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FLAVOUR-MEAL SIZE CONDITIONING IN THE RAT (*RATTUS NORVEGICUS*): FAILURE TO CONFIRM SOME EARLIER FINDINGS

Leickness Chisamu Simbayi
University of Port Elizabeth

ABSTRACT: A series of experiments was carried out in order to explore further the possibility that hungry rats, both mature and weanling, might learn to associate flavours with different sizes of meals made from the same diet. The general procedure used involved providing rats with either a large meal (e.g. 5 gm), usually consisting of wet mash with an added flavour such as anise, or a small meal (e.g. 1 gm) of the same diet with a second flavour such as vanilla added, on alternate days. Following a number of such discrimination training days, subjects were given a two-jar extinction choice test to assess their relative preferences for the two flavours. It was originally anticipated that rats would come to prefer the flavour associated with the larger meal (i.e., conditioned appetite), because the larger meal provided more calories. However, this result was never obtained. When a significant preference was acquired, this was for the flavour of the small meal instead, (i.e. conditioned satiety). The conditioned effects not only extinguished very rapidly but were also rather elusive at times. It is thought that the observed conditioned satiety effects were probably due to flavour-calorie rather than flavour-flavour associations.

A central theme in a number of current theories of food intake control is the idea that omnivores such as rats or human beings regulate their food intake on a short-term basis, that is, within a meal, by associating the caloric consequences of ingestion with the flavour of foods (e.g., Booth, 1985; Deutsch, 1987; Le Magnen, 1987). This phenomenon which is known as conditioned satiety is considered to be very important because it means that the omnivores do not necessarily have to wait until they have actually experienced the delayed results of digestion, namely, calories, before they terminate feeding. They can instead simply rely on their previous experience with familiar flavours

Address correspondence to Leickness Simbayi, Psychology Department, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, South Africa.

as cues for satiety. Accordingly, inability to make such associations may be responsible for inducing some pressing human problems such as obesity (Booth & Mather, 1978), alcoholism (Deems, Oetting, Sherman & Garcia, 1986) and drug withdrawal problems (Le Magnen, Marfaing-Jallat & Miceli, 1980).

A complementary process known as conditioned appetite which also involves learning about flavour-food relationships has been implicated as a food selection mechanism on a more long term basis whereby omnivores choose their food after learning about the caloric values of different foods (Bolles, 1983; Bolles, Hayward & Crandall, 1981; Hayward, 1983; Mehiel & Bolles, 1984; Rozin, 1977). It is thought that rats are perhaps adept at learning about both of these types of conditioned preferences in much the same way as they acquire conditioned taste aversion (CTA) learning or bait shyness. In contrast to the very considerable and unequivocal evidence for CTA learning in rats which has been accumulated over the past three decades or so of research (see Riley & Tuck, 1985), evidence for positive conditioned flavour preferences, which include both conditioned satiety and conditioned appetite, is relatively less strong and unconvincing. This seems rather surprising in view of the fact that the idea of the involvement of such learning mechanisms in the regulation of feeding behaviour was originally proposed as early as 1955 by Le Magnen (see Le Magnen, 1969).

Although there is mounting evidence in support of the idea that rats are capable of learning about positive flavour preferences (e.g., Boakes & Lubart, 1988; Boakes, Rossi-Arnaud & Garcia-Hoz, 1987; Capaldi, Campbell, Sheffer & Bradford, 1987; Simbayi, 1987; Simbayi, Boakes & Burton, 1986) most of the evidence demonstrated conditioned appetite rather than conditioned satiety. It is interesting to note here that most of these studies had employed fluids such as glucose, saccharin and ethanol rather than solid food as reinforcers. In contrast, a relatively small number of studies have also demonstrated conditioned flavour preferences using solid food in other animals such as humans (e.g., Booth, Lee & McAleavey, 1976; Booth, Mather & Fuller, 1982) and chicks (e.g., see Capretta, 1961; Hogan, 1977, 1980). These studies could be considered more informative about conditioned preferences than those that used fluids as reinforcers, because most of the food of omnivores is in solid rather than liquid form.

The fact that the experimental demonstration of conditioned satiety has proved to be rather elusive has been hitherto acknowledged by Smith and Gibbs (1979). According to them, only two studies, one by Booth (1972) and the other by Booth and Davis (1973), had successfully demonstrated conditioned satiety learning in rats. In his initial study, Booth (1972) found evidence for the ability of flavours to elicit conditioned satiety in rats. In this research, flavours were paired with high or low calorie diets during training and presented to the rats one at a time. During testing, when the two flavours were presented one at a time in isocaloric diets, the "low calorie" flavour was preferred more than the "high calorie" flavour. However, in a two stimulus preference test in which the flavours were presented simultaneously in isocaloric diets, the high-calorie flavour was preferred more than the low calorie flavour. This latter result demonstrated conditioned appetite. Similar findings have also been reported by Booth and Davis (1973). However, similar studies carried out by Bolles et al. (1981) and Hayward (1983) were only able to demonstrate conditioned appetite but not conditioned satiety. Perhaps even more interesting was Hayward's findings which also showed that young rats were capable of more diverse learning than adult rats.

The experiments reported in the present paper were undertaken in an attempt to explore further the positive conditioned flavour preference effects reported by Booth (1972), Bolles et al. (1981) and Hayward (1983) using wet solid food as a reinforcer. To test the validity of Haywood's (1983) developmental finding, conditioned flavour preferences were investigated in adult rats in Experiments 1, 2 and 4, and in rat pups in Experiment 3.

