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THE ROLE OF CENTRAL FACTORS IN DIFFERENTIATION

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Right at the beginning of this report it should be mentioned that it does not represent the main stuff of the studies carried out by me and my associates, but rather a by-product which has been obtained again and again, and for a long time has waited for synthesis and systematization. Therefore, when I was asked by the organizer of this Symposium to present a paper concerning integration of the sensory input and its "decoding", I soon realized that I have at my disposal a great body of experimental evidence which throws some light on the problem of utilization by the animal of information provided by the sensory channels.

And so the aim of the present paper is to report some experiments concerning this problem and to discuss conclusions which may be drawn from them.

Experiment I

To begin with I would like to remind you of an old fact, described long ago by Pavlov (1927), and very familiar to everybody involved in the study of conditioned reflexes. It is this.

Suppose that we have established in a dog a classical alimentary conditioned reflex, measured by the amount of saliva flowing from the salivary fistula, to a certain acoustic stimulus, e.g. a tone of definite pitch. Now we introduce into the experiments a tone of another pitch which is not reinforced by food. The typical course of events is the following one. At its first application among the positive conditioned stimuli the new tone elicits a quite distinct orientation reacton, while salivation in response to it is negligible. However, in spite of the fact that this tone is not reinforced, at its following presentations the salivary response grows bigger and bigger, and after a few trials may equal, or sometimes even exceed, that to the original conditioned stimulus. Only later, with further applications of this stimulus among the positive stimuli, differentiation is developed, and salivation in response to it drops nearly to zero.

What is the conclusion from this simple experiment? The animal *perceives* at once the difference between the new tone and the old one, and the orientation reaction to the novelty of the stimulus suppresses the salivary response due to generalization. Only when the animal becomes habituated to that stimulus, which process occurs more rapidly than the process of differentiation, does the true conditioned effect of the new tone become apparent. In other words the *information* about the novelty of the second stimulus is obtained at once, while its *utilization* for conditioning occurs very slowly.

This is, by the way, why I cannot agree with those American psychologists who replace the Pavlovian term "differentiation" by "discrimination". You see that both these terms have different meanings, the latter one denoting perception of the difference between stimuli, here evidenced by the orientation reaction produced by the novel stimulus, while the former denotes the process of formation of two different conditioned reflexes to two stimuli similar in some respects to each other.

In this connection we would like to quote other interesting experiments reported long ago by Lentz *(Pavlovian Wednesdays,* Vol. I, 1949). This author established in a young lady the classical alimentary conditioned reflexes, both positive and inhibitory, to a number of stimuli by using Krasnogorski's salivary method; however, in contradistinction to the dogs, the subject wrote in her diary her impressions from the experiments. One day a reversal training was introduced in which the positive stimuli were not reinforced while the negative ones were now reinforced. Already on the first day the lady wrote in her diary: "now I understood that all will be reversed." However, the appropriate transformation of the conditioned responses took place only after a number of days. Here again the information about the change of experimental procedure came very promptly, but its utilization was much retarded.

Experiment II

In most experimental set-ups conditioned stimuli do not usually possess a single modality, but they supply a number of cues, and it is interesting to know which cues the animal utilizes to establish a given differentiation. I shall show you experiments which illustrate this (Chorazyna and Konorski, 1962).

We established, by instrumental conditioning, a differentiation between two widely separated tones according to the following procedure.

Tone A was a positive conditioned stimulus, the dog being taught in response to it to lift his right foreleg and put it on the platform in order to receive food. Tone A was applied several times in each session separated by intervals of about 1 min. Tone B, higher than A by two octaves, was applied once daily among tones A randomly, but never in the first place.

It is easy to notice that the animal can master this task by two methods: either by differentiation of the absolute frequencies of tones A and B, or by simple perception of the "oddity" of the negative tone in comparison with the sequence of the positive tones.

In view of the results of the preceding experiment showing that the animal immediately perceives the difference between two stimuli one would predict that he would rather base differentiation on the latter principle.

In order to answer this question, the frequency of both tones was decreased by one octave. As seen in Fig. 1 this did not disturb the animal's conditioned reflex activity, and he reacted to both tones correctly. However, when the frequencies of the tones were decreased by another octave, so that now the positive tone was the same as the original negative tone, this produced an immediate breakdown in his activity, and the dog developed a heavy experimental neurosis, becoming quite unfit for further experimentation. The same was obtained in other dogs, even when we changed the respective frequencies of tones more gradually.

