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# AN ATTEMPT AT MODELLING OF THE CENTRAL ALIMENTARY SYSTEM IN HIGHER ANIMALS

## I. PHYSIOLOGICAL ORGANIZATION OF THE ALIMENTARY SYSTEM

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### INTRODUCTION

A great number of experiments performed on classical and instrumental conditioned reflexes (CRs) established by means of food reinforcement gradually led to some general concept of the organization of the alimentary system, a concept which has been formulated in detail in a recent monograph of one of the authors (Konorski 1967). As it most commonly happens with such concepts in neurophysiology, many statements proposed by the author were formulated rather generally and even somewhat equivocally. The lack of complete precision was not inadvertent; it was dictated by the limitation of our knowledge in the field concerned, a limitation which did not allow us to make clear decisions as to the character of neural processes underlying the experimental data at our disposal. Moreover, the complexity of the proposed structure of the alimentary system, involving a number of feedbacks, made it difficult to clearly foresee its functional properties.

This being so, it seemed profitable to elaborate a more precise model of the alimentary system and to present it in the form of an artificial nerve-net in which various parameters would simulate the parameters used in true conditioning. In this way it became possible to compare the experimental data obtained in the CR experiments on dogs with those obtained on the artificial nerve net. The apparatus has been called by us Dewan (Dog endowed with artificial nerve net).

The plan of the present series of papers is the following. In Paper I we present our concept of the organization of the alimentary system, discussing the hypothetical connections which are supposed to exist between its centers. In Papers II and III the technical details of the artificial model and the intimate properties of its functioning are presented. In Paper IV the experiments with classical CRs in Dewan are described and in Paper V we deal with instrumental CRs.

In the present series of papers we are not concerned with the processes of the formation of CRs, but only with their final states, when they are already firmly established. In this respect our model simulates the prevailing type of experiments carried out in Pavlovian laboratories, where the properties of well overtrained conditioned responses were mainly investigated.

The general purpose of this series of papers is to show that modelling of the organization of particular parts of the nervous system may play an important role in understanding their activity and, moreover, enables us to predict the results of further experimentation.

## FOOD SYSTEM

The main assumption concerning the organization of the central alimentary system held in this paper is that it is composed of two mutually interconnected subsystems which may be denoted as the food system and the hunger system respectively.

The food system controls the consummatory phase of the food intake, starting from the moment when the edible substance is placed in the mouth and ending at the moment when it is swallowed. Thus the unconditioned food reflex (FUR) is elicited by the taste of food (T) determined by stimulation of particular chemical and tactile mouth receptors. The effect of this reflex consists of mastication, when the food is not slimy or liquid, salivation and deglutition. For simplicity we shall assume that our artificial dog is fed only with a uniform kind of food consisting of all necessary nutritive ingredients and presented in the form of uniform "pellets". Accordingly, we admit that there is only one taste of food.

Anatomically, the food system is composed of the ventral postero--medial thalamic nucleus and the gustatory area of the cortex, situated in dog in the anterior composite gyrus (Żernicki and Santibañez-H. 1961). For the purpose of the present analysis we shall consider the food system a functional entity without entering into the role played by its particular parts. We shall, however, take into account another organizational aspect of that system, hardly given any attention to in other studies: we shall assume that there are two types of gustatory receptors, namely on-taste receptors (T), reacting to the presence of food in the mouth and off-taste receptors (~T) which are activated when the oral cavity is empty. It is further assumed that whereas the on-taste receptors are activated with roughly the same strength throughout the taste stimulation, the off-taste receptors are most strongly activated after deglutition of food, and then quickly adapt to about a half of their original firing.

We believe that in normal animals the on-taste units (representing particular kinds of food) and off-taste units (representing the absence of food in the mouth) are situated in the same morphological "center". When, however, constructing the brain of Dewan, we considered it more convenient to separate these two sets of units and represent them by different subcenters, denoted as food subcenter (F) and no-food subcenter (~F).

The problem arises as to what are the interrelations between the units of these two subcenters. On the one hand it may be supposed that they are quite independent from each other being activated, respectively, by T or ~T receptors. On the other hand, we may postulate the existence of reciprocal relations between these subcenters, owing to which activation of the F subcenter inhibits the ~F subcenter and vice versa. In our further considerations we have given advantage to the second alternative because this arrangement is in harmony with the organization of other double centers in the nervous system representing antagonistic functions.

Our foregoing discussion was concerned with the activity of the food system, when this activity is evoked by the unconditioned stimulus represented by the taste of food (FUS). We know, however, that if a neutral stimulus is presented in overlapping sequence with the FUS, it becomes a food conditional stimulus (FCS) being capable of eliciting the food conditioned reflex (FCR), simulating the FUR. This occurs owing to the formation of functional connections between the center of the neutral stimulus and the center of the FUS.

It is well known that the strength of the FCR depends to a great extent on the intensity and/or quality of the FCS, that is that even in well overtrained animals the salivary response to a "strong" CS is greater than that to a "weak" CS. This is the Pavlovian rule of the "strength of CSs" (Pavlov 1940, Maiorov 1954, Konorski 1968). Of course this rule will be simulated in Dewan. In other words this dog is so constructed that whereas the FUS is always of the standard strength, the strength of the FCS may vary within wide limits. Since the FCR is established on the basis of the FUS, the conditioned food response cannot exceed the corresponding unconditioned food response.

