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THE EFFECTS OF INSTABILITY OF THE VISUAL DISPLAY ON PATTERN DISCRIMINATION LEARNING BY MONKEYS: DISSOCIATION PRODUCED AFTER RESECTIONS OF FRONTAL AND INFEROTEMPORAL CORTEX*

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Abstract—Rhesus monkeys with anterior frontal ($N = 7$), posterior parietal ($N = 4$), or inferotemporal ($N = 4$) lesions and normal controls ($N = 3$) were trained on visual discrimination problems under conditions in which the stimulus display either remained in the same place or shifted randomly over a wide range of positions from trial to trial. Naive monkeys with frontal lesions were significantly impaired in learning the discrimination problem under the condition of shifting spatial context; their impairment disappeared with sophistication, but they continued to find this condition more difficult than one in which the display remained stable. The performance of monkeys with inferotemporal lesions was markedly improved by the random-position display condition.

THE CLASSICAL deficit in monkeys with bilateral anterior frontal ablations is an inability to perform spatial delayed response [1, 2] and spatial delayed alternation [3, 4]. On the other hand, monkeys with such lesions are able to learn to discriminate simultaneously presented visual stimuli as well as normal monkeys [5–8]. Hence, when a group of monkeys was trained on a series of simultaneous visual discriminations in an automated apparatus (Discrimination Apparatus for Discrete Trial Analysis, DADTA) [9] simply to adapt them to the apparatus before proceeding to a series of more complex problems [10], it was expected that the monkeys with frontal lesions would have no difficulty with these initial visual discriminations. Contrary to expectation, these monkeys did show a significant deficit. An earlier study from this laboratory [11] using the same automated apparatus had reported that monkeys with frontal lesions have significant difficulty in maintaining high levels of performance on a simultaneous visual discrimination problem. It therefore seemed possible that some feature of the training in the DADTA was tapping frontal lobe function.

One significant feature of the DADTA is that the stimuli are randomly presented on any of sixteen response panels; that is, *their locations change over a considerable range from trial to trial.* By contrast, all of the studies reporting normal visual discrimination performance by monkeys with frontal lesions have used a hand-operated two-choice apparatus

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in which a pseudo-random sequence determines whether the correct stimulus will be on the left or on the right from trial to trial. In this apparatus *the locations of the stimuli are relatively stable.*

The purpose of the present study was to determine if the stability of the stimulus display is a relevant factor for monkeys with cortical ablations when they are learning to discriminate visual stimuli. The monkeys with frontal lesions who had shown a deficit in the DADTA together with the original control monkeys were given visual discrimination problems in the standard two-choice hand-operated Wisconsin General Testing Apparatus (WGTA). They were then reintroduced to the DADTA and given a problem in which the stimulus display remained stable, as in the WGTA, and an additional problem in which the stimulus display randomly shifted over the sixteen response panels. In addition, the effect of stability of the stimulus display was examined in monkeys with inferotemporal lesions since such monkeys are known to be impaired on visual discrimination problems.

METHODS

Subjects

Fourteen immature rhesus monkeys (*Macaca mulatta*) began this study as naive subjects (weight range at surgery was 2·8–3.6 kg). Three of these remained as normal controls (Group N), four sustained bilateral posterior parietal lesions (Group P), and seven sustained bilateral anterior frontal lesions (Group F). When twelve of these fourteen monkeys were trained as sophisticated adults (one monkey from each of Group N and Group F having died of intercurrent disease) during Phase 3 of the experiment (see below), four additional comparably sophisticated adult monkeys with bilateral inferotemporal lesions (Group IT) were included.

Surgery and histology

Prior to surgery all monkeys were tranquilized with Ketamine (11 mg/kg i.m.) and the anesthetized with intravenous sodium pentobarbital until eyelid reflexes were absent. An intravenous saline drip was maintained throughout surgery during which additional doses of pentobarbital were administered as required. Following surgery long-acting bicillin (300,000 U i.m.) was routinely administered. All ablations were performed as a one-stage bilateral aseptic procedure. For the frontal and parietal ablations the cortex was exposed by making a full calverium flap; for the inferotemporal ablations two openings were rongeured in the skull. The grey matter was removed by subpial aspiration using a 19-gauge Pribram sucker designed to avoid damage to underlying white matter. Bleeding was controlled by gentle packing with cottonoid patties or, rarely, electrocauterization. The dura was closed with individual silk sutures, and muscle, subcutaneous tissues, and skin were closed in layers. Dexamethasone (2 mg) was given immediately following surgery to the monkeys sustaining the frontal ablations.

