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EFFECT OF FOOD-SATIATION AND FOOD-DEPRIVATION UPON THE CONDITIONED REFLEXES ESTABLISHED BY THE ELLISON-KONORSKI SEPARATION PROCEDURE

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Ellison and Konorski (1964, 1965) proposed the procedure by which the separation of the instrumental motor and the classical salivary responses was possible within the same trial. Namely, two chained conditioned stimuli (CSs) were used; the first elicited a multiple instrumental response and the second, immediately following the first one, was merely a well established signal of food. In our previous study (1968) a somewhat modified procedure was employed. The dogs were trained, to perform 14 lever-presses in response to a metronome, the instrumental CS (CS_{in}), which was followed by a buzzer, the classical CS (CS_{cl}) and food-reinforcement. It was shown in this study that the CS_{in} elicited active lever-presses but also a fair rate of conditioned salivation, a result far from perfect separation between motor and salivary responses such as shown in the Ellison and Konorski studies. This discrepancy has been discussed in the previous paper (Miyata and Sołtysik 1968).

The primary purpose of the present investigation was to study the effect of manipulation of the hunger-drive upon CRs established by the separation procedure described fully in our previous paper. Four tests were carried out to observe: (i) the effect of gradual satiation with food during prolonged session, (ii) the effect of acute satiation, (iii) the effect of increase of the hunger-drive, and (iv) the effect of prolongation of the CS_{in} under increased hunger drive.

MATERIAL AND METHOD

Subjects. Five dogs were selected as the subjects of the present study from eight dogs previously trained. In all the dogs a carotid loop (van

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Leersum 1911) and a chronic fistula of shortened Stensen's duct (Sołtysik and Zbrożyna 1957) had previously been prepared for the measurement of cardiac and salivary responses.

Apparatus. The experimental arrangement were described fully in our first study. Two auditory stimuli, a metronome (120 beats per min) and a buzzer, were used as CSs. The unconditioned stimulus (US) was a portion of boiled meat and bread cubes soaked in broth. About 70 g of food was delivered as one reinforcement by the automatic feeder. The dogs' lever-presses were recorded electrically on a polygraph together with the cardiac and salivary responses.

Training. The dogs were trained with nearly the same routine as in the Ellison and Konorski study, i.e. in the four consecutive phases.

1. Classical conditioning of a buzzer as a signal of food. The buzer was presented for 4 sec and the food was delivered 2 sec after the onset of the buzzer. This procedure was continued for seven days.

2. Instrumental conditioning of lever-pressing. Whenever the dog pressed the lever with his right foreleg, the buzzer and food were presented as in phase 1. The duration of this training varied from 3 to 13 days in different dogs.

3. Differential conditioning of lever-presses to the metronome. The metronome was sporadically presented and only the lever-presses performed during its operation were rewarded as in the phase 2. After 10-17 days of training the dogs learned to wait quietly for the presentation of this CS_{in} and the intertrial lever-presses gradually disappeared, or in some dogs decreased considerably.

4. The number of lever-presses required in each trial for delivery of CS_{cl} and food was gradually increased to 14 while the duration of the CS_{cl} was extended to 8 sec. It took nearly 30 days to complete this phase.

Throughout the whole training period the daily session consisted of four trials and the intertrial intervals varied from 3 to 5 min.

Testing. When the training was completed, the following tests were performed.

1. The effect of gradual satiation of the hunger-drive upon the CRs was tested on three nonconsecutive days.

2. The effect of acute satiation of the hunger-drive upon the CRs was tested on three nonconsecutive days. The difference between the two satiation-tests was that in the gradual satiation-test the dog was given the CS_{in}-CS_{cl}-US [2] trial repeatedly until the dog ceased to eat, while in

[2] In the satiation-test 140 g of food was delivered in one food-reinforcement to save the number of trials which would be needed to make the dogs satiated.

the acute test the dog was fed ad libitum after two normal trials and then, the remaining two trials were performed to observe the effect of acute satiation. In the gradual and the acute satiation-tests, the food was left for 2 min after refusal of eating to insure the degree of completion of satiation. Morevever, the dogs were given the same food in a large bowl at a different place after being taken out of the chamber, and checked again to determine whether or not they had been satiated. The duration of CS_{in} was fixed to 10 sec in these first 2 tests.

