

AN ATTEMPT AT MODELLING OF THE CENTRAL
ALIMENTARY SYSTEM IN HIGHER ANIMALS
V. INSTRUMENTAL CONDITIONED REFLEXES

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MECHANISM OF ALIMENTARY INSTRUMENTAL CONDITIONED REFLEXES
AND ITS MODELLING

According to the ideas put forward by Soltyśik (1960) and Konorski (1967) one of the main effects of hunger (or, for that matter, of every drive) is activation of the motor behavioral system manifested by general motor excitement and increased motor efficiency. If in such a condition a given motor act is provoked which leads to the satisfaction of hunger by offering the animal a morsel of food, then this very act becomes consolidated and is elicited when the animal is hungry. The reason for this consolidation is seen in the fact that inhibition of hunger produced by the taste stimulus prevents the continuation of the motor excitement and protects the last performed movement from being erased by retroactive inhibition caused by the following movements. In consequence, the general motor excitement produced by hunger is, so to speak, channeled and directed to one definite effector.

The presence of hunger is thus the indispensable condition both for the formation of alimentary instrumental responses and for their performances: in the absence of hunger the instrumental response fails to occur.

There is a great body of experimental evidence to show that the presence of hunger is not a sufficient agent for elicitation of the learned instrumental response. The occurrence of this response depends also on the external situation or a sporadic stimulus in whose presence that

response led to presentation of food. This stimulus will be denoted as instrumental conditioned stimulus (ICS).

A great number of experiments on instrumental conditioned reflexes (ICRs) to sporadic CSs performed in dogs has led to a model of these reflexes represented in Fig. 1 (Wyrwicka 1952, 1960). According to this model the center of the ICS is connected with the center of hunger (because the stimulus was always presented when the animal was hungry) and with the kinesthetic center controlling the trained movement (because the stimulus was followed by that movement). On the other hand, the center of hunger is connected with the kinesthetic center of the trained movement, because this movement was always elicited in the state of

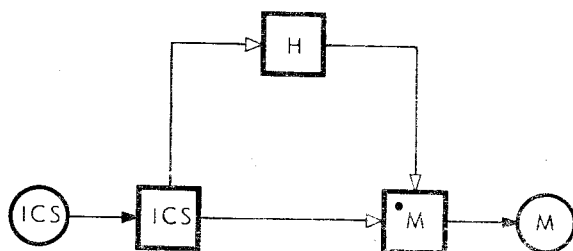


Fig. 1. Simplest model of ICR arc. ICS, receptor (circle) and center (square) of ICR. H, hunger center. M, center (square) and effectors (circle) of movement. Point in the center of M means that this center is activated by joint operation of H-M and ICS-M connections.

hunger. Thus, the center of the ICS is connected with the center of the learned movement both "directly" and "indirectly" through the intermediary of the hunger center. Only in the presence of the joint operation of these two types of connections is the learned motor act elicited.

Further experimental evidence shows that although both types of connections must be active for the elicitation of the movement, they mutually complement each other: the stronger the "direct" connections between the center of the CS and the center of the motor act the weaker hunger is sufficient to elicit that act (Dobrzecka and Wyrwicka 1960, Dobrzecka and Konorski 1962); similarly, the weaker the "direct" connections, the stronger must be the hunger to produce the movement.

In the first paper of this series (Konorski and Gawroński 1970a) a model of the central alimentary system was proposed which satisfactorily accounts for all major properties of the consummatory food unconditioned reflexes (FUR) as well as classical food conditioned reflexes (FCR) described in the preceding paper. For the convenience of the

reader this model is reproduced in Fig. 2. It may be noticed that the above considerations concerning the mechanism of the ICR can be easily incorporated into this model. As seen from Fig. 3 the *spiritus movens* of the instrumental CR is the activation of the H subcenter, which is connected (through the motor behavioral system) with the center of the given

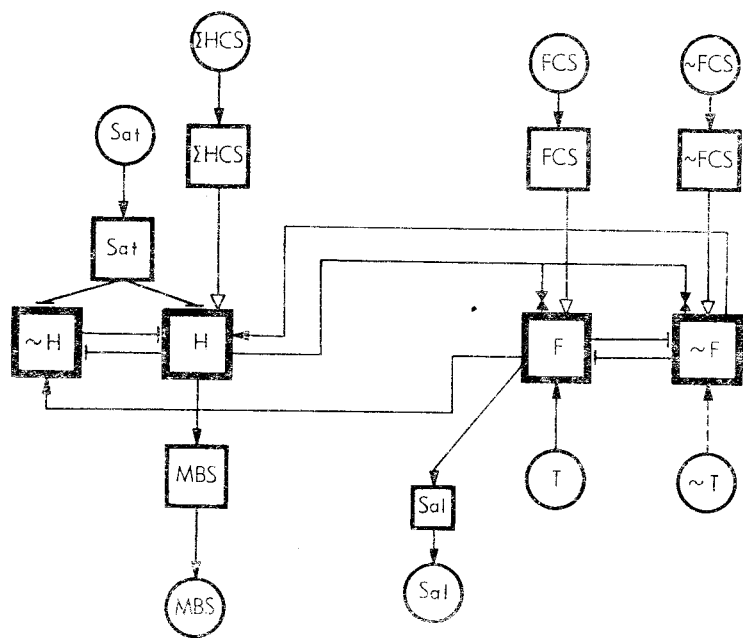


Fig. 2. Model of central alimentary system. Squares, centers, circles, receptors or effectors. H, \sim H on- and off-hunger subcenters; Sat, satiation center; F, \sim F, food, no-food subcenter; T, \sim T, on and off-taste receptors; Σ HCS, hunger CS; MBS, motor behavioral system; FCS, \sim FCS, food and no-food CS; Sal, salivation. Black triangles, excitatory unconditioned connections; white triangles, excitatory conditioned connections; double triangles, facilitatory connections; stopped lines, inhibitory connections; dashed line denotes adaptive connection.

movement M¹. In addition, the center of the ICS is connected both with the H subcenter and directly with the center of M. The latter center is activated when the impulses arrive at it jointly from the H subcenter and the ICS center.