The intended extent of the anterior frontal lesion included all of von Bonin and Bailey's [12] areas FD, FDγ, and FDΔ. Thus, it was to extend from the midline to the lip of the lateral surface through both banks of the sulcus principalis, and from the depth of the anterior bank of the arcuate sulcus rostrally to include the entire frontal pole.

The intended extent of the posterior parietal lesion included all of von Bonin and Bailey's areas PF, PG, PE, and the more dorsal portions of areas OA and TA on the lateral surface as well as PE and OA on the medial surface. Thus, on the lateral surface the lesion was to include the anterior bank of the lunate sulcus and to extend rostrally from the lunate through both banks of the dorsal portion of the superior temporal sulcus to include the posterior bank of the intraparietal sulcus. In addition, the lesion included a several-mm-square area superior to the intraparietal sulcus at the preoccipital notch as well as the anterior bank of the intraparietal sulcus at this level. The ventral limit of the lesion was defined by a line drawn from the tip of the intraparietal sulcus to a point several mm below the tip of the Sylvian Fissure and then directly in a line perpendicular to the lunate sulcus. On the medial surface the lesion was intended to extend ventrally almost to the calcarine fissure and was to include the anterior bank of the parieto-occipital sulcus and all of the tissue rostral to that sulcus for approximately 10 mm.

The intended extent of the inferotemporal lesion corresponded to area TE of von Bonin and Bailey. The lesion was to extend from a point several mm anterior to the ascending limb of the inferior occipital sulcus, usually marked by the vein of Labbé, continuing rostrally almost to the temporal pole, dorsally to include the depth of the inferior bank of the superior temporal sulcus, and ventrally to the occipito-temporal sulcus.

Following completion of behavioral testing, the monkeys were perfused intracardially under deep barbiturate anesthesia with saline and then 10% formalin, and the brains were blocked sterotaxically in the frontal plane. They were then hardened in formalin and 30% sucrose-formalin and, after they were embedded in

gelatin–albumin and frozen, 50 μm sections were taken in the coronal plane. Every tenth section was mounted and stained with cresyl violet for microscopic analysis of the lesions. Lateral, medial and ventral views of the lesions were reconstructed from enlarged tracings, using serial sections every one mm. The minimum and maximum extent of damage for the frontal, parietal and inferotemporal lesions are presented in Fig. 1. Reconstructions of individual brains are presented elsewhere [13, 14].

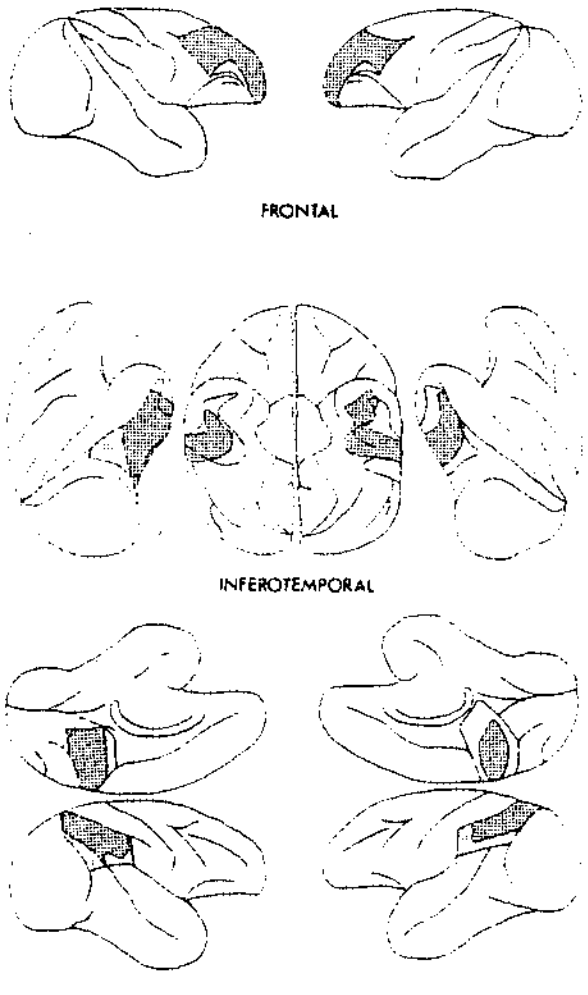

FIG. 1. Minimum and maximum extent of lesion in monkeys sustaining anterior frontal, posterior parietal, and inferotemporal ablations.