3. The effect of increase of the hunger-drive was observed on 4 consecutive days. The level of hunger-state was increased day by day by limiting the daily diet to the amount eaten during the training session.

4. The CS_{in} was prolonged to 30 sec and then followed, as usually, by CS_{cl} and food, but under the increased hunger-states.

Special caution was taken not to spoil the previously established CRs by applying the tests in too close succession. Therefore, the dogs were trained normally for at least five days before the next test was applied.

Feeding schedule. During normal training, the dogs received their meal after the daily session at their home cage. Since the daily order of running the dogs was fixed throughout the experiment, the training was performed under the condition of food-deprivation of approximately 22 hr. The daily meal was omitted on days with the satiation-test, since the dogs were fed enough at the experimental chamber. In the food-deprivation condition, the daily diet was also withdrawn and the animals were restricted to the four portions of food presented during the four session trials as a reward.

RESULTS

Effect of food-satiation upon CRs

As shown in Table I, our dogs differed in the number of trials which were needed to satisfy their hunger in the gradual satiation-test, i.e., the dog (H) needed nearly 20 trials before he stopped eating on the satiation-test while the dog (TK) seemed satiated after only four trials with food-reinforcement. In the two consecutive gradual satiation tests this difference between dogs remained unchanged although the amount of food eaten decreased in the dogs that ate greater amounts of food. In order to determine the effect of satiation on the CRs, the data from the first two trials were compared with those on which the dogs refused to take the food.

In Fig. 1*A*, the effect of gradual satiation upon the latency of salivation and lever-pressing, their rates, and the heart rate change of the dog

(H) are shown. It is clearly seen that the gradual satiation of hunger affected strikingly all the observed responses.

In our procedure of the acute satiation-test, all the dogs again consumed various amounts of food when fed ad libitum between the 2nd and 3rd trials, as shown in Table I. The amount of food they took in the gradual satiation-test was also added in the seventh column. An interesting fact is revealed by comparing the amount of food eaten during these two tests (two last columns of Table I). Some dogs eat more on acute satiation tests (dogs Q and Tk) whereas the other dogs eat more during the gradual satiation tests. The difference is particularly striking in the dog Tk which seemed satiated after only four trials though on acute satiation test he ate twice as much.

TABLE I

The number of trials and amount of food needed to satiate the dogs[a]

Dogs (weight in kilograms)	Numper of trials[b]				Amount of food (in grams)	
	GS test				AS	GS
	T–1	T–2	T–3	Mean		
H (16.9)	19	13	14	15.3	1740.0	2146.7
S (19.5)	13	7	8	9.3	676.7	1306.7
K (11.3)	11	7	9	8.7	1050.0	1260.0
Q (15.4)	7	7	6	6.7	1073.3	933.3
Tk (16.4)	4	4	4	4.0	1146.7	560.0
Mean	14.8	7.6	8.2	8.9	1137.3	1241.3

[a] Key: AS, acute satiation; GS, gradual satiation; T, test

[b] The trial on which the dogs refused to eat was not included.

In Fig. 1*B*, changes observed in CRs after complete acute satiation are shown, and it can be concluded that the effect of satiation upon CRs are of the same character in both tests. Therefore, the data obtained from two tests were combined hereafter to determine the general effect of satiation upon CRs. In Fig. 2 mean changes in latency, response rate, and heart rate change obtained from the five dogs are presented. It should be noted that nearly all satiated dogs responded unexpectedly to the CS_{in} by pressing the lever, though with a lower frequency and lesser vigor than when not satiated. However, salivation was rarely elicited during the action of CS_{in} in a satiated state. The amount of change in the heart rate also decreased markedly when the dogs were satiated. In Fig. 3 the recording obtained from the dog (Q) is shown. Lever-pressing was observed even after feeding ad libitum between the 2nd and the 3rd trial.