Further course of events is this. The performance of movement M leads to presentation of food, that is, to the stimulation of T receptors producing activation of the F subcenter. This in turn produces activation

¹ The notion of "the center of movement M" denotes the kinesthetic representation of that movement which programs and initiates its performance (Konorski 1967).

of the $\sim H$ subcenter which inhibits the H subcenter; as stated above, this inhibition is indispensable for the formation and preservation of the ICR.

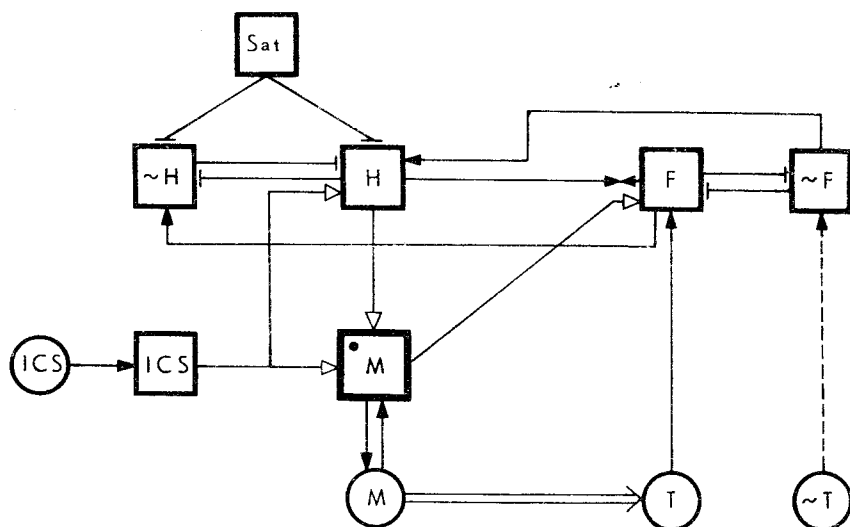


Fig. 3. Diagram of centers and connections involved in instrumental conditioning in Dewan. Denotations as in Fig. 2. Double line arrow between M and T denotes the causal bond. Note the connection between M and F which is in operation when kinesthesia of M becomes a FCS.

One more connection drawn in the diagram of Fig. 3 is that linking the center of movement M with the F subcenter. Since movement M always precedes the presentation of food, its kinesthesia may easily become a FCS. Although this is actually so, we have shown that the FCR established to movement M plays no role whatsoever in instrumental conditioning and is not indispensable for its occurrence (Ellison and Konorski 1965, 1966). This fact is well replicated in our model in which the connection leading from M to F (not to be confused with the causal link between M and T!) is completely irrelevant for instrumental conditioning.

BASIC EXPERIMENTS ON ICRs

The simplest experiment on instrumental conditioning is that in which the response (for instance, lever pressing) is established to the experimental situation in such a way that each movement performed in that situation is reinforced by presentation of food. The record of such an experiment mode on Dewan, which closely imitates a natural experiment, is pre-

sented in Fig. 4. As may be seen from this record Dewan, like a normal dog, behaves in such a way that he performs the trained movement, obtains food, eats it and immediately afterwards performs the next movement. The extremely regular performance is due to the fact that the end of the consummatory response leads to the temporary increase of hunger due to the $\sim F-H$ connection (see Fig. 3). During the act of eating Dewan, like a normal dog, never performs the trained movements. This is because, as seen in Fig. 4, the excitation of the $\sim H$ subcenter during the food intake inhibits to a large extent (although not completely) the H subcenter.

In a regular experiment, in which every movement is reinforced with food, we observe salivation only to the reinforcing stimulus, because the intervals between successive food intakes are too short to detect the conditioned salivary responses. In order to detect these responses we withdraw for a short period food reinforcement, allowing the animal to perform the instrumental movements repeatedly in close succession. We may observe that each movement is then followed by a "quantum" of salivation (Fig. 4).

According to our concept, wholly replicated in the model, the intensity of the ICR depends directly on the strength of excitation of the H subcenter. In Fig. 4 the instrumental responding is shown at strong (a) and weak (b) humoral hunger. It may be seen that the stronger the hunger, the more rapid the sequence of movements when the food reinforcement is withheld.

We shall turn now to that experimental procedure in which the animal is trained to perform the instrumental response not to a continuous CS provided by the experimental situation, but to a sporadic CS. In the first stage of training the animal performs the trained movements very frequently in intertrial intervals, but gradually these movements, not being reinforced, become extinguished, and the animal reacts only to the sporadic stimulus, in whose presence the motor response is immediately reinforced.

We cannot enter here into the problem of the mechanism of this extinction, because it postulates some mechanisms not described in our model (cf. Konorski 1967, Chapter X). To put it briefly we assume that since during the intertrial intervals the dog never receives food excitation of the H subcenter provided by the ΣHCS is attenuated below the threshold of the motor response. On the other hand, the center of the ICS becomes connected both with the H subcenter and with the motor center. Therefore, that stimulus increases the excitation of the subcenter H which fires to the motor center, and stimulates that center directly, thus providing necessary conditions for elicitation of movement M .

The simulation of such an experiment on Dewan is presented in Fig. 5. It may be seen that although in the intertrial intervals the H subcenter is activated, this activation is not sufficient for elicitation of movement M. However, that movement appears immediately in response to the ICR.

For better understanding the mechanism of instrumental conditioning it was necessary to create such experimental conditions in which it would

a)