So we see that the animal sticks to the absolute pitch of the respective tones and is not able to utilize their relative values. By the way, the experimenter based *his* differentiation of these tones exclusively on their relative values, and he hardly noticed the difference in the positive tones from one day to another.

However, it could be argued that this solution was due to the fact that in the first training always the same pair of tones was applied; in consequence, the animal could learn to base the differentiation on their absolute values, and thereafter was not able to switch to another principle.

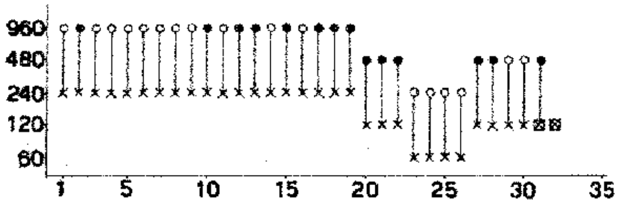

Fig. 1. The course of experiments with tone differentiation. Abscissae, successive experimental sessions, ordinates, frequencies of tones. Crosses, positive conditioned stimuli. Circles, inhibitory conditioned stimuli. Cross in square denotes that in a given session the CS did not elicit instrumental response in the majority of trials. Empty circles denote that inhibitory CS produced the positive response. Full circles denote that inhibitory CS produced the inhibitory response. Note that at first the dog was trained to differentiate between tone 240 (positive) and tone 960 (negative). Differentiation was fully established after 17 trials. The application of tones 120 and 480 did not disturb differentiation. However, application of tones 60 and 240 produced a full disinhibition of inhibitory CR. Although tones 120 and 480 were again applied, the CR activity became chaotic and soon the dog refused to react at all (Chorazyna and Konorski, 1962).

So in another series of experiments, all tones within some range were made positive but in a given sessions only one and the same tone was applied as a positive conditioned stimulus. The differential tone was always higher by two octaves than the positive one applied on the given day.

As seen in Fig. 2 the dog was not able to solve this problem, and soon he developed a heavy neurosis.

Another supposition was that perhaps the dogs would recur to the relative method of differentiation when the difference between the positive and negative tone is very small. In order to test this assumption differentiation between a 600 cycle-tone (positive) and a 500 cycle-tone (negative) was established, and in one session they were replaced by 700 and 600 cycle-tones respectively. The dog, however, reacted positively to the 600 cycle-tones although it was preceded by tones of 700 cycles.

On the other hand, it has been proved in another series of experiments, which shall not be discussed here in detail, that if we radically change the experimental procedure, the differentiation based on the relative differences of successive tones can be achieved

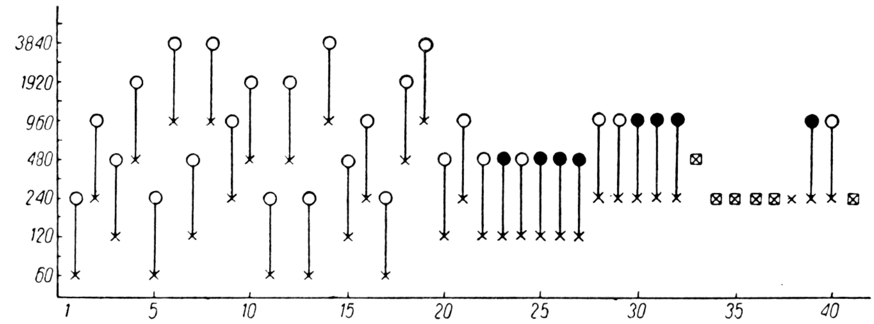

Fig. 2. The course of experiments with tone differentiation. Notation as in Fig. 1. Note that when different pairs of tones are applied each day differentiation cannot be established, and eventually the dog refuses to react at all (Chor~iyna and Konorski 1962).

(Chorazyna 1959, and unpublished experiments). Namely when we apply *pairs of tones* in such a way that, for instance, two identical tones of any frequency applied in quick succession signal presentation of food, while two different tones (e.g. lower-higher tone) do not, or vice versa, the animal *is* able to solve this problem, although it is based exclusively on the comparison of relative values of the tones.

