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THE ORIENTING-EXPLORATORY RESPONSE HYPOTHESIS OF DISCRIMINATIVE CONDITIONING

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Abstract. Behavioral and electrophysiological manifestations occurring under conditions of spatial discontiguity of CS and reinforcement (or response) are described. It is concluded that the conflict or learning difficulties which arise in such situations are the result of a competition between the signal directed conditioned orienting response and the goal directed approach response which require different or opposite directional movements. Considerations are offered to prove that the complex orienting-exploratory response emerging as a result of reinforcement corresponds to the real conditioned response and accordingly the CS to a new independent goal with comparable attractiveness as the primary (consummative) goal. Arguments are brought up against the validity of the stimulus substitution theory of signal directed activities. Findings obtained in fimbria-fornix lesioned animals are presented to show that the orienting-exploratory mode of coping with spatial tasks necessitates the intactness of the limbic system. The conclusion is drawn that an apparently more adaptive mode of behaving in spatial discontiguity, where the CS only releases or triggers the goal response (used occasionally by intact but exclusively by limbic lesioned animals) corresponds to a relatively inferior mode of adaptation.

If fifty years ago you had consulted an expert of conditioning about an experimental design in which CS and US were separated in space you would have been cautioned that no conditioning might occur in such situation. If you insisted to know why, you got an answer not entirely devoid of Aristotelian flavor: because temporal and spatial contiguity are indispensable conditions of association and learning. Times are changing. In the last two decades the paradigm of spatial discontiguity has become increasingly popular because the phenomena which become accentuated by it, signal directed responses, auto-shaping, or sign tracking, seem to offer a new and common approach to the basic problems of classical and instrumental conditioning. Beyond this insight we were also prompted to select this topic for the present occasion because the late Professor Konorski and his coworkers were among the first who paid close attention to and offerred challenging interpretations of such phenomena. Let us introduce the topic by showing our first meeting with that problem.

In the late fifties we reported (6) a correlation between the theta

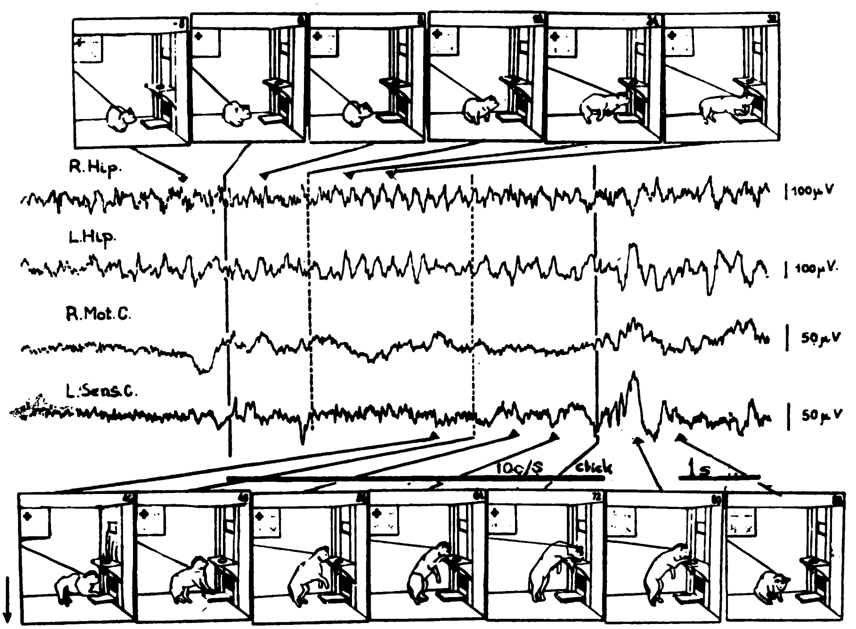

Fig. 1. Simultaneous motion picture and EEG recordings during the performance of a discriminated food reinforced approach response. The acustic CS is delivered through a loudspeaker (black rectangle in the lower right side of each motion picture frame) fixed below the feeding device. The solid horizontal line below the EEG records and the crosses appearing in the left upper corner of each frame mark the presentation of the CS. The numbers in the right upper corner correspond to the number of the motion picture frame copied. R. Hip. and L. Hip., right and left dorsal hippocampus; R. Mot. C., right motor cortex; L. Sens. C., left sensory cortex. From Grastyán et al. (6).

