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OBJECT PERMANENCY AND DELAYED RESPONSE AS SPATIAL CONTEXT IN MONKEYS WITH FRONTAL LESIONS

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Abstract—Frontally lesioned monkeys (*Macaca fascicularis*) were significantly impaired relative to controls on a task (similar to that used by Piaget to test the development of object permanency) which required subjects to retrieve a grape hidden under one of three baskets. All monkeys with such lesions completely failed to reach criterion on an additional set of tasks in which the baskets were moved (i.e. the spatial context was modified) while controls performed these tasks with relative ease. Both deficits were shown to be attributable to an inability of "frontal" monkeys to process a varying spatial context.

INTRODUCTION

IT HAS now been almost a half century since JACOBSEN discovered the special relationship between resections of the anterior frontal cortex of non-human primates and the delayed response task. During this period the task has been used to good advantage to clarify the role of frontal cortex (c.g. MALMO, WADE, PRIBRAM, STAMM and ROSEN, KUBOTA and NIKI [1-5]. However, despite several attempts (e.g. MEYER, MISHKIN and PRIBRAM [6, 7] to experimentally analyze the meaning of the delayed response test, our understanding of the task has progressed little beyond that of its inventor. HUNTER [8] had devised the procedure to investigate whether animals and children could form "ideas" that would bridge a temporal gap and so allow appropriate responding in the absence of a specific cue.

It occurred to us that this initial formulation had a great deal in common with one of Piaget's which he termed "object constancy". PIAGET [9] had developed a graded series of tasks as tests of the object constancy concept which resembled to some considerable extent the delayed response procedure (Table 1). Both involve the hiding of an object which a

Table 1. Stages in the development of the object concept

Stage	Time	Description
Stages 1 and 2	0-4 months	sucking reflexes; transient images;
Stage 3	4-10 months	primary circular reactions interrupted prehension;
Stage 4	10-12 months	secondary circular reactions coordination of secondary schemes; retrieval of hidden object
Stage 5	12-18 months	sequential displacements
Stage 6	18-24 months	invisible displacements

subject is required to subsequently retrieve. Despite this patent similarity, nothing had been done to bring together the two experimental traditions that have grown up around these procedures (PRIBRAM [10]).

We felt therefore that understanding might be enhanced within both traditions if we could "monkeyfy" the games played by Piaget with his children. We chose 3 tasks which signified the fourth, fifth and sixth stages in attaining the object concept since they displayed the most essential features of the delayed response task.

In addition we modified these tasks to explore their relationship to the concept "context dependency" which one of us (PRIBRAM [11, 12]) had developed for frontal lobe function on the basis of its singular relationship to the delayed response test. Context dependent behavior is defined as that which must vary as a function of the context in which it occurs—i.e. behavior which is not guided by the invariant properties of some environmental cue. The modifications of the task were readily made and presented us with the possibility of inquiring whether the delayed response deficit indicated a loss of object constancy or an inability to deal with context dependent processes. The results of the experiment indicate that this was an inappropriate question: object constancy and context dependency turn out to be related conceptualizations.

METHODS

Subjects

The subjects were 10 mature iris monkeys (*Macaca fascicularis*) ranging in age from approximately 3 to 7 yr and weighing 3.0–6.8 kg. Seven of the animals (the frontal group) had received frontal lobectomies about 2 yr previous to the experiments reported here. Single-stage bilateral subpial resection of dorsolateral frontal cortex extending from the arcuate sulcus to the lip of the lobe and including the frontal pole was performed on 3 of the 5 males and 4 of the 5 females. Recovery from surgery was uneventful. Anatomical reconstruction of the lesions is presented in another report (PRIBRAM, PLOTKIN, ANDERSON and LEONG [13]). All animals had been trained intensively on delayed alternation tasks in an automated apparatus, DADTA IV (PRIBRAM, DAY and GLICK [14]; DRAKE and PRIBRAM [15].) They were maintained on a standard diet of Purina monkey chow and obtained all their fruit in the test situation.