To sum up we may ascertain that according to the results of Experiment I the dog grasps at once the difference of two tones applied one after the other, and no special training is needed for this purpose. In a special type of experimental procedure consisting in differentiation of *the pairs of tones* this ability is utilized. However, when the dog has to do with simple tone differentiation, he does not make any use of this capacity, probably because the conditioned significance of the absolute values of the respective tones has an overwhelming importance for him, and he is not able to get rid of it, even when this is necessary for the solution of the given task.

Experiment III

It could be concluded from these results that the perception and memorization of the absolute pitches of tones is for the dog the simplest and main source of information to be used in tone differentiation. However, the following experiments performed recently by Lawicka convincingly prove that this is not the whole story.

Suppose that we establish in a dog a tone differentiation not by the method of one tone being reinforced and the other not, but by the method of one tone being reinforced from the left foodtray and the other one from the right foodtray.

Against our expectation it has been proved that such differentiation is exceedingly difficult for the dogs, and is achieved only if the difference between the tones is relatively large; however, even then some dogs are not capable to master this task.

In Fig. 3 we present the mean rate of training in a group of dogs in which go left-go right differentiation was established, as compared with food-no-food differentiation in another group of dogs. We see that the difference between the two groups is quite considerable.

The close observation of the dogs in the go left-go right differentiation training has revealed that, although both tones are given from the same loudspeaker, the animals display a slightly different orienting reaction to each of them. Usually in response to the higher tone the pricking up of the ears and the head movement were stronger than in response to the lower tone. It was seen that the more pronounced was this difference, the better was the animal's performance.

In view of these observations it has been supposed that, as a matter of fact, the dogs did not associate their responses with the respective frequencies of tones but *with different orienting reactions.*

In order to test this supposition in another group of dogs the go left-go right differentiation was established to two tones of the same frequency and loudness but coming from different loudspeakers, one situated on the floor and the other hanging 2 metres above the first. As seen in fig. 4 in this case the establishment of differentiation was much more rapid.

Finally, we would like to report the result of a crucial experiment in which a dog was trained to go to the right foodtray in response to the sound of a metronome and to the left foodtray to the sound of a buzzer. The buzzer was situated on the table, the metronome on the floor beneath the table. When the differentiation had been firmly established the buzzer was placed on the floor, and the metronome on the table. The dog without any hesitation now went right in response to the buzzer and left in response to

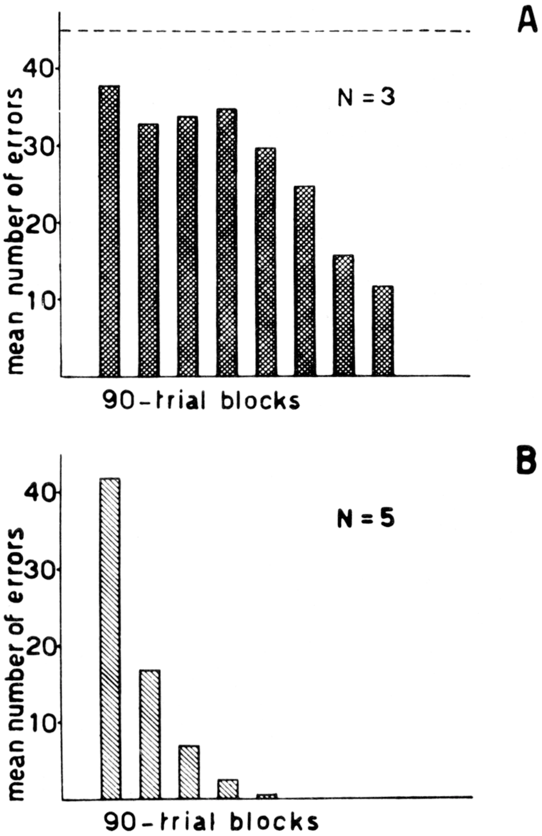

Fig. 3. Comparison of go left-go right differentiation (A) with food-no food differentiation (B). Each column denotes the mean number of errors in 90 trials. Note that food-no food differentiation is established much more quickly than go left-go right differentiation in spite of the fact that in the first case the difference of tones (700 versus 1000) was much smaller than in the second case (300 versus 1300). (Graph A is based on Lawicka's experiments, graph B is based on Brutkowski and Dabrowska's experiments).

