitative assessment was made of the extent of cortical damage in the individual animals. This analysis showed that although the TE + STP animals received the largest overall ablations, there were no group differences in the extent of damage outside the fundus and upper bank of the superior temporal sulcus.

RESULTS

Food board test

All group comparisons were based on a standard index of postoperative change (postoperative score minus preoperative score divided by postoperative score plus preoperative score). Over the entire test session it was found that although the animals in both the TE and TE + STP groups touched and mouthed more of the inedible objects postoperatively than preoperatively (Fig. 3) these increases were significantly greater in the TE + STP animals (in all cases, Mann–Whitney U = 0, P = 0.05). The TE + STP animals were not, however, indiscriminate in their behaviour, nor did they mouth a higher proportion of those objects that had been touched (Fig. 3).

Each test session was then divided between the period before all of the food items had been taken and the subsequent 30 s period of free access. Analysis according to this division showed that although there were no clear group differences in the numbers of non-food items selected before the food had all been taken (touched U = 1, mouthed U = 5), the TE + STP animals did touch and mouth more objects during the subsequent 30 s
Food preference

Before surgery both groups showed clear preferences among the various foods, selecting banana pellets, puffed wheat, and peanuts, in that order. Following surgery there was a flattening of the animals' preferences, which was perhaps more evident in the TE + STP group. But only one animal in this group, TE + STP1, appeared completely indiscriminate.

Statistical comparisons were based on the absolute postoperative changes in selection frequency, regardless of sign, for those 3 foods which all of the subjects ate (banana pellet, peanut, and puffed wheat). When the sums of these differences were compared it was found that although the TE + STP group showed a larger overall change in food preference (mean postoperative change, TE = 41.7, TE + STP = 83.3) this difference was not significant (U = 1, P = 0.01).

Postoperatively, all of the monkeys showed an increased willingness to pick up the meat, but only one animal from each group would readily eat it. Although the metal clip was occasionally picked up by monkeys from either group, this was infrequent, and the clip was never treated as food.

Reactions to aversive objects

All comparisons were based on an index of change in the total number of body and facial gestures following surgery (postoperative total minus preoperative total divided by postoperative total plus preoperative total). A negative score represents a decrease in defensive responses. Whereas both groups showed a postoperative decline in affective behaviour (Fig. 4), this change was greater in the TE + STP animals (U = 0, P = 0.05). The same pattern of results was found when those gestures which might be regarded as the most ambiguous to identify (head or eye avert, cower, sit hunched) were excluded. This modified analysis gave emotionality index scores of from −0.20 to −0.40 for the TE animals and from −0.43 to −1.0 for the TE + STP animals.

Following surgery, all of the TE + STP monkeys, but none of the TE monkeys, ate every banana pellet that was placed on the leather glove (object 3). This difference was further examined by recording the time taken to pick up a banana pellet in contact with 4 additional, aversive objects presented in a second test 7 months postoperatively. The animals' responses to the first object (glove) were highly variable and reflected the initial failure of some animals to notice the food. There was, however, a clear group difference in the total times taken to remove the food item from the 3 subsequent objects (range; TE 535–723 s, TE + STP 114–304 s; U = 0, P = 0.05).

Visual discrimination learning

Preoperatively, there were no group differences in acquisition scores, as measured by errors to
criterion, on either the colour (TE, range 12–62; TE + STP, 10–49) or pattern (TE, range 35–112; TE + STP, 55–157) discrimination.

Postoperatively, the two groups differed on some discriminations but not all. Table I shows the total number of errors and trials on each of the 6 discriminations. It can be seen that the TE group made fewer errors than the TE + STP animals on the first discrimination (red vs green, \( U = 0, P = 0.05 \)) but not on the next (cross vs square, \( U = 6 \)). A similar result was found for the next pair of discriminations (orange vs yellow and vertical vs horizontal) in that again there was a significant difference for colour \( (U = 0, P = 0.05) \) but not for pattern \( (U = 4) \). The same dissociation was found a third time on the last pair of discriminations, with a group difference emerging for mauve vs pink \( (U = 0, P = 0.05) \) but not for W vs N \( (U = 3) \). When the results of the 3 colour and 3 pattern discriminations were combined (Fig. 5) the selective differences in the effects of the TE and TE + STP lesions are striking.

**Object discrimination and reversals**

The error scores on the initial discrimination and the successive reversals are shown in Fig. 6. It can be seen that the TE + STP group performed more poorly than the TE group over the 7 reversals (total errors; TE 78–157; TE + STP 202–400). These differences were most apparent for reversals 3–7, the only overlap (a tied score) occurring on reversal number 4.

When the error scores were divided into 3 performance stages after the method of Jones and Mishkin, it was found that there was no consistent pattern within a group, the majority of the errors occurring in either Stages I or II (overall mean for groups TE and TE + STP combined; Stage I 64.7, Stage II 75.7, and Stage III 41.7). This pattern of errors is different to that seen after either orbital frontal or temporal pole plus amygdala lesions.

**Learning set**

Fig. 7 shows the overall mean performances of the TE and TE + STP groups on the 40 ‘baited’

|     | R/G   |  +/ | O/Y  |  ||-  | M/P   | W/N   |
|-----|-------|-----|------|-----|------|-------|-------|
| TE  |       |     |      |     |      |       |       |
| 1   | 416   | 52  | 172  | 154 | 449  | 343   |
| 2   | 310   | 304 | 280  | 638 | 477  | 575   |
| 3   | 352   | 525 | 142  | 386 | 329  | 439   |
| TE + STP |       |     |      |     |      |       |       |
| 1   | 167   | 637 | 33   | 541 | 69   | 500   |
| 2   | 240   | 138 | 71   | 164 | 90   | 166   |
| 3   | 108   | 331 | 113  | 316 | 326  | 379   |

**Fig. 5.** Mean total number of trials (bars) and errors (open circles) to criterion over the 3 colour and 3 pattern discriminations. The vertical bars show the range of total trials.

