Effects of Spatial Separation of the Conditioned Signal from the Reinforcement: A Demonstration of the Conditioned Character of the Orienting Response or the Orientational Character of Conditioning

ENDRE GRASTYÁN and LAJOS VERECZKEI[*]

Institute of Physiology, University Medical School,
Pécs, Hungary

When a continuously reinforced approach response in cats was brought under the control of a discriminative acoustic stimulus (CS) presented behind the starting place in a straight runway or T maze that is spatially separated from the reinforcement area, several behavioral and hippocampal electrical changes took place. After about 50-100 reinforcements, an ever increasing orienting-approaching tendency toward the acoustic CS appeared and began to interfere with and temporarily suppress the goal response. Simultaneously with this, some of the animals, although hungry, also refused to accept food in the experimental situation. After hundreds of additional trials, the approach response to the goal gradually reappeared, but the persistence of a quick, phasic orienting response toward the signal was observed during the whole course of conditioning. At the time of the emergence of this conditioned orienting response (COR), the CS elicited high amplitude and slow theta rhythm in the hippocampus; in the final stage of conditioning desynchronization was elicited.

These findings suggested that, as a consequence of reinforcements, the CS became a new goal and the interference between the orienting and goal responses corresponded to a competition between two goal responses. Evidence is cited to show that similar manifestations occur in any kind of learning and that spatial discontiguity is a proper method to unveil and amplify them. Based on these considerations and on the persistence of the orienting response during conditioning, the proposal is made that the conditioned orienting response is the real conditioned response. The implications of this hypothesis are discussed in the context of classical and instrumental conditioning.

INTRODUCTION

It is an old observation in classical conditioning that spatial separation of the conditioned signal (CS) and the unconditioned stimulus (US) may delay or even prevent the establishment of conditioned responses (CR) (Liddell *et al.*

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1934). Similar difficulties are caused by spatial separation of the cue and the reinforced response in instrumental conditioning (McClearn and Harlow, 1954; Murphy and Miller, 1955, 1958; Miller and Murphy, 1956, 1964). Curiously enough, the question of why spatial separation of stimuli causes difficulties in learning has not been explicitly raised as yet. Perhaps because spatial contiguity, like temporal contiguity, was assumed to be an indispensable and self-evident condition of learning. Or perhaps it was assumed that spatial separation necessarily interferes with temporal contiguity.

This latter assumption becomes more plausible with the observation that in most of the cited studies, the stimuli used were visual cues. In this case, spatial separation might indeed result in temporal separation, either because the distance between discriminative and reinforcing stimuli can physically prevent their simultaneous action, or because attention directed selectively to one of these stimuli prevents the perception of the other. The development of a material trace in the brain in the course of learning presupposes the temporal coexistence of the neural processes set up by the corresponding stimuli. For this reason, temporal contiguity is an indispensable condition of learning. Temporal contiguity is, however, not necessarily precluded if the spatially discontiguous CS is an acoustic stimulus. Therefore, in this case we might expect the occurrence of conditioning of the usual goal response.

The findings of the present study apparently corroborate this expectation. The experiment was originally devised to insure better conditions for recording the behavioral and hippocampal electrical correlates of orienting responses occurring in the early stage of conditioning (Grastyán et al. 1959). Free instrumental approach responses were elaborated in cats in a straight runway and a T maze and then brought under the control of a discriminative auditory stimulus. In order to separate the effects of the stimuli of the goal from those of the CS, the latter was placed at the starting place of the situation. Essentially, it was found that even such an extreme spatial separation of signal and reinforcement did not prevent the establishment of discriminative approach responses. However, conditioning did not proceed without troubles.

After a certain number of reinforcements, a gradually increasing orienting-approaching tendency to the CS appeared, began to interfere with the goal response, and finally completely suppressed it. This conflict could only be overcome with several hundreds of additional trials. That finding clearly indicated that the difficulties of learning occurring under the conditions of separation of discriminative and reinforcing stimuli cannot be simply reduced to the problem of temporal contiguity.

Spatial discontiguity, although a highly unnatural learning situation, proved to be useful in the present study in revealing some important characteristics of the orienting response usually hidden by spatial contiguity. These characteristics, in addition to explaining the paradoxical effects of

spatial discontiguity, also offered a complete reinterpretation of the role of the orienting response in learning.

METHODS

Subjects. Twenty-one adult cats of both sexes and two 6-week-old cats were used. An approach reaction was established in 17 animals and an avoidance response in four animals. Electroencephalographic activities of hippocampal, hypothalamic, and some neocortical structures were recorded in 9 animals.

Apparatus. The food-reinforced instrumental approach response was elaborated in a straight runway in one group and in a simple T maze in another group of animals (Fig. 1). The straight runway consisted of a 2-m-long, 50-cm-wide, and 80-cm-high corridor. The longer arm of the T maze was 2 m, its shorter arm 1.5 m; the rest of its dimensions were identical with those of the straight runway. Both were light-gray solid panels, except for a clear Lucite wall permitting direct observation of the animal. Both cages were brightly lit by two 100-W bulbs fixed to the ceiling of the cage. The experimental room was dark to minimize external stimuli.

A silent, automatic feeding device, also controllable by the experimenter, was fixed to one of the narrower endwalls of the straight alley, and two feeders were fixed to the ends of the shorter arm of the T maze. Stepping on the cover of the food delivery device delivered a pellet (usually 5 g) of raw meat or liver in a little dish which appeared in the opening of the cover. An elevated starting platform (30 cm high and 50 cm long) was located on the wall opposite the feeding device in the straight runway and in a corresponding place in the longer arm of the T maze.

Loudspeakers were placed above each feeding device on the wall behind the starting platform and at the midpoint of the long arm of the runway. The acoustic CS was produced by a pulse generator through any of these sources, according to the particular experimental requirements.

The avoidance apparatus was built by a transformation of the straight runway. The floor in front of the platform was covered with a metal grid for the administration of electric shock. The grid sector and the platform were separated by a guillotine door. Stepping on a pedal below the door during the presentation of the CS opened the door, stopped a timer for latency from CS onset, and allowed the animal to escape from the grid onto the platform. The CS was presented through the wall loudspeaker at the end of the platform opposite to the grid and the guillotine door.

EEG. Usually four or six pairs of recording electrodes were chronically stereotaxically implanted in the dorsal and medial regions of both hippocampi as well as lateral and medial regions of the hypothalamus. In some
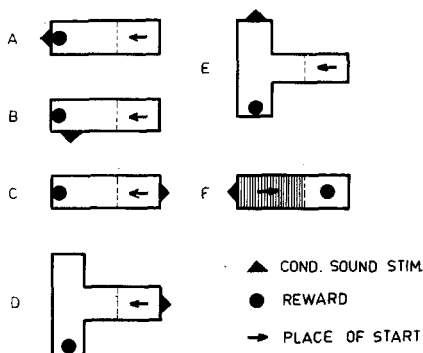
Fig. 1. Sketches of the spatial arrangements of loudspeaker, reinforcement, and place of start in the runway and the T maze. A-E: approach situations. F: avoidance situation, where the shaded area corresponds to the electrified grid and the area with the shaded circle to the platform.

cases, electrodes were also placed over the somatomotor and auditory cortices. The recording electrodes consisted of pairs of 0.2-mm-thick steel needles insulated except for a 0.5-mm tip, with a tip separation of 1 mm, connected via a light, flexible cable not interfering with movement to an 8-channel EEG machine and a two-channel oscilloscope. The experiments began after full recovery from surgery, usually 3–4 weeks postoperatively.