rhythm of the dorsal hippocampus and the orienting response paid to the conditioned signal in discriminative approach conditioning in cats. Actually this finding was an unexpected by-product of the spatial arrangement of the stimuli in the conditioning situation. The CS, an acoustic stimulus was delivered through a loudspeaker placed below the food dispenser, the place of reinforcement. The essence of our findings was that in the initial stage of conditioning an orienting response directed to the loudspeaker was the first and dominating response among all the reactions induced by the CS and strictly coincided with the appearance of hippocampal theta waves. These direct observations were reaffirmed more accurately by motion picture analyses (Fig. 1).

Originally our interest centered around a purely neurophysiological problem, the functional significance and intimate mechanism underlying the hippocampal theta rhythm. In pursuing this interest we attempted later to make a behavioral separation of the orienting response from the rest of conditioned activities by progressively removing the CS from the goal. As an extreme degree of this attempt finally the source of the CS and the feeding device were placed at the two opposite walls of a straight alley, a T or L maze. More precisely the loudspeaker was fixed to the wall behind an elevated platform functioning as the starting place for the approach response.

The findings obtained in that situation (7) considerably surpassed our expectations. Namely, in the first two or three experimental sessions of discriminative approach conditioning in the great majority of cases a progressively increasing orienting and approaching tendency toward the CS appeared. At the same time a progressively decreasing tendency to approach the goal could also be observed. The behavioral observations left no doubt that this was the outcome of competition between the effects of the CS and of the goal. The ensuing conflict reached different degrees in different animals. In about one third of the cases the goal response became entirely suppressed following the first few trials of the 2nd and 3rd experimental sessions and only slowly reappeared in subsequent sessions. Sometimes conflict was so serious that we became suspicious of an intervening sickness of the animals. This suspicion might have gained more weight if we were aware at that time of the findings of Stępień and Stępień (13). The syndrome they described as "magnetoreaction" in a similar situation following the lesions of the precruciate frontal cortex and accordingly regarded as a pathological phenomenon, exactly corresponded to our findings. The consistent emergence of the same phenomenon and the fact that at the climax of the conflict no loss or even decrease of appetite could be observed outside the experimental situation finally convinced us that the competition between the orienting and the goal response was a physiological phenomenon and accordingly what Stępień and Stępień had found was a pathologically exaggerated form of it. In subsequent experimental sessions the signs of conflict gradually vanished and the goal response became restored with progressively decreasing latencies. However, the conditioned orienting response, in most cases in the form of a quick head turn toward the loudspeaker persisted also in the final stage of conditioning after several hundreds of reinforcements (Fig. 2).