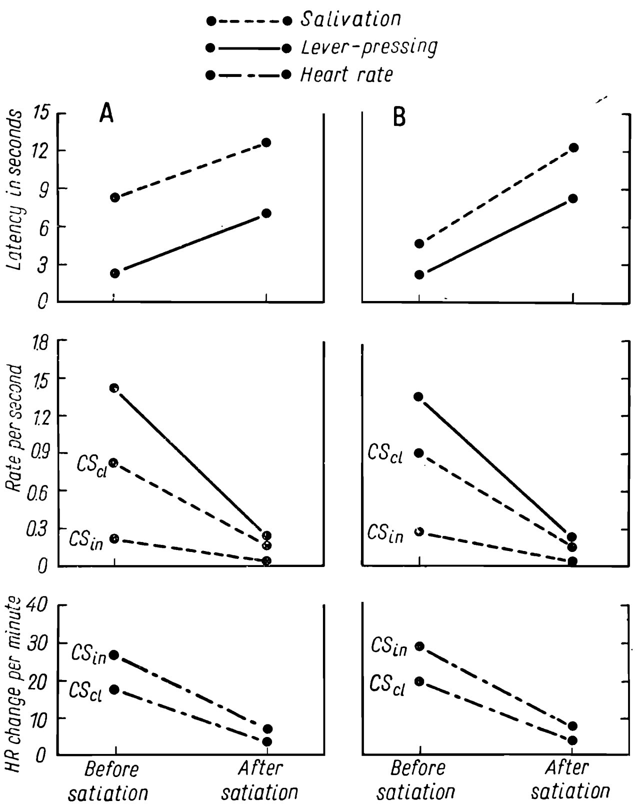

FIG. 1. The effect of gradual (*A*) and acute (*B*) satiation upon the latency of salivation and lever-pressing, their rates, and heart rate change obtained from the Dog H.

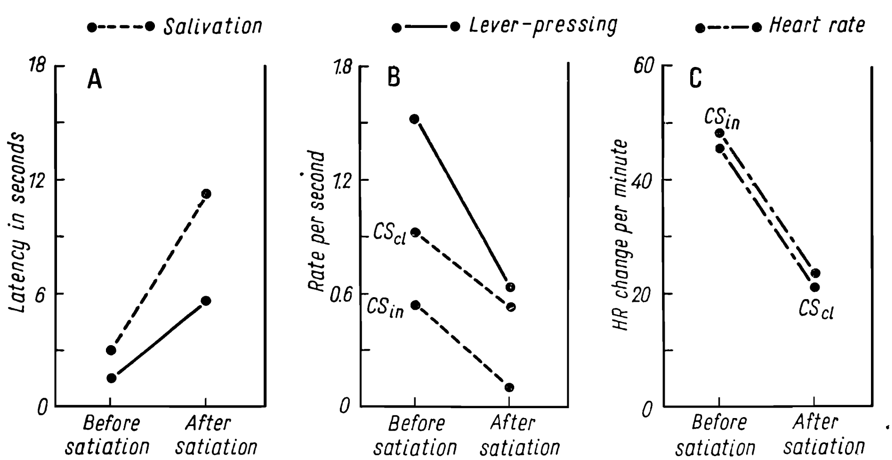

FIG. 2. Mean changes in latency of salivation and lever-pressing, their rates, and heart rate obtained from five dogs.

The general behavior on the trials on which satiation was attained was very similar in all five dogs namely, when the SC_{in} was presented, they showed still the orienting head-turning to it; they often showed a quick stepping leg-movement, sometimes with a low whining; and often they began to press the lever, though usually only a few times. When the CS_{in} was replaced by the CS_{cl}, they became quiet, looking at the