Conditioning procedures. Conditioning with spatially contiguous conditioned stimuli (CS) was essentially identical with the conventional procedures: reinforcement with food was contingent upon approach to the feeder from a fixed starting place during the presentation of a discriminative sound stimulus (Fig. 1A and B). The discrimination was assumed to reach criterion when the number of intertrial responses became smaller than 10% of the elicited responses.

Conditioning with spatially discontiguous conditioned stimuli (DisCS) was carried out in separate steps in both the straight alley and the T maze (Fig. 1C and D). Before the onset of training, the animals were kept in the experimental situation for 1 or 2 hr on several subsequent days. The behavioral and electrographic effects of the stimuli to be used as conditioned signals were checked in this habituation period. Afterwards, the animals were taught to secure food from the feeding device either by spontaneous exploratory activities or with the help of the experimenter. Following the consumption of food, the animal was returned to the starting platform, and only those approach reactions which were initiated from the platform were reinforced with food. With this procedure, a stable spontaneous return to the starting platform usually appeared in two or three experimental sessions of 20–25 trials each.

With the exception of two cases, the DisCS was consistently applied from the very beginning of training. In the first stage of conditioning, the DisCS was presented during spontaneous approach responses. These were gradually transformed into discriminative responses by omitting reinforcement after approach responses performed in the absence of the DisCS. Intertrial periods varied randomly between 0.5 and 3 min. The duration of the DisCS depended on the animal's behavior: it was consistently terminated at the moment of presentation of food. In all approach conditioning, the DisCS consisted of a 10-sec click stimulus with an intensity well above the hearing level but not unpleasant.

In the case of avoidance conditioning (Fig. 1F), the DisCS was a continuous 400-Hz tone. Release of the guillotine door within 10 sec of tone presentation made the shock avoidable. Reaching the safe end automatically terminated the DisCs.

RESULTS

Conditioning with the conventional CS. Although the behavioral mani-festations occurring in such situations were well-known from our earlier studies, additional measurements, mainly of temporal behavioral parameters, were required to provide a reliable control for the experiments conducted with DisCS.

After 2-4 daily sessions of 20-30 trials each, the animals spontaneously returned to the starting place and usually reached the criterion of discriminated response.

A strong orienting-exploratory tendency toward the source of the CS was displayed during the initial 20-30 trials. Under the condition of partial spatial discontiguity (Fig. 1B), this orienting tendency was characteristically expressed by the gradual deviation of the goal response toward the source of the CS. An opposite process, i.e., a gradual straightening of the goal response, occurred during subsequent reinforcements as the criterion of discriminative response was reached. In other words, after temporarily dominating the behavior, this orienting response gradually disappeared and finally was replaced by a fast, seemingly automatic, goal response. These automatic responses showed little variation during the rest of the experiment. The average latency times, always below 4 sec both in the straight alley and the T maze, showed a significant and abrupt lengthening only after 80-100 consecutive reinforcements in a single session.

DisCS conditioning. DisCS conditioning resulted in essentially similar outcomes in the alley and T maze; therefore, the main behavioral findings are treated together. In the initial stage of conditioning, when a nondiscriminated

continuously reinforced approach to the goal and a return to the starting place has been taught, no consistent reactions directed to the DisCS could be observed. Occasionally, at this time as well as during habituation, the sound stimulus elicited a quick pricking of the ears. At this first stage of conditioning, the animal was fully preoccupied with the goal. Approach responses began immediately after the return of the animal to the platform. Later, as a consequence of the nonreinforcement of the intertrial approach responses, the time spent on the platform became progressively longer. The greater part of this time was spent in grooming, a regular consequence of the discriminative procedure in cats. If the application of the DisCS did not coincide with grooming activities, an automatic approach response was immediately released. The fact that in this stage of conditioning many other stimuli, including those produced by the animal itself, similarly initiated approach suggested that the effect of the DisCS should be regarded as a disinhibitory effect rather than a real conditioned response. A definite difference between the DisCS and the irrelevant stimuli was, however, found in the rate of the extinction of the corresponding behaviors. The releasing effect of indifferent stimuli ceased after two or three repeated unreinforced applications, while that of the DisCS nonetheless persisted. However, in contradistinction to real automatic conditioned responses, these responses still did not appear if the DisCS was applied while the animal was engaged in grooming.

The emergence of the orienting response and the diffuse orientation stage. Usually in the second and third experimental session, definite behavioral reactions directed toward the sound stimulus began to appear. As a first manifestation, the approach response was preceded by a short, phasic turning of the head toward the source of the stimulus. In subsequent trials, this response appeared more frequently and also became prolonged, i.e., after the phasic head turning, the animal remained in a frozen posture, gazing at the loudspeaker. Finally, the animal approached the DisCS and performed a thorough investigation around it—sniffing and searching. Some of the animals also used their paws or teeth, and exploration often assumed a definitely aggressive manner (Fig. 2).