Apparatus

Testing for the present experiment was done in a modified Wisconsin General Testing Apparatus (WGTA) in a darkened, sound-shielded room. Instead of the usual opaque screen separating the subject from the experimenter, a piece of clear plexiglass was used that could be raised and lowered by the experimenter to allow the monkey access to a sliding tray 8 in. by 28½ in. Three wicker-type baskets, 3 in. in dia and 1 in. high, were inverted and placed 8 in. apart on the tray (which contained no foodwells). Beneath these baskets the reward (one green seedless grape) was placed. A black curtain, hung 2 ft in front of the plexiglas window and the animal's cage (20 × 20 × 18 in.), left only the experimenter's hands visible to the subject during the baiting procedure.

Procedure

Pretraining. All subjects were first trained to accept grapes from the tray without the imposition of the plexiglas window and without their being hidden under a basket. Grapes were then placed on the tray with the window down; the monkeys were required to take the reward when the window was raised. They were then trained to retrieve grapes from under a single basket, and finally, to retrieve grapes that had been planted under that basket while the window was down.

Active search for hidden objects (Piaget's Stage 4). Each trial began with the tray 4 in. from the plexiglas window. All manipulations of the baskets and the grape were visible to the monkey through the plexiglas. According to a random sequence, one of the three baskets was lifted a few in. above the tray by the experimenter, and a grape was placed beneath a basket. The instant the basket was placed over the grape, the experimenter simultaneously pushed the tray forward to the subject and raised the plexiglas window. The animal was then allowed to select a single basket (Fig. 1). If he selected the basket containing the grape the response was scored as correct. Choosing any other basket was an error. The trials were presented in sets of 20 trials/day. Criterion was 95% correct on one set of trials of 90% correct over two sets of trials. Upon achievement of criterion the subjects graduated to the next task.

Visible displacement (Stage 5a). This procedure was similar to that of the previous task except that the food object was hidden under the same basket for two consecutive trials. On the third trial, the grape was

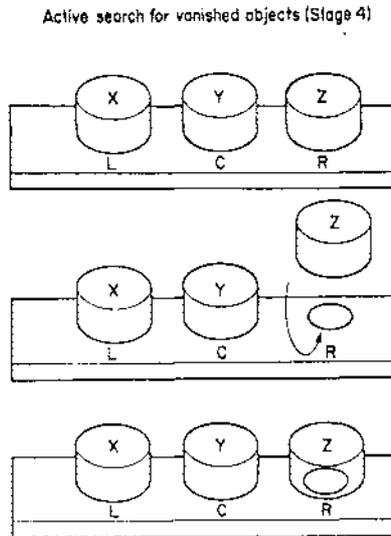


FIG. 1.

hidden first under the same basket as in the two previous trials and then removed and within full view of the monkey hidden under one of the other baskets. Only the third of each triplet of trials was scored. The subject was tested on 7 such triplets/day. The criterion was 6 out of 7 third trials correct.

Sequential displacements (Stage 5b). This procedure was identical to that of Stage 4 except that following initial concealment the basket was lifted, and within full view of the monkey the grape was moved and concealed under a second basket, and similarly, under a third, whereupon the window was lifted and the tray pushed forward to the animal. The criterion was the same as for Stage 4.

Invisible displacements (Stage 6). A small paper cup was inverted and placed over the grape and this combination hidden under a basket. The cup-grape combination was then treated as was the grape-alone in Stage 5. To insure total continuous concealment of the grape, the paper cup was slid along the tray when being moved from one basket to another. The criterion was the same as that of the Stage 4 task.

Transient context modification (a) single displacement. This is essentially the well known "Shell game". A grape was placed under one of the baskets. Then, within full view of the monkey that basket was lifted while another of the baskets was carried from its position and placed over the grape. This second basket was then slipped back to its original position with the grape under it, and the first basket was put back down so that all the baskets were returned to their initial positions (Fig. 2). Immediately the plexiglas was raised and the tray pushed forward. The criterion for this and all other context dependent tasks was the same as for the Stage 4 task.

Transient context modification (b) double displacement. Two operations such as that described for the preceding task were performed before the plexiglas window was raised. In full view of the monkey, the grape was hidden under a basket, captured by a second basket, and captured from the second by either the third basket or the original.

Permanent context modification (a) single displacement. A grape was placed under one of the baskets and that basket was switched with one of the other baskets by interchanging the baskets by sliding them in opposite directions. The grape continued to remain hidden under the original basket, but the baskets exchanged positions.