When a given neutral stimulus is never accompanied by presentation of food, that is, it always signals that food will not be offered, it can become a ~FCS. As a matter of fact the mere absence of the FCS is also a ~FCS, since in the intertrial intervals food is never presented. However, the intervals have rather an ambiguous character, because, if their duration is roughly constant, the moment closely preceding presentation of the FCS-FUS sequence also becomes a FCS.

The properties of the food system so far described are visualized in Fig. 1. This figure manifests among other things an important difference between the reflex arc of the FUR and FCR, which was hardly

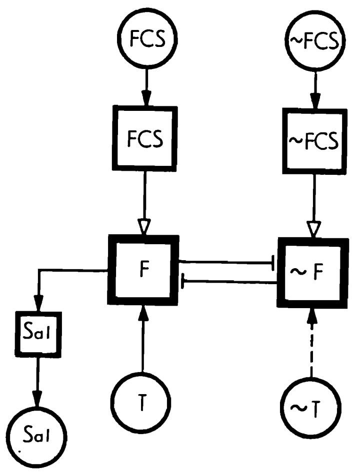


**Fig. 1. The organization of the food system in Dewan. FCS, receptors (circle) and center (square) of FCS. ~FCS, receptors (circle) and center (square) of ~FCS. F, food subcenter. ~F, no-food subcenter. Sal, salivary center (square) and salivary gland (circle). T, receptors for food taste. ~T, receptors for absence of food in the mouth. Lines ended by black triangles denote unconditioned connections; lines ended by white triangles denote conditioned connections; lines ended by perpendicular dash denote inhibitory connections. Interrupted line denotes adaptive connection.**

noticed by students concerned with classical conditioning. During the operation of the FUS T receptors are stimulated while ~T receptors are silent. Consequently, the F subcenter is fully active while the ~F subcenter is inactive, so that the reciprocal relations between both subcenters are not involved. On the contrary, during the operation of the FCS the ~F subcenter is activated because the food is not in the mouth, and in the same time the F subcenter is activated by the FCS. Because of the reciprocal relations between the two subcenters various effects of the conditioned activation of the F subcenter may be obtained, depending on the strength of the FCS, the strength of the excitatory effect of the ~T stimulus upon the ~F subcenter and the character of inhibitory connections between F and ~F subcenters (see below). Accordingly, even if the FCS is as strong as to maximally activate the F subcenter, its net effect may be (and frequently is) lower than that of the FUS, because the F subcenter is partially inhibited by the excitation of the antagonistic ~F subcenter.

To end these remarks on the functional properties of the food system it must be stressed that, as we shall see later, its activity depends to a large extent on the hunger system, and even more, the active state of the latter is assumed to be indispensable for the functioning of the food system. Therefore, the connections presented in Fig. 1 can be brought into action if, and only if, the hunger system is in operation.

## HUNGER SYSTEM

The physiological role of the hunger system is to provide nutritive substances to the organism, whenever it is in need of them. This is effectuated in such a way that the organism, when being hungry, is in a state of motor arousal performing a number of motor acts; those acts which eventually lead to placing food in the mouth are selected and consolidated. These are referred to as instrumental conditioned responses.

A large body of evidence based on instrumental conditioning experiments and on the effects of electrical stimulation of, or lessions in, the structures concerned with the control of hunger allow us to propose a following concept of the organization of the hunger system (cf. Konorski 1967).

To begin with, it is clear that hunger depends to a large extent on humoral factors, that is on the contents of nutritive substances in the blood. These substances activate the units of the satiation center, situated in the ventromedial hypothalamus, which in turn exerts an inhibitory influence on the units of the hunger center, situated in the lateral hypothalamus. When the satiation center is inactive because of the lack of the nutritive substances in the blood, the hunger center is free of inhibition and can be thrown into action by suitable stimuli. It will be convenient to denote the opposite of satiation as humoral hunger; the stronger the satiation, the weaker the humoral hunger and vice versa.

Among the external agents producing unconditional hunger (HUSs) we can indicate: 1° smell of food and 2° the post-deglutitional after-effect, when a bole is swallowed and the mouth becomes devoid of food. Conditional hunger-producing stimuli (HCSs) are those neutral stimuli which coincide with HUSs. In normal alimentary CR experiments, the very situation in which the sessions take place becomes a powerful HCS (we denote it as ΣHCS).

In normal animals there is not one hunger concerning all sorts of food, but various hungers concerning particular nutritive substances. Since Dewan is fed on only one stuff, it experiences one sort of hunger. We assume, however, that the hunger center consists not only of on-hunger units activated by the above listed HUSs and HCSs, but also of off-hunger units thrown into action by the presence of food in the mouth, that is, by food taste units. In other words, whereas activation of on-hunger units elicits food-seeking or food providing behavior, activation of off-hunger units elicits calmness connected with "satisfying state of affairs".

We have many reasons to believe that in normal animals both types of units are intermixed in the lateral hypothalamus; hence electrical stimulation of that region may produce either food-seeking effect, or food--simulating self-rewarding effect. In Dewan these two sorts of units are spatially separated; thus the hunger center is composed of on-hunger (H) subcenter and off-hunger (~H) subcenter.

As was the case with food system, here, too, the problem arose as to whether on-hunger units and off-hunger units are functionally independent, or whether they are in reciprocal relations. Here, too, we have adopted the latter hypothesis assuming that excitation of the H subcenter inhibits the ~H subcenter, and vice versa.