Fig. 2. Behavioral and hippocampal EEG manifestations occurring in an L maze during approach conditioning in the stage of the emergence of the orienting response to the DisCS. Upper row: (1) cat waiting on the starting platform, (2) turning toward the loudspeaker at the presentation of the DisCS (5 Hz), (3) approaching and biting, and (4) searching around the loudspeaker. Bottom row: (1) in the course of diffuse searching, leaving the platform, (2) catching sight of and turning toward the goal, (3) jumping on feeder and waiting for the appearance of food, (4) catching food with paw from the bowl of the feeder. Corresponding changes in the hippocampal EEG are indicated by arrows. Note that the frequency of the hippocampal theta waves becomes progressively higher and the duration of single waves shorter as the animal gets close to the goal: 4-Hz waves during the waiting periods, 5-Hz waves during orientation toward the signal, 7-Hz spikelike waves when the animal catches sight of and approaches the feeder. Theta waves are
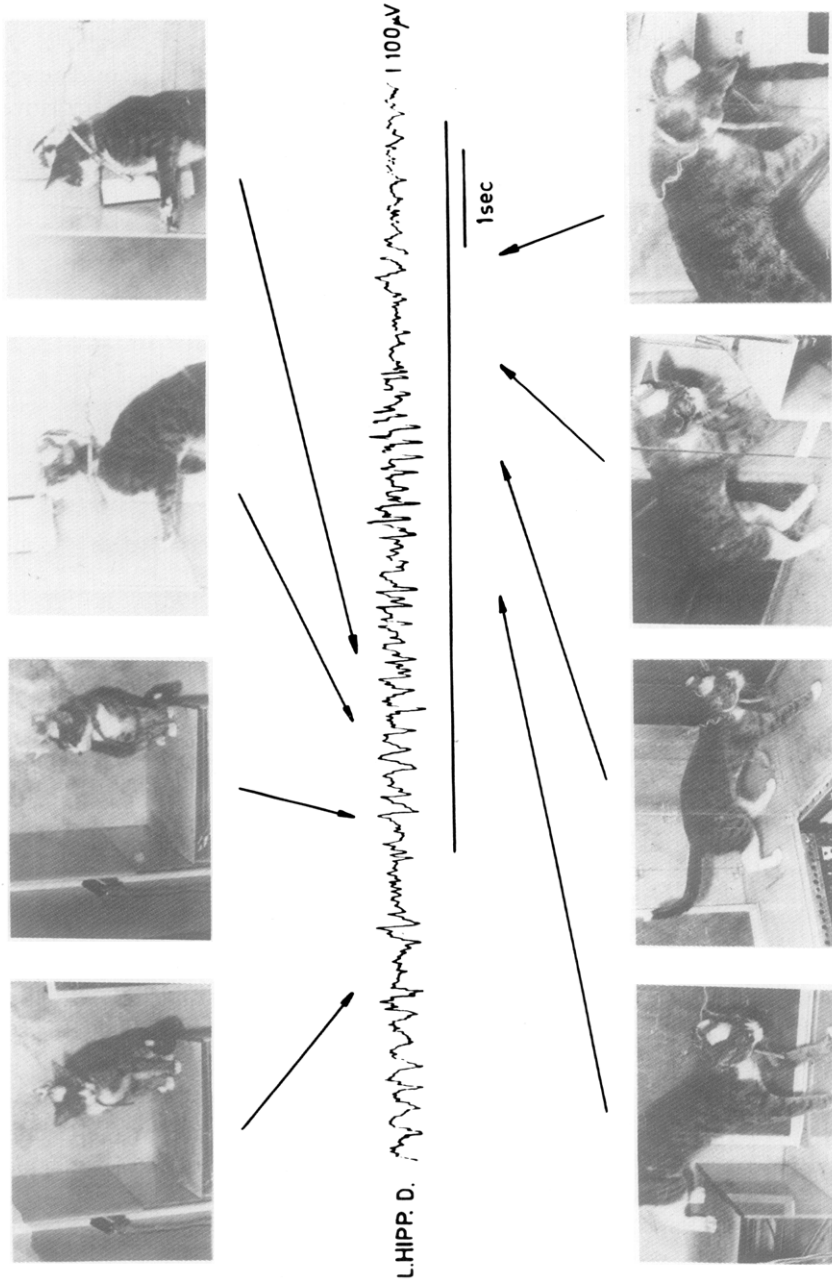
absent occasionally during the waiting period and regularly when the animal leaves the platform, waits for food, and eats. Continuous line under the EEG recording indicates DisCS presentation.

In its initial stage, the orienting response was an unstable process: it alternated with the automatic, disinhibited responses described above. A strong orienting response usually appeared after a series of short-latency automatic goal responses, suggesting that its release was due to a cumulative process, progressively built-up during successive reinforcements. A slower progressive build-up manifested itself both within a single experimental session and over sessions (Fig. 3A and B).
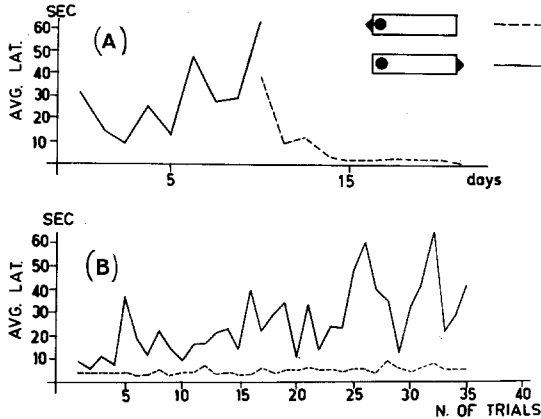

Fig. 3. Learning curves in terms of the response latency obtained in the straight runway during the elaboration of an approach response with the DisCS (continuous line) and then the CS (dashed line) conditions for one animal. (A) Session averages over days. (B) Trial averages for sessions 4 and 15 over trials within sessions.

The behavior of the animal left no doubt that the periodic lengthening of the latency of the goal responses was a consequence of the orienting response displayed toward the DisCS. However, it was found that an important additional event significantly contributed to this delay. Namely, when the animal turned away from the source of the stimulus, its attention became directed to the whole situation. In the course of this activity, any potential stimulus in the situation, even as insignificant as spots on the walls or floor of the cage, could become a target of minute and lasting investigation. It was usually in the course of this diffuse orienting behavior that the animal finally found the goal. It is important to note that, during the climax of diffuse exploration, stimuli directly related to the goal had no more, or perhaps less, influence than any other stimulus in the environment. Although it regularly appeared, this phenomenon was largely overlooked in our earlier studies.

Conflict between signal and goal-directed responses. If conditioning with the DisCS was continued beyond the stage when the orientation response culminated, a new phenomenon appeared (Table 1). Signs of diffuse orientation

TABLE 1

The Appearance of the Orientation Response and the Conflict During Conditioning
with the DisCS in the Alley and the T Maze in 8 Animals[a]

Animal	Orientation		Conflict		Animal	Orientation		Conflict	
	Day	Trial	Day	Trial		Day	Trial	Day	Trial
1	2	50	9	250	5	2	50	11	262
2	2	42	9	206	6	5	140	15	299
3	3	73	9	260	7	2	25	12	235
4	2	34	10	303	8	3	75	8	180
	2	49	9	254		3	72	11	244

[a]Numbers in the bottom row correspond to mean (rounded down) values of the two situations. Triangle: CS location; shaded circle: reinforcement location; arrow: starting location.

decreased, but, at the same time, orienting approach responses directed to the DisCS became more pronounced and finally began to compete with the goal response. Conspicuous behavioral signs of uncertainty were seen during the presentation of the sound stimulus. Abortive approach responses toward the goal and the signal occurred in alternation. Under the effect of these opposing influences, a lasting circling on the platform sometimes occurred with periodic accelerations toward the corresponding "goal". In the course of this behavior, the tendency to approach the feeder often won out over the attraction of the signal. Curiously, however, instead of strengthening the goal response, reinforcement strengthened the orienting response (Fig. 4). Finally, complete
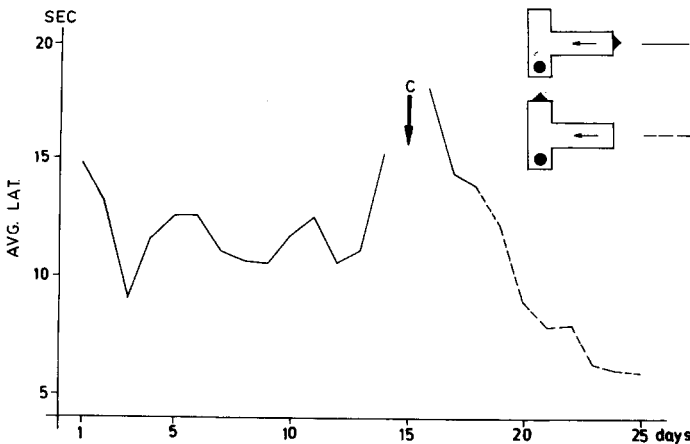