Permanent context modification (b) double displacement. Two operations such as that described for the preceding task were performed before the plexiglas window was raised. Each trial consisted of two switchings of the baskets while the grape remained hidden under the original basket.

Three-color discrimination. Three differently colored cups (red, yellow, blue) were used. Unlike the previous tasks, the red cup was invariably baited out of the subject's view, behind a black curtain. Then the tray was pushed forward and the plexiglas raised.

RESULTS

Active search for vanished objects (Stage 4). The subjects in the normal group achieved criterion on this task in 80 trials or less. The monkeys with frontal lesions divided into two

Transient context modification (a) single displacement

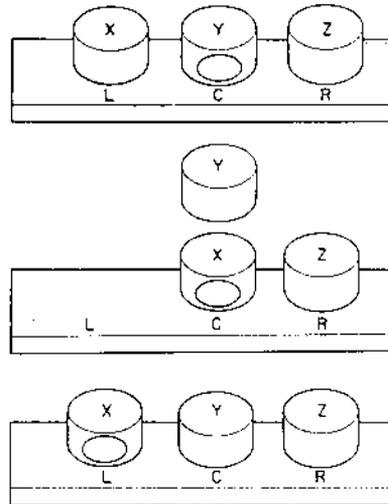


FIG. 2.

groups. Frontal Group I was run first on the Stage 4 task and then, after the other Piaget-type tasks, on the transient context modification task. Although 3 of the 4 subjects in this group obtained criterion within 500 trials, they took an average of 380 trials. There was thus a significant difference between this group and the normal group on the task (one-tailed Mann-Whitney U test, $P < 0.05$ for $U = 0$, $P = 0.028$). For Frontal Group II, consisting of 3 monkeys, the task order was reversed with the transient context modification task first, followed by the Stage 4 task. The subjects in this group took an average of 336 trials to reach criterion on the Stage 4 task. Thus the scores of all monkeys with frontal

Active search for vanished objects (Stage 4)

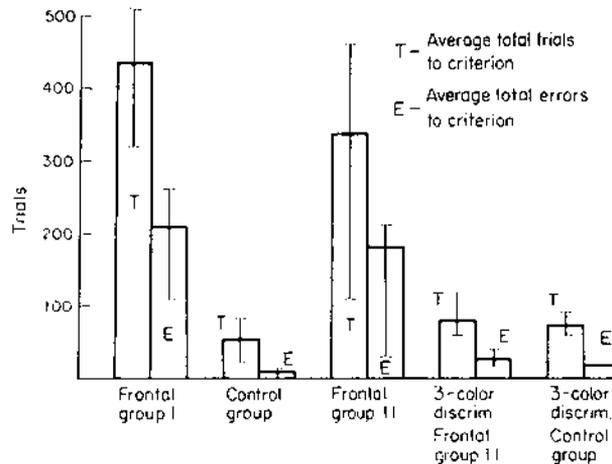


FIG. 3.

lesions differed from their controls (one-tailed Mann-Whitney U test, $P = 0.008$) irrespective of the order in which they were trained on this task. Table 2 and Fig. 3 show the scores and averages of the performances on this task of the three groups of monkeys.

Visible displacement (Stage 5a). Although the unoperated control group did a little better than either of the frontal groups, the difference was not statistically significant (Table 2).

Sequential displacements (Stage 5b). The control group did a little worse than the frontal group on this task due to the difficulty one of the normal monkeys had with the task. The

Table 2. Trials (T) and Errors (E) to criterion on Piagetian tasks

		Stage 4		Stage 5a		Stage 5b		Stage 6	
		T	E	T	E	T	E	T	E
Control group	HEN	40	10	7	1	60	8	20	1
	GRO	80	16	21	5	220	56	20	1
	PON	20	1	7	0	20	0	20	0
	X	47	9	12	2	100	21	20	1
	PAT	440	191	21	5	60	11	60	13
Frontal group I	GRI	320	125	6	1	180	40	40	5
	WHI	380	147	77	30	20	2	20	2
	PET	500	260	—	—	—	—	—	—
	X	410	181	35	12	87	18	40	7
	JER	500	207	—	—	—	—	—	—
Frontal group II	NAM	400	189	—	—	—	—	—	—
	FRI	108	24	—	—	—	—	—	—
	X	336	104	—	—	—	—	—	—

other 2 normal monkeys achieved criterion within 40 trials (Table 2). There were no statistically reliable differences between group performances.

