ON THE FUNCTIONAL STRUCTURE OF CONDITIONED REFLEXES TO SERIAL STIMULI IN DOGS

L. P. RUDENKO

Institute of Higher Nervous Activity and Neurophysiology Moscow, USSR

Abstract. The functional structure of conditioned reflexes to a stimulus series has been studied. The serial stimulus consisted of a tone of 600 Hz, passive lifting of the right forepaw, and a puff of air directed at the eye, the latter component of the series being reinforced by food. Four dogs were used. Objective registration of the effector manifestations to each component stimulus has shown that, during the elaboration of a conditioned alimentary reflex to the serial stimulus, conditioned connections are formed by each component with the alimentary center and by each preceding stimulus with all subsequent stimuli, irrespective of their position in the series. All excitation foci which function in the given stimulus set become interconnected. Direct connections of each stimulus component with the alimentary center are never inhibited. The multiplicity of duplicating direct connections and the presence of backward connections impart to composite reflexes the reliability and adaptive strength which is necessary for the formation of behavioral acts.

The integrative activity of the brain has been a subject of study almost from the inception of the doctrine of higher nervous activity. In Pavlov's view, the formation of a conditioned reflex (CR) already represents an act of synthesis, an instance of integrative activity by the cerebral hemispheres. For a special study of integrative activity of the brain, various composite and chain CRs underlying complex behavioral acts have long been investigated in the Pavlovian laboratories.

In the USSR, CRs to a series of stimuli have often been studied (e.g., 1, 6, 9, 11–13, 16, 18, 23). Many diverse and interesting facts have been discovered relevant to the formation and properties of serial CRs and the role and significance of their individual components in the process
of synthesis. The functional structure of this type of composite reflex has not yet been fully elucidated, however. The present investigation differs from the previous ones in that each component of a composite stimulus had an objectively recorded effector response, which made it possible to assess the interconnections between the individual components of the series.

METHOD

The composite serial conditional stimulus (CS) consisted of a tone of 600 Hz, passive lifting of the right forepaw, and puffs of air directed at the eye of the dog. Each component stimulus occurred for 10 sec, while the interval between stimuli was 5 sec. The last stimulus coincided with presentation of food. During exposure to the tone, electromyographic recording was made of the orienting response from muscles moving the pinna; during forepaw lifting, mechanographic and myographic records were made from forepaw extensors; and during feeding, salivation was recorded. The components of the serial stimulus were always presented in the same sequence. Intervals between presentations of the serial stimulus were varied. Four dogs were used. Recording was done on an universal ink recorder.

RESULTS

In the serial stimulus, each succeeding component served to reinforce each preceding one; food, however, was a biologically important (rewarding) agent and exerted the strongest reinforcing effect on all other components.

It took very little time to elaborate an alimentary CR to the serial stimulus. Each component of the series was accompanied by salivation (Fig. 1). Therefore, each component became connected with the alimentary center, although it had never been reinforced with food; that is, direct connections of each component with the alimentary center were established.

Analysis of the individual components of the CS indicated that early in the reflex elaboration, the "law of strength", was in operation, that is the stronger the stimulus the greater was the CR. The greatest salivation developed in response to the third component (air puffs), the reflex to the first component (the tone) was less strong, and the weakest reflex was to the second component (passive forepaw lifting). As the reflex was further elaborated and consolidated inhibition developed, with shifting of the beginning of the CR to the end of the serial CS, closer to the re-
inforcement, irrespective of the stimulus force (Fig. 2). The development of inhibition, as in the case with the use of a single stimulus, suggests that the serial stimulus is perceived by the nervous system as a unique, integrated entity.
Apart from direct connections of each component with the alimentary center, it was also possible to observe from the very outset the elaboration of successive connections between individual components of the series. The tone of 600 Hz invariably preceded passive forepaw lifting, and after several combinations the dogs began to lift the forepaw actively in response to the tone, as can be clearly seen from the mechanogram and especially the myogram of the forepaw extensors. Such a response was noted in 95–97% of the cases. Passive forepaw lifting always preceded the air puffs to the eye, and as a consequence elicited blinking in 70–75% of cases. This implies the establishment of successive connections between the serial components, as also reported by others along with direct connections with the alimentary center. The present experiments, in addition to confirming the existence of the above two kinds of connections, have also shown that each stimulus not only becomes a signal for the stimulus that follows it, but also for all the subsequent stimuli irrespective of their position. A particularly striking demonstration of this was the application of the first component, the tone of 600 Hz, which usually was followed by passive forepaw lifting, air puff, and food presentation. During presentation of the tone, all three responses were elicited, i.e., active forepaw lifting, blinking and salivation (see Fig. 1 and Fig. 31). During passive forepaw lifting, a blinking CR and salivation were observed, respectively. But salivation also followed all other preceding stimuli, because they all were linked by direct connections with the alimentary center.

