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THE EFFECT OF INFEROTEMPORAL OR FOVEAL PRESTRIATE ABLATION ON SERIAL REVERSAL LEARNING IN MONKEYS

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Abstract—Visual discrimination performance during serial reversal learning was studied in monkeys with inferotemporal or foveal prestriate lesions. Both groups were equally impaired in acquisition of the discrimination when compared with normal monkeys. They also learned the reversal series more slowly than control subjects. The reversal deficit of monkeys with inferotemporal lesions was more severe than their acquisition deficit though over successive reversals they achieved normal performance. Monkeys with foveal prestriate lesions were less impaired in reversal learning than in acquisition of the discrimination problem. These results are interpreted in terms of qualitative differences in the effects of the two lesions.

INTRODUCTION

IT IS now well established that bilateral removal of inferotemporal cortex interferes with the ability of monkeys to remember visual discrimination habits learned preoperatively and to acquire new problems postoperatively (e.g. [1, 2]). BUTTER [3] has suggested that this deficit is most pronounced when subjects are required to maintain high levels of correct performance. His suggestion may be relevant to a discrepancy in the literature concerning the ability of monkeys with inferotemporal lesions to perform the serial reversal of a visual discrimination. PRIBRAM [4] showed that these monkeys formed a serial reversal learning set as rapidly as intact animals. However, other investigators have shown that inferotemporal ablation retards reversal learning with objects [5] and patterns [6]. Since Pribram's animals were trained to a criterion of ten consecutively correct and criterion for subjects in the other studies was 90% correct, it may be that the deficit is apparently only when a continuously high level of correct performance is demanded before each reversal. If this hypothesis is correct, operated animals would be expected to achieve a criterion of 70% and perhaps 80% correct as easily as normal subjects, but be impaired in finally attaining 90% criterion.

Selective impairments at various stages of learning have also been discussed in a comparison of the effects of inferotemporal and foveal prestriate lesions on reversal learning. MANNING [6] hypothesized that the two lesions would differentially disrupt the two processes thought by some to comprise discrimination learning [7–9]. According to two stage models, subjects acquire discrimination habits by first learning to attend to the stimulus

dimension which is relevant to solution of the problem and then establishing correct choice behavior based on stimulus reward associations. Several studies suggest that foveal prestriate or foveal prestriate plus posterior inferotemporal lesions disrupt basic attentional mechanisms while lesions placed in the more anterior portions of inferotemporal cortex seem to interfere with "associational or mnemonic" capacities [10–13]. Manning predicted that subjects with foveal prestriate lesions would be impaired in the early stages of original learning as they attempted to discern the features by which the stimuli could be discriminated, but that they would acquire the discrimination normally thereafter. They should also be unimpaired in reversal learning since the stimuli remain unchanged throughout the series. By contrast, he predicted that monkeys with inferotemporal lesions would show normal performance in the early stages of original learning but be impaired in actually attaining criterion. They should also be impaired in reversal learning since the task requires subjects to alter their choice behavior as the reward contingencies change with each reversal.

The data reported by Manning failed to show differences in the stage of learning disrupted by the two lesions, though there was a trend in the expected direction. In addition, the reversal deficit of the foveal prestriate group equalled that observed in the inferotemporal group. However, it is important to note that these foveal prestriate lesions included removal of a considerable portion of posterior inferotemporal cortex. CHRISTENSEN and PRIBRAM [14] have shown that deficits seen after removal of foveal prestriate cortex are less severe than those reported for lesions which include posterior inferotemporal cortex as well. The absence of significant qualitative and quantitative differences between the deficits reported by Manning may be due to the inclusion of posterior inferotemporal cortex in the lesions of his foveal prestriate group.

In this paper we have reexamined the serial reversal learning of monkeys with inferotemporal or foveal prestriate lesions and characterized their performance at various stages of learning the individual problems and the entire reversal series. The foveal prestriate lesions studied here were restricted in their anterior extent with minimal encroachment on posterior inferotemporal cortex.

METHOD

Subjects

Twelve adult rhesus monkeys (*Macaca mulatta*) were subjects in this experiment. Four animals (Group FPS) received bilateral resections of foveal prestriate cortex intended to remove the portions of the superior temporal, inferior occipital and lunate sulci which receive projections from foveal striate cortex. This lesion corresponds to a strip 0 lesion of IWAI and MISHKIN [10] with inclusion of a portion of strip 1 in some animals. Four subjects (Group IT) sustained bilateral removal of inferotemporal cortex corresponding to area TE of VON BONIN and BAILEY [15]. The remaining four monkeys (Group N) served as unoperated control subjects. All animals had received visual discrimination training prior to this experiment. Details of this training, as well as surgical procedures and lesion reconstructions have been published previously [14]. Figure 1 shows maximum lesion size and the area of removal common to all subjects for the two operated groups.

