HEDONESTHESIA: THE NERVOUS PROCESS DETERMINING MOTIVATED INGESTIVE BEHAVIOR

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Abstract. The hedonistic theory of motivated ingestive behavior is discussed against drive-reduction theories, which claim that ingestive motivated behavior is mainly determined by the urge to meet the basic needs of the organism, often ignoring the important role of sensations. Evidence is supplied that mere sensations derived by exteroceptors can play an essential part in motivated behavior. A view is put forward that the reinforcing properties of exteroceptive stimulation in motivated ingestive behavior should be related to their ability to generate positive emotional states experienced as pleasure. It was pointed out, however, that the same external gustatory stimulation may possess a different hedonic value, depending on the current nutritional state of the organism. Therefore, the existence of a special nervous process which makes these stimuli emotionally positive, neutral or negative, i.e., pleasant, indifferent or aversive, depending on the given state of need is postulated. We call this nervous process hedonesthesia, and claim that it plays a decisive part in motivated ingestive behavior. The possible mechanism of hedonesthesia is explained on the block model.

Up to now most investigators consider that ingestive behavior is mainly determined by the urge to fulfill the basic needs of the organism, often ignoring the important role of sensations. Food intake, for instance, was considered to be determined: according to the glucostatic theory (45) by the level of blood glucose, or rather by the degree of glucose utilization; according to the lipostatic theory (36) by the level of lipids; accord-
ing to the aminostatic theory (46) by amino acids; according to the thermostat theory (6) by the calorific effects of food; and according to the osmotatic theory (73) by information from osmoreceptors. As concerns motivated behavior, this particular trend was expressed by Hull (33) in his law of primary reinforcement, which became the basis of the need-reduction theory, better known as the drive-reduction theory.

On the other hand there are some experimental data indicating that mere sensations derived by exteroceptors can play an essential part in motivated behavior. Indeed, animals do perform instrumental responses in order to receive nothing but exteroceptive stimuli. Several authors succeeded in establishing an instrumental reflex reinforced with tasty substances which had no nutritive value (68, 69, 77), with a mere smell of food (42, 43), with small amounts of food not leading to satiation (15–18), with copulation without ejaculation (2, 70), with contact with another conspecific (3), with access to a new environment (7, 8, 49, 50), or with change of illumination (20, 37, 61).

Our experiments also proved the important role of external sensations in motivated ingestive behavior. We made several attempts to establish an instrumental reflex reinforced with liquids delivered directly into the stomach through a chronic nasopharyngeal gastric tube (21–24, 81). In this procedure exteroceptive stimulation of ororhinopharyngeal receptors of taste, smell and somatic sensations was virtually eliminated. Liquid food, 50% glucose, or water delivered intragastrically were used as a reinforcement. Increasing intensity of stomach mechanoreceptive stimulation was attained in various experiments by increasing the volume of reinforcement. In all of experiments, regardless of the kind of fluid used as a reinforcement, as well as its volume, we failed to establish an ingestive instrumental reflex. The level of responding was always very low and within the limits of spontaneous bar-pressing in the nonreinforced control group. In the second phase of experiments, when oral reinforcement was substituted for an intragastric one, the number of responses rapidly increased and an instant formation of instrumental reflex was obtained in all experiments.

The results of our experiments suggest that exteroceptive information from ororhinopharyngeal receptors of taste, smell and somatic sensations is indispensable for the formation of ingestive instrumental reflex. These results made us regard critically the drive-reduction theory of Hull (33). It appeared that an obvious reduction of the alimentary drive caused by intragastric infusions of nutrients has not ensured the formation of instrumental reflex. These data together with the results of other experiments mentioned before, strongly indicate the decisive role of sensations in motivated behavior. They show that animals are unable to satisfy their
biological needs if they are deprived of sensations. On the other hand, as has been said before, animals will vigorously work for sensations even if these are not accompanied by the reduction of their needs.

It is also possible to receive an instrumental reflex if it is reinforced not with exteroceptive stimulation but centrally, with electrical stimulation of certain brain structures, mainly within the limbic system (51, 52), or if an instrumental response is rewarded with application of some centrally acting drugs, like morphine (1, 19, 30, 81, 82).