Invisible displacements (Stage 6). All monkeys achieved criterion on this task within 60 trials and there were no statistically significant differences between group performances.

Transient context modification (a) single displacement. Normal monkeys all achieved criterion in 80 trials (Fig. 4). Both Frontal Group I and Frontal Group II were unable to

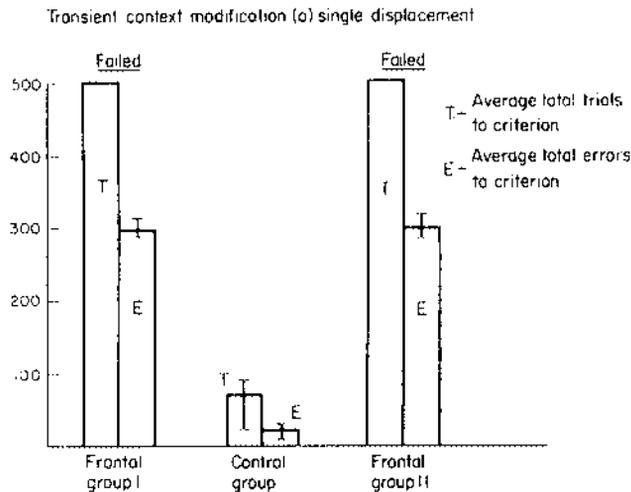


FIG. 4.

do this task in 500 trials and were performing at the 50% level when testing was terminated. (Comparing all monkeys with frontal resections with their controls shows them to differ significantly—one-tailed Mann-Whitney U test, $P = 0.012$.) Usually monkeys with frontal lesions responded to the basket under which the grape had been initially hidden. However, when the grape was moved from one of the two extreme lateral positions to the other, the operated subjects often chose the center basket.

Transient context modification (b) double displacement. Normal monkeys achieved criterion within 40 trials (Table 3). The monkeys with frontal resections were not run

Table 3. Trials (T) and Errors (E) to criterion on context modification tasks

		Transient context mod. (a)		Transient context mod. (b)		Permanent context mod. (a)		Permanent context mod. (b)	
		T	E	T	E	T	E	T	E
Control group	HEN	60	16	20	1	40	4	40	7
	GRO	80	21	40	6	340	127	140	27
	PON	80	15	20	0	40	5	120	32
	X	73	17	27	2	140	45	100	22
	PAT	500	277	—	—	—	—	—	—
Frontal group I	GRI	500	302	—	—	—	—	—	—
	WHI	500	260	—	—	—	—	—	—
	X	500	280	—	—	—	—	—	—
	JER	500	288	—	—	—	—	—	—
Frontal group II	NAM	500	295	—	—	—	—	—	—
	FRI	500	317	—	—	—	—	—	—
	X	500	300	—	—	—	—	—	—

systematically as they had not mastered the simpler task. However, attempts with several subjects showed that this task was hopelessly difficult for them.

Permanent context modification (single and double displacements). The normal monkeys achieved criterion on each of the two remaining tasks within 340 trials and the monkeys with frontal lesions were not run on these difficult versions.

Three-color discrimination. There was no difference between the performance of Frontal Group II and the normal group on this task. Subjects reached criterion within 120 trials.

DISCUSSION

The results of these experiments indicate that resection of the frontal cortex of monkeys impairs performance on an initial task designed to test whether they can respond to the "permanency" of an object which is no longer within sight. The initial deficit is present (in both frontal groups) irrespective of whether the task presented is the first such test or whether training on other problems had been given. The results also show that after such an initial deficit, once the monkeys have grasped the "concept", they readily master subsequent problems of this sort.

The results of the experiments also show that resection of the frontal cortex of monkeys decisively and, within the limits of testing, permanently impairs their ability to perform tasks designed to test performance of behavior which depends for its appropriateness on the context in which it occurs.

At first, therefore, we felt that we had demonstrated two separate deficits to follow frontal cortex resections in monkeys: one, a moderate difficulty in reaching the concept of

object permanency; the other a more profound loss in the ability to perform context dependent behaviors. Further analysis, however, convinced us that these deficits were in fact one and the same.