Apparatus

Both the automated PDP-8 computer-controlled DADTA and the hand-operated WGTA were used in this study. For training in the DADTA the monkeys were contained in a testing cage measuring 18 × 20 × 20 in., one side of which consisted of bars spaced at 1½ in. intervals. During testing the cage was placed in a small enclosure illuminated by a 15 W house light in the ceiling. The monkey faced a 20 × 20 in. square panel on which there was embedded a four by four regular array of clear round plastic push-panels 1 in. in dia. Microswitches mounted behind each of the response panels signaled the presses to the computer, and the stimuli were back-projected through these panels by IEE digital display projectors. The non-colored stimuli appeared as white patterns against a dark field. The sequence of stimulus location, the intertrial interval, and rewards were all controlled by the computer program, and the responses were recorded by teletype. A correct response caused the banana pellet food reward to be delivered by a mechanical feeder to a single food well centered just below the array of response panels.

For training in the WGTA the monkeys were contained in a testing cage identical to the one used in the DADTA. The monkey's compartment was illuminated by a 9 in. fluorescent light bulb which rendered a one-way vision door opaque to the monkey. This opaque door separated the monkey from the experimenter and the testing board, and was raised by the experimenter during testing to allow the monkey free access to the testing board positioned horizontally 6 in. above the level of the floor of the testing cage. The testing board was 28 in. long and 8 in. deep. The two food wells were spaced 15 in. from center to center and 3 in. from the center of the wells to the edge of the board facing the monkey. The stimuli were directly affixed to 3 in square plywood plaques painted a dull grey and attached via strings to the experimenter's edge of the board. These plaques served to cover the food wells during testing. Two sets of stimuli, a pair of objects and a pair of patterns were used. The objects were a red and yellow plastic tugboat, 4 in. in length, mounted diagonally on one plaque and a yellow and white pair of plastic soap bubble pipes, 4 in. in length, mounted criss-crossed together on the other plaque. The patterns, F(pos) ⋊(neg) were drawn in black ink on white matboard cut to exactly cover the plaques. The three lines making up the F and ⋊ patterns were respectively the same length and width. Raisins or apple cut into approximately raisin-sized pieces were used as rewards according to the monkey's preference.

Procedure

The problems for this study were trained in three phases. Groups F, P and N participated in all three phases. Group IT participated in Phase 3 only.

Phase 1. The naive monkeys began their training in the DADTA. Preoperatively, all monkeys were first shaped to respond selectively to lit panels on the sixteen panel array. They then learned to criterion a green (pos)/red(neg) color discrimination and its reversal. Criterion for these and all subsequent discrimination problems was 90 correct in 10 consecutive sets of 10 trials. Postoperatively, all monkeys were allowed to reattain criterion on the color discrimination in order to readapt themselves to the apparatus. They then began training on two new pattern discrimination problems: □(pos)/÷(neg) and 3(pos)/8(neg) in that order. For both the color and pattern two-choice discriminations the two stimuli appeared in random positions on the sixteen-panel array. These positions varied according to a pseudo-random sequence from trial to trial. One hundred trials with an 8 sec intertrial interval were given daily, 6 days a week, for all shaping and discrimination training in the DADTA.

Following completion of Phase 1 all 14 monkeys continued as subjects in a 3 yr study [10, 13] during which time they became sophisticated with both the apparatus and complex visual sequence and spatial problems. After completing the intervening study the monkeys were given one week's vacation and then Phase 2 was begun.

Phase 2. Phase 2 consisted of discrimination testing in the WGTA. Following a single day's shaping all monkeys were trained to a criterion of 90 correct out of 10 consecutive sets of 10 trials on two two-choice visual discrimination problems, using first the objects and then the patterns as stimuli. The object discrimination problem, boat(pos)/pipes(neg), was trained for 30 trials a day, 7 days a week. The pattern discrimination problem, F(pos)/ ⋊(neg), was trained for 50 trials a day, 7 days a week. For both problems the experimenter maintained an intertrial interval of approximately 7 sec. The position of the stimuli was varied pseudo-randomly according to a GELLERMANN [15] sequence. A modified correction procedure was used in which an incorrect trial was followed by another trial with the stimuli in the same position. However, on the fourth incorrect correction trial the monkey was permitted to self-correct and the following trial continued the Gellermann sequence.