It would seem that all these facts may be satisfactorily explained on the basis of the antidrive-activation theory of Konorski (39), which is the revised and most modern version of the drive-reduction theory. Konorski heavily stressed the very important role of sensory stimulation as the main activator of these nervous structures which he called antidrive centers, and which when activated reinforced the instrumental movement. Accepting the very important role of external stimulation in motivated behavior, Konorski, did not attach importance to the emotional aspect of reinforcing stimuli. As was remarked by Simonov (71) all versions of drive-reduction theories, though logically coherent, ignore the important part of emotional states in motivated behavior. For reinforcers, if they are to function on the basis of any drive-reduction theory, the emotional feature of the stimuli is needless. From a biological point of view it is unlikely that such a universal and apparent psychological phenomenon as emotion and the ability to experience stimuli-induced pleasurable states was meaningless for voluntary motivated behavior. An attempt to overcome this obviously vulnerable point of the antidrive-activation theory was undertaken by Żernicki (89) who included pleasurable processes in his models of conditionel reflexes.

In our opinion the reinforcing properties of stimuli actually depend on their ability to generate a positive emotional state, i.e., pleasure. In this respect we fully agree with the hedonistic theory of motivated behavior postulated by Young (87), and supported by Pfaffmann (55), Cabanac (9, 10) and Wyrwicka (85). There are many proofs that animals prefer some substances above others on the basis of gustatory value of these substances. As has been said before, instrumental reflexes may be successfully reinforced with tasty products which have no nutritive value. On the contrary, if a fully nutritious food tastes badly, for instance in the case of purified casein for rats, the animals will refuse to eat it (56, 88), and may even starve if it is the only source of protein (38, 64). The same happened with animals kept in magnesium deficiency which also refused to eat untasty magnesium containing diet (65).

The role of gustatory stimuli is still better manifested in animals with specific hypothalamic lesions. The addition of small amount of
quinine to food deters lateral hypothalamic recovered rats from eating and drinking (27, 80). The same applies to rats with ventromedial lesions of the hypothalamus. In spite of their hyperphagia they respond to a slightly bitter taste of food (31, 54, 78) or water (40) by complete rejection and they may even starve to death.

A particularly impressive demonstration of the role of pleasurable states are the recent experiments of Wyrwicka (86) in which cats, i.e., carnivorous animals, preferred bananas to meat if the consumption of bananas was rewarded with electrical stimulation of the lateral hypothalamus.

We are fully aware that the hedonistic theory has many opponents, because it utilizes psychological terminology which is difficult to transfer into the physiological way of thinking. However, pleasure, if understood as some kind of a positive emotional state commonly known from introspection, does really exist. By analogy with out introspection, and observing animal behavior, we can speculate that mankind is not an exception in this respect. In our opinion pleasure must be recognized not only as a psychological phenomenon, but also as a physiological mechanism which must have its neurophysiological substratum, and which exerts a decisive influence on motivated behavior. Indeed, the results of numerous studies on the so-called reward system of the brain seem to bring us closer to the knowledge of anatomical and neurohumoral substratum of pleasure. It seems that a reward system which in our opinion is in fact a pleasure system, is made up according to some authors of norepinephrine pathways (4, 57, 59, 60, 74, 75, 83), other claim that it is made of dopaminergic pathways (12–14, 41), both derived from the brain stem and sending their terminals to different brain structures, mainly within the diencephalon. Recently Belluzzi and Stein (5) put forward an interesting hypothesis that activation of enkephalin-containing neurons in the brain is related to euphoria and to rewarding properties of some categories of stimuli.

According to the hedonistic theory, as we brought out elsewhere (25), motivated ingestive behavior is directed toward stimuli possessing hedonic value. However, it is known that the same stimulus may be assessed as pleasant, indifferent or aversive, hence it may evoke different behavioral responses: an approach response, no reaction or even escape behavior, depending on the current nutritional state of the organism. Miller (47) reported that the degree of quinine adulteration of food required to inhibit eating parallels the time of food deprivation. It follows that food slightly adulterated with quinine is fully accepted by a hungry animal, a moderately sated animal ignores adulterated food still showing interest in more tasty substances, while a hypersated animal rejects normal food
and shows an apparent aversion toward the same quinine adulterated diet. Thus, the changes in the current nutritional state of the organism influence behavior. This may be easily observed as a shift in the preference-aversion curve. On the basis of this observation, as well as introspection, we can assume that the same gustatory stimulus may possess a different hedonic value depending on the current nutritional state of the organism. It follows that a special nervous process must exist which makes the same stimulation emotionally positive, neutral, or negative, in other words pleasant, indifferent, or aversive, depending on the given state of need which is signaled by peripheral interoceptors and central detectors. For this nervous process which presumably takes place within the limbic system, we propose the new term — hedonesthesia, by analogy with the term alliesthesia introduced by Cabanac (9).