Our last assumption concerning the organization of the hunger system is that excitation of the satiation center exerts an attenuating influence upon the whole hunger center, that is both upon the H units and ~H units. Speaking freely we may say that the stronger the starvation, that is the more the hunger center is released from the inhibitory influence of the satiation center, the more intense is the food-seeking behavior when food is not available, and the more intense the satisfaction (pleasure) when the food is in the mouth. Further, it is assumed that with full satiation both the hunger-producing stimuli and hunger-satisfaction stimuli are ineffective. This means, that with full satiation the animal will not try to provide itself food when the HUSs and/or HCSs are in operation, nor will the food mouth play any rewarding (pleasurable) role.

The organization of the hunger-satiation system proposed in our concept is presented in Fig. 2. Although the system includes in reality at least two levels (the hypothalamus and amygdala) these levels are not separated in our model.

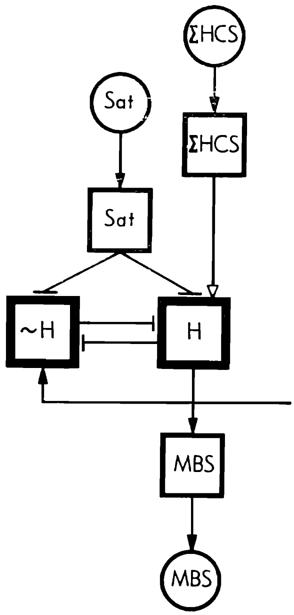


Fig. 2. The organization of the hunger system in Dewan. Sat, satiation receptors (cricle) and center (square). H, on-hunger subcenter. ~H, off-hunger subcenter. ΣHCS, the receptors (circle) and center (square) concerned with the HCS represented by the experimental situation. MBS, general motor behavioral system. Lines ended by black triangles denote unconditioned connections; lines ended by white triangles denote conditioned connections; lines ended by perpendicular dash denote inhibitory connections.

## INTERRELATIONS BETWEEN THE FOOD SYSTEM AND THE HUNGER SYSTEM

After presenting the main features of the food system and hunger system we should turn now to the problem of their cooperation. The connections between both systems are presented in Fig. 3, and below we shall disuss them in detail. We shall begin with describing connections leading from the hunger system to the food system, and then we shall turn to the connections leading in the opposite direction.

According to a great number of experimental data the functioning of the food system strongly depends on the intensity of hunger. The main fact substantiating that view is that when this intensity is zero (because of either full satiation of the animal or the absence of external hunger--producing stimuli), then te FCRs are null; with moderate hunger (that is, partial satiation) the FCRs to strong stimuli are generally well preserved, whereas those to weak stimuli can be null; on the contrary, with strong hunger, there is a tendency to some equalization of responses to weak and strong stimuli (the Pavlovian "equalization phase on the high level") (Pavlovskie sredy 1949, Maiorov 1954). These rules show that there are connections leading from the H subcenter to the F subcenter.

What is the character of these connections? We have good experiment-

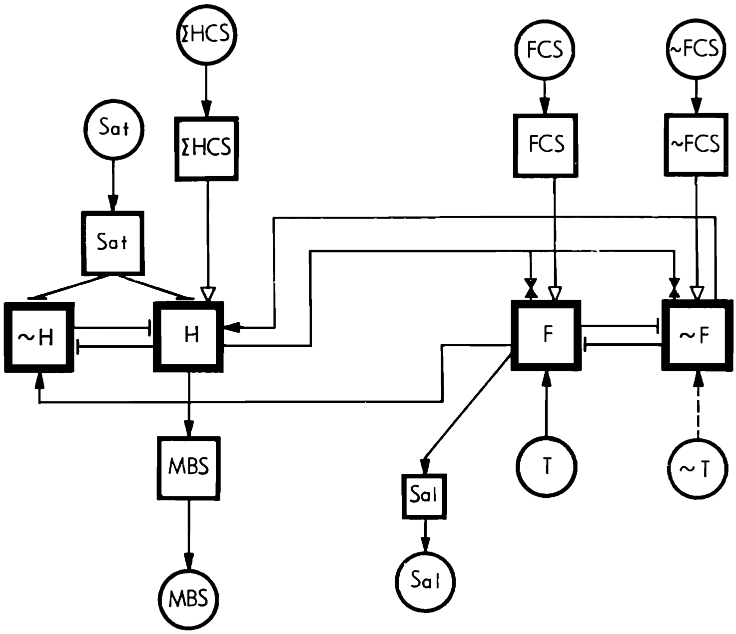


Fig. 3. The organization of the alimentary system. Denotations as in Fig. 1 and 2. Lines ended by two-triangle figure denote facilitatory connection.

al evidence to show that even if the intensity of hunger is very high, it does not lead to the actual excitation of the F subcenter. This shows that hunger is not an activating but a facilitating factor with regard to the food subcenter. To put it in plain language we can say that hunger is not able to activate the taste units (represented in F), but it sensitizes them and allows them to be activated if the FCS is in operation [1].

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[1] In this study for the sake of simplicity we disregard a mechanism which seemingly contradicts this statement. We know from human experience that if a subject is hungry, he can easily imagine the natural CSs heralding food (for instance, the view of the favorite dishes) and this image as a substitute of the CS will evoke salivation. In our diagrams this would correspond to the connection linking the H subcenter with the FCS center. Since this conditional connection is unstable and not well understood, we prefer not to include it into connections operating in Dewan.