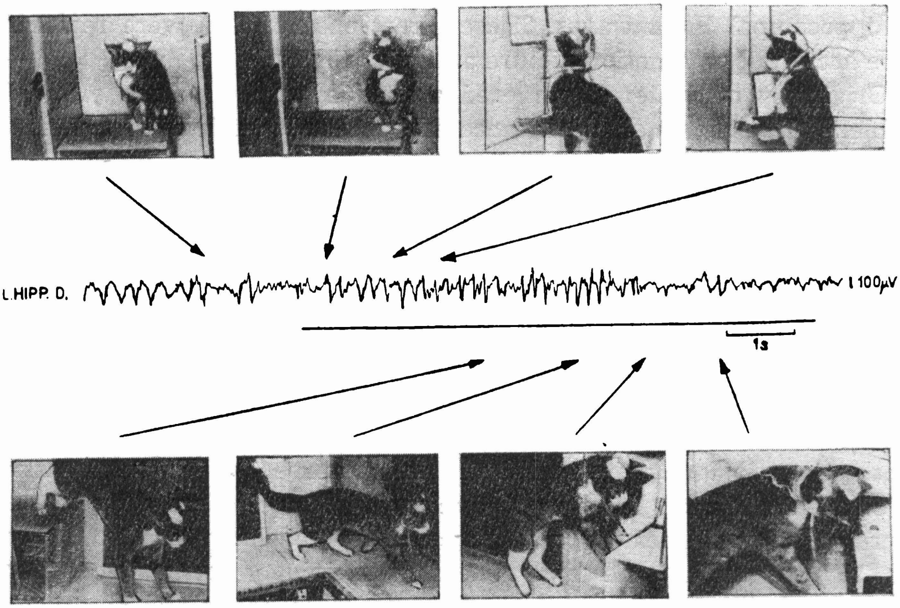

Fig. 2. Behavioral (video-tape recorded) and hippocampal electric manifestations in a L maze induced by a spatially discontiguous acustic CS. Upper row: the conditioned orienting-exploratory response directed to the loudspeaker on the starting platform. Bottom row: the goal response occurring during the second part of presentation of the CS. From Grastyán and Vereczkei (7).

Following this initial study several series of experiments were conducted with the same or modified versions of spatial discontiguity and for reasons of comparison also in the rat. These studies (2–5) confirmed most of the original findings. In addition aversive conditioning was also examined and in this case signal directed responses were not observed. I should like to show some relevant findings from a recent study of ours which make easier to confront our interpretation with others, mainly those based on the auto-shaping phenomenon and conditioning studies operating with spatial variables (3–5). The most conclusive studies of the latter sort were conducted in the Nencki Institute with the leadership of Professor Konorski (9) and by his coworkers (10-12). Before describing our new results let me outline briefly the basic traits of our initial theoretical framework.

The way that we had come to obtain the findings described above made it natural to suppose that the orienting-approaching tendency directed to the spatially discontiguous signal corresponded to the usual conditioned orienting response well known from the classic studies of Pavlov. This is assumed to be an obligatory, or unavoidable, consequence of any kind of discriminative conditioning at least in its initial stage. Under traditional conditions of spatial-contiguity, however, its strength and persistence is hard to assess,' because of its spatial and temporal overlap with goal directed responses. Thus, we thought that spatial discontiguity only unveils, and thereby amplifies a response which also exists and has the same significance under conditions of spatial contiguity. The competition between the CS and the goal was partly attributed to their opposing spatial directions. It seemed obvious that under traditional conditions of spatial contiguity the two tendencies coincide in space, and therefore easily merge so that no conflict ensues.

Up to this point our interpretation does not seem to differ significantly from that proposed by Konorski and his coworkers. Namely, in studies involving spatial tasks with either spatial contiguous or discontiguous conditions, they also attribute a positive or negative (parasitic) role to the conditioned orienting or, to use Konorski's term, the "targeting reflex" (10). There is, however, a basic difference as to the nature of the latter between his and our interpretation. Namely, we do not share the traditional view that the orienting response emerging during conditioning is identical with the inborn, unconditioned or consummative form of

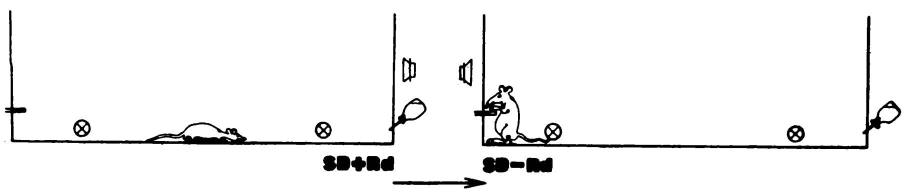

Fig. 3. Schematic of the experimental design. DS, loudspeaker delivering the discriminative signal; Rd, water reward.