Apparatus

All behavioral testing was carried out in the DADTA IV automated test apparatus [16]. The stimulus display of DADTA IV is a vertically aligned metal panel containing nine 1¾ in. round, plexiglass buttons arranged in a 3 × 3 array. These buttons serve as the site of presentation of stimuli and as manipulanda. Stimuli are projected upon a television screen placed directly behind the panel. This screen is driven by a scan converter programmed to display stimuli behind one or more of the clear buttons. Presentation of stimuli, delivery of food rewards and registration of responses were controlled by a PDP-8E computer located in an adjacent room. A dim light illuminated the testing chamber and a ventilating fan masked extraneous sounds.

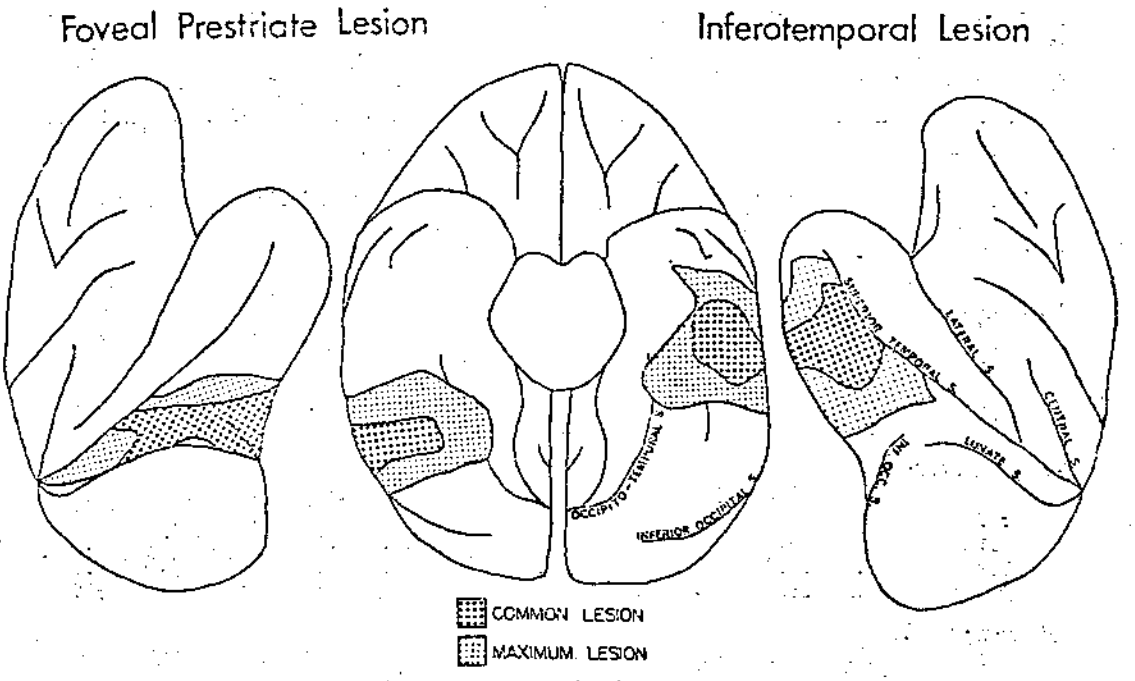


FIG. 1. Lateral and ventral views of the cerebral hemisphere showing the lesion common to all subjects and the maximum lesion for monkeys with inferotemporal lesions (right) and those with foveal prestriate lesions (left).

Procedures

Since the DADTA IV was unfamiliar to these animals, they were pretrained to respond to lighted panels by rewarding presses of the numeral 1 as it appeared randomly on two of the nine panel positions. Pretraining continued until the subject responded 50 times in one day's session. At that time the subject was presented with discrimination of the numerals 3 and 8. Subjects were tested 100 trials/day until a criterion of 90% correct in 100 consecutive trials was achieved. After acquisition of this task, the reward contingencies were reversed and training continued until criterion was again met. Testing continued through a series of ten reversals.