Phase 3. The monkeys were reintroduced to the DADTA with one day of training on a shaping program. They were then given one discrimination problem using a stable display; that is, the stimuli, *(pos)/ *(neg), always appeared in the same two panels on the response panel array. These two panels were the center panels of the second row from the top. As in the WGTA (Phase 2) the position of the two stimuli on the two panels was varied pseudo-randomly according to a GELLERMANN [15] sequence, but a non-correction procedure was used. The monkeys were given 100 trials a day with an 8 sec intertrial interval until they attained the 90% criterion previously described. The monkeys were then given a second discrimination problem, 9(pos)/6(neg), using the random-position display; that is, as in Phase 1 the stimuli could appear on any two of the 16 panels. The same program that controlled the discriminations in Phase 1 was used for this final discrimination and the monkeys were trained to the same 90% criterion. This order of training applied to Groups F, P and N. Group IT learned the two problems in the reverse order, but in all other respects the training procedures were identical.

RESULTS

Phase 1

The monkeys with frontal lesions demonstrated a striking and unexpected impairment when they were trained as naive subjects on their first two pattern discrimination problems in the DADTA (Fig. 2, Table 1). A Kruskal–Wallis one-way analysis of variance by

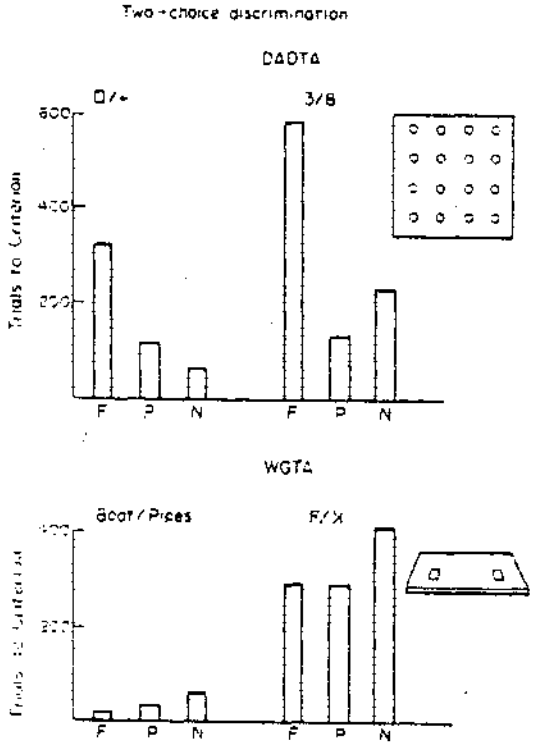

FIG. 2. Mean trials to criterion on visual discrimination problems trained in an automated (DADTA) and hand-operated (WGTA) apparatus by monkeys with frontal lesions (F), posterior parietal lesions (P), and normal controls (N).

ranks [16] for three independent samples yielded an $H = 7{\cdot}9$, $P < 0{\cdot}02$ for the □/+ and an $H = 7{\cdot}5$, $P < 0{\cdot}05$ for the 3/8, indicating that the groups differed significantly on both discrimination problems. Paired comparisons using the Mann–Witney U Test two-tailed for independent groups demonstrated that the significant differences were entirely due to the poor performance of Group F on both problems. For the first pattern discrimination, □/+, a comparison between Group F and Group P gave a $U = 3$, $P = 0{\cdot}021$ and between Group F and Group N gave a $U = 0$, $P = 0{\cdot}008$. For the second pattern discrimination, 3/8, the same respective comparisons gave a $U = 1$, $P = 0{\cdot}006$ and a $U = 3$, $P = 0{\cdot}058$. The performance of Group P was equivalent to that of Group N on both problems.

Phase 2

The monkeys with frontal lesions rapidly acquired both the object and pattern discriminations trained in the WGTA (Fig. 2, Table 1). In fact, the extremely good performance of these monkeys was in sharp contrast to their poor initial performance during Phase 1 in the DADTA. There were no significant differences between any of the groups on either the object or the pattern discrimination problem. The fact that Group F performed so well on the F/X discrimination in the WGTA was all the more surprising because both Groups N and P actually found this discrimination somewhat more difficult than the ones in the DADTA.