Fig. 4. Learning curve obtained during the elaboration of an approach response in the T maze. Continuous line: DisCS. Dashed line: CS conditions restored. The approach response practically disappeared during the 14th-16th sessions (Arrow:conflict).

suppression of the goal response ensued in almost every case. The phenomena of conflict showed many individual variations, which necessitated the introduction of an arbitrary criterion. Accordingly, cases were regarded as conflict only where no goal responses could be elicited during the continuous 60-sec presentation of the DisCS in 3 subsequent applications. Actually, most cases were characterized by a complete failure to respond in several subsequent sessions, with the exception of the first few (1-3) trials. Two young and two adult animals did not reach the above criterion, displaying instead normal learning curves (Fig. 5).
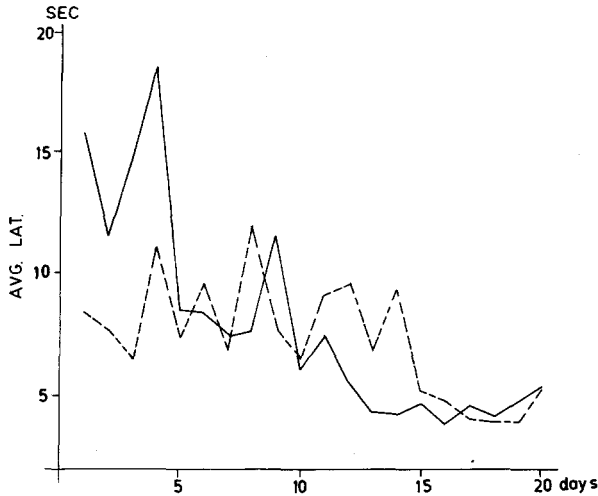

Fig. 5. Learning curves obtained in two cases where the criterion of conflict (60-sec latency) was not reached during the elaboration of approach responses with the DisCS in the T maze.

Characteristic side effects of conflict occurred in several individual cases. At the climax of conflict, two animals refused to eat the meat either after approaching the goal or when offered by the experimenter. The same animals ate ravenously outside the experimental situation. In two other animals, presentation of the DisCS elicited retching and repeated vomiting. The most consistent effect of the DisCs characteristic of all cases was an intense grooming. This further diminished the chances of occurrence of the goal responses. However, even in the gravest stage of conflict, short-latency goal responses were regularly elicited at the beginning of each experimental session, during the first two or three trials.

In the cases of two animals, after persistent conflict had occurred in three subsequent experimental sessions. the stimulus location was transferred to the vicinity of the goal, thus switching from DisCS to CS conditions. During the first several applications of the CS, a definite orienting head movement was displayed toward the former place of the stimulus. This "false"

TABLE 2

Latency Times of Approach Responses Elicited with CS and
DisCS Presented in Alternation[a]

TRIAL	14 th exp. session	
	⊏⊐ ⇇	⊏⊐ ⇨
1.	4,9	7,5 sec
2.	5,4	9,0
3.	5,8	7,7
4.	5,7	7,9
5.	5,9	6,3
6	5,6	6,6
7.	5,9	6,6
8.	5,2	7,5
9.	6,6	7,6
10.	5,5	8,3
	5,6	7,5 sec
t = - 5,57	p<.001	

[a]Symbols are the same as in Table 1.

orienting response disappeared during subsequent applications of the CS, and a
short-latency stable goal response could be established during the same session.
Simultaneously, all signs of conflict completely vanished and did not reappear
during the subsequent 500 trials. A restoration of spatial discontiguity failed
to produce a new conflict, but the reappearance of the orienting response to
the DisCS resulted in a permanent lengthening of the latency of the goal
response (Table 2).

In the rest of the cases, conditioning with the DisCS was continued
beyond the appearance of the conflict. It was found that in the course of 2-3
subsequent sessions (50-90 reinforcements), the orienting tendency progressively
weakened and the grooming reactions were gradually superseded by goal
responses. On the basis of the latency times, the final, stable goal responses
could be sorted into two groups. Those accompanied by a conspicuous
orientation response, still directed to the DisCS, had a longer latency than
those where no overt signs of orientation were visible (Table 3).

The orientation response also consistently appeared in those two cases
(Fig. 5) where the effects of conflict did not reach criterion. In these cases,
after 400-500 reinforcements the latency became stabilized at a value higher
than responses elicited by a spatially contiguous stimulus.

Is reinforcement enough to produce the conditioned orienting response?
The above-described facts clearly indicated that reinforcement (food reward)
was necessary to induce orienting responses. The question arose if reinforce-
ment was not only necessary but also a sufficient condition to obtain
orientation. The present experimental situation offered an easy way to decide
it. In two animals, after they had learned to approach the goal (continuous
reinforcement) and spontaneously returned to the platform, the DisCS was

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TABLE 3

The Latency Times of Fast Approach Responses Devoid of Overt Signs of Orientation
(A) and Preceded by a Quick Orienting Head Movement (O) Toward
the CS[a]

Trial	8th		9th		11th exp. session	
	A	O	A	O	A	O
1.	6.2	7.4	5.0	7.1	4.4	7.7
2.	6.6	9.6	5.4	7.5	4.3	7.6
3.	6.2	6.9	5.8	7.8	4.0	8.0
4.	7.1	9.1	4.4	6.7	5.2	7.3
5.	7.0	7.4	4.8	7.6	4.2	6.0
6.	8.1	9.4	5.9	9.0	5.5	7.0
7.	7.1	9.9	4.4	6.9	5.4	6.9
8.	7.6	9.2	5.4	7.1	5.6	7.0
9.	8.7	9.3	5.8	8.0	4.7	6.8
10.	6.6	9.4			5.3	8.1
	7.1	8.7	5.2	7.5	4.8	7.1 sec

Trial	15th exp. session		Trial	15th exp. session	
	A	O		A	O
1.	4.0	5.0 sec	1.	5.6	5.8 sec
2.	5.1	5.9	2.	5.9	10.2
3.	4.8	7.5	3.	4.7	6.9
4.	5.6	7.8	4.	5.5	7.5
5.	5.6	7.5	5.	4.7	8.9
6.	6.0	7.9	6.	4.2	8.8
7.	5.2	8.2	7.	6.7	11.4
8.	6.3	6.5	8.	5.7	10.4
9.	6.2	7.8	9.	5.9	15.3
10.	6.2	10.0		4.8	8.5 sec
	5.5	7.4 sec			

[a]Recordings were made in three different animals in the T maze.

consistently presented when the animal was about to leave the platform and until it obtained the reward at the goal. In spite of the fact that all of these approach responses were reinforced by food, not even traces of orienting responses were observed during 400-500 consecutive trials in the two cases. Orienting toward the DisCS began to develop only when approach responses performed in the absence of the DisCS were consistently not reinforced (20-30 randomly distributed nonreinforced trials). This has clearly shown that temporal contiguity between signal and reinforcement is not a sufficient

condition to produce orientation. The applied experimental procedure indicated that the inhibitory processes whereby the DisCS became differentiated from the rest of the stimuli of the environment were also necessary to produce the signal-directed orienting response.