According to PIAGET [16], one has the object concept if one has the understanding that certain things exist independently of one's own experiences and actions, and these things have a permanence and substance of their own. In his researches, Piaget discovered that the object concept does not exist in the child full-blown at birth, but develops as the child matures. He distinguished 6 stages in the development of the object concept, and developed tests to determine whether a child had achieved each of these stages. During the first 2 stages of development until about 4 months of age, children's behavior is primarily reflexive in nature, and their visual experience is composed solely of transitory images. When things come into the infant's field of view, they exist and the infant responds; when they leave, for the infant, they cease to exist. (Note the similarity of this description to JACOBSEN's [17] description of his monkeys with frontal resections. "It is as if 'out of sight, out of mind' were literally applicable.") At the third stage of development the child will continue an activity that is involved with an object (e.g. grasping a ball) even after the child loses the object (if he drops the ball, he continues grasping—interrupted prehension). The child at this stage does not initiate any novel or search behavior to find the missing object. Piaget tested Stage 4 development by hiding an object of which the child was fond under chairs, cushions, hats, etc. while the child watched. The child was then allowed to retrieve the object. If the child generally could retrieve the object, he was judged to have reached Stage 4.

We attempted to mimic Piaget's test for Stage 4 and the more advanced Stages 5 and 6 (which involved movements or displacements of objects) in the WGTA with monkeys. The plexiglas window was used to prohibit the animals from finding the basket covering the grape by simply reaching for the grape as it was hidden and following the rule, "lift the basket I am reaching for". Thus without the glass the task would be a Stage 3 task with the monkey only required to perform an interrupted prehension; he would not be required to distinguish clearly between his own act and the object, as is required by Stage 4. One important difference between our experimental set-up and that of Piaget was that the baskets we used as obstacles under which to hide the grapes had no differentiated markings, whereas Piaget's obstacles (chairs, cushions) could be distinguished by their pattern. This was done as a concession to the delayed response paradigm.

Pretraining. Even in their initial training the frontal group appeared to be deficient with respect to the control group in terms of the object concept. Normal animals from the very beginning were very careful in overturning the basket so as not to knock the grape off the tray. Monkeys with frontal lesions, on the other hand, were very careless and usually hit or knocked the basket instead of picking it up. When they did manage to pick up the basket, they often registered surprise on discovery of the grape.

Active search for vanished objects (Stage 4). All previous studies using the delayed response set up with no delay interval and no dropping of the opaque screen had found no frontal deficit (HARLOW, DAVIS, SETTLAGE and MEYER [18], BATTIG, ROSVOLD and MISHKIN [19], PINSKER and FRENCH [20]). We therefore hypothesized that there would be no deficit on this task and we expected that Stages 5 and 6 involving displacements would reveal a deficit. Contrary to our hypothesis, however, the frontals had quite a sizeable deficit on the initial stage. This disagreement with previous studies is probably due to either our use of three baskets instead of the usual two and/or the use of the plexiglas window rather than

having air and bars intervening between monkey and tray. PINSKER and FRENCH [20] found no deficit in their frontal group using a clear screen; the task, however, was indirect delayed response and the frontal group had preoperative training). The window came down close to the bars of the cage, prohibiting the subject from reaching out toward the correct basket during the baiting phase.

Since the normal animals had no trouble with this task while the operated animals had great difficulty, it appears that monkeys with frontal resections do have a deficiency in the acquisition of the object permanency concept. This finding is consonant with the fact that myelination of the connections of the anterior frontal cortex is delayed until approximately 20 yr when their ability to handle object permanency becomes well established.

However, this deficiency in the object permanency concept cannot simply be attributed to a failure of the monkeys with frontal resections to map the vanished object. Neither the state of mind of the infants tested by Piaget nor the processing deficit of our monkeys can be properly described as "out of sight, out of mind". BOWER (BOWER and WISHART [21]) in a recent critique of Piaget's studies of object permanency demonstrated that infants who were unable to retrieve an object hidden under an occluding object could reach out for and grasp an object first hung in total darkness. Similarly, MALMO [1] showed that monkeys with frontal lesions could do delayed response if the experimental set up was kept in the dark except for illuminated food cups.