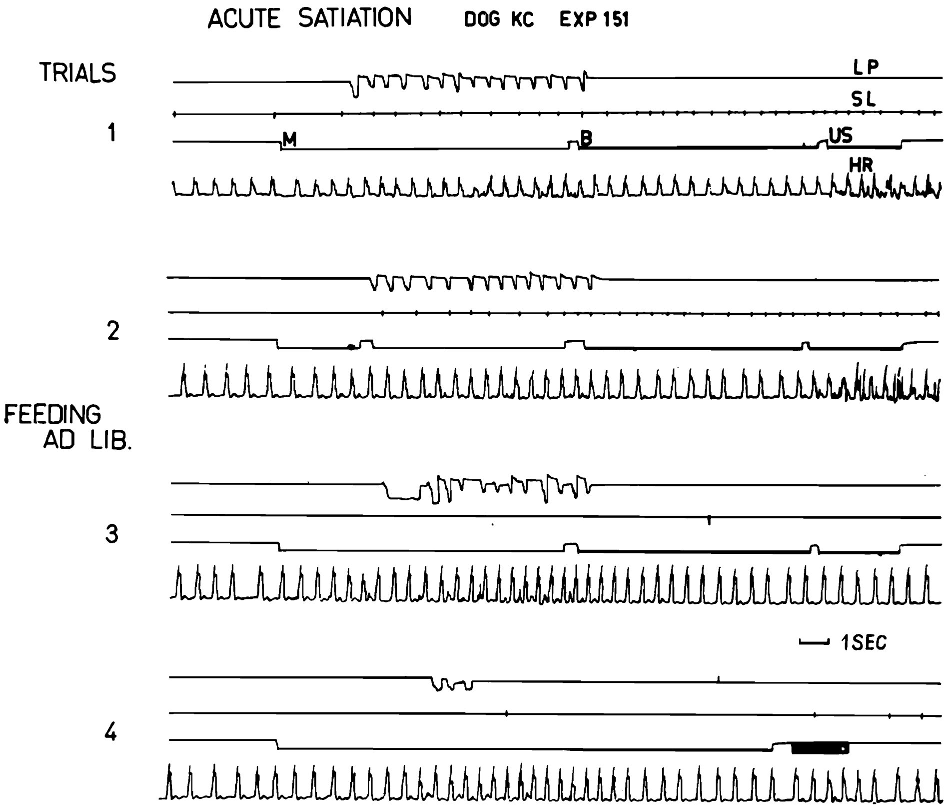

FIG. 3. Recording obtained from the dog Q before and after the acute satiation. M, metronome (CS_{in}); B, buzzer (CS_{cl}); LP, lever-pressing; SL, salivation; US, unconditioned stimulus (food); HR, heart beats. Note the dramatic reduction of salivation on trials 3 and 4, and virtually no change in motor response on trial 3.

food-cup and then seemed to have lost interest in it. But at the moment of presentation of the food they again gazed at it for a short while. The restlessness and escaping behavior from the stand described elsewhere (Sołtysik 1969) rarely occurred in our dogs during satiation-test.

Effect of food-deprivation upon CRs.

Five dogs were deprived of the daily diet for four days, and the effect of increasing of the hunger-drive was determined on each day. It is clearly evident in Fig. 4 that only the conditioned salivation was highly influenced; the latency was greatly shortened on the second day, and the rate of the responses to both CS_{in} and CS_{cl} was increased. It

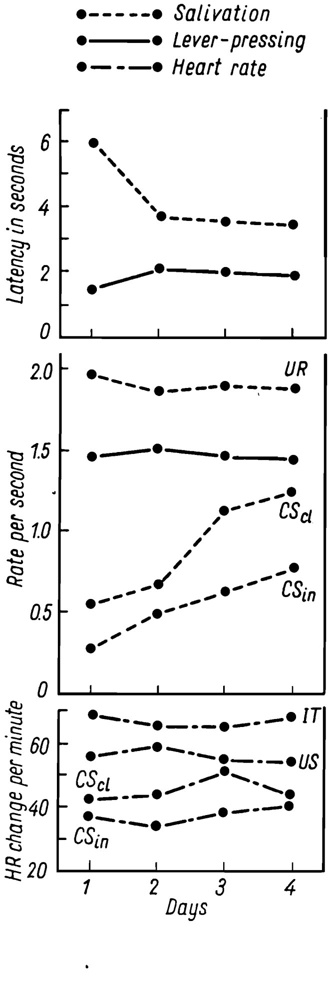

FIG. 4. The effect of food-deprivation upon the latency of salivation and lever-pressing, their rates, and the heart rate change obtained from five dogs. UR, unconditioned response; IT, heart rate between trials; US, heart rate change during eating.