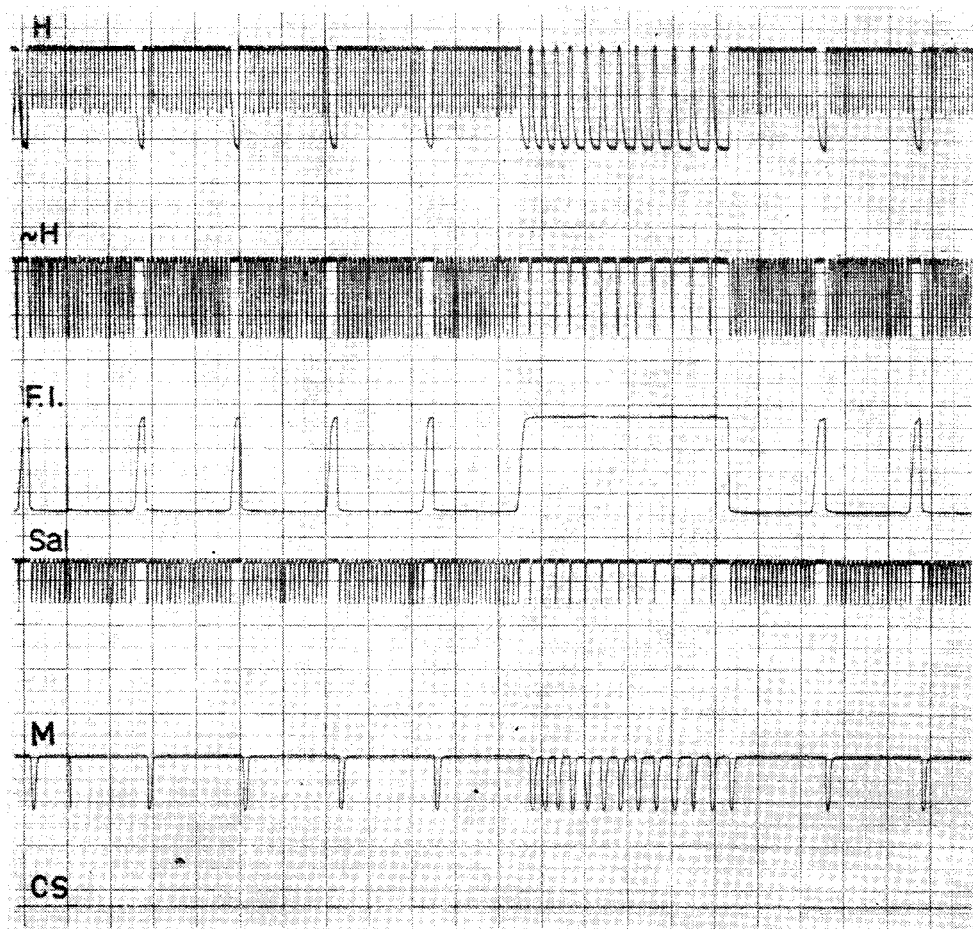
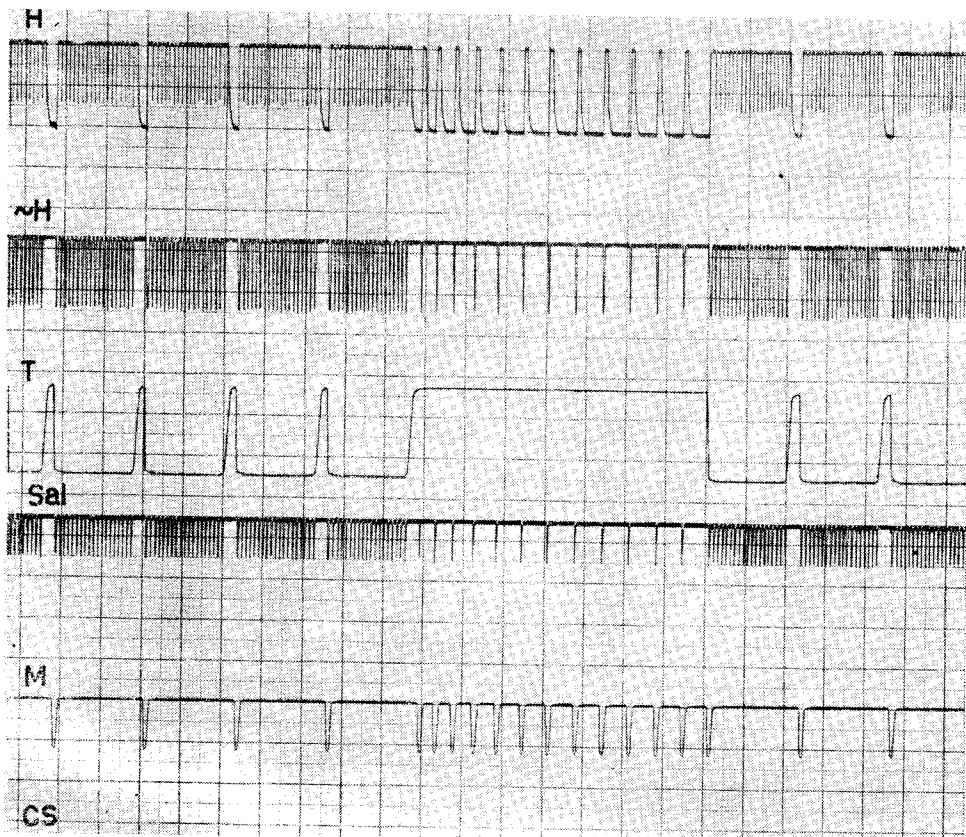


Fig. 4. Record of experiment in Dewan in which the ICR is established to the experimental situation. From top to bottom: activity of H subcenter (H), activity of \sim H subcenter (\sim H), acts of eating (F.I.), salivation (Sal), instrumental movement (M). All active states are denoted by downward deflection of the record. After several movements reinforced by food, the presentation of food is withdrawn; this leads to a rapid sequence of movements. *a*, relatively high level of humoral hunger; *b*, lower level of humoral hunger. Presentation of food leads to excitation of F subcenter (copious salivation), which partially inhibits the H subcenter (rel-

be possible to record parallelly both motor and salivary responses. This was achieved by introducing "fixed ratio" of motor responses. For instance, the animal has to perform during the CS-US interval twelve movements to obtain food. The rate of the motor performance and salivation gives the measure of the intensity of instrumental and classical CRs respectively.

It was found that the relations between both responses are rather complex. On the one hand, as noted before, each motor response is accompanied by salivation because of the strong M-F connection. On the

b)



atively low rate of impulses), excites the $\sim H$ subcenter, inhibits movements. When food is digested immediately the activity of the H subcenter is increased, the $\sim H$ subcenter is silenced, movement is performed. Each performance of the movement produces conditioned salivation, shortlasting decrease of H and increase of $\sim H$. This is seen in the period when food is not presented. Note that with higher humoral hunger the rate of motor acts in the absence of food reinforcement is greater than with lower humoral hunger.

other hand, this connection may fail to be established; this happens when the series of movements is not immediately followed by food reinforcement, but it is followed by the classical FCS which precedes the presentation of food (Ellison and Konorski 1965). Finally, when the ICS is regularly reinforced by food (because the animal performs quickly the whole ratio of movements), it tends to become by itself a FCS and evoke salivation regardless of whether it does or does not evoke movements.