RESULTS

Scores for original learning* and the ten reversal problems are presented in Table 1. The group means of these data are plotted in Fig. 2. The data show that monkeys with inferotemporal lesions ($t = 2.04$, $P < 0.05$) and those with foveal prestriate lesions ($t = 3.02$, $P < 0.025$) were severely impaired in acquiring the discrimination. The magnitude of the impairments produced by the two lesions was approximately equal ($t = 0.199$).

As can be seen in Fig. 2, the operated animals maintained their visual discrimination impairments during reversal learning ($F = 4.60$; $df = 2, 8$; $P < 0.05$). The deficit was especially pronounced in Group IT. Monkeys in this group acquired the first two reversal problems even more slowly than they had learned the discrimination originally. By contrast,

*These animals had previously learned and been tested for retention of a 3⁺–8 visual discrimination. We chose the same stimuli for this study in order to hasten assessment of their reversal performance. As can be seen in Table 1, our assumption that the subjects would rapidly reattain criterion on this problem was erroneous. The original problem was trained on DADTA III and the stimuli were slightly different from those presented on DADTA IV in the present study. This may be the reason that all subjects responded to the discrimination as if it were unfamiliar. We have described the 3⁺–8 discrimination learned in DADTA IV as original learning, though in the strict sense, this designation is inaccurate.

monkeys with foveal prestriate lesions were less impaired on the reversal problems than they were on acquisition. Though they were still impaired relative to intact animals on the first reversal ($t = 2.99$, $P < 0.025$), their performance was significantly better than that of monkeys with inferotemporal lesions on this problem ($t = 2.16$, $P < 0.05$; all t tests are one-tailed).

Table 1. Trials accumulated by individual subjects during the serial reversal of a visual discrimination (scores are trials including criterion)

	O.L.	1	2	3	4	5	6	7	8	9	10
Normal Ss											
337	254	479	450	441	343	350	250	318	236	200	250
338	550	850	2478	1471	1050	1350	900	800	350	400	300
339	200	295	250	300	250	200	250	250	150	150	200
342	200	325	289	463	514	423	494	521	434	300	372
$\bar{X}$	301	487	867	669	539	581	474	472	293	263	281
Foveal prestriate Ss											
308	1323	822	852	550	550	550	1443	1615	1247	1180	1600
310	2433	1314	1301	1053	1100	781	1198	1600	1250	1600	2150
315	1400	2150	3545	2809	2650	2000	350	950	1050	952	1300
369	4200	1300	1150	750	1250	750	700	800	1850	500	250
$\bar{X}$	2339	1397	1712	1290	1388	1020	923	1241	1349	1058	1325
Inferotemporal Ss											
340	1698	2550	2433	2590	2200	1500	300	150	1050	150	300
393	5647	6000	5350	3250	4200	1900	1500	1400	550	200	700
407	400	1600	1400	900	466	550	650	1455	844	1039	1000
391	2650	(7062)	(9745)	(10201)							
$\bar{X}$	2599	3383	3061	2247	2289	1317	817	1002	815	463	667

Parentheses indicate that S391 was not included in group means.

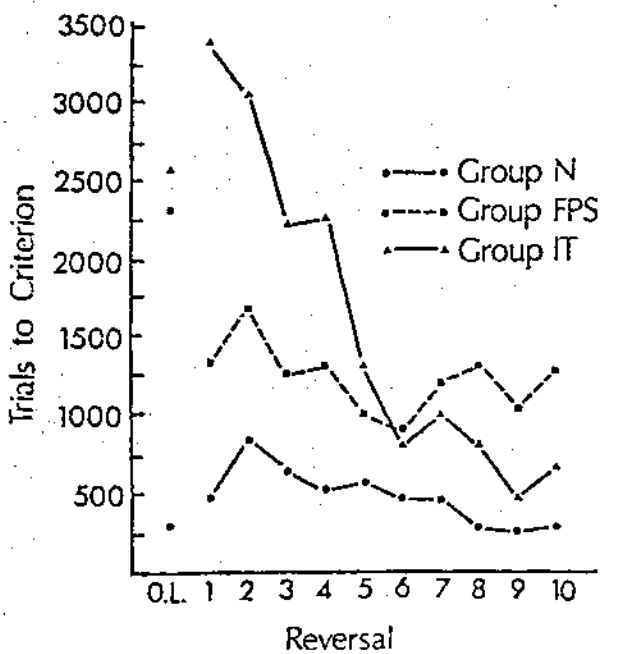


FIG. 2. Mean number of trials to 90% criterion for normal monkeys and those with inferotemporal or foveal prestriate lesions during original learning (OL) and ten reversals.