The concept of hedonesthesia throws a new light on motivated ingestive behavior and permits better comprehension of the role of interoception versus sensations in this respect, as well as of their mutual relations. Figure 1 explains the concept of hedonesthesia. As shown, two categories of stimuli, extero- and interoceptive ones, determine together

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**Fig. 1.** A model of functional organization of central regulation of food intake. Explanations: circles, peripheral structures (receptors and effectors) and actions taking place beyond the central nervous system; rectangles, central structures and actions taking place within the central nervous system; arrows, excitatory connections or positive influences; stopped lines, inhibitory connections or negative influences; solid horizontal bars, levels subjected to regulation within the limits denoted by dashed lines as show dashed arrows in the rectangle of hedonesthesia; dashed rectangle encloses the central nervous system. Further explanations in text.
the motivated ingestive behavior. The current nutritional state of the organism through adequate interoceptive activation is signaled to the central nervous structures which function as a homeostat. Hypothalamic centers which receive sensory information both from intero- and exteroceptors, contain chemosensitive neurons, and are subjected to facilitatory and inhibitory influences from the limbic system (53), most probably function as this homeostat. Within the homeostat interoceptive information is compared with the set point (level of regulation). When the current nutritional state of the organism seemingly differs from the set point, as in the case of hunger (deficiency) or hypersatiety (excess), the alimentary drive is activated or inhibited respectively. Simultaneously, due to the process of hedonesthesia, hedonic evaluation of gustatory stimuli, both actual and their memory traces, shifts toward the pleasure or aversion. Nutritional deficiency results in lowering the threshold for pleasurable processes (lowered level of hedonic indifference). Thus, primarily indifferent or sometimes primarily unpleasant gustatory stimuli can be assessed as pleasant. An inverse shift of the level of hedonic indifference occurs in the case of nutritional excess. If the actual gustatory stimuli, or their traces, are evaluated as pleasant, a further increase of the alimentary drive occurs. If they are evaluated as aversive, the alimentary drive is secondarily inhibited.

Being under the influence of the alimentary drive, the animal, through its motivated behavior, prefers those categories of stimuli which due to the process of hedonesthesia have a positive hedonic value. The animal continues this behavior until its biological need is satisfied. When this is done, the same gustatory stimuli may even appear aversive, again due to the process of hedonesthesia.

The above-described homeostatic system is characterized by some degree of inertia, which results mainly from the process of digestion and resorption. Due to these processes the current nutritional state of the organism changes only after some delay. Thanks to the inertia of the homeostatic system, feeding behavior is to some degree independent of current stimuli. Otherwise the animal would have to cease and resume feeding behavior too frequently.

To summarize, hedonesthesia is a nervous process that determines hedonic value of a given gustatory stimulus depending on the current nutritional state of the organism, or sometimes on previous sensory stimulation. This nervous process, although it cannot be identified with the alimentary drive, greatly influences this drive and hence the feeding behavior. However, it has to be stressed that hedonesthesia should not be considered as a sensory process but rather as a central integrative mechanism. In some respects the process of hedonesthesia resembles that
of kinesthesia. Indeed, as in the case of kinesthesia there are no receptors of movement, so in the event of hedonesthesia there are no receptors of pleasure. As was pointed out by Konorski (39), the sense of movement is a result of integrative activity of the cerebellum, which converts proprioceptive information about the tension of muscles into information about movements. In the case of hedonesthesia, impulses derived from gustatory exteroceptors, after being compared with information about the current nutritional state of the organism, acquire an adequate hedonic value, again due to the integrative activity of the brain, presumably of some limbic structures.

Speaking of hedonesthesia we should like to stress again that we fully agree with the hedonistic theory which claims that a state of pleasure constitutes the real reinforcement for motivated behavior (9, 10, 55, 87), as we brought out earlier (25). However, it should be remembered that the hedonic value of stimuli changes depending on the current state of the organism. There is experimental evidence for this statement. Sharma (66, 67) found that changes in nutritional state of the organism induced by such agents as gastric distention, pretreatment of gastric mucosa with nutrient substances, changes in blood glucose level, chronic food deprivation, etc., influence gustatory discharges at multi-levels, as well as responses of hypothalamic neurons. Sharma (66) also suggests that the nutritional state of the organism through this effect on hypothalamic neurons influences the motivational and reinforcing systems. In fact, it was discovered earlier by Hoebel and Teitelbaum (32) that hungry rats self-stimulate the lateral hypothalamus more frequently than sated animals. If electrical stimulation of the lateral hypothalamus evokes an emotional state somehow related to the pleasure of eating it follows that the hedonic value of this central stimulation depends on peripheral information as well.