EXPERIMENT 1

This experiment was a partial replication of experiments carried out by Bolles et al. (1981), except for the following changes:

a) The ratio of meal sizes was increased to 5:1 instead of 2:1. It was hoped that the ratio increment would serve to make the meal sizes more easily discriminable.

b) To prevent rats from learning to anticipate or predict specific flavours during each subsequent training day, semi random presentations of flavour-meal size correlations replaced the alternating presentations every other day adopted by Bolles et al (1981).

c) Control groups were added for which supplementary food (wet mash of standard laboratory chow) was made available 15 min after the presentation of small meals. These control groups were somewhat similar to the Oral Group used in Bolles et al.'s (1981) Experiment 4 and were meant to equate the total caloric consequences of both meal sizes and thereby controlling for any possible confounding effects of differential hunger.

Basically, rats were given experience with two meal sizes of the same diet, each of which was marked by a distinctive flavour (anise oil or vanilla). Thus, the two distinctive flavours were correlated with the same pattern of oral cues and caloric density but different caloric consequences: that is, large meals yielded more calories than smaller ones. The conditioning of flavour preferences was assessed by the degree to which the animals tracked the flavours in an extinction choice test when they were no longer correlated with meal size.

METHOD

Animals

Twenty male hooded Lister rats were obtained from Sussex University's Laboratory of Experimental psychology breeding colony. They had been used previously in a food neophobia experiment but had no experience with either the reinforcer or flavours used in the present experiment. The rats were fed for only 2 h each day beginning at 1500 hrs and were food deprived for the rest of the day except for 30 - 60 mins beginning at 1000 hrs each morning when training or testing was conducted. More importantly, the animals also had some previous experience with feeding from jars and their mean consumption time for 5 gm of wet unflavoured mash was about 5 min. The average age and weight of the rats at the beginning of the experiment were 100 days and 250 gm respectively.

Materials

The experimental flavours, which were added to the chow diets, were made by adding 0.5 ml anise oil (Sigma London Chemical Company Limited, Poole, Dorset, England) and 2.0 ml vanilla (E.F. Langdale Ltd., New Addington, Surrey, England) extracts to 100 ml water. These flavour concentrations were chosen following a titration experiment which tested for sensitivity of rats to flavours relying on food neophobia as the dependent variable. Both the conditioning and testing diets consisted entirely of standard laboratory chow (Spratt's Expanded

Rodent Diet, Spiller's Limited, Newmarket, Suffolk, England) to which some water was added and yielded about 2 cal/gm.

All conditioning and testing was carried out in the animals' home cages where both the conditioning and testing diets were presented in feeding jars with holes in the lids large enough for the rats to insert their heads in order to reach the food. During testing the jars were attached in pairs to prevent rats from altering the position of each jar relative to the other. In addition, the pairing arrangement also made it possible to effectively counterbalance for any positional biases.

Experimental design

A 2 x 2 factorial design was used with large meal flavours (anise vs. vanilla) and supplementation (whether or not the animal had received supplementary food on small meal days during conditioning) as factors. The experiment had two major phases during which conditions were reversed. For each subject the treatments in each phase were identical except that the relation between flavour and meal size was reversed. Each phase consisted of two 8-day conditioning cycles, each of which were followed by a single test day. Finally, a 5-day interval separated the two phases during which no flavours were presented and the same food deprivation schedule as used in the actual experiment was also maintained.

Procedure

Conditioning involved presenting flavour-meal size correlations for blocks of 8 days in semi random order, that is, a total of 4 days with each flavour. The animals were randomly assigned to four equal groups (n = 5) namely, Groups V, VS, A and AS. Groups V and VS were presented with a large meal (5 gm) flavoured with 2.0 % vanilla on some days and a small meal (1 gm) flavoured with 0.5 % anise oil on other days. On the other hand, Groups A and AS were both presented with a large meal (5 gm) flavoured with 0.5 % anise oil on some days and a small meal (1 gm) flavoured with 2.0 % vanilla on the other days. However, in addition, Groups VS and AS also received a supplement of 4 gm of unflavoured plain chow (also in wet mash form) 15 min after consuming the small meals. On any given conditioning day, all the animals received the same flavour: for example, on a typical 'vanilla day', Group V and VS received large vanilla flavoured meals, while Groups A and AS received small vanilla flavoured meals, and only Group AS received the 4 gm of supplementary food after 15 min. The flavoured meals used for conditioning were presented at 1000 hr while maintenance food was presented for 2 h beginning at 1500 hr.

Testing was done using a two jar extinction choice paradigm which involved comparing the consumption of two diets presented simultaneously in equal amounts in two feeding jars. Each jar contained 20 gm of either anise or vanilla flavoured food in wet mash form. Testing lasted for only 10 min beginning at 1000 hr on each test day. The positions of test foods were counterbalanced for each pair of animals to minimise any positional biases. The first test was done on Day 9 (Phase 1) after which the conditioning cycle was repeated for another 8 days. Then, another choice test followed on Day 23 (Phase 2).

In order to further demonstrate the consistency and resilience of the phenomenon under investigation, the above procedure was repeated exactly except that the flavours were reversed during Phase 2 as mentioned earlier. A 5-day interval was allowed to reduce the chances of rats confusing flavour-meal size pairings used in Phase 1. However, no tests were carried out to ascertain whether or not preferences had remained unchanged during the intervening period. Thus, during Phase 2 Groups V and VS were presented with anise-flavoured large meals on some days and vanilla-flavoured small meals on other days while Groups A and AS were presented with vanilla-flavoured large meals on some days and anise-flavoured small meals on other days. Note that these flavour meal size correlations are exactly the opposite to treatments given in Phase 1. In addition, Groups VS and AS were retained as controls as in Phase 1, and they both received supplements of 4 gm of unflavoured plain mash 15 min after the presentation of food on 'small meal' days. However, as in Phase I, Groups V and A did not receive any supplementary food on their small meal days.