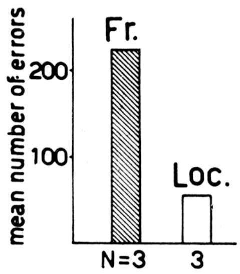

Fig. 4. Comparison of go left-go right differentiation of frequencies of tones (Fr.) versus various localizations of tones (Loc.) Note that differentiation of tone frequencies is much more difficult than differentiation of tone localizations (Lawicka's experiment).

the metronome. So even a marked difference in the quality of the two sounds had less importance in go left-go right differentiation than their localization.

As seen from these experiments the dog utilizes different cues depending on what type of responses is differentiated; while in food-no food differentiation he makes use of frequencies of tones, sticking to their absolute values (Experiment II), in go left-go right differentiation he associates his responses rather with different orienting reactions.

Experiment IV

One of the dogs used in the preceding experiment, who was not able to learn tone differentiation go left-go right, developed a strong tendency to run alternately to the left and right foodtray quite independently of which tone was applied. Therefore, it was decided to apply the two tones in alternating sequence. In this situation the responses of the animal became nearly faultless, except sometimes for the first trial in which the animal reacted at random (fig. *5a).* The substitution of the two tones by one and the

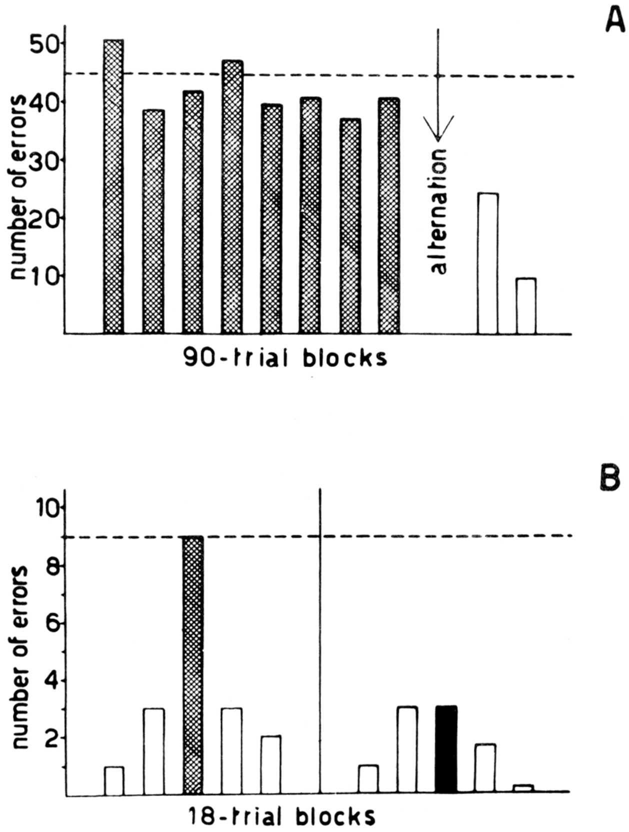

Fig. 5. Go left-go right tone differentiation versus alternation. Crossed columns, tone differentiation. Empty columns, two tones in alternative sequence. Black column, alternation to buzzer. Interrupted line, chance level.

A. Tone differentiation could not be established in this dog in spite of 560 trials. Application of tones in alternating sequence was almost immediately effective.

B. Left: returning to the random order of tones totally destroys alternation. Right: substitution of tones by buzzer did not change the animal’s performance. (Lawicka’s experiments).

same stimulus, the buzzer, did not change the animal's behaviour, but returning to the randomized order of tones made the animal quite confused (fig. *5b).*

In two other dogs two tones, signalling two foodtrays, were applied in alternating sequence from the very beginning. When the task had been mastered, the buzzer was introduced instead of both tones. The animals reacted in the same way as in preceding sessions, i.e. they ran alternately to the left and the right foodtray.

The results of these experiments show that when the dog can choose between two methods of solving go left-go right differentiation, either by performing alternate responses, or by associating his run with the pitch of the tone, he definitely chooses the first method. In other words, it is easier for the dog to remember what was his run in the preceding trial and react now in the opposite direction, than to establish differentiation according to the actual pitch of the tone. This result shows once more bow difficult it is for the dog to differentiate between two tones in case they signal two different positive responses.