The more dubitable and uncertain is the role played by hunger with regard to the FUR, that is, to the excitation of the F subcenter produced by the taste of food. Here the following possibilities are conceivable.

1. The FUR is completely independent of hunger, that is, whenever the food is in the mouth, there is a full (maximal) activation of the F subcenter [2]. This suggestion is supported by the fact, that salivary unconditioned responses, in contradistinction to conditioned responses, are virtually independent of hunger.

2. The FUR is facilitated by hunger, but hunger is not indispensable for its occurrence. In other words, the FUR, in contradistinction to the FCR, does occur when the H subcenter is completely silent, which may happen either in the state of full satiation, or when the ∼H units are strongly excited by the taste of the food in the mouth. Indeed, in the latter situation the subject is in a state of complete satisfaction produced by the taste of food with strong inhibition of hunger, and nevertheless his consummatory act of eating will occur.

3. The effect of hunger upon the FUR is exactly the same as that upon the FCR, that is, "no hunger – no consummatory reflex". The virtual independence of the salivary and masticatory responses from hunger would be in that case explained by the conjecture that the FUR may be mediated by the lower feeding centers in the medulla, which, in contradistinction to the higher centers, are not subjected to the control of hunger.

Even if the first supposition of the full independence of the FUR from hunger is rejected, we are still in a difficulty between choosing the second and the third supposition. Therefore, for the sake of uniformity of rules governing the FURs and FCRs, we shall adopt the third supposition, according to which excitation of the F subcenter, either by a FCS or by the FUS, is not possible without the facilitating influence of hunger.

We turn now to the problem of what is the effect of hunger upon the ∼F subcenter, that is on the off-taste units. Here the most reasonable assumption is to accept that the ∼F subcenter is under the facilitatory influence of hunger exactly in the same way as is the F subcenter. This means that the stimulation of the ∼T receptors in the absence of hunger fails to activate the ∼F subcenter, in other words, that the "taste" of no food in the mouth is perceived only if the animal is hungry.

Now we turn to the description of connections leading from the food system to the hunger system.

[2] The argument that when the subject is not hungry he stops taking food is irrelevant, since taking food (either by mouth or by hand) is an instrumental act and consequently it is fully controlled by hunger, not belonging to the consummatory phase of the feeding process.

The main connection, whose acceptance is essential for our entire concept of the alimentary system, is the one leading from the F subcenter to the ~H subcenter and causing the latter subcenter to be activated by the former one. The physiological aspect of the activation of this connection is the satisfying state of affairs, or the pleasure, furnished by the taste of food or its palliative provided by the FCS; its physiological aspect is "drive reduction" provided by reciprocal inhibition of the H subcenter, a phenomenon playing an essential role in reinforcement of instrumental alimentary CRs (Sołtysik 1960).

No less important is the second connection linking the ~F subcenter with the H subcenter. This connection is responsible for the increase of hunger after swallowing the bole of food, the increase, compelling the subject to take the next morsel. The interplay between the inhibition of hunger produced by the presence of food in the mouth and the "rebound" produced by its disappearance constitutes the main mechanism of intermittent food intake occurring in most higher animals.

We should draw attention to the fact that there exists a strong positive feedback provided by the loop H → ~ F → H. In fact, the presence of hunger facilitates the perception of the absence of food in the mouth, and this perception in turn increases the intensity of hunger. This positive feedback is, however, attenuated by rapid adaptation of the off-taste receptors: a few seconds after the food is swallowed firing of these receptors is reduced to such a level, as to preclude the H subcenter from overexcitation (cf. Gawroński and Konorski 1970a). This fact explains why hunger is strongly increased after swallowing a morsel of tasty food and thereafter returns to its original level.

## THE FINAL CIRCUITRY OF OUR MODEL AND ITS FUNCTIONING

Having described the organization of the food system, the hunger system and their interrelations, let us analyse now the whole alimentary system from the point of view of its inputs, outputs and interconnections (Fig. 3).

*Inputs.* 1. Food intake. Placing of the food into the mouth is signalled by stimulation of T receptors which are active till the bolus is swallowed. During that period the ~T receptors become silent. Dewan is fed by regular pellets of food, whose consuming lasts a definite period of time and ends abruptly. The pellets are supposed to be so small that they virtually fail to increase satiation.

Taste receptors send impulses to the F subcenter which becomes activated provided that it is facilitated by excitation of the H subcenter.

The F subcenter fires impulses to the ~H subcenter which partially inhibits the H subcenter. All these effects are presented in a record from a typical experiment on Dewan (Fig. 4).