Relative preferences for anise-flavoured food in the extinction choice tests which followed each 8 day training cycle were calculated in terms of percentages of total food consumption by each subject during each test as follows:

$$\text{Preference for anise (\%)} = 100 \times \frac{\text{intake of anise}}{\text{intake of both anise and vanilla}}$$

Data analysis

Data obtained during each of the two phases of the experiment were initially assessed using separate three way analyse of variance (ANOVA) with repeated measures, comprising large meal flavour (anise versus vanilla), supplementation (supplement versus no supplement) and test session (Test 1 versus Test 2) as factors. In order to determine how flavour preferences shifted after each 8 day training cycle, data obtained during each of the two test sessions in each phase were also separately assessed using two way ANOVAs with large meal flavour and supplementation as factors.

RESULTS

During conditioning, all animals ate all of the portions of food given to them every day. The data obtained from the extinction choice tests carried out at the end of each of the four 8 day training cycles in Experiment 1 are illustrated in Figure 1. This figure shows that although all groups highly preferred vanilla compared with anise in all choice tests (as revealed by low anise preferences ranging from 2 % to 35 %), quite clear group differences could still be seen.

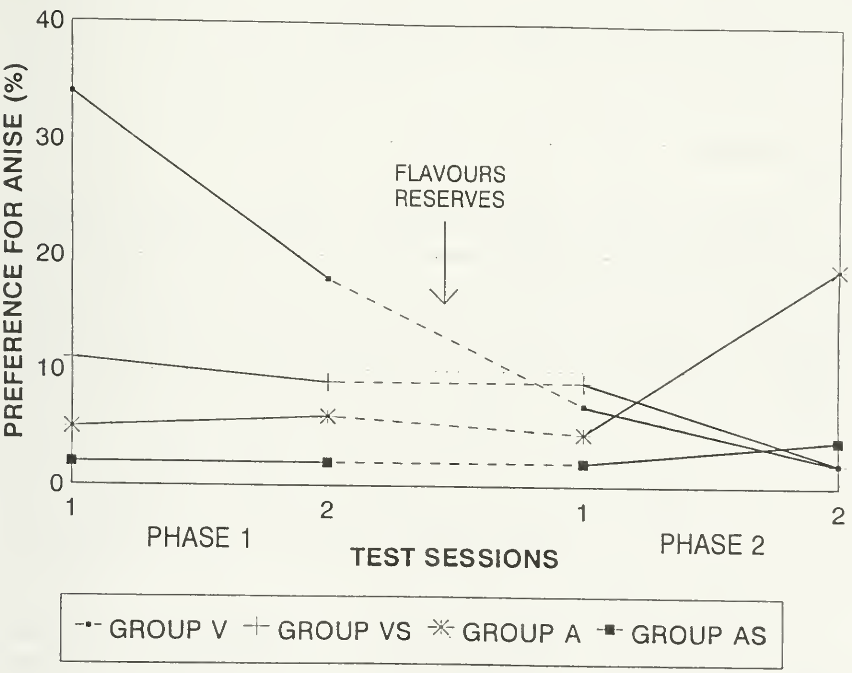

Figure 1. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 1 (n = 5). Note: Flavour-meal size pairings were reversed during Phase 2.

The ANOVAS performed on data obtained during each of the two phases of the experiment revealed a significant main effect of large meal flavour during Phase 1 only, $F(3,16) = 5.69$, $p < 0.01$. As can be clearly seen in Figure 1, this indicates that both Groups V and VS consumed significantly more anise-flavoured food than Groups A and AS during Phase 1. However, there were no such major flavour preference shifts observed during Phase 2 following reversal training, although the direction of the small preference shifts that had occurred was similar to that observed during Phase 1.

A two way ANOVA of data obtained during Test 1 of Phase 1 revealed reliable main effects of both large meal flavour and supplementation, $F(1, 16) = 8.17$ and 5.32, $p < 0.01$ and 0.05, respectively. However, there was no significant interaction between the two factors. As can also be clearly seen in Figure 1, supplementation of meals significantly reduced the magnitude of flavour preference shifts during Test 1. Another two way ANOVA of data obtained during Test 2 of Phase 1 revealed a significant main effect of large meal flavour only, $F(1,16) = 5.32$, $p < 0.05$. Similar statistical analyse of data obtained during each of the two tests in Phase 2 of the experiment failed to reveal any significant main effects or interactions.

DISCUSSION

Three main findings emerged from Experiment 1. Firstly, adult rats learned to prefer a particular flavour when it was previously correlated with small meals more than when the same flavour was correlated with larger ones. Secondly, supplementation of small meals initially slightly reduced the preferences for the flavour previously paired with the small meal, but had no effect on the preferences afterwards. Even though the rats had clearly a positive preference for vanilla and what appeared to be an unconditioned aversion to anise, it was also clear from the data that the flavour tracking effect was quite consistent throughout the experiment. Thirdly, although reverse flavour-meal size pairings reduced the preferences to non significance, they were still in the direction determined by meal sizes.

Although the first finding appears to be consistent with Booth's (1972) conditioned satiety findings, the extinction testing procedure which was used in the present experiment was different from that utilised by Booth. For instance, Booth's testing procedure involved presenting the two test flavours one at a time whereas in the present experiment the testing procedure involved simultaneous (or side by side) presentation of the two test flavours. However, the same finding clearly contradicts reports by Bolles et al. (1981) and Hayward (1983) that adult rats can not learn taste preferences based on differing caloric outcome.