orienting which is supposedly induced by any kind of unfamiliar environmental event. The unconditioned orienting reflex is usually restricted to short phasic reactions by organs of the corresponding receptors, like pricking the ears or moving the eyes, and habuitates quickly. In contrast, conditioned orientation is a complex, holistic response of a tonic character, which directs the whole organism towards (or away from) a specific object or goal in its environment; it may involve locomotion and, after completion of an approach reaction, even manipulation of the target (Fig. 3). This conceptualization assumes that the conditioned orienting response is a complex learned phenomenon capable to direct the organism in its environment toward new and specific goals (specified by reinforcement).

Accordingly the generalization seems also justified that the orienting response occurring in conditioning is not only a conditioned response, but the only response that is conditioned. Perhaps it was a mistake for us to term this phenomenon "orienting response" because of the traditional connotations it suggests. If it can be identified with the "targeting response" described by Konorski (9) or "sign tracking" used in recent auto-shaping literature (8) then we would not hesitate to accept either of the two terms.

The conflict described earlier also suggests a more feasible interpretation of the above concept of what will be called from now on, the orienting-exploratory response. If it corresponds to the real conditioned response, then the CS is also a new independent goal and the conflict becomes interpretable as the result of competition between a new and an older goal. The objection can, however, be raised that this is hard to reconcile with the requirement of the biological adaptiveness of the learning process. The following reasoning may resolve the paradox. The severity of conflict between CS and consummative goal is proportional to the degree of spatial discontiguity. Spatial discontiguity, however, hardly occurs in the natural settings of the organism, thus we can regard it more or less as a laboratory artefact. Under natural conditions signal and signalled are usually close together or even coincide (e.g., the sight of food). Accordingly the orienting exploratory response directed to the CS leads the organism to the consummative goal, therefore its adaptive nature cannot be questioned.

However, this explanation also fails if we accept the stimulus substitution theory of signal directed conditioned responses. This interpretation which goes back to Pavlov, has became popular recently in the context of auto-shaping. If we assume that the signal becomes a substitute for the reinforcer, then in the case of perfect spatial contiguity the theory works well. However, in the case of even minor spatial discontiguities, which unquestionably also exist in natural circumstances, the unadaptive nature of the signal directed response becomes obvious. Because of such discrepancies we could only accept the substitution hypothesis in a modified form, whereby the signal directed response is viewed as a reinforcement-specific orienting-exploratory response which helps the organism to attain the consummative goal, but the stimulus object does not become identical with it. Fortunately, evidences obtained in recent studies of auto-shaping, mainly in mammals, has considerably devalued the generality of the stimulus substitution theory, thus, even the above mild concession may prove unnecessary (for corresponding literature see the review of Boakes, 1).

We have, however, still another trouble with our interpretation, partly raised by some of our own data which has not been mentioned so far. Namely, we have consistently noticed that a small minority of our animals (about 10% in every experimental group) adapt to spatial discontiguity with an entirely different strategy than that described earlier. No signs of orienting or any kind of signal directed activities were observed during the whole course of conditioning in these cases and consequently no manifestations of conflict could be observed. It seemed that the CS became a potent factor by simply releasing, permitting or triggering the goal directed approach response. The performance of those animals which have shown signal directed responses was significantly slower even in the latest stages of conditioning when the orienting response decreased to its possible minimum level. These facts inevitably raised the critical question of whether there might exist two entirely different learning strategies in solving spatial tasks. An affirmative answer to this question has been given in a recent article by Ławicka and Szczechura (12). The data we are going to show from a recent study (2) seem to confirm their conclusion, but we hope to be able to give a more consistent interpretation within the framework of our own concept.