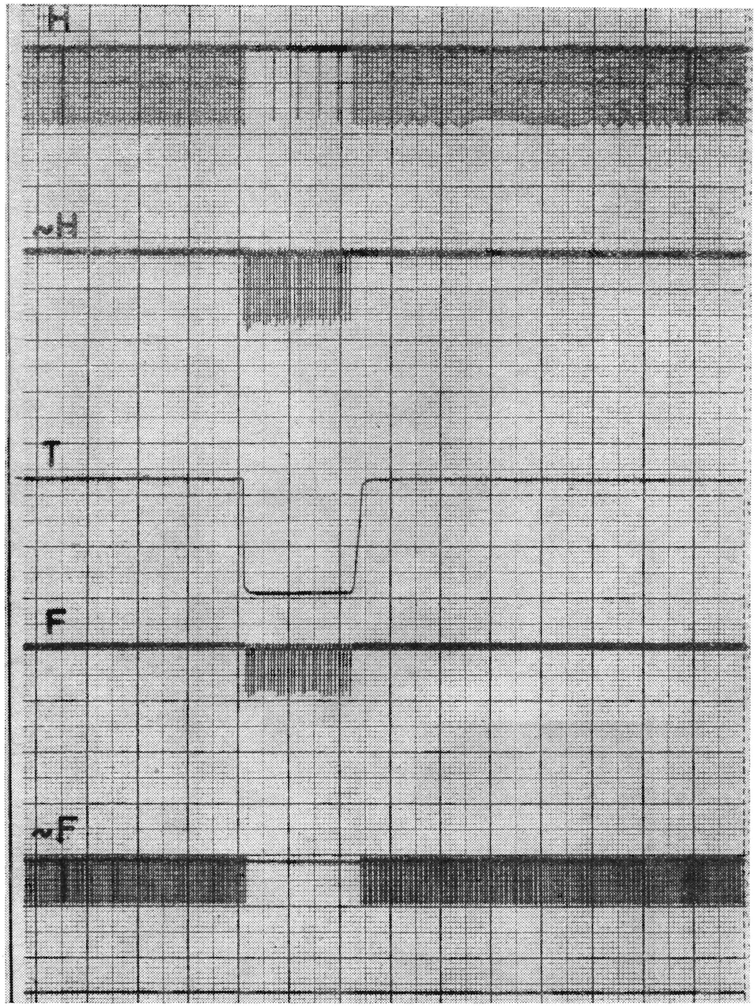


Fig. 4. The record of an experimental session in which at a moderate hunger food was presented. From top to bottom activity of H, ~H, F, ~F subcenters. In the middle, T, presentation of food and the act of eating. All records downward. Note that before and after the food intake there is a considerable activity of H subcenter and of ~F subcenter, whereas ~H subcenter and F subcenter are silent. When food is presented H subcenter is strongly (but not completely!) inhibited, ~H subcenter and F subcenter are strongly activated, ~F subcenter is silent because ~T receptors are not active. Note that record of the activity of each subcenter has different rate and therefore they are mutually uncomparable. Equalization of all the rates proved to present serious difficulties.