The persistence of the orienting response in the final stage of conditioning. In the majority of cases, the approach response was consistently preceded by at least a quick orienting head movement directed to the DisCS, even after the latency of the approach response became stable. However, automatic goal responses devoid of any behavioral signs of orientation could be elicited in some animals by applying the DisCS at a moment when the animal was watching the goal or the way leading to it. This correlation was so consistent that it enabled us to induce and measure the two kinds of responses alternately (Table 3).

Since the behavioral and electrical manifestations accompanying the automatic responses were in every respect identical with those observed at the beginning of training, it seemed highly probable that they were also produced by disinhibition. This idea was supported by the observation that approach responses, particularly at the beginning of the experimental sessions, could occasionally be released by completely indifferent stimuli even in the final stage of learning.

The persistence of the orienting response raised serious problems. The false orienting response to the original position of the stimulus after the transposition from DisCS to CS indicated that it corresponded to instrumentally conditioned movement rather than to a real orienting response. The electrographic evidence, as we shall see later, agrees with this assumption.

Apart from the question of its essential nature, the persistence of orientation in "true" conditioned responses also suggested that it might represent an indispensable link in the performance of the approach response by chaining those signals which finally lead to the goal. In other words, perhaps a seemingly automatic goal response was actually an automatic series of orienting responses. Accordingly, it might be expected that if stimuli related to the goal were not present during the orientation initiated by the CS, the animal would not know what it was seeking.

An attempt to answer this question was made by using the following procedure. In two cases a gauze curtain was imperceptibly lowered between the platform and the goal during randomly chosen trials while the animal's attention was engaged by the conditioned stimulus. Naturally, we were aware of the risk that the animal's attention might be distracted from the goal by this dramatic change itself. Fortunately, this fear proved to be groundless. One of the animals immediately returned to the loudspeaker while showing no signs of being interested in the curtain, then began to circle on the platform, and finally became immersed in grooming. No attempts to find the goal were shown during repetitions of this procedure.

In the second case, after similar initial reactions, a diffuse orienting response appeared, in the course of which the animal managed to find the goal behind the curtain. With repeated applications of the procedure, the latency of the approach response gradually became shorter.

The T maze, where the goal cannot be seen from the starting platform during the presentation of the DisCS, seemed to provide a more adequate situation for the examination of the above question. However, the expectation that a more serious conflict would appear in this situation than in the straight alley was not substantiated by the findings. Although the persistence beyond 1000 trials in two cases and the vigor of the orienting response in the T maze was prominent, the conflict did not appear earlier and did not last longer than in the straight alley. The conflict could be easily overcome by transposing the DisCS to the shorter arm of the T, opposite to the place of reinforcement (Fig. 1E and Fig. 4). In that case, there was still a spatial discontinuity between signal and reinforcement. However, the initial direction of the orienting response coincided with that of the goal. Mild orienting responses occurred transitorily when the animal reached the intersection of the T maze. However, these were easily overcome by the attraction of the nearby goal.

The secondary reinforcing effect of the DisCS. In the final stage of conditioning, when the DisCS elicited stable short-latency goal responses, a complete and lasting suppression of the goal response could be achieved again with the following procedure.

By presenting the DisCS within 1 sec after the animal's arrival at the platform, the usual quick orientation toward the DisCS and the following goal response became preceded by conspicuous behavioral signs of excitement and diffuse orienting and searching activities around the platform. During the sequential reptition of this procedure, these symptoms became progressively dominating and finally, usually in one session, the criterion of conflict was reached again. At the presentation of the DisCS beyond 1 sec on the animal's arrival at the platform, short-latency responding was immediately restored (Fig. 6). If the presentation of the DisCS within and beyond 1 sec after arrival was applied in alternating blocks of ten trials, a corresponding alternation of the latencies was recorded (Fig. 7). The progressive buildup to conflict could also be observed in this case during the trials with DisCS deliveries within 1 sec. If the DisCS was consistently applied within 1 sec of arrival at the platform, the complete disappearance of the suppressing effect required about 1000 trials.

The peculiar time characteristics of this phenomenon suggested that we were dealing with the secondary reinforcing effect of the DisCS. It is reasonable to suppose that the strict temporal contiguity between jumping onto the platform and the DisCS resulted in the selective reinforcement of the former as a distinct instrumental response with the resulting suppression of the goal response. This interpretation is supported by the fact that with unstable DisCS the described phenomena could not be reproduced.
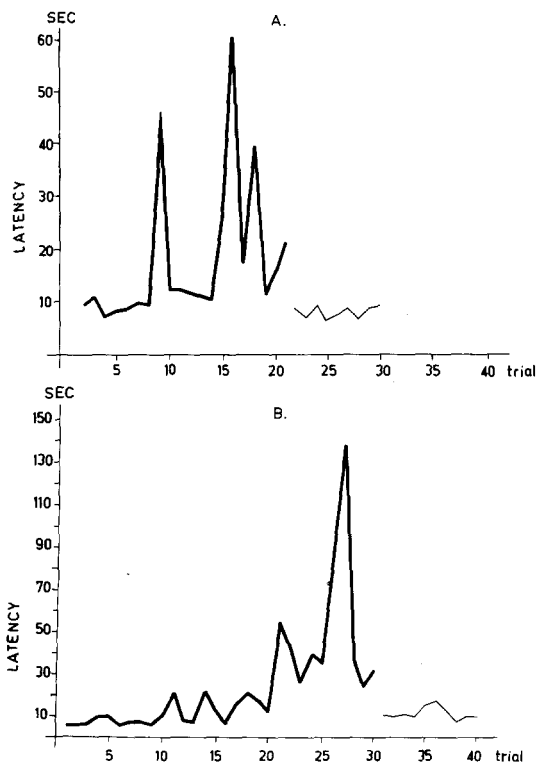
Fig. 6. The changes in approach latency in two animals when the spatially discontiguous CS was applied less than (heavy line) and more than (thin line) 1 sec after the animal's arrival at the starting place.

Extinction and differentiation of the DisCS. The findings obtained during extinction and the elaboration of a differential no-go DisCS did not add anything new to the above observations. The tendency to orient toward the signal was slightly increased at the beginning of both procedures. The differential stimulus produced no additional signs of conflict.

In one case, during the elaboration of differentiation, the animal several times agressively attacked the loudspeaker presenting the no-go stimulus.