The study used separate (intact, sham operated, and limbic lesioned) groups of hooded rats that were water deprived in a straight alley to secure water in the presence of an auditory signal (Fig. 4). Before training the fimbria-fornix system was destroyed electrolytically in one third of the animals. The delivery of the auditory signal was a consequence of repeated bar presses at one end of the alley after which the rats had to run for water available at the other end of the alley. Crossing a light beam in the end of the alley turned off the CS and simultaneously activated the water dispenser. In the first stage of the experiment the auditory signal was presented in spatial contiguity with reinforcement, that is at the place of the consummative goal (Fig. 5).

After reaching criterion performance, in the second stage of the experiments, spatial discontiguity was introduced, that is the auditory signal was placed above the bar, i.e., far from the place of reward. In accordance with our previous findings, with the intact animals this arrangement caused abrupt changes characteristic of conflict, that is, increase of latency of the goal response, perseveration of bar pressing and lengthening of duration of single presses. However, quite unexpectedly no signs of conflict appeared in the fimbria-fornix lesioned animals. They continued to respond as if no change had occurred at all.

Identical conditioning procedures were used in the second part of

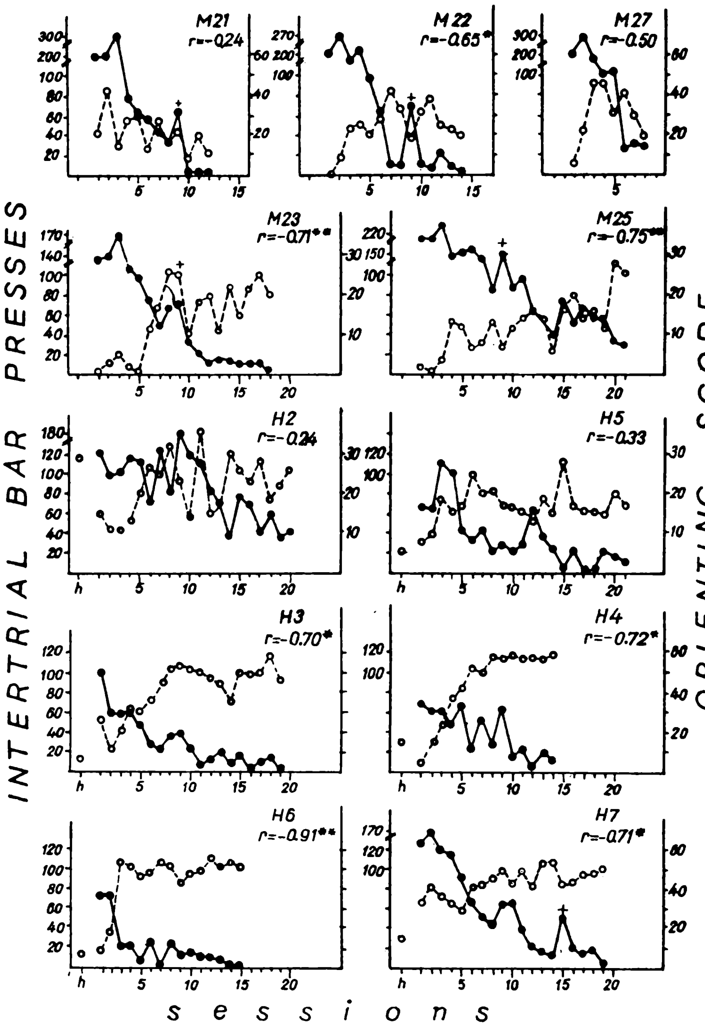

Fig. 4. Relationship between the total number of intertrial bar presses (heavy line) and orienting scores (dashed line) for individual animals; h, habituation session. Asterisks indicate the level of significance. * $P < 0.05$; ** $P < 0.01$. Sessions were conducted always in the afternoon except on days marked by +.

the study which employed three new groups of rats. In this case the limbic lesions were made surgically and followed initial training under the spatial contiguity condition. After recovery from surgery the introduction of spatial discontiguity caused similar, or even more accentuated, signs of conflict as in the control animals (Fig. 6) in the lesioned animals.