Table 1. Trials to criterion on visual discrimination problems trained in an automated (DADTA) and hand-operated (WGTA) apparatus

Lesion group	DADTA (Naive subjects) Pattern (□/+)	Pattern (3/8)	WGTA (Sophisticated subjects) Object (boat/pipes)	Pattern (F/Ж)
Normal				
N–Zld	70	230	60	400
N–Lns	30	170	20	220
N–Gld	90	240	100	620
x̄	63	213	60	413
Frontal*				
F–Clb	190	350	10	150
F–Dsc	120	160	20	220
F–Smn	390	360	30	380
F–Ali	260	920	40	320
F–Mdb	440	380	0	380
F–Pip	560	1560	—	—
F–Iss	320	340	—	—
x̄	326	581	20	290
Parietal				
P–Ths	150	60	50	340
P–Tag	40	300	10	230
P–Brc	50	10	20	330
P–Grf	230	130	40	250
x̄	118	125	30	288

*F–Pip was not trained in the WGTA. F–Iss died due to a metabolic disease before beginning Phase 2.

Phase 3

As sophisticated subjects the monkeys with frontal lesions learned the discriminations rapidly and with learning scores that completely overlapped those of the control subjects (Groups N and P) under both the stable and random-position display conditions in the DADTA (Table 2). However, despite this good performance there was still evidence that the random-position display disturbed the performance of Group F more consistently than it disturbed that of the control groups. All six monkeys in Group F took longer to reach criterion on the discrimination with the randomly positioned stimuli than on the discrimination with the stable display ($t = 2{\cdot}735$, $P < 0{\cdot}025$; one-tailed t test for correlated means). By contrast, the six monkeys in the control groups divided their preferences equally between the two discrimination problems; two of the four monkeys in Group P and one of the two monkeys in Group N learned the random-display discrimination even more quickly than they did the stable-display discrimination. The probability that all six monkeys in Group F would learn the random-display discrimination more slowly while half of the monkeys in the control groups would learn that discrimination more quickly is only 0·090 (Fischer Exact Probability Test, one-tailed; [16]).

The variable of stimulus position stability had a significant effect on the performance of monkeys with inferotemporal lesions which was opposite to the effect on monkeys with frontal lesions. As expected, the monkeys in Group IT were impaired in learning both pattern discrimination problems. But, in sharp contrast to the performance of Group F, each of the four monkeys in Group IT learned the discrimination with the random-position display considerably faster than the discrimination with the stable display (Table 2); the probability that this would occur by chance is 0·0625.

Table 2. Trials to criterion on two-choice pattern-discrimination problems presented in the DADTA under stable-position and random-position conditions by sophisticated monkeys

Lesion group	Stable-position (Patterns*/*)	Random-position (Patterns 9/6)	(Stable-position)–(Random-position) Performance
Normal*			
N-Lns	120	70	–
N-Gld	70	120	—
x̄	95	95	
Frontal			
F-Clb	60	70	–
F-Dsc	60	90	–
F-Smn	30	110	–
F-Ali	70	150	–
F-Mbd	70	260	–
F-Pip	110	370	–
x̄	67	175	
Parietal			
P-Ths	210	150	–
P-Tag	20	180	–
P-Brc	40	110	–
P-Grf	160	120	–
x̄	108	140	
Inferotemporal†			
IT-340	7858	1350	–
IT-391	2692	1300	–
IT-393	886	400	–
IT-407	1203	100	–
x̄	3160	788	

*N-Zld died with stomach bloat before beginning Phase 3.
†Data from these monkeys have been reported elsewhere [14, 17, 18].

DISCUSSION

The results from this study indicate that naïve monkeys with lesions of the anterior frontal cortex have a deficit on visual discriminations in which the stimuli are presented in randomly shifting positions from trial to trial. After they become sophisticated the deficit relative to normal monkeys disappears, but they still find a discrimination with the stimuli presented in stable positions easier than one with stimuli presented in randomly shifting positions. Thus, the data provide evidence that the lack of spatial stability in the DADTA display was affecting the performance of the monkeys with frontal lesions. These results are consistent with those from several other studies using the DADTA. GRUENINGER and PRIBRAM [19] reported that monkeys with frontal lesions were more distracted than normal monkeys by a distractor cue which shifted location from trial to trial. Furthermore, when the monkeys from the present study were trained on a series of complex spatial problems [10, 13], monkeys with frontal lesions were significantly impaired, *specifically* when the relevant stimuli shifted spatial position from trial to trial, but were not impaired when the stimulus display was constant from trial to trial.