The second finding appears to be entirely consistent with those of Booth and Davis (1973) and Booth et al. (1982) who found that although the latter supplements failed to condition meal size per se, they did actually manage to condition flavour preferences. Finally, the third finding could be explained in terms of either overshadowing or proactive interference (or inhibition) of the subsequent learning during Phase 2 by learning which took place earlier during Phase 1.

EXPERIMENT 2

One criticism of the conditioned satiety hypothesis, namely that the animal will prefer the flavour not associated with satiety, is that it might instead avoid the flavour with a prolonged exposure due to an acquired aversion. In order to rule out this possibility, in Experiment 2 flavours were presented for an equal amount of time but were followed or preceded by different sized supplements. Therefore, for one half of the subjects, one flavour was followed by 4 gm while a second flavour was followed by 1 gm of plain mash. Hence, this procedure controlled both for flavour exposure time and for the disturbance factor involved when supplements are given after the presentation of flavour cues. Another important issue concerns the extent to which the relationship between the flavour cue and the caloric supplement could also be important, since cues presented at meal onset may have a different value compared with those at the end of the meal. In order to investigate this issue flavour cues were preceded by supplements for the remaining half of the experimental subjects. This allowed comparisons to be made to examine the extent to which conditioned satiety depended upon the relative temporal positions of flavour cues and supplements.

METHOD

Animals and materials

The subjects consisted of 24 male hooded Lister rats obtained from the same breeding colony as in the previous experiment. They were aged about 160 days and weighed 325 - 480 gm at the beginning of the experiment. The rats had previously been used in another flavour conditioning experiment employing the Holman (1975) procedure using delayed reinforcement (Simbayi, 1987), but had no experience with the solid reinforcer, the two flavours (i.e., vanilla and anise) and the conditioning procedure used in this experiment. The subjects were allowed about 4 weeks of ad libitum feeding prior to being given another 2 weeks to adjust to new housing conditions and a new feeding schedule similar to that used in Experiment 1. In addition, they were allowed 6 days to accommodate to feeding on wet chow from feeding jars placed inside their individual cages before the actual experiment began.

All the materials used were similar to those used in Experiment 1.

Procedure

The rats were housed, watered, fed and tested exactly as in Experiment 1. However, some major changes were made during training. Discrimination training commenced at the same time of day as in Experiment 1 and flavours were also presented in a semi-random order for 8 days. The subjects were randomly divided into four groups (n = 6), namely, Groups VS, AS, SV and SA. Groups VS and AS received flavoured mash initially before supplements of plain mash were presented whereas supplements of plain mash preceded the presentation of flavoured mash in Groups SV and SA. All four groups received 1 gm of either vanilla or anise flavoured mash, each flavour separately for a total of 4 days. On any particular conditioning day, all groups received only one of the two flavours which served as the conditioned stimuli. Group VS received 4 gm of plain mash 2 min after the presentation of 1 gm of vanilla flavoured mash on some days and only 1 gm of plain mash also 2 min after the presentation of 1 gm of anise flavoured mash on other days. Groups AS received a similar treatment to Group VS, except that flavour-meal size contingencies were reversed, that is, 4 gm of plain mash 2 min after the presentation of 1 gm of anise flavoured mash on some days and 1 gm of plain mash also 2 min after the presentation of 1 gm of vanilla flavoured mash on other days. However, Groups SV and SA were presented with the same flavour-meal size pairings, as Groups VS and AS respectively, except that the order of the presentation of the flavoured and plain mash were reversed. Therefore, Group SV received 4 gm of plain mash 5 min before the presentation of 1 gm of vanilla flavoured mash on some days and also 1 gm of plain mash 2 min before the presentation of 1 gm of anise flavoured mash on the other days. Similarly, Group SA received the same treatment as Group SV, except that the flavour-meal size pairing was reversed, that is, 4 gm of plain mash was presented 5 min before the presentation of

1 gm of anise flavoured mash on some days and 1 gm of plain mash 2 min before the presentation of 1 gm of vanilla flavoured mash on other days. The 2-min and 5-min intervals were introduced to enable the animals to eat all of the initial plain and flavoured mash respectively before additional food was presented. This procedure was adopted to prevent mixing of flavoured and unflavoured food and a possible reduction of the potency of the conditioned stimuli due to dilution.

Testing for changes in preferences of either anise- or vanilla-flavoured mash was performed using two jar extinction choice tests on 2 consecutive days and lasted for 10 min on each day as in Experiment 1. Rats were simultaneously presented with 30 gm of vanilla flavoured mash and 30 gm of anise flavoured mash in separate jars. Both Tests 1 and 2 were held under conditions of food deprivation similar to those employed during conditioning.

RESULTS

All animals consumed their food portions on all training days. The results obtained from the choice tests carried out at the end of the single 8-day training cycle are shown in Figure 2. During Test 1, both Groups VS and SV which had prior exposure to large vanilla-flavoured meals and small anise-flavoured meals had higher preferences for anise-flavoured mash than Groups AS and SA which had been exposed to large anise-flavoured meals and small vanilla-flavoured meals. There was a similar pattern of group preferences during Test 2. During both Tests 1 and 2, Groups VS and AS (which had received cues before supplements) had higher preferences for anise-flavoured mash than Groups SV and SA, which had received flavour cues after the meal supplements.