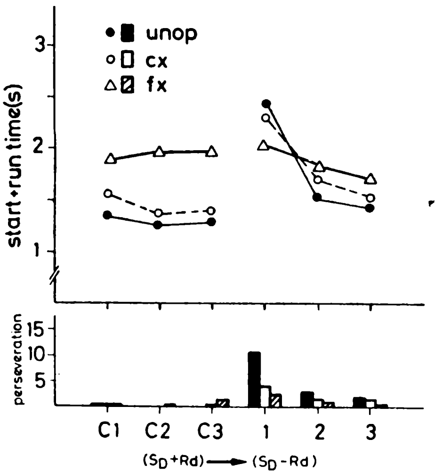

Fig. 5. Total time (start + run times) and lever press perseveration measures on the three criterion sessions (C1, C2, C3) and on the 3 days under S_D-Rd spatial discontiguity condition, unop, intact group; cx, sham operated. group; fx, fornix lesioned group. Lesions were inflicted before training. From Buzsáki et al. (5).

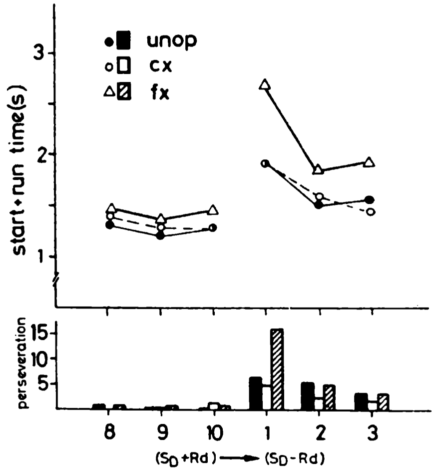

Fig. 6. Total time (start + run times) and lever press preseveration measures on the last three sessions under S_D + Rd spatial contiguity condition and on the 3 test days under S_D — Rd discontiguity condition. Others denotations as in Fig. 5.

The following conclusions are offered by this study:

The findings definitely support the assertion that in coping with spatial tasks two basically different learning modes can occur. In the majority of intact organisms signal-directed responses are obtained, either in spatial contiguity or discontiguity. On the other hand "release", or triggering, of goal responses by the conditioned signal is an exclusive mode of responding after the lesion of the limbic system. Although the adaptive value of this latter mode of responding under conditions of spatial discontiguity seems obvious, we cannot say that it corresponds to a better, superior or even equivalent solution to the former one. This is contradicted by the fact that the releasing mode of action of the CS is a less complex reaction, since it occurs without exception after limbic lesions and is only occasionally used by intact animals. This simple kind of reacting resembles an amplified or stabilized form of sensitization. Its underlying neural mechanisms or its integrative level are unknown. We know, however, that the orienting-exploratory mode of reacting, or the acquisition of this mode, presupposes the intactness of the limbic system, at least in the initial stage of learning. This is clearly demonstrated by the present finding, that the great majority of animals lesioned after training also use this more complex strategy.

If the paradox of unadaptivity of the orienting-exploratory mode under conditions of spatial discontiguity can be resolved by the consideration that the kind of situation containing spatial discontiguity which results in conflict is a completely artificial situation, then there is no obstacle to concluding that the orienting-exploratory mode is the single and highest developed mode of coping with spatial problems of any kind in higher organisms.

Accordingly, we would not regard the two different modes of responding as equivalent learning strategies, between which the organism could chose according to the requirements of the actual spatial task. The relationship between the two modes, however, remains still obscure. We guess that the orienting-exploratory mode of reacting might always be preceded by a short, elusive initial stage when the CS simply releases the goal response. This would become transformed, as discrimination proceeds, into the orienting-exploratory mode. It remains, however, still to be revealed why the minority of intact animals stick to this inferior solution forever.

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