seemed that the salivation to the CS_{cl} was more influenced by deprivation than that to the CS_{in} although the exact comparison was impossible because of the unequal initial levels of salivary secretion to both stimuli. The unconditioned salivation to food, however, was not affected, even after four days of fasting. It must be reconsidered that the food-deprivation did not produce any noticeable effect on the instrumental response, the lever-pressing, as well as on the cardiac response. In this test all the dogs had pressed the lever 14 times to bring about the CS_{cl} and the time needed to complete this criterion response was measured. Generally, they took approximately 10 sec to complete 14 pressings. Two dogs were selected after this test to examine further the effect of food-deprivation chiefly upon the instrumental lever-pressing, and 30 sec were allowed for them to perform the lever-pressing. The results showed that the dog (S) performed 37 pressings on the first day with a normal feeding schedule, while on the second and the third days, without a daily diet, the dog showed 47 and 50 pressings. In another dog (Q), the number of pressings was 36 under the normal feeding, 46 on the second day, and 47 on the third day. Thus the effect of deprivation significantly influenced the instrumental responding, if the duration of instrumental performance was prolonged to 30 sec.

Regarding the heart rate, only a neglegible increase in response to CSs was found under the elevated hunger drive and no changes were observed of the cardiac acceleration during eating or in the intertrial interval heart rate.

DISCUSSION

The Ellison–Konorski training procedure offers a unique opportunity to study the effect of drive manipulation upon classical-salivary and instrumental-motor CRs simultaneously though separately. By emploing this method under increased or decreased hunger drive it is possible to observe changes in performance of both appetitive and consummatory phases of feeding behavior and thus to infer the relationships between corresponding nervous centers. A brief resumé of the history of the theoretical approach to the "alimentary conditioning" may help in clarifying our position. Pavlov (1951) in his lecture of 1910 considered an "alimentary center" as a part of a gustatory analyzer with its efferent salivary, masticatory etc. reflexive output. Hunger state, i.e., humoral changes within an organism (e.g. "hungry blood") would control the excitability level of cortical and possibly subcortical taste cells. The instrumental response was, according to Pavlov (1936), produced by the reverse transmission of excitation from taste cells to kinesthetic cells representing movements which previously had been reinforced with food and had become conditioned signals of taste unconditioned stimuli. E. A. Asratian (1966) recently proposed a modified version of this concept.

The ethological approach to the concept of instinct with its separate drive and consummatory components, and the classic studies of Hetherington (1941, 1943), Anand, Brobeck and others (Anand and Brobeck 1951, Brobeck et al. 1943, Brobeck 1951, 1955) on the centers of hunger and satiety in the hypothalamic region led one of us (Sołtysik 1960) to a new concept of the central mechanism of instrumental and classical food CRs. Hunger and taste were assumed to have separate neuronal representation and to belong to separate reflexive mechanisms. Although in the first model of 1960 no definite interrelations between both systems (i.e. hunger system and food system) were postulated, it was clear from the observations of Konorski and Wyrwicka (1950) and the recent study of J. Konorski, T. Rentoul and S. Sołtysik (in prep.), that the gustatory system, including conditioned stimuli signalling food, exert an immediate and powerful inhibitory effect on instrumental behavior. On the contrary, the influence of the hunger system on the food-taste system was assumed (Konorski 1967) to be facilitatory. According to this view the salivary CRs should parallel the instrumental CRs under various hunger levels. This was actually the result of our experiments. However, difficulties are posed by the trials in which the dogs being obviously satiated still vigorously responded instrumentaly and at the same time *failed* to salivate. Webb (1952) in his article on the "response in the absence of the acquisition motive" proposed four explanations of such phenomena. The first is the theory of an "irrelevant drive" of Hull (1943). The second is the Allport's concept of "functional autonomy" (1937) which apparently has no relevance for our results, as it is concerned rather with maturation and ontogenesis of behavior. The remaining two theories belong to the class of "acquired tendencies theories" and need to be considered more carefully. According to the theory of automatization, the response could be elicited in the absence of drive by the conditioned stimuli due to the connection (or "habit") between the stimuli and response. Such a possibility really exists but, as shown in the study of Dobrzecka et al. (1965) is limited to stimuli that possess a natural strong connectivity with a particular response. The telereceptive CSs used in our experiment should not be able to form such a strong connection as to enable eliciting the movement without a support of drive. Finally, the last theory, assuming the conditionability of drive, stems from Anderson's concept of "externalization of drive" (Anderson 1941). According to this concept the instrumental CS is considered a conditioned hunger stimulus, and in our dogs which had been given over 600 trials under the hunger state this stimulus could be reasonably assumed to have acquired the capacity of eliciting a conditioned hunger drive. The observation of animals' behavior during satiation tests seemed to indicate that this was the case. The nearly satiated dog, apparently uninterested in food exhibited a new interest to the foodtray when after the instrumental response, a CS_{cl}