In Fig. 6 we present these three possible varieties of the animal

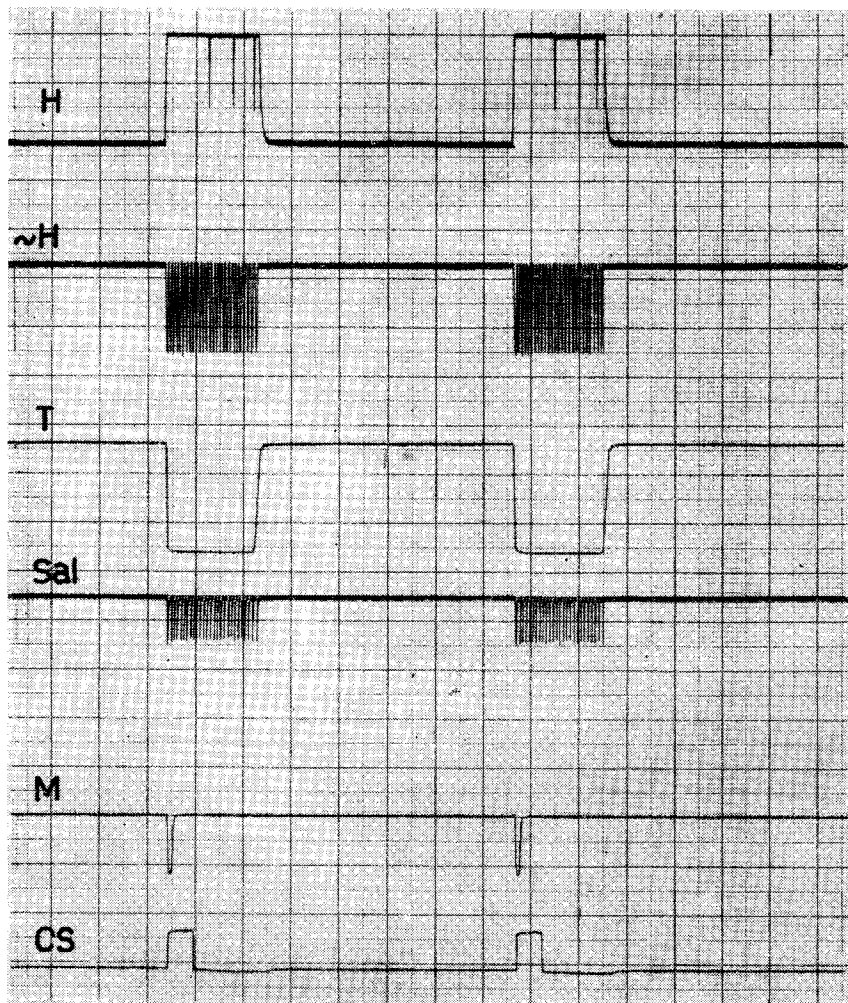


Fig. 5. ICR to sporadic CSs (marked upward on the bottom line). All denotations as in Fig. 4. Note that presentation of the ICS immediately evokes movement followed by presentation of food. Two such trials are shown. Very high hunger in the intervals drops considerably during the act of eating.