The avoidance response. In order to establish whether the phenomena described in the earlier sections were not confined to approach conditioning, a pilot study was made in four animals (Fig. 1F). The orientation response directed to the DisCS appeared somewhat earlier during avoidance than in approach conditioning and resulted in a transient lengthening of the latencies of avoidance. However, no definite and lasting signs of conflict were observed in any of the four cases. At the stage when the vigor of orientation began to decline, it was often found that the attention of the animal gradually became shifted from the signal to the grid through which the painful shocks were
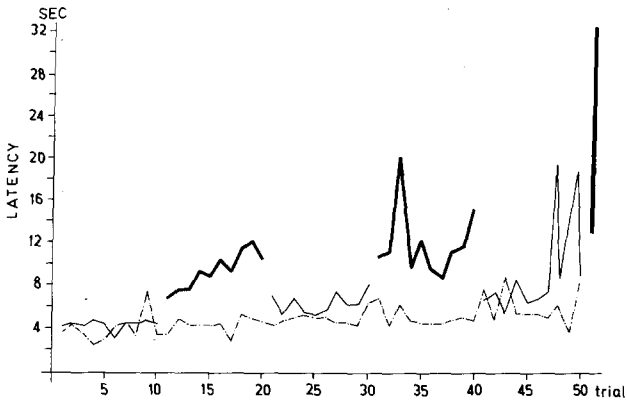
Fig. 7. The oscillatory changes of the latency times when the spatially DisCS was presented alternately in groups of 10 trials less than (heavy line) and more than (thin line) 1 sec after the arrival at the starting platform. The dashed line represents the latencies of a previous session when the DisCS had been presented consistently beyond 1 sec after arrival at the starting place.

delivered. In the final stage of avoidance conditioning, usually after 200 reinforcements, short-latency avoidance responses preceded by a short phasic orienting response, or seemingly pure automatic responses, appeared in alternation.

The Hippocampal EEG in Different Stages of Conditioning

The initial stage of disinhibited fast response. At the initial stage of conditioning, whether spontaneous or released by any stimulus, including the DisCS, approach responses were in the majority of cases accompanied by a dominant desynchronization in the hippocampus, i.e., by a low-amplitude relatively fast discharge with the random occurrence of slow waves (Fig. 8, top line). In other cases, the initial automatic response was accompanied by a fast theta activity, composed of spikelike waves, most pronounced in a region intermediate between the basal and dorsal parts of the hippocampus.

The stage of the emergence of the orienting response. Simultaneously with the appearance of the orienting response, a slow 4-5-Hz high-amplitude theta activity gradually became pronounced in all the recorded regions of the hippocampus (Figs. 2 and 8, second line). Different components of the approach response were consistently accompanied by characteristic changes in the hippocampus. The slow theta rhythm characteristic of both the orienting and the approach response directed to the signal became intermingled with fast components as the animal left the platform and made its way toward the goal. When the animal's attention became definitely attracted by the stimuli of the goal, e.g., upon entering the short arm of the T maze, the individual theta waves assumed a definite spikelike character, and their frequency

O:ORIENTATION
S:START
A:ARREST BEFORE FEEDER
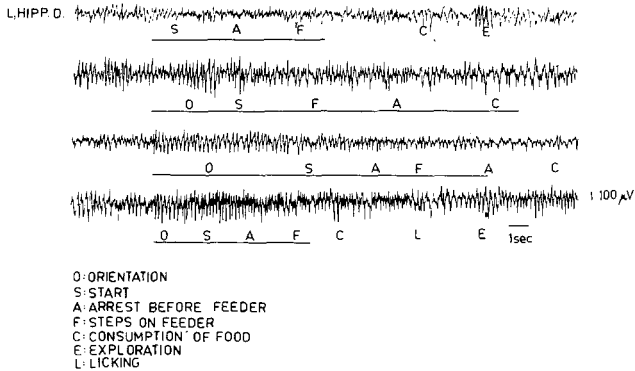F:STEPS ON FEEDER
C:CONSUMPTION OF FOOD
E:EXPLORATION
L:LICKING

Fig. 8. The electrical activities recorded in the dorsal hippocampus in different stages of conditioning with the DisCS in the T maze. Records from top to bottom: (1) initial stage of conditioning; (2) the stage of the appearance of the orientation response, (3) the diffuse orientation stage when the orientation response becomes dominant, (4) the final stage when the automatic approach responses begin to appear.

increased to 6-7 Hz (Fig. 2). The period while the animal was waiting for the appearance of food was consistently accompanied by desynchronization.

The stages of diffuse orientation and conflict. During the diffuse orienting response, an almost continuous 5-Hz theta activity of moderate amplitude became manifest in all hippocampal leads as well as in medial regions of the hypothalamus (Figs. 8, third line and 9). If the approach response failed to appear during the whole period of presentation of the DisCS, the theta rhythm was progressively replaced by a rather disorganized
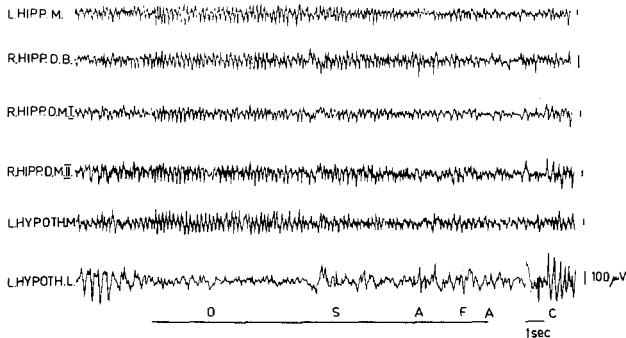

Fig. 9. The electrical activities of different hippocampal and hypothalamic regions recorded in the stage of dominance of the orientating response. Key same as in Fig. 8. L. Hipp. M., left intermediate region of the hippocampus, bipolar recording; R. Hipp. D.M.I. and II. right dorsal hippocampus, monopolar recordings. L. Hypoth.M. and L., bipolar recording in the medial and lateral hypothalamic regions, respectively.

electrical pattern of low-amplitude fast discharge with interspersed slow waves, also characteristic of intertrial periods (not shown in the figures).

The final stage of conditioning with DisCS. With the emergence of short-latency goal responses, the hippocampal activity became progressively faster. The frequency of the theta rhythm was shifted from 4-5 to 6-7 Hz, and the duration of single theta waves became shorter, assuming a spikelike character with much interspersed low-amplitude fast potentials (Fig. 8, bottom line). Finally, in certain electrode locations, the DisCS elicited a single large-amplitude slow wave, resembling an evoked potential followed by a short period of desynchronization coinciding with the orienting response. This desynchronization was usually followed by a high frequency (7-Hz) theta burst while the animal turned away from the signal and prepared to leave the platform (Fig. 10).
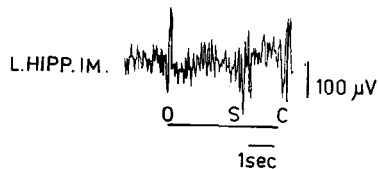

Fig. 10. Monopolar recording made in the posterior region of the dorsal hippocampus in the final stage of conditioning. The quick orienting head movement is accompanied by a large evokedlike biphasic slow wave and short period of desynchronization. A burst of 7-Hz theta activity appears when the animal turns away from the DisCS. The large potentials at S and C are most probably movement artifacts caused by jumping from the platform and by grasping the food with the mouth.

DISCUSSION

Is Spatial Contiguity an Indispensable Condition of Learning?

The essential finding of the present experiment was that during conditioning in a spatially discontiguous situation, the occurence of the orienting-approaching responses to the discriminative stimulus progressively increased. Simultaneously with this, the rewarded goal response became temporarily suppressed.