It should be noted that the serial CR also involved backward connections when isolated presentations of component stimuli elicited the effect of the preceding component (thus during food intake there was blinking; during air puffs the forepaw was actively lifted).

When the CRs to the serial stimulus had been elaborated and consolidated, a number of functional tests were carried out. In fact, all relevant tests known in the literature, were performed. These included isolated presentation of individual components, omission of components and their replacement with a pause, extinction of individual components and their substitution with indifferent stimuli, etc.

With the isolated presentation of either the first (600 Hz tone), second (passive forepaw lifting) or third (air puffs) component, the alimentary CR persisted in all the dogs at all stages of CR elaboration (Fig. 3). A total of 40 such tests were performed in the four dogs, yielding similar results. In these tests, a given stimulus was presented for the period equal to that of its duration as a component of a series (i.e., 10 sec) or else its presentation was extended to 30 sec, i.e., the duration the entire series. In both cases, the alimentary CR was elicited but in the latter
FUNCTIONAL STRUCTURE OF CONDITIONED REFLEX

Fig. 3. Isolated application of individual components of the serial stimulus: I, 600 Hz tone; II, passive forepaw lifting; III, air puffs to the eye. Designations as in Fig. 1.

case it often strongly diminished after 10 sec, and an orienting response was observed. This is probably because none of the components had normally lasted longer than 10 sec. The persistence of alimentary CRs during the isolated presentation of one of the components of the CS indicates that the direct connections of each component with the alimentary center had not been lost in the course of the elaboration and consolidation of the serial CR.

The tests with omission of one or two components and their replacement with a pause, produced the same result, i.e., the CR persisted. It likewise persisted when the sequence of components was altered. The next test consisted in the simultaneous presentation of all three components or of the second and third components when the first was still acting. In these cases the CR grew even stronger, apparently due to the phenomenon of summation.

In other tests particular components of the series were inhibited by presenting extraneous stimuli instead of any of the serial components (external inhibition) and by using acute intermittent extinction of one of the serial components (internal inhibition). The CR to the serial stimulus was most affected when indifferent stimuli were employed in place of the third component, which was closest to the reinforcement. The same picture was observed in the case of extinction. The CR to the series was impaired mostly following extinction of the CR to the air puffs (third component). During the first and second presentation of the composite stimulus following an extinction, the reflex was still inhibited and re-
stored completely only upon the third presentation of the composite stimulus. These results serve to emphasize the great importance of the third component associated with food reinforcement.

To sum up the results of all tests, it may be said that the alimentary CR persists following various changes of the serial components. This suggests, in the first place, that the direct (parallel, according to Voronin) connections of each stimulus are strongly linked with the alimentary center. The successive connections were temporarily disrupted in these tests but the CR persisted due to the parallel connections.

As has been shown earlier (7, 8, 17, 22) during the elaboration of feeding and defensive CRs the unconditioned responses (URs) to any

Fig. 4. Change in orienting reflex to the tone (5) during elaboration of alimentary CR to the stimulus series: A, 5th day of elaboration; B, 14th day of elaboration.

Designations as in Fig. 1.
CS become somewhat weakened and inhibited, while the CR becomes stronger. Asratyan (2, 3) believes this to be a most important prerequisite for the formation of a conditioned connection. The same phenomenon was observed here in the course of elaboration of CRs to serial CS. Each succeeding component exerted an inhibitory (induced-type) effect on the UR of the preceding stimulus resulting in its attenuation.

By recording the URs of the stimuli which were components of the series, the time-course of changes in the blinking reflex in response to air puff could be seen in the form of weakening of blinking movements (see Fig. 1); and of the orienting reflex to the tone from changes in the electromyogram of the muscle of the pinna (Fig. 4). Figure 4A shows the beginning of elaboration of a CR when the orienting reflex to the tone was very strong as manifested by an abrupt increase of potentials in the ear-elevating muscles upon presentation of this stimulus. Fragment B of this Figure shows that as the CR to the serial CS was elaborated, the UR (i.e., the orienting reflex) to the tone was inhibited. When any change in the experimental procedure was introduced (for instance, when the tone was prolonged or extraneous noise appeared in the chamber), the orienting reflex to sound recovered.