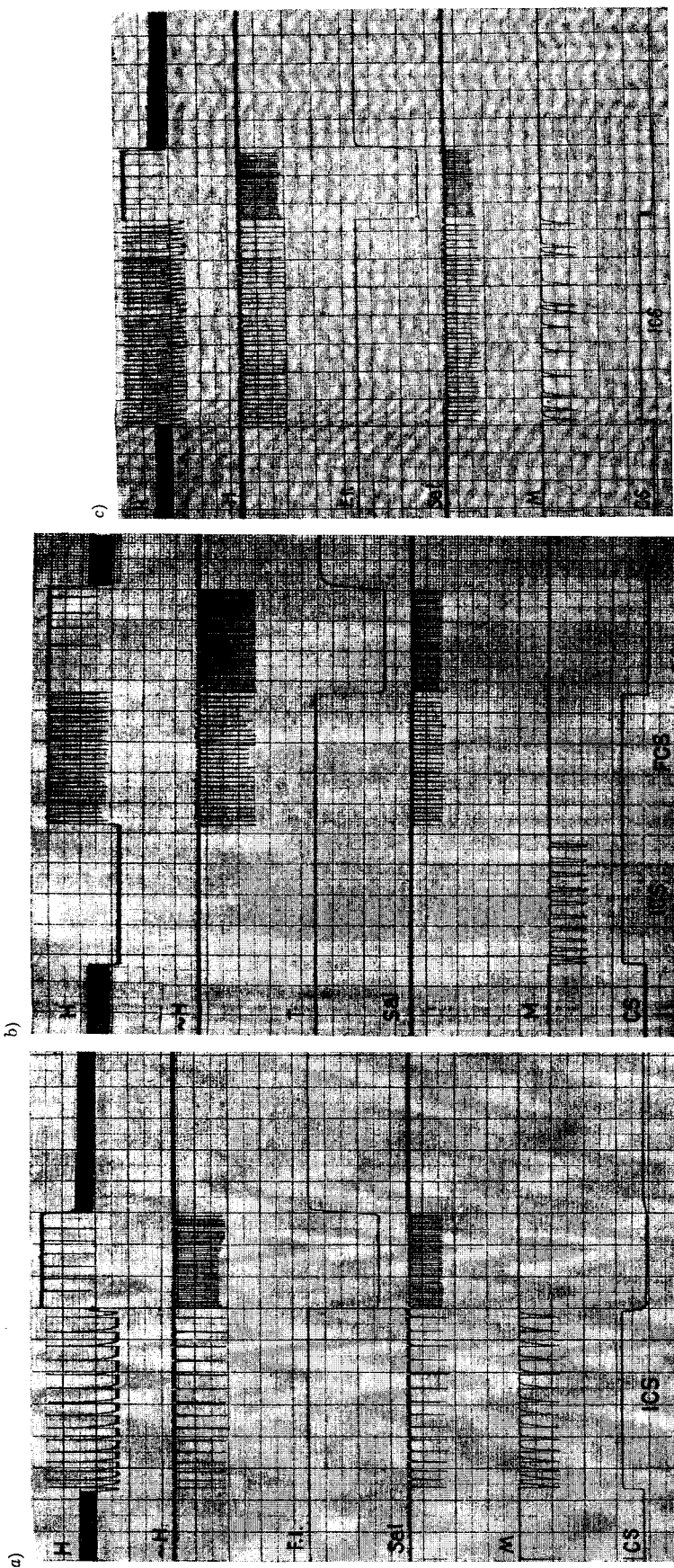


Fig. 6. Three possible varieties of the interrelations between motor and salivary responses in instrumental conditioning. All denotations as in Fig. 4 and 5. a, ICR to a sporadic ICS reinforced after 15 movements. A medium level of hunger in the interval is increased during the ICS; Dewan starts to perform the movement which is followed by short conditioned salivation. During short periods of FCRs following the motor acts, H subcenter is inhibited and \sim H subcenter is excited. b, Model of the Ellison and Konorski (1965) experiment. First, the ICS is presented, to which Dewan performs 11 movements. The H level increases (owing to the ICS-H connection), but, in contrast to the experiment presented in Fig. 6a, salivary responses do not follow the movements. The ICS is followed by classical conditioned stimulus (FCS) which produces copious salivation, decrease of the activity of the H subcenter and excitation of the \sim H subcenter. Presentation of food produces increased salivation, increased excitation of the \sim H subcenter and strong decrease of the excitation of the H subcenter. c, ICR to a CS which has a mixed character being partially classical and partially instrumental. CS produces salivary response increased in comparison to that in Fig. 6a and instrumental response at a slower rate than that in Fig. 6ab. Note slight antagonism between salivation and motor responses.

behavior simulated by Dewan. In *a* the CS is a "pure" ICS that is, it elicits no salivation, but the kinesthesia of movements performed produces salivation (Wolf 1963). In *b* neither the ICS nor the kinesthesia of movement M produces salivation (Ellison and Konorski 1965). In *c* both ICS and movement produce salivation, that is the external stimulus is a mixed instrumental and classical CS (this is the most usual case). It may be seen that while the intensity of instrumental response (measured by the period of the performance of twelve movements) is almost the same in case *a* and in case *b*, in case *c* it is definitely lower than in both preceding cases; this is because excitation of the F subcenter by the CS produces excitation of the \sim H subcenter attenuating the activation of the H subcenter (Konorski and Wyrwicka 1950, Ellison and Konorski 1966).

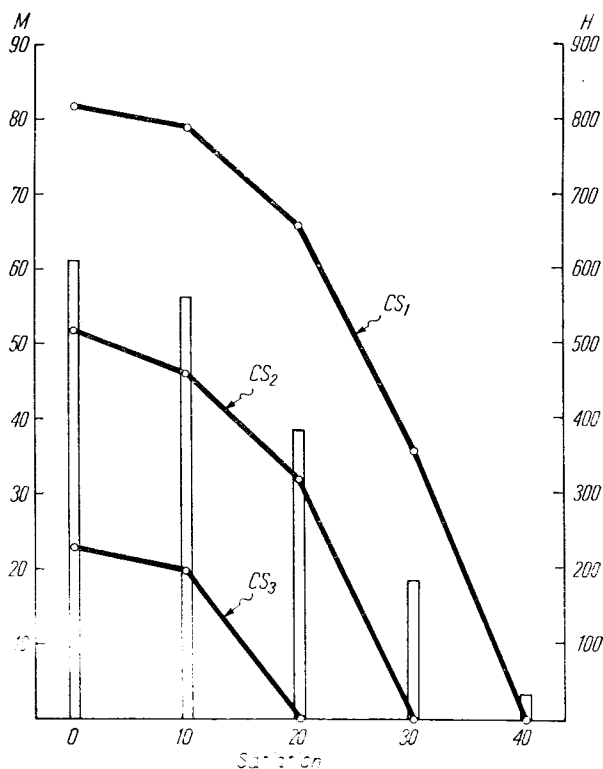


Fig. 7. Dependence of the ICR on levels of satiation and motogenic properties of the ICS. Abscissae, levels of satiation; ordinates, on the left the intensity of motor responses, on the right the intensity of hunger. Columns denote the intensity of hunger at various levels of satiation. Curves denote various intensities (rates) of motor acts. CS₁, strongly motogenic ICS, CS₂, moderately motogenic ICS, CS₃, weakly motogenic ICS.

As stated before, the activation of the H subcenter is not the only factor regulating the intensity of the ICR, since the weight of the direct connection linking the ICS center with the M center plays also a significant role. In natural experiments on dogs this was proved by comparing the strength of the ICR to an auditory CS and to the tactile CS administered to the wrist of a leg performing the trained movement (lever pressing): the strength of the instrumental response to the tactile stimulus was much stronger than that to the auditory stimulus, although the former stimulus did not produce stronger HCR (Dobrzecka and Wyrwicka 1960, Dobrzecka and Konorski 1962).

The dependence of the strength of ICRs on these two variables is presented in Fig. 7. On the one hand, the more motogenic the given ICS, that is the greater the weight of the ICS-M connection, the more intense is the motor response, although the intensity of excitation of the H subcenter remains the same. On the other hand, the ICS being the same, the intensity of the instrumental response depends on the strength of the excitation of the H subcenter.

THE INTERRELATIONS BETWEEN THE ICRs AND FCRs

In the preceding section we were concerned with the relations of instrumental (motor) and classical (salivary) effects in the ICRs. In the present section we shall deal with the influence of the classical FCSs on instrumental responding.

The method which was adopted from the very beginning of the studies on this problem, and which seems most suitable for this purpose is the following (Konorski and Miller 1933, 1936, see Konorski 1967, Chapter VIII). First, the classical FCRs are established to a number of stimuli. Thereafter, the CSs are no longer presented, and the animal is trained to perform the instrumental response to the experimental situation, as shown in Fig. 4. When this is achieved, we present the earlier established FCSs against the background of instrumental responding. Since the repeated food reinforcements would obviously disturb the relations between the ICR and FCR, the procedure is such that the presentation of food to instrumental movements is withheld for a few seconds and the FCS is given during the "net" instrumental responding.