If instrumental learning corresponds to an increased probability of appearance of an occasional response, then, by definition, the instrumentally *conditioned* orienting response meets this criterion. Accordingly, spatial contiguity of CS and reinforcement cannot be regarded an essential condition of learning. The opposite view might have been deduced from the findings that under conditions of spatial discontiguity, the goal response, i.e., the traditional indicator of learning, failed to appear. However, in the present experiment

with the extreme spatial separation of CS and reinforcement, it became obvious that the orienting response was a learned consequence of reinforcement which suppressed the goal response. The conditions of earlier experiments were highly unfavorable for such observations. In parametric studies of spatial variables of conditioning, the interest of the experimenters was mainly centered on that minimal spatial discontiguity which already interfered with learning. This critical distance between discriminative stimulus and reinforcement can be small enough (6 in. in the case of monkeys, Murphy and Miller, 1955) to conceal signal directed responses from observation.

Accordingly, we can state that the primary but not sufficient condition to create a conditioned signal is its temporal contiguity with reinforcement. Another essential condition brought to the fore by the present experiment is the nonreinforcement of responses (or environmental stimuli) occurring in the absence of the conditioned signal. Accordingly, the orienting response is the product of a process of differentiation. Since the latter is also a necessary (though implicit) condition to form a conditioned signal in classical conditioning, it reaffirms our assumption that the orienting response is a real learned phenomenon.

The Significance of the Inhibitory Effect of the Conditioned Orienting Response

The finding that the conditioned orienting response supresses the goal response and, often, also the consummatory response, is undoubtedly an unusual finding. The simplest way to explain it would be to regard the suppressing effect as a special manifestation of spatial discontiguity. However, this would run against well-known facts. Namely, the orienting response lawfully emerges also under the traditional conditions of classical conditioning, even after previous habituation of the orienting response to the CS. Because of this and similar findings, some authors are inclined to regard the orienting response as a reliable predictor of learning (Maltzman and Mandel, 1968, Morgenson and Martin, 1968, Zeiner and Schell, 1971). The inhibitory effect of the conditioned orienting response on goal and unconditioned responses is also a long-known phenomenon (Pavlov, 1927, Sokolov, 1963). These facts make it highly probable that spatial discontiguity only accentuates a phenomenon that also occurs in the traditional conditioning situation. Thus, we cannot avoid explaining the inhibitory effect of the orienting response as a real and important problem of conditioning.

A wide-spread interpretation originating from the Pavlovian concept is that the inhibition exerted by the orienting response is closely related to an accentuated perception of the developing CS. There are evidences to show that the sensitivity of the receptors becomes increased during orientation, i.e., the orienting response optimizes the conditions for the perception of the

future CS (Sokolov, 1965). The underlying mechanism of this process is supposed to play an important facilitory role in bringing about the neural connection between the conditioned and unconditioned functions (Anokhin, 1965). With the widely accepted view that the orienting response disappears when the performance of the CR becomes automatic, the problem of inhibition becomes seemingly settled.

However, one obvious contradiction warns against the acceptance of this interpretation. Namely, we can wonder how could the orienting response facilitate the formation of the conditional connection if its inhibition exerted on one member of the future connection (the UR) prevails until the connection becomes formed. This contradiction cannot be resolved by any known neurophysiological mechanism of inhibition.

Might the Orienting Response be the Real Conditioned Response?

The proposition we are going to entertain in the following resolves the above contradiction but, of course, at the price of introducing new difficulties. The essence of the proposition is that *the conditioned orienting response is not only a learned response, but it is the only response learned*! We assume that as a consequence of reinforcement, it is the signal and not the goal or the object to be consumed which the animal learns to approach or avoid. Or, in other words, we suppose that under the effect of reinforcement, it is the CS itself which becomes a new and independent goal, and that is why the animal insists on approaching the signal instead of the goal.

As the present experiment clearly demonstrates, in the case of spatial discontiguity, responding to the signal results in inadequate behavior. It is unquestionably maladaptive if the hungry animal approaches a signal which does not offer food. This discrepancy, however, becomes resolved by the observation that spatial discontiguity of signal and reinforcement is a highly artificial learning situation. Under natural conditions of learning, signal and signalled always coincide in space or are close to each other. Under such conditions, the approach or avoidance of the signal is purposeful because it carries the animal to the vicinity of the consummative goal or removes it from a harmful object. However, in the case of spatial contiguity, it is just the closeness of the stimuli which makes it difficult to ascertain whether the animal reacts to the signal or the signalled.

According to the above proposition, the inhibition exerted by the orienting response expresses the dominance of a newly acquired response over older habits. The adaptive significance of this mechanism can be interpreted as follows.

In most cases of learning, distance receptors play an overwhelming role. The primary importance of these stimuli obviously consists of directing the behavior of the organism while the final goal object is still remote. On the

other hand, it is easy to realize that, in most cases, unconditioned or consummatory responses anticipatorily elicited by distant stimuli would not serve adaptation at all. If distant stimuli signalling the prey or the predator would respectively elicit salivation or some local defensive reflex instead of approach or avoidance, the organism would be left hungry or defenseless. (Theories about the fractional anticipatory goal responses (Hull, 1943, Spence, 1956) assigning a role to them in behavioral chaining remain unconvincing until a reliable demonstration of their existence.) Probably no theoretician would deny that the animal would react with approach or avoidance to the distant CS; this, however, does not necessarily follow from any of the present learning theories (perhaps with the exception of Tolman's, 1959). The fact that the importance of signal-oriented responses remained relatively neglected in our present theories might be attributed to the inadequacies of the conditioning procedures. In classical conditioning, the spatial limitations of the situation, and in instrumental conditioning, the lack of a controllable stimulus, might have concealed such responses from systematic observation. The recently discovered phenomenon of autoshaping (Brown and Jenkins, 1968, Williams and Williams, 1969, Gamzu and Williams, 1971), which definitely shows that signal-directed responses regularly occur also in instrumental conditioning, may finally discredit Skinner's (1938) emitted response hypothesis.

According to our present proposition, learning essentially consists of responses related to stimuli (orientation, exploration, attention, approach, withdrawal). If we adhere to the behavioral classification originally proposed by Sherrington (1906), this would also mean that learning exclusively occurs in the preparative and not in the consummative sphere of behavior.

The Difficulties of the Orienting Response Hypothesis (The Problem of Inhibition)

Our present behavioral findings and those based on GSR changes obtained during conditioning (Gale and Ax, 1968) strongly indicate that, contrary to common belief, the orienting response does not disappear during conditioning. This also supports our presumption that the orienting response might be the *final* conditioned response. However, it is an undisputable fact that finally the consummatory response also reappeared in the present experiment as in the case of the conventional procedure of conditioning. This raises the paradoxical problem: How can the consummative response appear in spite of the persistence of the orienting response if the latter inhibits the former? The following alternative solutions offer themselves.