Analysis of the scores for all ten reversals reveals that while both operated groups were impaired relative to normals, ($F_{fps} = 9.29$; $df = 1, 6$; $P < 0.05$; $F_{it} = 6.56$; $df = 1, 5$: $P < 0.05$), only Group IT improved significantly over the reversal series ($F = 3.97$; $df = 9, 45$; $P < 0.01$). No significant reversal effect was noted in the comparison of Groups N and FPS. The performance of monkeys in both of these groups was relatively constant across the ten reversals with the scores of Group FPS elevated above those of Group N.

Even though the operated animals achieved criterion very slowly during the early reversals, they were frequently observed to make long strings of correct responses. They performed well above 70% correct performance for many days before actually achieving criterion suggesting that the magnitude of their deficit was due in part to the high level of correct performance demanded of them. The reversal data were therefore reanalyzed with criterion set at 80% correct. This analysis failed to show a significant lesion effect; the learning of monkeys with inferotemporal or foveal prestriate lesions could not be distinguished from normal when criterion was less stringent. Though this analysis cannot be taken as an independent manipulation of level of criterion, it does suggest that the discrepancy between the data from inferotemporal subjects studied here and those reported earlier by Pribram is related to this variable.

In order to further characterize the learning of subjects during the final stages of learning, backward learning curves of the data from Table 1 were plotted according to the method of HAYES [17]. This procedure more clearly represents the performance of subjects near criterion than when learning curves are plotted conventionally. Backward learning curves for acquisition and reversals 1 and 5 are presented in Fig. 3. This representation elaborates findings already described. The acquisition impairments of the two operated groups are apparent in Fig. 3 (a). Figure 3 (b) shows that on the first reversal the performance of Group FPS improved while that of Group IT deteriorated. These representations also show that animals in both operated groups acquired the discrimination and the first reversal by gradually achieving higher levels of correct performance. The slopes of their learning curves differ markedly from the steeply accelerated function of the normal subjects. In addition a prolongation at chance is apparent in the original learning of Group FPS and

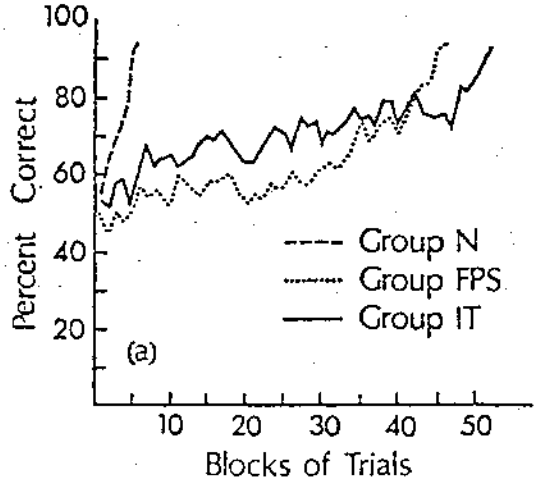
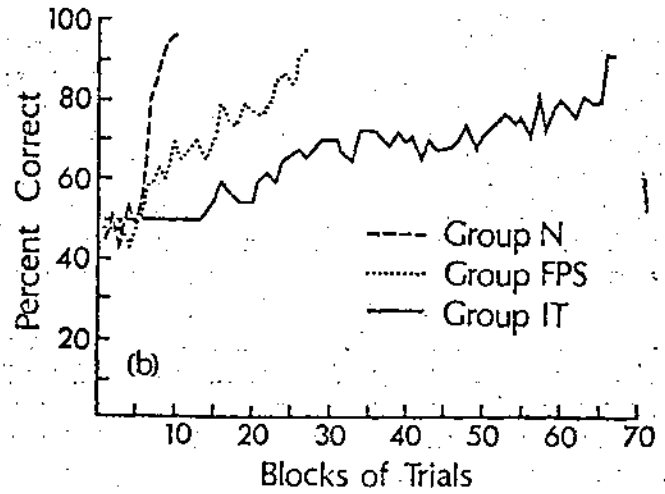
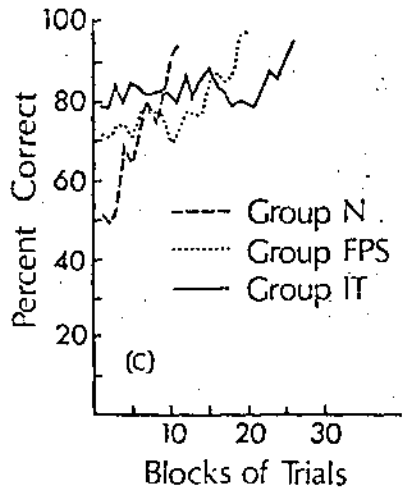