Experiment V

In our last experiment it was shown that go left-go right alternation is not a very difficult task for a dog even with 1 min. interval between trials. So now we shall pass to

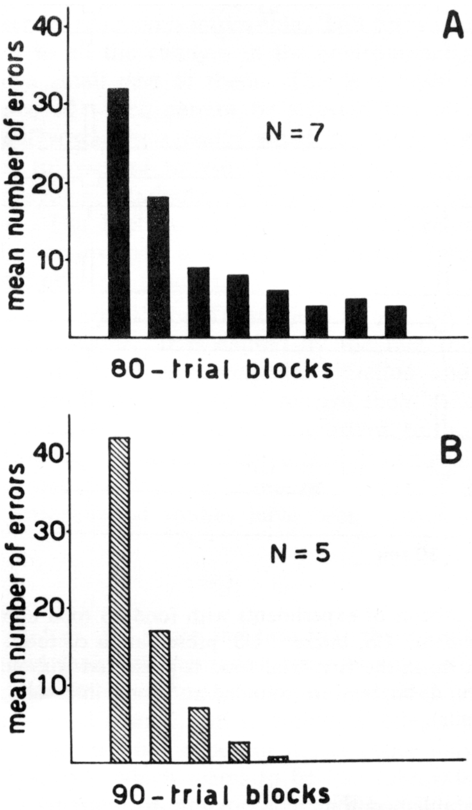

Fig. 6. Comparison of food-no food alternation (A) with food-no food tone differentiation (B). Note that alternation is more difficult than tone differentiation. (Graph A based on Szwejkowska's experiments, graph B based on Brutkowski and Dabrowska's experiments).

the analogous experiment in which one and the same stimulus will signal alternately food and no food (unpublished experiments performed by Lawicka and Szwejkowska).

The dogs were trained to perform a simple movement consisting in putting the right leg on the platform in response to a stimulus (buzzer), but now only every second buzz was reinforced by food. The intervals between trials were 1 minute.

The establishment of such alternation was in most dogs rather difficult. Again and again they displayed a positive response to the unreinforced buzzer, and only gradually did they learn not to do so (fig. 6).

When this aim was achieved several variations of the experiment were carried out to make clear on which basis the animals had mastered this task.

First, it was established that if food was presented in a given moment without preceding it by a buzz, and then, after 1 min., the buzzer was applied, the animal displayed a negative response to it. This showed that presentation of food and not the stimulus by which it was signalled played a decisive role in alternation (fig 7b).

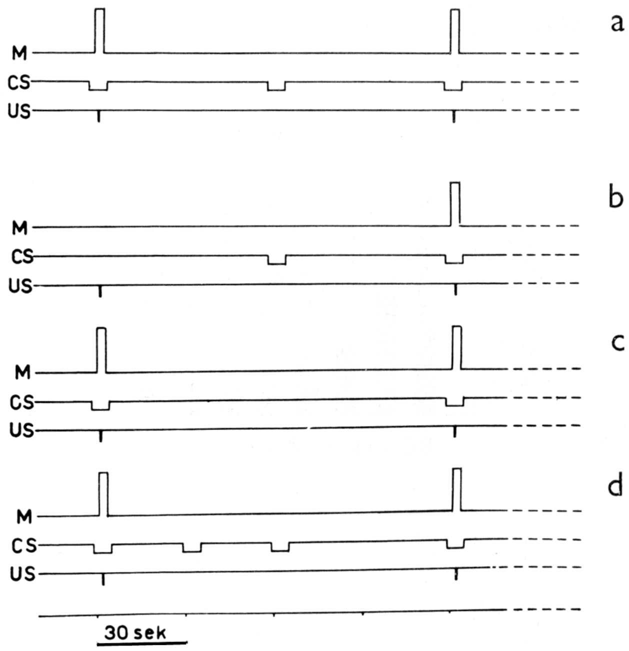

Fig. 7. Fragments of protocols of experiments with food-no tood alternation (Semi-schematic). M, instrumental movement. CS, buzzer. US, presentation of food.

a, normal experiment. b, in the first trial food is presented without CS. c, interval between trials prolonged to 2 min. d, buzzers are sounded at 30 sec. intervals. (Based on Lawicka's and Szwejkowska's experiments).

Then, it has been established that it is possible to intersperse the buzzer between the positive and the negative trial one or even two times, and this did not disturb the negative response to the buzzer applied in its right place (fig. 7d). On the other hand, if the negative trial was omitted and the next application of the buzzer was separated from the preceding trial by 2 min., the animals unhesitatingly displayed the positive response (fig. 7c).