A two way ANOVA of data obtained during Test 1 revealed significant main effects for both large meal flavour and the timing of the supplement, Fs $(1, 20) = 10.43$ and 6.22, ps < 0.01 and 0.05, respectively. However, there was no significant interaction between the two factors. The former main effect indicates that Groups VS and SV had significantly higher preferences for anise-flavoured mash than Groups AS and SA, whereas the latter one shows that flavour cues were more effective as conditioned stimuli during conditioning when they were presented at meal onset as in Groups VS and AV than at meal offset as in Groups SV and SA. When data obtained during Test 2 was also statistically assessed, neither the main effects nor the interaction between the two factors were found to be significant.

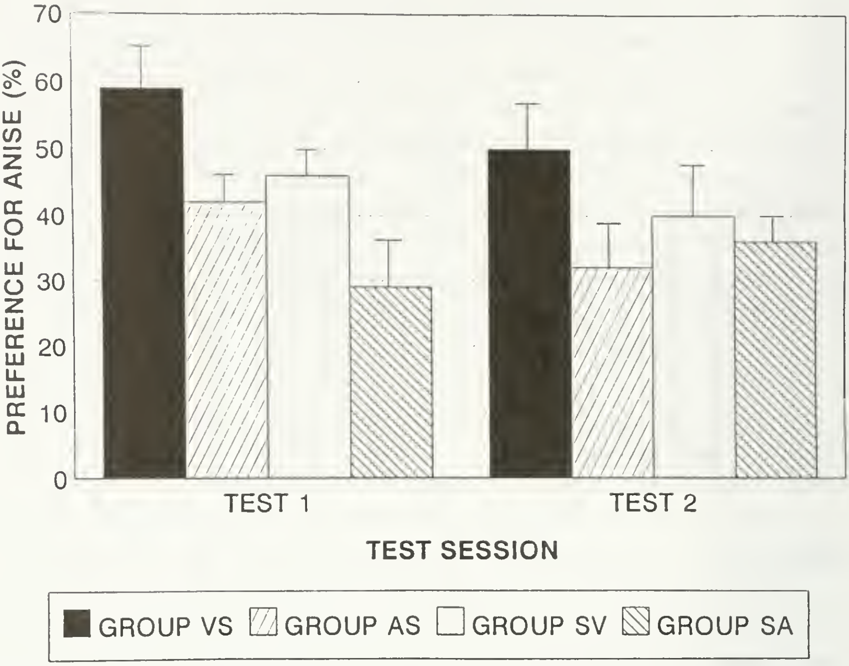

Figure 2. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 2 (n = 6). Bars represent standard errors.

DISCUSSION

Three main findings emerged from Experiment 2. Firstly, it confirmed the finding in Experiment 1 that adult rats are capable of learning about flavour-meal size associations. Even when flavour-exposure time was controlled, the rats learned to prefer a flavour previously associated with a small meal better than when the same flavour was paired with a large meal. Secondly, flavour-meal size effects were stronger when flavour cues were presented at meal onset than at meal offset. Thirdly, the conditioned effects extinguished very rapidly.

The finding that conditioned satiety effects could still emerge when flavour exposure time was controlled provides further evidence that satiety associated with the ingestion of large meals has no positive reinforcement properties. Similar conclusions have been arrived at by Van Vort and Smith (1983). The present finding also weakens the argument that conditioned flavour preferences observed in Experiment 1 were due to an acquired aversion towards prolonged flavour exposure which was associated with large meals during conditioning.

The second finding that flavour cues were presented at meal onset rather than at meal offset suggested that the cues may be more salient and less interfered with at the former than at the latter stage. The presentation of flavour cues following supplements was still effective in conditioning satiety but it reduced the effects considerably. It is possible that when supplements preceded flavour cues, they interfered with the learning of the discrimination between the two flavours and the appropriate satiety signals derived from the two meal sizes. The result of such interference was probably some weakening of the effects of the conditioning.

An alternative explanation would be that the rats became satiated after consuming the supplements and perceived the appropriate satiety signals immediately afterwards before the flavour cues were even presented and perceived. Therefore, it would appear from the present data that the strength of any flavour-meal size conditioning is stronger when the flavour cues precede supplements than vice versa. This finding appears to contradict the findings reported by Booth and Davis (1973) in rats and Booth et al. (1982) in humans, where the later supplements failed to condition meal size per se and conditioned only flavour preferences at most. The third finding that the conditioned satiety effects were weak and extinguished rapidly was surprising when compared with the extreme persistency of the other types of flavour conditioning based phenomena (see Capaldi, Myers, Campbell & Sheffer, 1983; Logue, 1979; Revusky, 1974; although see Simbayi, 1987). The effects had disappeared as early as the second test day after an 8-day conditioning cycle during which each flavour-meal size pairing was presented four times only. Perhaps, the effects could have been more persistent and more resistant or less susceptible to extinction with additional conditioning.

EXPERIMENT 3

Both previous experiments demonstrated flavour-meal size conditioning in adult rats. The aim of Experiment 3 was to test Hayward's (1983) claim that rat pups are apparently capable of more diverse learning than adult rats. As indicated earlier, Hayward showed that rat pups, but not adult rats, could acquire a conditioned taste preference for a flavour paired with a diet that provides more calories than another diet of equal caloric density. In particular in her Experiment 3, she obtained stronger conditioning of caloric effects with rat pups when a 4 cal/gm novel diet represented the major part of the animal's daily caloric intake for just 4 conditioning days. The pups were given unlimited access to 20 gm of the 4 cal/gm diet on one day, and three quarters of the previous day's consumption on alternate days. In order to control for differential hunger experienced on days when rats had inadequate food, the food supply of half of the animals was topped up with laboratory chow 8 h after presentation of the novel diet. Thus, the present experiment was meant to confirm such caloric effects by using a procedure almost identical to that employed by Hayward except for the following four minor changes which were made. Firstly, rats were first familiarised with the diets to reduce neophobia. Secondly, on small days the rats received only half of the amounts of food they received on large meal days to make the meal sizes more easily discriminable but, as indicated above, their training diets were also supplemented by laboratory chow pellets. Thirdly, the duration of testing was extended to cover a period of up to 24 h with intervals at 30 min and 4 h instead of only after 30-min and 3-h intervals as per Hayward (1983). This allowed monitoring of intake rates for a period longer than a meal which in turn made it possible for one to distinguish between aversions taking place early and throughout the meal as opposed to those taking place later. This in turn made it possible to distinguish between conditioned aversion and conditioned satiety respectively. Finally, in order to facilitate comparisons with other experiments reported in the present paper, conditioning lasted for 8 days instead of only 4 as in Hayward's study.