FIG. 3. Backward learning curves for normal monkeys and those with inferotemporal or foveal prestriate lesions for (a) original learning (b) first reversal and (c) fifth reversal.





in the first reversal performance of Group IT. The actual number of trials accumulated in the period of 40–60% correct performance for original learning and the first reversal is presented in Table 2. Monkeys in Group FPS accumulated more trials during the presolution period of original learning than did normal subjects ($t = 3.66$, $P < 0.02$) or those with inferotemporal lesions ($t = 2.90$, $P < 0.05$). Monkeys in Group IT did not differ from normal subjects during original learning on this measure ($t = 1.83$). However the length of chance performance of monkeys with inferetemporal lesions was significantly prolonged on the first reversal when compared with Group N ($t = 7.51$, $P < 0.001$) and Group FPS ($t = 5.63$, $P < 0.01$). (All t tests are two-tailed.)

A different learning profile is apparent in Fig. 3 (c). By the fifth reversal the performance of both operated groups had improved, yet they continued to be retarded in actually achieving criterion. Although most operated monkeys immediately performed above 70% correct, they required many days of training to complete the problem. For example, the most impaired subjects, IT-393 and FPS-315, required approx 2000 trials to reach criterion

Table 2. Trials accumulated in moving from 40 to 60% correct performance

	Original learning	First reversal
Group N		
337	0	100
338	150	250
339	0	150
342	0	50
$\bar{X}$	38	112
Group FPS		
308	673	50
310	1783	293
315	650	200
369	1750	300
$\bar{X}$	1214	211
Group IT		
340	171	550
391	300	789
393	500	600
407	0	750
$\bar{X}$	243	672

even though their performance on the first block of 50 trials was 72 and 80% correct respectively. Impairments which were observed on subsequent reversals followed this same pattern.

DISCUSSION

The results reported here confirm our earlier findings concerning the effects of foveal prestriate ablation [14] and elaborate the nature of the dysfunction produced by this lesion. In addition these results more completely characterize serial reversal learning in monkeys with inferotemporal lesions. The data show that both lesions impair the ability of subjects to acquire a visual discrimination and retard formation of a reversal learning set provided a criterion of 90% correct in 100 consecutive trials is demanded. When the data are reanalyzed with a less stringent criterion of 80% correct, the reversal deficit is not manifest. The learning set deficit appears to stem from an inability of the lesioned subjects to steadily maintain a high level of correct performance. Discrepancies among earlier reports are thus resolved.

The remaining deficits produced by the two lesions appear to be due to different disorders, although the data do not provide evidence for a complete dissociation of function between these areas. The deficit produced by removal of foveal prestriate cortex results in prolongation of the presolution period during original learning and only during original learning in these subjects. ZEAMAN and HOUSE [18] have reported that prolongation at chance characterizes the visual discrimination learning of retarded children who are impaired in discerning the stimulus dimension relevant to solution of the problem. Monkeys with foveal prestriate lesions did not display the effect on the first or any subsequent reversal which suggests that their deficit is related to initial detection of the relevant attribute of the stimulus configuration during original learning. Disappearance of the prolongation of the presolution period is in large part responsible for the improvement of Group FPS on the first and subsequent reversals.

Do these data also clarify the nature of the inferotemporal deficit? The results are consistent with the hypothesis that the disorder is related to a disruption of associative capacities. Monkeys with this lesion were disrupted by alteration of reward contingencies. All four subjects were more impaired on the first reversal than in original learning as might be expected if they were particularly vulnerable to the change in choice demanded by the task.

Monkeys in Group IT were also retarded in moving from chance to higher levels of correct performance during the first reversal though they had shown no such prolongation in learning the problem originally. The following explanation may account for this result.

WILSON, KAUFMAN, ZIELER and LIEB [19] have suggested that the inferotemporal deficit in a match to sample task is related to intrusion of errors associated with past reinforcements. Vulnerability to intrusion errors should also disrupt reversal learning. In effect these intrusions from the previous problem would change the reward contingencies to a partial reinforcement schedule for inferotemporal subjects. MANNING, GROSS and COWEY [20] demonstrated that monkeys with inferotemporal lesions are greatly disrupted by partial reinforcement schedules and it has been demonstrated that partial reinforcement retards reversal learning [21]. The prolongation of performance at chance observed in inferotemporal subjects may be explained by this effect.