Beneath we present the simulation of this type of experiment in Dewan. As usual, the experiment is much enriched in comparison with the original one by introducing several CSs of various intensities and several satiation levels, just as it was described in the preceding paper of this series (Konorski and Gawroński 1970b).

Table I

F

S Sat	0	CS				us	Sum
		9	11	13	15		
0	0	19	33	35	40	47	174
5	0	15	32	34	36	47	164
10	0	0	22	31	30	42	125
13	0	0	0	9	25	33	67
15	0	0	0	0	6	29	35
Sum	0	34	87	109	137	198	565

~ F

S Sat	0	CS				us	Sum
		9	11	13	15		
0	60	56	43	17	19	0	195
5	59	54	44	26	0	0	183
10	49	50	32	15	15	0	161
13	29	32	30	21	0	0	112
15	0	0	0	0	0	0	0
Sum	197	192	149	79	34	0	651

H

S Sat	0	CS				us	Sum
		9	11	13	15		
0	745	590	297	134	91	24	1881
5	629	500	297	135	71	24	1656
10	326	317	174	121	74	29	1041
13	118	106	105	80	51	16	476
15	21	23	23	23	19	14	123
Sum	1839	1536	896	493	306	107	5177

~ H

S Sat	0	CS				us	Sum
		0	9	11	13		
0	0	10	47	116	178	297	618
5	0	8	20	52	90	108	278
10	0	0	11	15	30	98	154
13	0	0	0	5	13	30	48
15	0	0	0	0	3	14	17
Sum	0	18	78	188	284	547	1115

M

S Sat	0	CS				us	Sum
		9	11	13	15		
0	56	33	13	0	0	0	102
5	46	27	9	0	0	0	82
10	15	11	0	0	0	0	25
13	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
Sum	117	71	22	0	0	0	210

The classical CRs for various CSs and various satiation levels are presented in Table I. We may easily observe the essential similarity between our present experiment and that described in the preceding paper (Experiment I). The typical characteristics of "normal" FCR activity are present, namely the dependence of the FCRs on the humoral hunger and on the strength of CSs, the partial "equalization phase" obtained at the high humoral hunger, and the relative stability of the food responses (salivation) to the FUS at different satiation levels.

On the same table in the bottom tablet the numbers of trained movements for 20 sec periods are presented, when the FCSs are given during instrumental responding. The column 0 presents the control numbers of movements, observed in the absence of the CSs; the following columns present the numbers of responses during the operation of CSs of various strength and the US. It may be immediately seen that the operation of CSs, even weak ones, drastically inhibits the instrumental responding. At 0 satiation level partial inhibition is observed for CS 9 and CS 11, while stronger CSs and the US produce full inhibition of the ICR. At higher levels of satiation the instrumental responding is weaker and it is easier inhibited.

Figures 8 and 9 show the relation between instrumental responding in the presence of CSs and the strength of excitation of the F subcenter and the H subcenter respectively. It may be seen in Fig. 8 that there is a clear reverse relation between the excitation of the F subcenter and

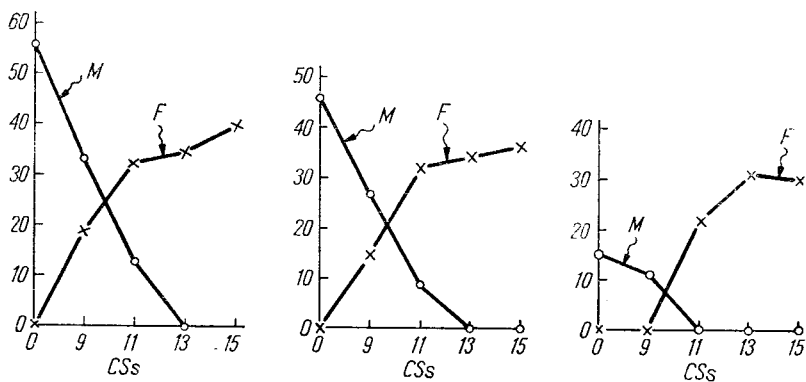


Fig. 8. Relation between instrumental responding (M) in the presence of FCSs of various strength, and the intensity of excitation of F subcenter. Abscissae, strength of FCS; ordinates, intensity of motor responses (circles) and intensities of excitation of F subcenter (crosses). Left graph, zero level of satiation, middle graph, moderate level of satiation, right graph, high level of satiation. It may be seen that the stronger the excitation of the F subcenter the smaller the rate of motor acts at all levels of humoral hunger.

instrumental responses: the stronger the excitation of the F subcenter, the stronger the inhibition exerted by the subcenter upon motor responses. This relation is true at all three levels of humoral hunger, but it is far from being quantitatively precise. In fact, roughly the same excitation of the F subcenter produces different degrees of inhibition of motor responses, depending on the level of humoral hunger. On the other hand, as seen in Fig. 9, there is a good quantitative relation between the decrease of instrumental responding and the decrease of excitation of the H subcenter when the strength of the FCSs is increased.

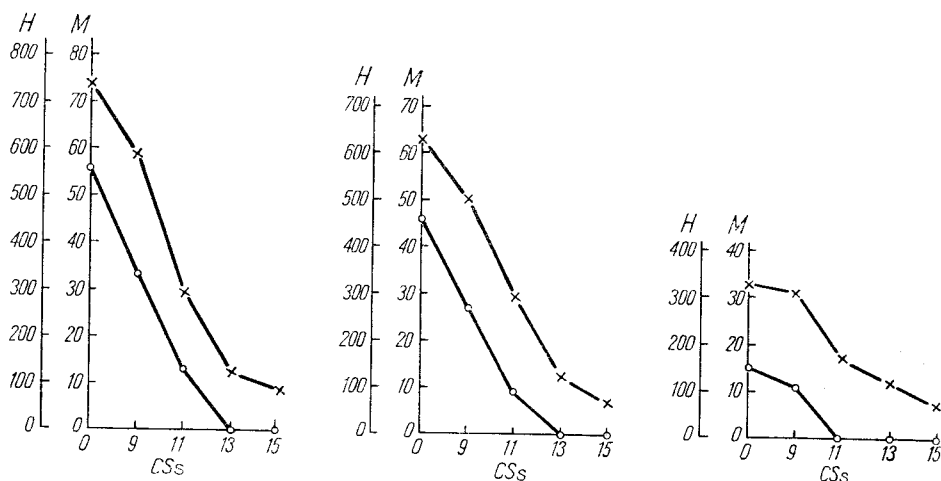


Fig. 9. Relation between instrumental responding (M) in the presence of FCSs of various strength, and the intensity of excitation of the H subcenter (H). Abscissae, strength of FCSs; ordinates, intensity of motor responses (circles) and intensities of excitation of H subcenter (crosses). Left graph, zero level of satiation, middle graph, moderate level of satiation, right graph, high level of satiation. Note the close parallelism between the intensity of hunger and the rate of instrumental responding.