was presented. Turning to the opening in the foodtray, sniffing, and attentive watching of the foodtray did not however, last long and usually after a few seconds, still during the action of the CS_{cl} the dog turned away. Thus a momentary arousal of the hunger drive could be inferred from the overt behavior of the animals.

Now the poblem arises why the salivary conditioned secretion does not profit from this temporary increase of hunger drive? Sołtysik (1971) postulates that satiation does not significantly affect unconditioned salivation, and that the effect of diminished hunger upon conditioned secretion might be executed indirectly by changing the attentiveness to CSs and attenuating the food-oriented behavior. This is not confirmed in the present study where a marked reduction in salivary CRs was observed in spite of hunger inciting action of the CS_{in}. Thus, either conditioned salivation is controlled directly the by satiety center in addition to, or instead of the facilitatory control from the hunger center, or the salivary reflexes need a more tonic, longlasting facilitation and a fleeting increase of drive is not sufficient.

The heart rate responses, similarly as in the earlier study on the effect of satiation of conditioned food reflexes (Sołtysik 1969) were markedly diminished in the satiated state. However, they did not increase when the hunger was increased by starvation. Perhaps, the well developed self-regulation devices within the cardiovascular system prevent the increase of cardiac responses beyond a certain limit, and therefore using of the heart rate responses as an index of drive is justified only below that value which is determined by the ordinary 24 hr deprivation.

SUMMARY

The purpose of the present study was to determine the effect of food-satiation and food-deprivation upon CRs established on five dogs by a modified Ellison-Konorski procedure. The dogs were trained to perform 14 lever-pressings in response to the instrumental conditioned reflex, which was followed by the classical conditioned reflex and food-reinforcement. In order to investigate the effect of satiation upon CRs — a lever-pressing instrumentally established, the salivation classically conditioned, and the heart rate response during the peformance of CRs — the gradual and the acute satiation-tests were performed. In the former test the trial was repeated until the dog refused to accept the food, and in the latter the dog was fed ad libitum in the middle of the four trials session. The general effect of satiation was the inhibition of both classical and instrumental CRs but it was also found that the instrumental lever-pressing was often provoked in response to the CS_{in} in spite of the

fact that the dogs were completely satiated. It is concluded that this continuation of responding even in the absence of the acquisition drive is due to the externalization of the hunger-drive, i.e., due to the conditioned hunger reflexes elicited by the CS_{in}.

The second part of this study was to observe the effect of food-deprivation upon CRs. The dogs were not fed at their home cage during three days, and the changes observed in CRs were measured on each day. It was found that the deprivation enhanced both the instrumental and classical CRs, but it did not change the heart rate responses.

The interesting fact that satiation inhibits more readily the consummatory food reflexes than the drive reflexes is discussed in terms of Konorskian concepts of the central neuronal circuitry of the alimentary system.

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