These results clearly show that what the animals did learn in the food-no food alternation was not to perform the instrumental response to every second application of the buzzer, but to react positively to the buzzer applied about 2 min. after the last ingestion of food, and not to react to buzzers applied earlier.

In conclusion we can see again that seemingly the same problem of alternation is solved by totally different methods depending on whether the animal has to alternate two positive reactions, or to react to every second application of the stimulus. In the first case true alternation is established independently (up to some limit) of the intervals between trials, while in the second case the animals developed simply a conditioned reflex to time intervals, ingestion of food being the decisive landmark.

In addition to the above, I would quote from Tinbergen's monograph *The Study oj Instincts* (1951) where he says:

"A mere knowledge of the potential capacities of the sense organs never enables us to point out, in any concrete case, the actual complex of stimuli responsible for the release of action. From a study of sensory capacity we can infer what changes in the environment can or can *not* be perceived by the animals, but a positive answer about what *does* release the observed reaction is impossible. This turns upon the peculiar fact that an animal does not react to all the changes in the environment which its sense organs can receive, but only to a small part of them. This is a basic property of instinctive behaviour, the importance of which cannot be stressed too much. For instance, the carnivorous water beetle *Dytiscus marginalis*, which has perfectly developed compound eyes and can be trained to respond to visual stimuli, does not react at all to visual stimuli when capturing prey, e.g. a tadpole. A moving prey in a glass tube never releases nor guides any reaction. The beetle's feeding response is released by chemical and tactile stimuli exclusively, for instance, a watery meat extract promptly forces it to hunt and to capture every solid object it touches.

The occurrence of such "errors" or "mistakes" is one of the most conspicuous characteristics of innate behaviour. It is caused by the fact that an animal responds "blindly" to only part of the total environmental situation and neglects other parts, although its sense organs are perfectly able to receive them (and probably do receive them), and although they may seem to be no less important, to the human observer, than the stimuli to which it does react. These effective stimuli can easily be found by testing the response to various situations differing in one or another of the possible stimuli. A small number of such experimental studies have been carried out; they have led to important results."

General Conclusions

All experiments reported in this paper indicate that the acquisition of various types of conditioned reflexes and their differentiation obey two important principles. One is that in solving the given conditioning problem the animal does not utilize all the information supplied by conditioned stimuli, but it definitely selects certain cues neglecting the other ones. As is well known much experimental evidence may be quoted to support this issue. The second principle, which seems to be less acknowledged than the first, is that the animal extracts different cues from the same conditioned stimuli depending on which type of conditioning it is confronted with. In other words, it is not so, as we would be inclined to think according to our introspection, that the receipt of information and its utilization are two separate processes which can be combined one with the other in any way; on the contrary, information and its utilization are inseparable constituting, as a matter of fact, one single process.

If we take into account the general principles of the functioning of the nervous system, we may see that our conclusion can be directly deduced from them. As is well known, the basic principle of the functioning of the spinal cord is that each type of reflex is selectively elicited by definite patterns of stimulation in which usually different types of receptors are involved. It means that here "information" is immediately and rigidly linked with its utilization. The same rule holds true in respect to higher forms of innate animal activity, as clearly illustrated by Tinbergen's experiment quoted above. As far as the acquired animal behaviour is concerned the following considerations empower us to draw a similar conclusion.

In our analysis of the mechanisms of conditioning presented in detail elsewhere (Konorski, 1948), we have put forward an idea that a conditioned reflex is formed by a transformation of *potential* connections established between some centres in the ontogenetic development of the nervous system into the *actual* connections. This thesis is supported by a great body of evidence and seems to be true quite independently of what is the intimate nature of this transformation and which parts of the nervous system are engaged in it. According to that principle only those activities of the nervous system can become interconnected by the conditioning process which are potentially predisposed to do so. In consequence, the acquired activities of the nervous system obey the same rules as the innate ones, except that here potential and not actual connections determine the patterns of future conditioning.

The evidence from Experiment III that in food-no food differentiation and go left-go right differentiation different sensory cues are involved is a good illustration to this issue. In fact, in the first type of differentiation the conditioned connections are formed between the "centre" of the conditioned stimulus and the "centre" of the reinforcing stimulus, i.e. the central representation of taste. Probably the higher parts of the nervous system are endowed with potential connections joining all sensory systems and in particular various modalities of sensory input with taste. In consequence, in this case the particular acoustic stimuli themselves become the signals of both food reinforcement and food nonreinforcement. This occurs by establishing connections between the central representation of a given stimulus with the central representation either of taste of a given food, or of the taste of its absence in the mouth.