METHOD

Animals

Twenty four male naive Lister rat pups, 24 - 28 days old and weighing 46 - 91 gm at the beginning of the experiment, were used. The rat pups were weaned at the age of 21 days old and reared in colony cages (4 - 6 animals per cage). They had ad libitum access to dry laboratory chow pellets (Scientific Foods, Croydon, England) and tap water for 3 - 7 days before the experiment commenced. Following selection and assignment to groups, the weanling rats were housed individually in wire cages in a cage rack in an experimental room and had ad libitum access to water throughout the experiment.

Materials

The recipe for the novel diet used was identical to that utilised by Hayward as the high calorie food. It consisted of 50% dextrin (Sigma), 15% calcium carbonate (chalk, East Anglia Chemicals), 2.5% mineral oil (liquid paraffin, British Drug Houses, now M. W. Scientific, Ltd., Poole, Dorset, England), 7.5% ordinary (domestic) vegetable cooking oil and 25% lactic casein (Sigma). The diet provided approximately 4 cal/gm. Either vanilla or anise extract was added to the diets separately in the following proportions: for vanilla, 10 ml of flavour was added to 100 gm of the diet mixture; for anise, 0.50 ml of flavour was dissolved in 20 ml of water and also added to 100 gm of the diet mixture.

Procedure

The rats were assigned randomly to four groups (n = 6), namely, Groups R-A, R-V, Ad-A, and Ad-V, with R and Ad standing for restricted and ad libitum conditions respectively, as explained below. Groups R-A and R-V represented Groups A and V in Experiment 1 in the present study whereas Groups Ad-A and Ad-V represented Group 2 (the chow group) in Experiment 3 reported by Hayward (1983). On familiarisation days, all the weanling rats were exposed to the unflavoured novel 4 cal/gm diet. First, all groups received 40 gm overnight. Then, Groups R-A and R-V received only 5 gm while Groups Ad-A and Ad-V continued to receive unrestricted access to 40 gm for every 24 h beginning at 1200 hrs for the next 3 consecutive days.

On conditioning days, Groups R-A received anise flavour in 5 gm of the novel 4 cal/gm diet on some days and vanilla flavour in 1 gm of the same diet on other days. The flavour-meal size pairing was reversed for Group R-V. Group Ad-A received anise flavour in 20 gm of the novel 4 cal/gm diet on some days and vanilla flavour in 10 gm of the same diet on other days. Similarly, the flavour-meal size pairing was reversed for Group Ad-V. Therefore, for all rats, the two flavours were correlated with the same pattern of oral cues but differing caloric consequences (i.e., 20 vs. 4 calories for Groups R-A and R-V and 80 vs. 40 calories for Groups Ad-A and Ad-V, both respectively). Altogether, rats in Groups Ad-A and Ad-V experienced 4 days with sufficient food (i.e., large meals) and another 4 days with an inadequate amount of food (i.e., small meals). In order to avoid the problem of differential hunger on days of inadequate food, the food supply was supplemented by 5 pellets of dry laboratory chow (weighing approximately 10 gm and containing 40 calories) 5 h after the presentation of the training diet.

For both Groups R-A and R-V, laboratory chow was removed 2.5 h prior to the presentation of the novel diet and returned 5 h afterwards. The remaining rats in both Groups Ad-A and Ad-V received no additional food except only as specified above, that is, on small meal days. Flavours were also presented in semi-random order as in previous experiments.

All groups were given an extinction choice test between the anise and vanilla flavoured diets on Day 9. Two jars of the 4 cal/gm food were presented simultaneously, and consumption was recorded at the end of 30 min, 4 h and 24 h for all four groups. As in previous experiments, preferences for anise-flavoured food were calculated as percentages of total food intake.

Data analysis

The data were first assessed using a three way repeated measures ANOVA with the following factors: duration of exposure to the training diet (restricted vs. ad libitum), the large meal flavour (anise vs. vanilla) and cumulative test intervals (30 min vs. 4 h vs. 24 h). Follow up limited pair-wise comparisons between groups trained under similar conditions of exposure to the training diets at each test interval were also carried out using independent t tests.

RESULTS AND DISCUSSION

All animals completely consumed their food portions on all training days. Figure 3 outlines the results obtained during the three cumulative intervals of the extinction choice test held on Day 9. It shows that the two groups which had received vanilla flavour paired with the larger meal during training (i.e., Groups R-V and Ad-V) generally had higher preferences for anise than the other two groups (i.e., Groups R-A and Ad-A) which had received anise paired with the larger meal during training. This effect was particularly marked after 24 h than after both the 30 min and 4 h cumulative intervals of the extinction choice test.