Thus, an essential aspect of the synthesis of both elementary and composite reflexes appears to be some weakening of the response to that stimulus which is transformed into a signal for the succeeding stimulus. (The proposition must be accepted that any external or internal stimulus acting on the nervous system invariably brings about its own UR).

DISCUSSION

In the literature devoted to CRs established to consecutive sets or series of stimuli, the test with isolated presentation of individual CS components is usually regarded as a special test revealing that a composite stimulus has been transformed into a single integrated stimulus in which each component produces a conditioned effect only when it is a part of the series, and loses its signalling significance when presented separately. That is, in the process of serial reflex elaboration, the parallel (in Voronin’s terminology) or direct connections of each stimulus with the alimentary center become inhibited while the successive connections persist.

However, analysis of the available data in the literature reveals that different authors have obtained differing results not only for different species, but also for the same species. For instance, stimuli were found to lose their signalling significance when presented separately in studies
by Ivanov-Smolensky (10), Beritov (5), and Alekseeva (1) on dogs; by Tagiev (20) on rabbits and pigeons; by Prazdnikova (14) on fishes; and by Shirkova (19) and Tkhan (21) on rats. Conversely, they retained their signalling significance in studies by Kunstman (12), Voronin (23), and Rokotova (16) on dogs; and by Tagiev (20) on fishes.

In the present experiment, parallel, or direct connections were never inhibited at any stage of elaboration or maintenance of CRs to serial stimuli, which has led to the conclusion that the absence of a CR in the test involving the isolated use of one component of the CS cannot serve as an indicator of the animal's ability to perform analytic–synthetic activity, as believed by certain authors.

The results in which inhibition was established in response to the first component of the serial stimulus speaks in favor of the view that integration is of importance in the consolidation of the serial CR. This is also attested to by the formation of successive connections which unite, in a reflex manner, the individual stimuli to make them a single entity. As regards direct connections, they are neither lost nor diminished, and even show no tendency to inhibition, but exist along with the successive connections and duplicate their function.

The experiments confirm the presence in composite reflexes of parallel and successive connections (in Voronin's terminology) and, in addition, have revealed some other, previously unnoticed connections. Registration of the effects produced by each component of the serial stimulus has indicated that all of them are interconnected. Each preced-
ing component is connected by both direct and mediated connections with all subsequent components (Fig. 5). A schematic representation of all connections observed in these experiments, yields a picture of multiplicity of forward and backward connections. Whether these connections enter a current reaction sequentially or some of them remain unoperative, is not yet known. But the evidence suggests that all of them are in a functional state and are never inhibited or inactivated.

The question arises as to why multiple connections possessing the same function arise in composite reflexes, taking into account that a single connection or a series of successive connections would be sufficient for the successful performance of a particular function?

As is well known, the principle of redundancy is an important factor in the reliability in the living organisms as well as in technology. The redundancy of elements in any system underlies the principle of reliability both in structural and functional respects (e.g., 4, 15). The redundancy of conditioned connections observed here appears to provide for the reliable functioning of composite reflexes. If, for whatever reason, one of the functioning connections suddenly becomes inoperative, it will be replaced by another duplicate connection, and the function will not be impaired. If there were only one such connection, composite reflexes would be liable to all kinds of accidental influences, they would be constantly disrupted, and no behavioral activity would be possible. Apparently, the more complex the nervous activity, the more conditioned connections are formed to provide for the reliability and perfection of neural organization; and some of this was seen here when studying the CRs to serial stimuli.

CONCLUSIONS

1. Objective registration of effector manifestations of each stimulus which formed a part of a serial conditional stimulus has shown that during the elaboration of a conditioned alimentary reflex to such a stimulus, conditioned connections are formed by each component stimulus with all subsequent ones, irrespective of their position. All excitation foci which function in a given composite reflex become interconnected.

2. Direct connections with the alimentary center are never lost by any component of the serial stimulus.

3. The multiplicity of duplicating direct connections having the same function, as well as the presence of backward connections, appear to impart to composite reflexes the reliability and adaptive force which are necessary for the formation of behavioral acts.
REFERENCES


21. TKHAN NHUEN TKHIEN 1959. The formation of conditioned reflex and dif-


Received 3 July 1972

L. P. RUDEKO, Institute of Higher Nervous Activity and Neurophysiology, Academy of Sciences of the USSR, 48 Pyatnitskaya, Moscow, USSR.