To sum up we may conclude that the inhibitory influence of the classical CSs on instrumental responding is due exclusively to the attenuation of the activity of the H subcenter caused by the increase of the activity of the \sim H subcenter. The illustration of this mechanism is presented in Fig. 10.

DISCUSSION

There are three general rules governing the formation and occurrence of the instrumental conditioned reflexes. These are:

1. The ICR is driven by drive, the strength of the instrumental

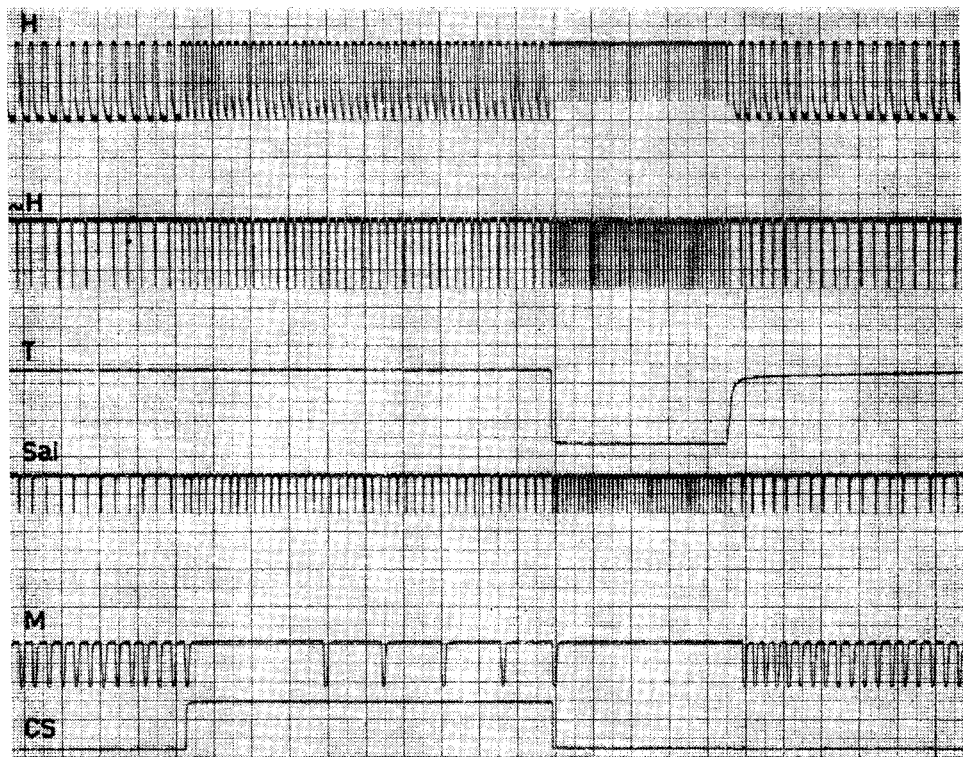


Fig. 10. An example of the record of the effect of FCS (of moderate strength) on instrumental responding. It may be seen that the FCS increases the activity of the $\sim H$ subcenter, which leads to the decrease of excitation of the H subcenter, and this leads to the dramatic decrease of the rate of instrumental responding.

response being proportional to the intensity of drive, in our case, the intensity of activation of the H subcenter.

2. The ICR is determined by the external stimulus (ICS) which specifies the movement to be performed in the presence of the given drive.

3. The ICR must be reinforced by inhibition of drive due to the activation of a corresponding antidrive (in our case activation of the $\sim H$ subcenter inhibiting the H subcenter).

Since in this series of papers we are dealing only with elicitation of CRs, but not with their elaboration and preservation, we are obviously concerned with the first two rules and are not directly interested in the discussion of the third one. Indirectly, however, we are concerned also with that rule, because the problem of reinforcement of the ICR is closely related to the effect of the FUS and FCS upon instrumental responding.

Let us discuss now each of these rules separately.

When we speak of the close dependence of the ICR upon the hunger drive we have clearly in mind the activity of the H subcenter and not the humoral hunger itself. Obviously this distinction is a most important one. On the one hand, humoral hunger may be very high and nevertheless the H subcenter may be strongly inhibited by the \sim H subcenter, as is the case when food is in the mouth of a non satiated animal. As we know, the instrumental response is then completely inhibited. On the other hand, the humoral hunger may be relatively low because of the partial satiation of the animal, and nevertheless the activation of the H subcenter may be relatively high because of the strong positive influence of the HCS or the afterdeglutitional rebound due to the \sim T- \sim F-H adaptive connection. These are the motives for having connected the center of the instrumental response M with the H subcenter and not directly with the satiation center (which would, by the way, require obviously inhibitory connection). The model proposed clearly corresponds to the obvious fact that instrumental responding is not directly dependent on the absence of nutritive substances in blood, but on the urge to eat — a state denoted by many authors as appetite.

Another factor which determines the ICR is provided by the external situation and/or sporadic stimuli in the presence of which the instrumental training took place. According to the diagram presented in Fig. 1 these stimuli not only control the instrumental response through the H subcenter, being the conditional signals of hunger (HCS), but also being directly connected with the kinesthetic center of M. The role of this factor is not only to determine which of a number of instrumental movements will be elicited in a given moment (a role, which was not modelled in Dewan, who has only one instrumental movement at his disposal), but also to facilitate the elicitation of the instrumental response. This role was proved in experiments on specific tactile stimuli (Dobrzecka and Wyrwicka 1960, Dobrzecka and Konorski 1962) in which, under a definite state of satiation or extinction, the tactile stimulus applied to the leg involved in the instrumental response did evoke this response, while a "normal" ICS failed to do so. This fact was simulated in Dewan, in which the two roles of a ICS (as a pure motogenic factor and drive-eliciting factor) were clearly separated.