The repeated measures ANOVA failed to reveal any significant main effects (all $ps > 0.05$). However, the interaction between all three factors was significant, $F(2,40) = 5.82$, $p < 0.01$. Additional between-group comparisons also revealed a highly significant difference between Groups Ad-A and Ad-V after 24 h of testing only, t (10, one tailed) = 5.07, $p < 0.001$ (see Figure 3). This shows that the rat pups were clearly capable of learning to associate a taste with the size of the meal under

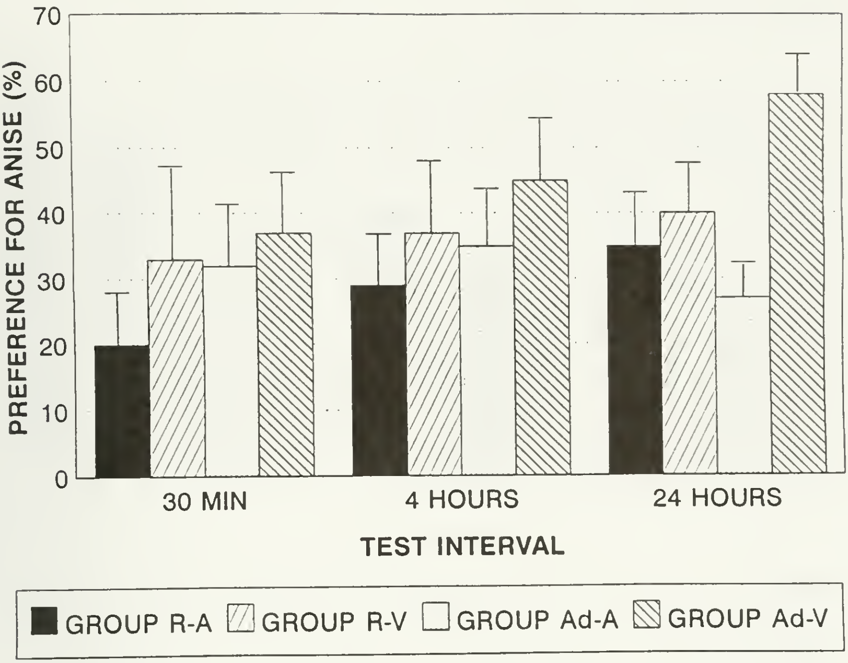

Figure 3. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 2 (n = 6). Bars represent standard errors.

the ad libitum feeding conditions, whereas they were not able to do so under restricted feeding conditions. Even more interesting was the fact that flavour preference shifts were most pronounced after 24 h of testing than earlier. This finding suggests that the flavour-meal size conditioning effects observed in these experiments might be attributed to satiety rather than aversions, because if the latter were involved, flavour preference shifts would have been observed throughout the test period. In particular, they would have commenced at the beginning of the test period rather than later, as occurred in the present experiment. The results are consistent with Booth's (1972) conditioned satiety ideas but they clearly contradict Hayward's (1983) findings. It is important to note here that the present experiment used a procedure similar to Hayward's except that the meal sizes and one flavour were different. However, her findings generally supported a conditioned appetite hypothesis whereby only young rats learned to prefer a taste which was previously associated with larger meal sizes or more calorific diets.

EXPERIMENT 4

As both the training and testing procedures employed in Experiment 3 did differ somewhat from those employed in both earlier experiments (i.e., Experiments 1 and 2), it is not only difficult but also rather unfair to make direct comparisons between their respective findings. Clearly, the best way to achieve such a goal would be to replicate Experiment 3 using naive adult rats. This was the aim of Experiment 4. According to Hayward (1983), an adult rat no longer attends to post-ingestional feedback since it is rarely hungry and therefore is not capable of learning conditioned taste preferences based on differing caloric outcome. Therefore, Experiment 4 investigated whether naive adult rats could be as responsive as naive young rats to flavours paired with differing caloric outcome when novel diets provided either only a small proportion or most of the rats' daily caloric needs.

METHOD

Animals

Twenty four naive male hooded Lister rats 81 - 126 days-old and weighing 245 - 420 gm at the start of the experiment were used.

Materials and Procedure

The materials and procedure were the same as for Experiment 3 except for the following three minor changes: both Groups R-A and R-V were allowed 25 gm of supplementary solid laboratory chow pellets at 17.00 hrs each day; during familiarisation, both Groups Ad-A and Ad-V received 30 gm of unflavoured and novel high calorie diet instead of 20 gm only as in Experiment 3; during training, both Groups Ad-A and Ad-V received 30 gm of the novel diet with no supplements on large meal days and 15 gm of the novel diet plus another 15 gm supplement of solid laboratory chow pellets on small meal days. All the changes were made to compensate for the larger size of animals used in the present experiment compared to those used in Experiment 3.