These results suggest an alternative characterization of the difficulty of both the infants and monkeys with frontal lobe lesions. Both appear less able than normal adults to ignore irrelevant features of the context within which an object is being hidden and thus are prevented from focusing in on features essential to encoding the continued existence and position of the object. In the experiments with children both the occluding object and the other objects in the test room act as distracting features of the context. For monkeys with frontal lesions, the occluder, screen (whether clear or opaque), and other parts of the apparatus as well as the basket itself may act as distractors.

In an experiment to test the impact of distractors on monkeys with frontal lesions, GRUENINGER and PRIBRAM [22] showed that such animals were more susceptible to distraction than control subjects and that the enhanced distractibility was especially marked for spatial cues. In the present experiment the contextual cues were spatial and therefore can be assumed to be especially potent for the frontally lesioned group. Our conclusion, therefore, is that the tests of object permanency which we modelled after Piaget's tests uncovered an impairment in the ability to withstand distraction from the spatial context in which the object appears and disappears.

Transitory context modification (a) single displacement. The spatial context hypothesis is given further support by the utter failure of both frontally lesioned groups, irrespective of the order of presentation of task, on a series of tasks (unlike any used by Piaget to test sensorimotor development) which involved moving the baskets with a grape concealed beneath one of them. Since in these tasks the baskets provide a context within which the grapes are moved and hidden, it seems appropriate to consider these new tasks as involving modification in context.

The frontally lesioned monkeys were foiled by one simple manipulation of the context—moving the basket to capture a grape from under another basket. At 500 trials the frontalized monkeys still showed no signs of learning the task. The normal monkeys had little difficulty. Since it took about 2 sec to perform the operation and lift the screen it might be objected that this deficit is due to the time interval. However, BATTIG, ROSVOLD and MISHKIN [19] found that frontalized monkeys could learn screenless delayed response with a 5-sec

interval in 300–700 trials a day. The explanation for the inability of the frontalized monkeys to reach criterion on the transitory context modification task must, therefore, be sought in other factors than the time interval. A more likely explanation is that frontally lesioned monkeys are not able to encode changes in spatial context (perhaps because they are distracted by them) that must be noted in order to find the grape.

On all of the tasks involving manipulations of the context normal animals had little difficulty. The fact that the normal animals could perform even the more difficult of these tasks so readily and the monkeys with frontal resections could not even begin to perform them, further emphasizes the deficit of the operated monkeys on tasks involving modifications of context.

In conclusion, therefore, we feel that the results of these experiments suggest that the performance of the delayed response task involves the ability to process a varying spatial context upon which appropriate behavior depends.

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Résumé :

Des singes (*Macaca Fascicularis*) avec lésions frontales se révélèrent déficitaires de façon significative par rapport à des contrôles sur une épreuve (similaire à celle utilisée par Piaget pour examiner le développement de la conservation de l'objet) qui réclamait des sujets de retrouver un raisin caché sous un des trois paniers. Tous les singes avec de telles lésions échouaient totalement à atteindre le critère sur un ensemble additionnel d'épreuves dans lequel les paniers étaient déplacés (c'est-à-dire avec modification du contexte spatial) tandis que les singes contrôles accomplissaient cette épreuve avec une facilité relative. On montre que les deux types de déficits peuvent être attribués à l'incapacité des singes "frontaux" de traiter les variations d'un contexte spatial.

Deutschsprachige Zusammenfassung:

Affen mit frontalen Läsionen waren Kontrolltieren gegenüber signifikant schlechter bei der Lösung von Testaufgaben, bei welchen eine Traube gesucht werden mußte, die unter einem von 3 Körbchen versteckt war. (Die Versuchsanordnung entsprach etwa der wie sie PIAGET bei Prüfung der Entwicklung einer Objektkonstanz anwandte). Alle Affen mit solchen Läsionen versagten auch vollkommen bei einem zusätzlichen Test bei dem die Körbchen an einen anderen Ort versetzt wurden. In diesem Falle wurde der räumliche Context verändert. Kontrolltiere lösten diese Tests relativ leicht. Beide Versagenszustände wurden als Ausdruck dessen angesehen, daß frontale Schädigung bei Affen zu einer Unfähigkeit führen, Aufgaben mit wechselndem Raumcontext zu lösen.