This explanation is also relevant to the data reported by BOLSTER and CROWNE [22] for monkeys with lesions of anterior inferotemporal cortex. Like the monkeys with inferotemporal lesions studied here, their subjects appear to show prolongation at chance in reversal learning though not in original acquisition. These findings suggest a similarity between the dysfunction by lesions of area TE and smaller lesions placed in the anterior segments of this area.

Our findings regarding the deficits produced by inferotemporal and foveal prestriate lesions conflict in part with those reported by MANNING [6]. In both studies the subjects of both groups were equally impaired in original learning. However in Manning's study the magnitude of the reversal deficit of the two groups was also indistinguishable. His subjects were severely impaired in the early reversals but they attained normal performance midway in the series. In our subjects the early reversal deficit of the foveal prestriate group was less severe than that of the inferotemporal group and, unlike Manning's animals and our inferotemporal group, the foveal prestriate subjects maintained an impairment throughout all the reversal problems.

Differences in the magnitude of the initial reversal deficit observed in the two groups of foveal prestriate subjects is probably attributable to inclusion of posterior inferotemporal cortex in the lesions of Manning's subjects. The effects appears to be due to the size of the lesion rather than to the disruption of two distinct processing capabilities in the region of foveal prestriate and posterior inferotemporal cortex. The presolution prolongation observed in the original learning of monkeys with foveal prestriate lesions in this study is also evipent in the original learning of monkeys with posterior inferotemporal lesions studied by BOLSTER and CROWNE [22] suggesting some functional equivalence of these areas.

The maintenance of a reversal deficit by monkeys with foveal prestriate lesions in this study may be due to task difficulty. As judged by the number of trials to criterion in original learning, the discrimination presented here was more difficult than that taught by Manning. The inability of monkeys to maintain high levels of correct performance is especially pronounced when they are required to learn difficult tasks [23]. As already discussed, the reversal deficits observed here are attributable to instability of performance during the final stages of learning.

In conclusion, the results of this study have resolved some of the discrepancies among earlier reports concerning the effects of inferotemporal resections on discriminations reversal learning set. The results also support earlier suggestions that two separate functions are disrupted by inferotemporal and foveal prestriate lesions, albeit in the current study, as in previous studies, the dissociation is not complete. The evidence points to a difficulty in detecting relevant stimulus attributes in monkeys with foveal prestriate lesions. The exact nature of the inferotemporal deficit is less clear, though the dysfunction results in increased susceptibility to interference effects and intrusion errors across problems.

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Résumé :

La performance de discrimination visuelle pendant un apprentissage de renversement en série a été étudiée chez des singes avec lésions inféro-temporales ou pré-striées fovéales. Les 2 groupes étaient également déficitaires dans l'acquisition de la discrimination s'ils étaient comparés avec des singes normaux. Ils apprenaient aussi plus lentement les séries de renversement que les singes de contrôle. Les déficits de renversement des singes avec lésions inféro-temporales étaient plus sévères que leur déficit d'acquisition encore que sur des renversements successifs, ils parvenaient à la performance normale. Les singes avec lésions pré-striées fovéales étaient moins déficitaires dans l'apprentissage de renversement que dans l'acquisition du problème de discrimination. On interprète ces résultats en termes de différences qualitatives entre les effets des 2 lésions.

Deutschsprachige Zusammenfassung:

Das optische Unterscheidungsvermögen während des Reihen-Rückwärtslernens wurde bei Affen mit inferotemporalen oder foveal-prästriären Läsionen untersucht. Beide Gruppen waren gleicher maßen beeinträchtigt beim Erlernen der Unterscheidung im Vergleich zu normalen Affen. Auch lernten sie die Rückwärtsreihen langsamer als Kontrolltiere. Das Rückwärts-Lern-Defizit von Affen mit inferotemporalen Läsionen war schwerwiegender als ihr einfaches Lern-Defizit, obwohl sie über mehrfache Rückwärtsreihen normale Leistungen erzielten. Affen mit foveal-prästriären Läsionen waren weniger beeinträchtigt beim Rückwärtslernen als beim Normallernen des Unterscheidungsproblems. Diese Ergebnisse werden interpretiert i. S. qualitativer Unterschiede der Auswirkungen der beiden Läsionen.