According to one supposition, orientation, instead of being an unspecific response, is always specified by the actual reinforcing event which induced it. In the case of food reinforcement, this would mean that the animal approaches the source of the signal as an object to be consumed. In other

words, we can suppose that the signal becomes a substitute of the signalled. If this is correct, then in the case of normal spatial contiguity, the problem of inhibition automatically disappears. Findings supporting this hypothesis have been reported by Pavlov (the dog licking the lightbulb as the source of the CS; 1927) and recently in connection with instrumental conditioning (Peterson et al. 1972). Observations of a similar sort are obtained also in the present experiment (the cat biting the loudspeaker; Fig. 2). There are, however, reasons to accept this seemingly sound hypothesis with reservation. First, the oral tendencies observed cannot necessarily correspond to feeding behavior. As common experience shows, they can quite as well represent explorative or emotional tendencies. Also, the appearance of the oral tendencies was not consistent enough to be taken seriously. Most of our animals showed, in a definite stage of conditioning, passionate interest in the CS without, however, any trace of oral tendencies. Thus, it seems possible that the orienting response induced by any kind of reinforcement is an aspecific process and corresponds to a particular stage of conditioning postulated once by Woodworth (1947) as the stage of "indefinite expectancy".

A second solution of the inhibitory paradox would be to suppose that the underlying mechanism of orientation progressively changes during conditioning in the course of which its inhibitory effect disappears. The best supporting evidence of this is the marked difference between the hippocampal electrical patterns accompanying the early and late stages of conditioning. Spatial discontiguity enabled us to clearly establish that in the final stage of conditioning, instead of the slow theta rhythm, a definite desynchronization took place during orientation. It is noteworthy that consummatory actions correlate with a highly similar or identical electrical pattern. This might be related also to the fact that if, in that stage, the CS was made contingent upon a well-defined response, it proved to be a potent reinforcing event. (Since a detailed discussion of the hippocampal electrical changes as well as the controversies about their functional significance would divert attention from our present purpose, they will be dealt with at another place.)

The antagonistic nature of the early and late hippocampal electrical correlates of the orienting response suggests that its initial inhibitory effect finally becomes a disinhibitory effect, and the reappearance of the consummatory response is a consequence of this latter event. In addition, it is also conceivable that at the cessation of the inhibitory effect, the CS and the stimuli of the consummatory goal fuse into a common stimulus configuration and become represented as a complex pattern in the CNS. This might correspond to Woodworth's (1947) "definite expectancy" stage of learning.

Familiarity Versus Novelty in the Induction of Orientation

It is generally accepted that the orienting response corresponds to an inborn capacity of the organism to react to unfamiliar stimuli or to various

kinds of novelty (Pavlov, 1927, Berlyne, 1960, Sokolov, 1963). This view, of course, reduces the significance of our proposition to a minimum. Namely, if, as our hypothesis claims, the orienting response, i.e., an inborn reaction of the organism, is the only consequence of learning, then learning produces something which the organism already knows without learning. An assumption surmounting this difficulty would be that the stimulus is perceived with a different meaning while it becomes transformed from an indifferent stimulus into a CS. Actually, what our proposition claims is more than that. Namely, we also suppose that most of the unfamiliar or indifferent stimuli which reach the organism do not have the capacity at all to arouse orientation, i.e., to induce perception. We regard the orienting response as an exclusive product of reinforcement, i.e., a learned response. The following considerations support this view.

The orienting response appears in ontogeny late enough to relate it to processes of learning (Obraztzova *et al.* 1965). During ontogeny, the organism becomes familiar, directly or through generalization, with an immense amount of stimuli. Consequently, in the case of grownup organisms, it is difficult or impossible to decide whether it was the novel or familiar character of a "new" stimulus which elicited orientation. The validity of the novelty hypothesis seemed so unambiguously guaranteed by everyday experience that its rigorous experimental testing remained lacking so far. An attempt at that has been made (Grastyán *et al.* 1964, Karmos *et al.* 1965. Lissák *et al.* 1966). Adult cats were isolated for several weeks in a spacious stimulus-rich home-cage with the intention to create a complex and stable stimulus background where the effects of solitary stimuli alien to the situation (e.g., sounds produced by a generator) could be checked. According to Sokolov's well-known hypothesis (1960), an interference or mismatch between the effects of these new stimuli and the neuronal model established by the background stimulus complex could be expected to induce strong orienting responses. However, contrary to this expectation, the new stimuli induced, instead of orienting responses, automatically (i.e., in a time-locked manner) and regularly those habits which had developed in the situation during isolation. The experiment did not offer any conclusive clues to decide whether the mechanism underlying these effects was disinhibition or some kind of aspecific energizing effect. This is, however, irrelevant in the present context. We could definitely establish that a stimulus, the novelty of which was guaranteed in this case, did not elicit orientation. The first orienting responses directed to the new stimuli appeared only after a series of frustrative performances of the previously learned habits, i.e., as a result of experience.

A recent experimental finding of Wilz and Bolton (1971) according to which the spatial rearrangement of the stimulus objects of a familiar situation is enough to induce strong orienting activities is in line with the above argument. It also agrees with Hebb's (1949) notion that it is the unusual

spatiotemporal sequence of the familiar elements of a situation rather than its complete novelty which is responsible for the orienting activities.

A frequently cited experimental fact of the novelty hypothesis is that a relatively slight change of a habituated stimulus will immediately result in orientation. This fact, however, supports rather than weakens our present argument. It is highly improbable that a slight change of a habituated stimulus could make it completely unfamiliar. More probably the animal reacts to the changed stimulus as to a familiar one and because the well-known selectivity of habituation does not prevent the reaction. The fact itself that the orienting response, like learned and unlike unconditioned responses, can easily be habituated could have made the present arguments long overdue.

If the novelty hypothesis were correct, it would necessarily follow that the enormous mass of irrelevant stimuli reaching the organism from the environment would only become ineffective through habituation. According to the present hypothesis, stimuli would only become effective after having obtained relevance through experience. The latter view seems more compatible with the economy of the organism.

Some Theoretical Consequences of the Orienting Response Hypothesis

Our proposition would offer a vantage point to a combined approach of classical and instrumental conditioning. We suggest that reinforcement results, in both cases, in the appearance of stimulus-directed responses. In the case of classical conditioning, this stimulus is the CS. As we have attempted to show in natural circumstances of learning, an orienting-approaching (or withdrawing) response to the CS is more adaptive than the appearance of the UR. In the case of the instrumental response, the target of orientation can be an environmental stimulus which preceded or played a latent role in the first elicitation of the future instrumental response. Besides, it is also conceivable, e.g., in the case of learning skilled actions, that the target of orientation are those peripheral or central feedback impulses which accompany or precede the performance of the response. This supposition is strongly supported by the recent neurophysiological discovery (Asanuma, Stoney, and Abzug, 1968) that the feedback impulses accompanying a given motor reaction exert a facilitatory influence on the cortical representation of the same reaction. If the orienting response directed to the feedback impulses increases their effectiveness, then this mechanism is equivalent with a higher probability of appearance of the corresponding response. That is, it meets the criterion of instrumental learning.

Our proposal may contribute to the reconciliation of one of the basic discrepancies between S-R and cognitive theories of learning. If learning results in the emergence of stimulus-directed responses, then even the simplest adaptive act is at the same time a cognitive act. The most frequent objection

brought against cognitive theories was that they failed to explain how the cognitive event was translated into action. Our proposal overcomes this difficulty by showing that orientation toward a signal is not only a passive mental event or the reorganization of the perceptual field but at the same time a well-defined somatic response. Paraphrasing Guthrie's famous joke, we suggest Tolman's rat would not remain buried in deep thought in an intersection of a maze, but would find its goal by learned orientation.

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