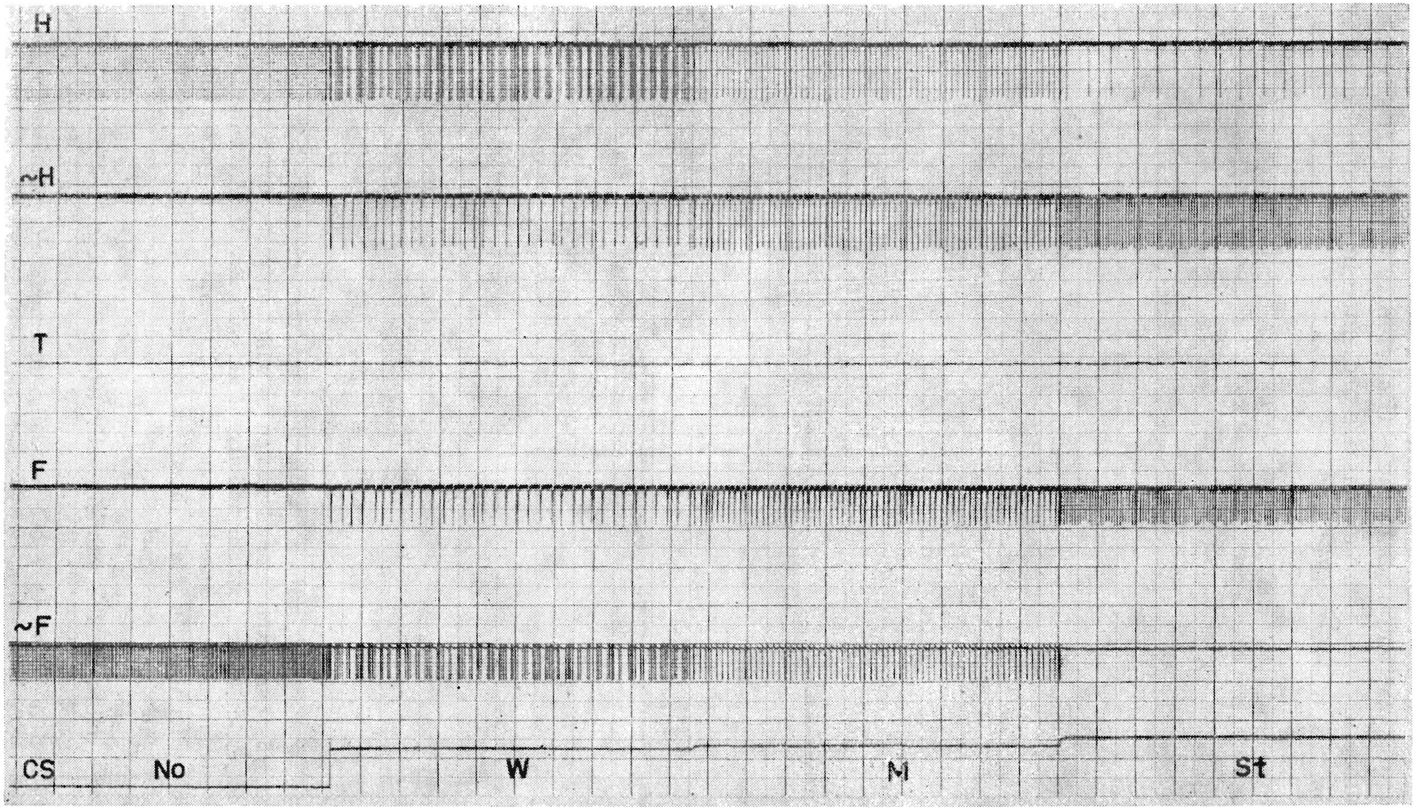


Fig. 5. Fragments of records of the responses of H, ~H, F, ~F subcenters to FCSs of different strength: No, no CS presented, W, weak CS, M, moderate CS, St. strong CS. Bottom line, CS marker. Hunger level the same as in Fig. 4. Note that the stronger the CS, the stronger the inhibition of the H subcenter, the stronger the activation of the F subcenter, and of the ~H subcenter, and the stronger the inhibition of the ~F subcenter by the F subcenter. Note the complex patterns of discharges in all the records but particularly in H and ~F records (cf. Gawroński and Konorski 1970b).

2. FCSs. FCS activates the F subcenter owing to the connections established between the FCS center and the F subcenter. This activation occurs when the F subcenter is facilitated by hunger. During the operation of the FCS off-taste receptors ($\sim$T) are active; these fire impulses to the $\sim$F subcenter which partially inhibits the F subcenter and is reciprocally inhibited by it.

In our experimental set-up the strength of the CSs may vary within large range, thus producing stimulation of the F subcenter with various intensities. The FCS, like food, activates the $\sim$H center. The appropriate record is presented in Fig. 5.

3. $\sim$FCSs. $\sim$FCS simply increases the activation of the $\sim$F subcenter provided that it is facilitated by hunger. Its action may be detected only if it is presented simultaneously with the presentation of the FCS.

4. Satiation. The animal may be brought to the experimental session under various degrees of satiation. Zero satiation means a state in which the satiation center is not activated at all, thus not exerting any inhibiting influence upon the hunger center. On the contrary, full satiation means that the hunger center is completely inhibited by the satiation center. Between these two extreme states various degrees of satiation are possible which partialy inhibit the hunger center. It should be emphasized that the satiation center inhibits in the same degree the H subcenter and the $\sim$H subcenter, that is, it attenuates both the hunger when food is not directly available and the state of satisfaction when food is in the mouth or a FCS is in operation (Fig. 6).

5. HUS and HCSs. It was already emphasized that the release of the hunger system by lack of, or partial, satiation is effective only when either the HUS or HCS is in operation. In a usual experimental set-up a strong HCR is elicited by the whole experimental situation because hunger reflexes, in contradistinction to food reflexes, have not a phasic but a tonic character (Konorski 1967). In consequence, the HCS lasts throughout the experimental session and its strength is more or less constant. Since it is composed of a number of elements we denote it as $\Sigma$HCS.

The $\Sigma$HCS activates the H subcenter provided that this subcenter is not completely inhibited by the satiation center. The H subcenter sends facilitatory impulses to the F and $\sim$F subcenters and inhibitory impulses to the $\sim$H subcenter.

*Outputs.* In normal CR experiments on dogs two main outputs are used: in classical CRs, salivation, and in instrumental CRs the trained motor response.