**TABLE I**

*Total number of errors and trials (in parentheses) made by each animal to reach a criterion of 90 correct responses in 100 trials*

R/G, red vs green; +/☐, plus vs square; O/Y, orange vs yellow; ||–, vertical vs horizontal; M/P, mauve vs purple; W/N, letter W vs letter N.
DISCUSSION

The addition of superior temporal sulcal damage to an area TE lesion led to a selective exacerbation of the effects of area TE damage alone on tests assessing the Klüver–Bucy syndrome. Thus, the animals with TE + STP lesions displayed a greater tendency to touch and manipulate inedible objects, and a lesser tendency to react defensively or aggressively to fearful and otherwise aversive objects, than the animals with TE lesions. Those with the TE + STP lesions did not, however, exhibit either indiscriminate selection of food and non-food items or excessive oral exploration of the non-food items that they touched, nor did they exhibit coprophagia or a sudden willingness to eat meat. In all of these respects, i.e. with regard to the sets of both positive and negative findings, the effects of TE + STP lesions match closely those reported to follow total disconnection of the amygdala from the visual system. Taken together, the results indicate that both area TE and STP independently provide the amygdala with the information needed for visual identification of the inedibility and aversiveness of objects. At the same time, neither area alone nor both in combination appears to supply the amygdala with information essential for identifying these attributes through any sensory modality other than vision: hence, for example, the absence of excessive orality or of dietary changes. Presumably, only if the amygdala were disconnected from all of its sensory inputs, visual and non-visual alike, would the full Klüver–Bucy syndrome emerge, i.e. a syndrome comparable in kind and degree to that observed after amygdalectomy itself.

The addition of an STP to a TE lesion led to a selective exacerbation not only of Klüver–Bucy signs but also of the visual learning impairments caused by damage limited to area TE. Two learning impairments that showed significant augmentation were those on the serial reversal task and the ‘unbaited’ problems of the object discrimination learning-set task, whereas two that failed to show such augmentation were those on the ‘baited’ problems of learning set and the pattern discriminations. Paradoxically, the deficit produced by TE lesions on the colour discrimi-
nations resembled the first pair of visual learning deficits listed above rather than the second, in that the colour discrimination deficit also was augmented significantly by the additional damage to STP; this result poses an interesting puzzle which will be considered after all the other findings have been discussed.

Discrimination reversal learning, in contradistinction to discrimination learning itself, is known to be markedly disrupted by amygdalectomy\textsuperscript{3,7,23,32}. It has been proposed that this is because reversal learning is a particularly sensitive measure of object–reward and object–non-reward association, which, like identification of an object’s inedibility or aversiveness, taps what may be the amygdala’s primary function, namely, that of linking the physical qualities of a given object with its emotional or motivational qualities\textsuperscript{2,23}. Considered in this light, the ‘unbaited’ problems of the learning-set task may well tax the same function, in that such problems require the animal to reverse its initial choice by learning to associate non-reward with an initially preferred, perhaps attractive, object and, conversely, to associate reward with an initially non-preferred, perhaps aversive one. Evidence for this comes from the finding that, like the TE + STP animals in the present study, amygdalectomized monkeys are differentially impaired on the ‘unbaited’ or ‘shift’ condition in a learning-set task\textsuperscript{32}. According to this analysis, the increase in impairments on the serial reversal and ‘unbaited’ problems of the learning-set task may be understood in the same way as the increase in the visually related Klüver–Bucy signs. In both cases, area TE and STP must independently supply visual information about objects to the amygdala and other medial temporal limbic structures that mediate the association of that visual information with the emotional or motivational consequences signalled by the objects.

As indicated above, in contrast to various forms of reversal learning, discrimination learning itself is relatively insensitive to the effects of amygdalectomy or of even larger medial temporal removals\textsuperscript{30,41}. Discrimination learning in vision does depend substantially on area TE, but there is evidence that the learning in this case is a form of habit formation that can be supported by a system involving projections from area TE and other cortical visual areas to the posterior neostriatum\textsuperscript{26,27,30,31}. Whatever system underlies visual discrimination learning, however, the present results suggest that STP makes little or no contribution to it. First, there was no difference between the TE and TE + STP groups in pattern discrimination learning, a finding confirming an earlier observation that superimposing removal of the entire superior temporal gyrus, including STP, on an inferior temporal lesion did not increase a pattern discrimination relearning impairment produced by the inferior temporal lesion alone\textsuperscript{16}. And second, a negative result was also obtained on the ‘baited’ problems of the learning set task, a type of problem that is formally similar to pattern discrimination learning. Why STP does not contribute to either of these forms of learning is unclear, but one possibility, which invokes the hypothetical corticostriatal mechanism described above, is that, compared with area TE, STP may have only sparse projections to the posterior neostriatum.

A difficulty with the foregoing suggestion, however, has already been alluded to, namely, that unlike the impairment in the other two forms of discrimination learning examined in this study, the impairment in colour discrimination learning was clearly exacerbated by the addition of STP damage (even though colour discrimination learning appears to be completely unaffected by STP damage alone\textsuperscript{17}). Assuming for now that all 3 forms of visual discrimination learning – pattern, object and colour – depend upon the same hypothetical corticostriatal mechanism, we arrive at the tentative conclusion that STP projections to the neostriatum, unlike its projections to limbic structures, must carry colour information selectively. However curious this conclusion may seem, the results from which it is derived seem clear-cut, and, in any event, it is subject to direct experimental test.

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