Returning to gustatory stimulation, it seems that its hedonic value may also change during a prolonged exposure of taste receptors to the same stimulation. At least such conclusion may be drawn from experiments of Hull et al. (34) who found that esophagotomized animals stopped eating after a period of sham feeding in spite of the fact that during sham feeding the food has never reached the stomach and has not satiated animals neither by activation of interoceptors nor by its metabolic effects. Also, Janowitz and Grossman (35) found that sham feeding of hungry esophagotomized dogs inhibited their subsequent eating. Judging from the feeding behavior we may assume that in both above cases the food lost its attractiveness for the animals after a prolonged gustatory stimulation. In our model of functional organization of central regulation of food intake this effect of prolonged gustatory stimulation is depicted as
the ability of exteroceptive stimulation to shift the level of hedonic indifference within the process of hedonesthesia (Fig. 1).

Alteration of hedonic value of stimuli according to the current nutritional state of the organism, or prior stimulation, constitutes an important biological mechanism which allows the animal to choose those stimuli from among a vast variety derived from its environment, which are biologically useful at the given moment. In fact palatability of the available food, but not its caloric or nutritive value is the only feature which allows the animal to recognize the value of the food, and thereby to decide whether to ingest or to refuse it.

Of course, the mechanism of hedonesthesia, similarly to other biological mechanisms, sometime fails. This happened to mankind where thanks to culinary art it became possible to prepare highly palatable food which gave maximum satisfaction to the senses, thus contributing to overeating and the phenomenon of obesity.

There are also justifiable assumptions put down by Rado (58) that the principal defect in schizophrenia — the most dangerous mental disease harassing human beings — consists in severe impairment of the ability to experience pleasure. In our opinion this defect is actually a malfunction of the physiological process which we call hedonesthesia. Although schizophrenic patients sense stimuli, these do not have any hedonic value for them. In consequence, this defect leads to a lack of interest, initiative, motivation for a goal directed activity, and lack of an emotional attitude to environmental stimuli. Stein and Wise (75, 76) presented an interesting explanation of the pathogenesis of schizophrenia which they relate to the damage of norepinephrine reward system of the brain. This view was mainly based on the results of postmortem measurements of the activity of dopamine-β-hydroxylase (the enzyme that converts dopamine into norepinephrine) in the brains of schizophrenics, which activity was found to be significantly reduced (84).

Malfunction of the process of hedonesthesia can also be produced experimentally. The effect of specific hypothalamic damages may serve as such an example. The ventromedial hypothalamic rats are not hungry, because they have no nutritional deficit, nor do they display an enhanced alimentary drive, because they do not show food-deprivation-induced locomotor activity (44, 79), and they are less motivated to work for food reinforcement (48, 72, 79), none the less they eat voraciously. It follows that for them the hedonic value of gustatory stimuli is elevated due to this brain damage. On the contrary, lateral hypothalamic rats are hungry, i.e., they suffer severe nutritional deficit, and if carefully observed they show signs of alimentary drive because they display increased locomotor activity associated with food deprivation (11), nevertheless they refuse to
eat and drink. From their behavior we can suppose that as a result of this brain damage another malfunction of the process of hedonesthesia occurred, and for these animals gustatory stimuli appeared to be highly aversive, hence their finickiness.

Experiments of Fonberg (28, 29) may be considered as a still better example of impairment of the process of hedonesthesia. Severe emotional disturbances accompanied with aphagia and adipsia were observed in dogs with lesions of the dorsomedial amygdala (28). These effects were similar to those observed in dogs with lesions of the lateral hypothalamus (62). The animals not only showed no interest in food, but they actively resisted forced feeding. When food was placed in their mouth they spat it out or even vomited. On the contrary, dogs with lateral amygdala lesions (29) or with lesions of the ventromedial hypothalamus (63) strove for food and ate voraciously. It shows that as a result of these two categories of brain damages the hedonic value of food was shifted either towards aversion or towards pleasure.

Except for these aberrations, in normal conditions the animal satisfies its biological needs perfectly through its motivated behavior. However, this is done in a very sophisticated manner. Actually the animal is not seeking calories, nutritive values, preservation of species, etc. All these are abstract ideas invented by scientists. The animal is simply seeking pleasurable sensations. Searching for pleasure, the animal unintentionally satisfies its biological needs. When this is accomplished the stimuli are no longer pleasant due to the process of hedonesthesia.

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