Now, let us turn to the third decisive factor determining the occurrence of the alimentary ICR, namely that of food reinforcement. As noted above, the mechanism of this factor was not built in Dewan. The problem of how to simulate this mechanism is most intriguing. If, however, the drive inhibition theory of reinforcement of ICRs is accepted, our model certainly fulfills this requirement, because presentation of food does

inhibit the H subcenter by activation of the reciprocal \sim H subcenter. Moreover, as shown in our experiments simulated in section 3 of this paper (Konorski and Miller 1933, 1936, S. Soltysik, T. Rentoul and J. Konorski, in preparation) not only the taste of food (FUS), but also classical FCSs strongly inhibit instrumental responding by activating the \sim H subcenter and inhibiting the H subcenter. This fact is in good harmony with Ellison's and Konorski's (1965) results showing that a classical FCS interspersed between ICS and FUS in no way thwarts the ICR even after hundreds of such trials. On the contrary, it seems that such a training is rather beneficial for the strength and stability of the ICR, since instrumental responding is not contaminated by classical FCR (cf. Fig. 6bc). Thus, although the facts just described do not explain the reinforcing significance of the F- \sim H activation in alimentary ICRs, they make the proposed explanation quite acceptable.

In one of the previous papers (Gawroński and Konorski 1970a) it was stressed that a model proposed for understanding the given neurophysiological processes not only should fit to experimental facts, but also it should not be replaceable by any simpler model. In this context the question may be raised as to whether the \sim H subcenter is indeed indispensable for our concept, and whether the excitatory connections directed to this subcenter could be simply substituted by inhibitory connections directed to the H subcenter.

We do not think that this important problem can be unequivocally solved now. One general argument for the correctness of our concept is that it is in harmony with the general organization of the nervous system, in which such double reciprocal centers are rather a rule than an exception. Beside this, the main difference between the two models is that concerning the influence of the satiation center. In our model this center inhibits both the H subcenter and the \sim H subcenter, that is, it influences both antagonistic processes. In a model excluding the \sim H subcenter the inhibitory influence of satiation would affect only hunger, but not the opposite process arising when the consummatory food reflex is in operation. On the contrary, satiation would rather enhance this process but not inhibit it.

Almost certainly such an assumption cannot be true. If the \sim H subcenter represents "satisfaction" generated by the taste of food, satiation does not enhance it, but on the contrary thwarts it. Satiation cannot be considered as the same process as satisfaction produced by taste of food, because these two phenomena have quite different neurophysiological and psychological features. The fact that both of them inhibit hunger and thus suppress the instrumental responding does not mean that they are the same process.

SUMMARY

This paper was concerned with the problem of modelling of instrumental conditioning on an artificial nerve-net. The modelling was based on the following assumptions: (i) the instrumental response is driven by drive and it is consolidated by drive inhibition, (ii) the instrumental response depends not only on drive but also on the direct connection linking the center of the ICS with the center of instrumental movement. The following facts were reproduced by the model: (i) instrumental responding to the experimental situation and sporadic stimuli, (ii) the complex relation between motor and salivary conditioned responses in instrumental conditioning, (iii) the dependence of the instrumental response not only on drive but also on motogenic properties of the ICS, (iv) the inhibitory influence of classical FCSs and of the FUS upon instrumental responding.

REFERENCES

- DOBZECKA, C. and KONORSKI, J. 1962. On the peculiar properties of the instrumental conditioned reflexes to "specific tactile stimuli". *Acta Biol. Exp.* 22: 215-226.
- DOBZECKA, C. and WYRWICKA, W. 1960. On the direct intercentral connections in the alimentary conditioned reflex type II. *Bull. Acad. Pol. Sci., Sér. Sci. Biol.* 8: 373-375.
- ELLISON, G. D. and KONORSKI, J. 1965. An investigation of the relations between salivary and motor responses during instrumental performance. *Acta Biol. Exp.* 25: 297-315.
- ELLISON, G. D. and KONORSKI, J. 1966. Salivation and instrumental responding to an instrumental CS pretrained using the classical conditioning paradigm. *Acta Biol. Exp.* 26: 159-165.
- KONORSKI, J. and MILLER, S. 1933. Foundations of physiological theory of acquired movements (in Polish, French summary). *Książnica Atlas, TNSW, Warsaw.* 168 p.
- KONORSKI, J. and MILLER, S. 1936. Conditioned reflexes of the motor analyzer (in Russian, English summary). *Trudy Fiziol. Lab. Pavlova* 6: 119-278.
- KONORSKI, J. and WYRWICKA, W. 1950. Researches into conditioned reflexes of the second type I. Transformation of conditioned reflexes of the first type into conditioned reflexes of the second type. *Acta Biol. Exp.* 15: 193-204.
- KONORSKI, J. 1967. Integrative activity of the brain. *Chicago Univ. Press, Chicago.* 531 p.
- KONORSKI, J. and GAWROŃSKI, R. 1970a. An attempt at modelling of the central alimentary system in higher animals. I. Physiological organization of the alimentary system. *Acta Neurobiol. Exp.* 30: 313-331.
- KONORSKI, J. and GAWROŃSKI, R. 1970b. An attempt at modelling of the central alimentary system in higher animals. IV. Experiments on classical conditioning. *Acta Neurobiol. Exp.* 30: 371-395.

- SOŁTYSIK, S. 1960. On the intercentral connections in the reflex arc of the alimentary conditioned reflex (in Russian). In E. A. Asratian (ed.), *Tsentralnye i perifericheskie mekhanizmy dvigatelnoï deyatel'nosti zhivotnykh*. Izdat. AN SSSR, Moscow, p. 58-60.
- WOLF, K. 1963. Properties of multiple conditioned reflex type II activity. *Acta Biol. Exp.* 23: 133-150.
- WYRWICKA, W. 1952. Studies on motor conditioned reflexes. 5. On the mechanism of the motor conditioned reaction. *Acta Biol. Exp.* 16: 131-137.
- WYRWICKA, W. 1960. An experimental approach to the problem of mechanism of alimentary conditioned reflex, type II. *Acta Biol. Exp.* 20: 137-146.

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