Although each monkey in Group F learned the discrimination with the stable display faster than the one with the random-position display, they all learned both problems at a normal rate despite the fact that as naïve monkeys they had shown a striking deficit in

learning similar pattern discrimination problems. Apparently the sophistication they gained from the intervening study [10] enabled them to compensate for whatever difficulty was causing the earlier deficit. That study also had shown a significant effect due to sophistication. Only the naïve members of Group F were impaired relative to the control monkeys on visual sequence problems. The sophisticated monkeys in Group F demonstrated rapid, normal learning of the same problems.

The results of the present study are consistent with the conclusion of several concurrent studies [13, 20]: the frontal area seems to be particularly essential to the monkey's ability to impose organization on its stimulus input when the spatial aspects of the cues are unreliable. However, when the spatial position of the cue is only a distractor rather than a relevant cue to be discriminated, sophistication enables the animal to learn to ignore the shifting spatial context. Thus, when the unreliable spatial factor is a relevant part of the cue, as in delayed response, monkeys with frontal damage have a permanent impairment [4, 21] while the difficulty they have in learning visual discriminations in an irrelevant unstable spatial context decreases markedly with training.

In contrast, damage to the inferotemporal region does not impair the monkey's ability to impose organization on an unreliable spatial array. Rather, the continuously shifting spatial context seems to attract the attention of the monkeys with inferotemporal lesions to the stimuli, resulting in improved performance. Some earlier data also tend to support this hypothesis. Unlike normal monkeys, monkeys with inferotemporal lesions were unable to learn to fixate the positive stimulus in a display composed of two visual patterns [22]. However, after the stimuli were mounted on a disc and rotated, additional training enabled these monkeys to track the positive pattern at least 75% of the time each session. Data from one of the earlier studies [17] using the same four monkeys in Group IT of this study suggest that flickering stimuli as well as moving stimuli increase the ability of monkeys with inferotemporal lesions to attend to patterned stimuli. In that study a 60 Hz flicker was created by rapidly turning the stimulus bulbs on and off. All four monkeys in Group IT learned a 3/8 pattern discrimination faster under the flicker condition while all four normal controls learned the discrimination faster under the steady illumination condition. A Fisher Exact Probability Test indicates that this distribution of scores between Group N and Group IT is unlikely to occur by chance ($P = 0{\cdot}028$, two-tailed).

In summary, monkeys with anterior frontal lesions find it difficult to compensate for a shifting spatial context during visual discrimination problems, but the same shifting context serves to attract the attention of monkeys with inferotemporal lesions and paradoxically allows improved performance.

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Résumé :

On a entrainé des singes rhésus avec lésions antérieure frontale (N = 7), pariétale postérieure (N = 4), et inféro temporale (N = 4) et des contrôles normaux (N = 3) sur des problèmes de discrimination visuelles sous des conditions dans lesquelles la présentation du stimulus restait à la même place ou se déplaçait aléatoirement sur une grande quantité de positions d'essai en essai . Les singes naïfs avec lésions frontales étaient significativement déficitaires dans l'apprentissage des discriminations sous la condition de déplacement du contexte spatial; leur trouble disparaissait à mesure qu'ils étaient habitués à la tâche mais ils continuaient de trouver cette condition plus difficile que celle dans laquelle la présentation restait fixe. La performance des singes avec lésions inféro temporales étaient nettement améliorée par la condition de présentation avec position aléatoire du stimulus.

Deutschsprachige Zusammenfassung:

Rhesusaffen mit vorderen frontalen (N = 7), hinteren parietalen (N = 4) und inferotemporalen (N = 4) Läsionen sowie normale Kontrolltiere (N = 3) wurden darauf trainiert einen optischen Diskriminationstest zu lösen unter den Bedingungen, daß der Reiz entweder am gleichen Ort blieb oder von Versuch zu Versuch seine Lage änderte. Nicht trainierte Affen mit frontalen Läsionen waren signifikant unfähig das Diskriminationsproblem zu lösen, wenn der räumliche Context wechselte. Dieser Mangel verschwand nach Training, es blieb aber auch in diesen Falle eine größere Erschwerung als wenn der Reiz am gleichen Ort blieb. Die Leistung von Affen mit inferotemporalen Läsionen war deutlich besser unter zufällig verschiedenen Reizpositionen.