The situation is quite different in respect to the go left-go right differentiation. Here *both* conditioned stimuli are reinforced by food, and therefore both of them are connected with the same taste centre. The differentiation concerns the problem *whether to go left or to go right* in response to the given tone.

It follows from our experiments that the central nervous system of the dog is not endowed with potential connections joining acoustic stimulation with turns of the body, but it is certainly endowed with connections joining various bodily reactions between themselves, since this is indispensable for the adequate behaviour of the animal in the surrounding world. In consequence, only the orienting reaction elicited by the conditioned stimulus may become connected with the reaction to the proper foodtray. As tones of different frequencies differ very much in their acoustic properties, but differ only slightly in the orienting reactions elicited by them, it is quite conceivable that differentiation based on the latter cues is very difficult. * It is of course made easier if the tones (even if identical) are sounding from different sources, since then the difference

By the way, Lawicka noticed that such a differentiation is facilitated when one of the tones becomes *stronger* than the other, which is comprehensible in view of the fact that then the difference between orienting reactions becomes greater.

between the respective orienting reactions is increased. Hence we can easily understand the, at first sight, almost unbelievable fact that even if two quite different sounds signal two runs to different foodtrays, the dog totally disregards the *quality* of the sound and bases his reaction exclusively on its localisation.

Other experimental results reported in this paper can be easily accounted for on the basis of this principle. In Experiment I, when the animal is confronted with a new stimulus similar to that being already conditioned to food, he at once perceives the difference, as judged from the orientation reaction, but cannot utilize it for differentiation, for the new stimulus possesses elements already connected with the given reinforcing agent. In consequence, the animal achieves differentiation between the two stimuli by a sort of countertraining applied to the new stimulus.

From this point of view experimental findings reported by Chorazyna and Konorski also seem to be clear (Experiment II). Since the animal has a strong tendency to establish sensory-sensory associations, particularly if the second stimulus has a strong reinforcing value, the differentiation based on the relative and not on the absolute value of tones *must* be difficult because it violates this very tendency. However, when a pair of successive tones, and not one particular tone, is conditioned (as is the case in Chorazyna's experiments), this firm association has no chance to be established, since the first element of the pair, whatever it is, is never reinforced.

Again, our assumption explains why according to Lawicka's experiments go left-go right alternation is easier than go left-go right tone differentiation (cf. Experiment IV). In alternation the differential cue to go to the proper foodtray is provided by the direction of the last run, i.e. by a very strong proprioceptive stimulus, although not immediately preceding the reaction. On the other hand, the tone differentiation is very difficult because, as was said before, the differential cue provided by two different proprioceptive stimuli generated by different pitches of tones is insignificant.

The above reasoning explains why the animal cannot apply the same solution in food-no food alternation, as is used in go left-go right alternation (Experiment V). In the case of food-no food alternation the buzzer becomes first a conditioned stimulus in spite of the fact that it is, from the dog's point of view, irregularly reinforced. Some dogs stick to this principle for a long time and continue to react positively to every application of the buzzer. But then they gradually learn that during some period after food ingestion food is not presented in spite of the application of the buzzer and so they develop an appropriate inhibitory conditioned reflex analogous to that described by Pavlov as "conditioned inhibition". In consequence, while go left-go right alternation is a true alternation, here we have to do rather with a sham alternation since the animal's reactions are controlled by the time elapsed since the last feeding.

Summary

The present paper presents a number of experiments showing the following rules concerning the selection of information comprised in conditioned stimuli: 1° When solving the given conditioned reflex problem the animal does not utilize all the information supplied by the conditioned stimuli, but selects certain cues neglecting the other ones. **2°**The selection of cues does not depend only on the species of animal we are experimenting upon, but also on the problem the animal has to deal with. In particular, while in go-no go differentiation the animal utilizes the acoustic properties of sound conditioned stimuli (such as pitch of tone), in go left-go right differentiation, he makes use preferably of proprioceptive cues provided by the respective orienting response.

It has been shown that these rules concern both innate and acquired responses, and their possible physiological mechanism is discussed.

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