As it was proved in our earlier papers, salivation may be regarded

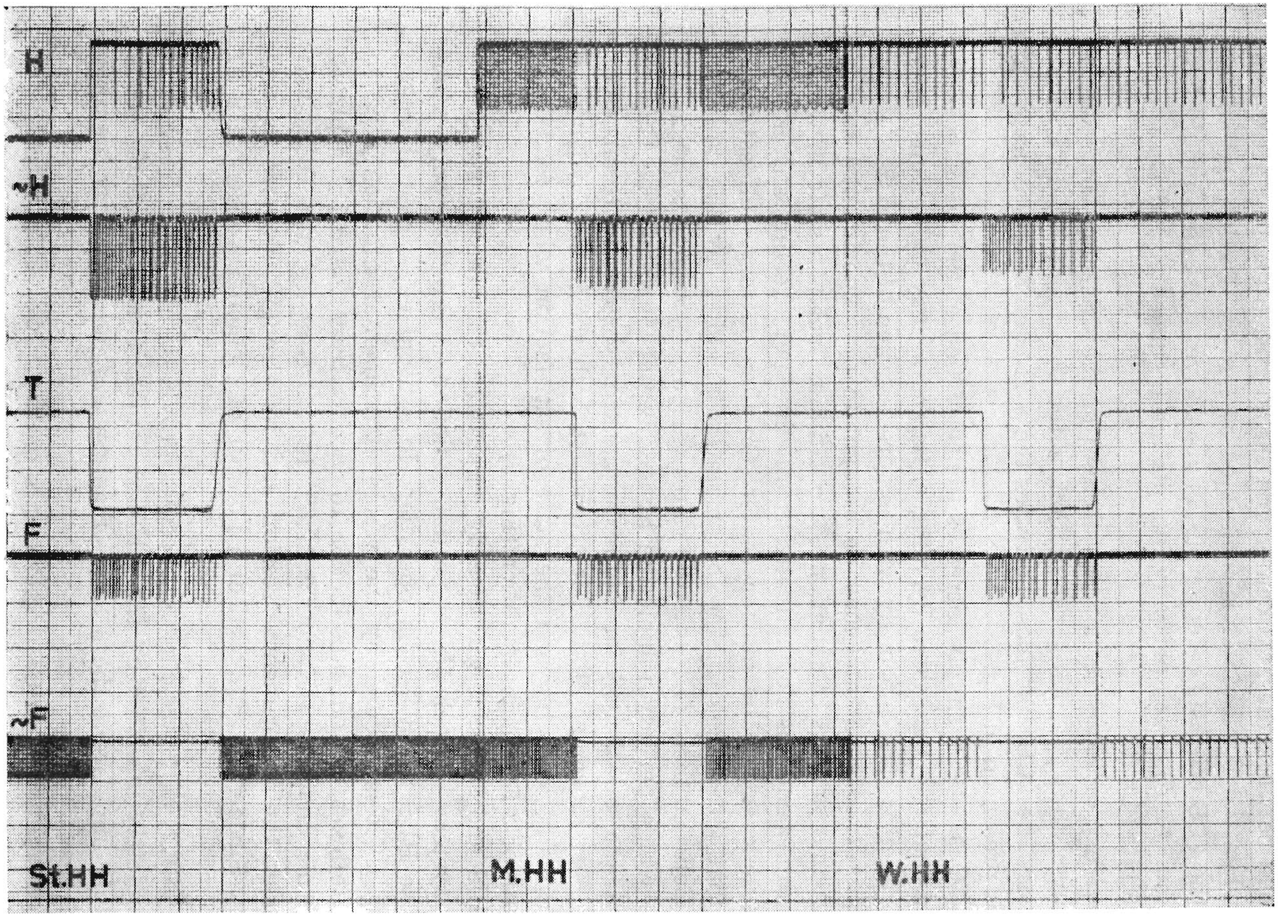


Fig. 6. Fragments of sessions in which food was presented against the background of strong, moderate, and weak humoral hunger (St.HH, M.HH, W.HH respectively). Denotations as in Fig. 4. Note that before and after food presentation activation of H subcenter and ~F subcenter is proportional to the humoral hunger (reverse to the level of satiation), ~H subcenter and F subcenter being silent. During food intake the stronger the humoral hunger, the stronger the activation of ~H and F subcenters, but the effect of humoral hunger is insignificant because of the stabilizing influence of the F–~H–H–F inhibitory loop (see Gawroński and Konorski 1970b, Konorski and Gawroński 1970a).

as a direct effect of activation of the F subcenter, roughly proportional to its strength. It certainly does not depend directly on hunger because it may be null even when the hunger is very intensive (Ellison and Konorski 1965).

On the other hand, the instrumental response takes its origin of, and is based on, the general arousal of the motor behavioral system, being the effect of any drive, among others of hunnger drive. The fixation of this response is due to the fact that it is immediately followed by drive inhibition due to the occurrence of antidrive. In experiments on alimentary CRs this inhibition is caused by food reinforcement producing activation of ∼H subcenter.

However important are these two overt responses as measures of activation of F subcenter and H subcenter respectively in experimentation on normal dogs, their roles in Dewan are largely reduced. This is because in Dewan we have a direct access not only to both these subcenters but also to the ∼F subcenter and ∼H subcenter, whose activation does not produce any direct overt response. Therefore, our documentation obtained in experiments on Dewan is much richer than that obtained on normal dogs and the analysis of experimental data can be more exhaustive.

According to these considerations the methodology of our experiments on Dewan is this. First we set all the weights of intercentral connections of the alimentary system, and then we record the values of activations of F, ∼F, H and ∼H subcenters in response to FCSs of various intensities and at various levels of satiation. By changing the weights of particular connections we alter the functional properties of Dewan and thus modify his responses to the applied agents. In Paper IV of this series of papers some examples of these modifications will be presented.

## DISCUSSION

The proposed concept of the organization of the central alimentary system, which is an improved version of the last Konorski concept (1967), differs in many respects from the views put forward by other authors (Brobeck 1955, Grossman 1955, Anand 1961, 1963, De Ruiter 1963, and others). The best exemplification of most other views is the concept of Anand (1961, 1963) which we shall discuss in some detail (Fig. 7). By comparing his model of the alimentary system with that of ours we may see that they differ in the following points:

1. According to our concept the alimentary system is composed of two parallel systems denoted as consummatory and preparatory. The consummatory system includes on the afferent side: the medulla taste center,

the VPM taste center and the cortical gustatory area, and on the efferent side the corresponding centers controling mastication, salivation and swallowing. The preparatory system includes hypothalamus and the limbic brain and subserves the preparatory alimentary behavior. According to Anand (and other authors) these two systems are not longitudinally separated and the corresponding centers are simply superimposed one upon the other, as the levels of a single system. By the way, this was the view held by one of the authors in his earlier paper (cf. Konorski 1960).

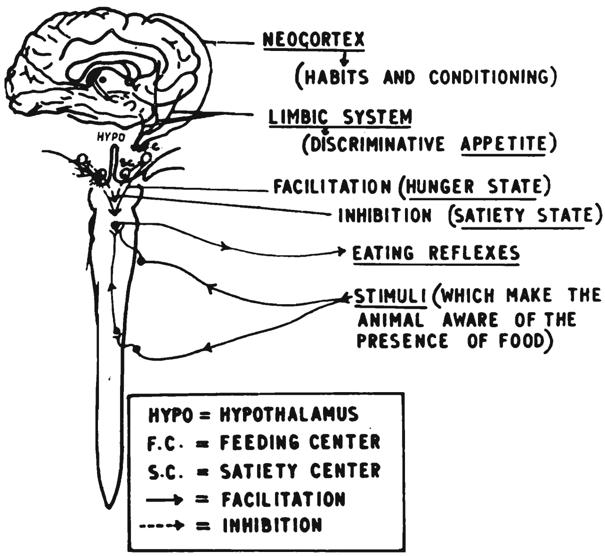


Fig. 7. Model of the central alimentary system according to Anand (1963).

2. According to Anand (and most other contemporary authors), the diencephalic alimentary system is composed of the feeding center and satiety center which are in reciprocal relations. According to our view, the feeding center, better called the hunger center, is composed of two types of units, namely on-hunger units and off-hunger units. The former represent food- appetite, the latter food-satisfaction. The satiation center is a regulatory center in respect to the hunger center, inhibiting both on-hunger units and off-hunger units.

3. According to both Anand's model and that of ours, the satiation center is stimulated by humoral factors (nutritive substances in blood), distension of the stomach, tissue dehydration, rising heat production and others. The only input of the "feeding" center is, according to Anand, the

release from the inhibitory influence of the satiety center [3]. According to our concept this release does not excite by its own the hunger center; the on-hunger units of this center are excited by the smell of food, by the disappearance of food from the mouth due to its swallowing, and by hunger conditional stimuli. The off-hunger units are excited by the actual taste stimuli and food conditional stimuli.

4. According to Anand (and other authors) both the state of hunger, when the animal is in the search of food, and the state of satisfaction of hunger, when food is in the mouth, are the manifestations of the activation of the unique alimentary system. The only type of satisfaction of hunger is thought to occur when the animal is satiated. According to our view these two states are in antagonistic relations, since the activation of the consummatory system inhibits the hunger system.

It seems that our present concept gives a good physiological theory for distinguishing three separate states clearly manifested both in behavioral performances and in introspection. These are:

1. Hunger (appetite) when the subject wants food and attempts to secure it (excitation of on-hunger units).

2. Satisfaction of hunger, when food is already in the mouth (excitation of off-hunger units).

3. Satiation, when food is no more wanted (excitation of satiation center).

If hunger belongs to the category of central processes denoted as drives, the satisfaction of hunger and satiation should be regarded as opposite central processes, which have been denoted as antidrives (Konorski 1967). It is clear from our considerations that various antidrives can have quite different physiological mechanisms and by no means should be confused with one another. Very important for our concept is the realization of the fact that the satiation antidrive, that is the appeasement of the hunger drive by statisfaction of the nutritive needs of the organism inhibits both on-hunger units and off-hunger units, that is it suppresses in exactly the same way the desire of food and the pleasure of its acquisition.

Another important point of our concept is the acceptance of two sorts of food units, namely on-food units, stimulated by taste-of-food receptors and responsible for the perception of food in the mouth, and off-food units, stimulated by the lack of food in the mouth and responsible for the perception of no food in the mouth. We have assumed that the off-food units are stimulated by receptors reacting to the cessation of food taste.

[3] It is agreed that Cannon's assumption to the effect that hunger contractions of the stomach are the cause and not the effect of hunger cannot be held.

We further assume that both on-food units and off-food units are thrown into action by the relevant stimuli only when they are under the facilitatory influence of hunger; in other words, hunger directs the attention of the subject to the receptors of the oral cavity and thus enables the perception of either the presence of the food in the mouth or its absence.

We were not concerned in this paper with the physiological significance of particular levels of both the food system and the hunger-satiation system. This problem was dealt with in Konorski's recent monograph and little may be added to his discussion in this matter. Concerning other aspects of the central alimentary system its model in this monograph is roughly the same as that in the present paper, however, its exposition is now more precise and clear. Beside this, the important duality of food units and no-food units was not manifested in our earlier diagrams.

## SUMMARY

In this paper the physiological organization of the central alimentary system is presented on the basis of all relevant facts provided by electrophysiological and behavioral experimentation. It is assumed that the system is composed of two parallel and mutually interconnected parts, namely food intake system and hunger-satiation system.

The food consummatory system is composed of food units activated by the taste-of-food stimuli and corresponding CSs, and no-food units, activated by the off-taste-of-food stimuli or corresponding CSs. These two types of units are in reciprocal relations.

The excitability of the consummatory system is under the control of the hunger-satiation system composed of the hunger center and the satiation center. The satiation center is activated by nutritive substances in the blood: it exerts inhibitory influence upon the hunger center. The hunger center is composed of on-hunger units and off-hunger units. The on-hunger units are activated by smell of food and by off-taste stimuli, as well as by corresponding CSs. The off-hunger units are activated by taste-of-food stimuli and corresponding CSs. The on-hunger units and off-hunger units are in reciprocal relations. The activation of on-hunger units produces arousal of the motor behavioral system converted into the food-seeking and food-providing behavior, whereas activation of off-hunger units leads to the state of satisfaction produced by the taste of food.

The comparison of the present concept with those proposed by other authors is discussed.

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