RESULTS AND DISCUSSION

All animals completely consumed their food portions on all training

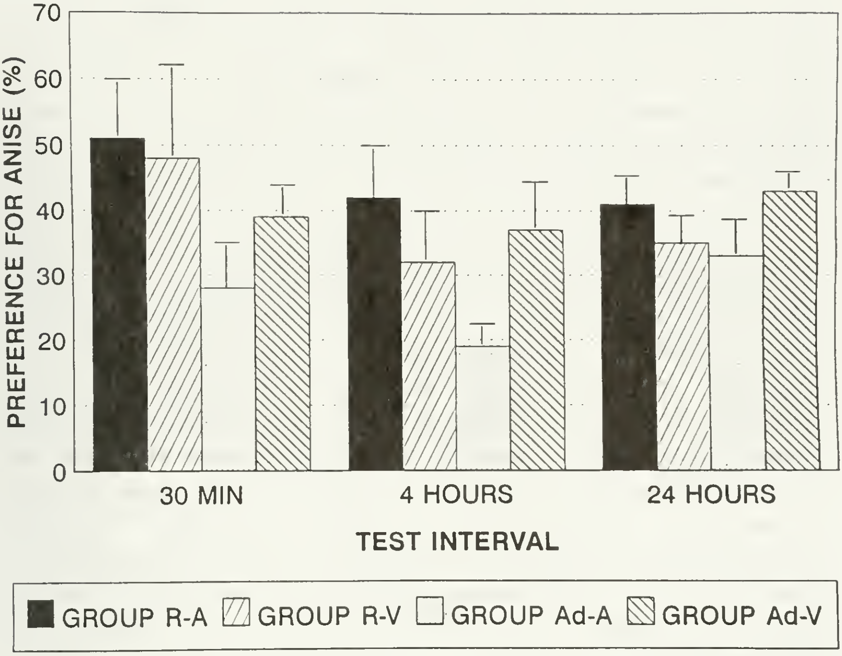

Figure 4. Mean preferences (%) for anise flavour during the two-jar extinction choice test in Experiment 3 (n = 6). Bars represent standard errors.

days. The results obtained during the three interval of the extinction choice test held on Day 9 are displayed in Figure 4. They show that Group Ad-V generally had higher preferences for anise flavour than Group Ad-A, whereas no such differences are evident between Groups R-A and R-V.

When the data were assessed using a three way repeated measures ANOVA as for Experiment 3, neither the main effects nor interactions were significant. However, additional between-group comparisons of anise preferences indicated that Group Ad-A had a significantly higher preference than Group Ad-V after the 4 h test interval only, t (10, one tailed) = 2.20, $p < 0.05$. Thus, these mature rats were also able to learn about flavour-meal size associations under ad libitum but not restricted feeding conditions, as did the weanling ones in Experiment 3. It is rather difficult to explain why adult rats appeared to learn conditioned satiety only when flavour-meal size pairings were presented on an ad libitum basis (30 gm vs. 15 gm) but not when access was restricted to much smaller amounts (5 gm vs. 1 gm). Perhaps, in the latter condition adult rats simply ignored post-ingestional feedback of the small snacks with a novel flavour and concentrated mostly on the bigger supplementary meals from which most of their daily caloric requirements were derived. Such a view is consistent with that of Bolles et al. (1981) and Hayward (1983) who used this fact to argue why adult rats should fail to learn to associate a flavour with a diet that provides more calories under such conditions. Nevertheless, the fact that, like weanling rats, adults can acquire flavour-meal size effects, appears to contradict these authors' findings. Another interesting aspect of the present results is that preference shifts in those groups which displayed them were most evident only after 4 h of testing. This differs from Experiment 3 where preference shifts were most notable in the groups concerned after 24 h of testing. Although the reasons for this disparity are unclear at present, one possibility is that older rats may experience the onset of satiety much sooner than younger ones. Nevertheless, this issue needs to be investigated further. Experiment 4, therefore, has shown that adult rats appear to learn to make flavour-meal size associations just as well as weanling rats especially when the diet provides for most of the animals daily caloric needs.

GENERAL DISCUSSION

The present research showed that both weanling and mature rats are capable of learning to associate a flavour with the size of a meal. In particular, these findings demonstrated flavour-meal size conditioning effects whereby an animal learns to prefer a flavour not associated with a larger meal. It is however important to note here that, as Capaldi and Myers (1982) and Davidson-Codjoe and Holman (1982) have pointed out, the preferences demonstrated in experiments of this sort are relative, rather than absolute. The data really do not distinguish a preference for the flavour consumed when rats received the small meal from an aversion for the flavour consumed when they received the large meal. Furthermore, as Capaldi et al. (1983) also pointed out, the word "preference" is usually intended as a neutral term accommodating either a learned aversion for the flavour associated with the large meal, learned liking for the flavour associated with the small meal, or both.

As the present results are consistent with Booth's (1972) and Booth and Davis' (1973) findings, a phenomenon very similar to Booth's conditioned satiety may be implicated. Conditioned satiety involves an increment in the size of the feeding bout on the dilute nutrient (or, small meal, few calories, etc.) more than on the more concentrated nutrient (or large meal, many calories, etc.) after several pairs of presentations. This takes place in order to compensate for calories depending on the nature of the concentrated diet. Booth suggested that such conditioning of satiety may be important in the control of food intake only under conditions which are put on the timing of meals, that is, under high food deprivation schedules. Perhaps, different mechanisms are involved under normal ad libitum feeding conditions. This might explain why stronger evidence of conditioned satiety learning was obtained under restricted feeding conditions in both Experiments 1 and 2 in the present study than was the case under ad libitum feeding conditions in both Experiments 3 and 4. Nevertheless, the present findings clearly demonstrated the existence of an acquired oral and/or olfactory sensory control of the satiation process just as Booth's conditioned satiety study did. The present findings are also in agreement with those of Le Magnen (1985) and Deutsch (1982).

The present findings suggest that oral qualities of a familiar food may enable a mammal to react in anticipation of that food's caloric value or the duration of its satiating effect. According to such a view, animals stop eating at an appropriate stage even though absorption has barely started or possibly has not even started at all as in the case of a rapid feeder such as a dog. However, our findings clearly contradict Hayward's (1983) findings which generally demonstrated conditioned appetite in weanling rats but not in adults. Apart from strain differences, it is unclear at present why our results contradict Hayward's.

One hypothesis which explains the present findings is that the flavour tracking may be due to an acquired difference in the development of feeding inhibition during meals. This is because there were no differences in basal acceptability since both meals consisted of the same diet, except for flavours which were added to them. This view is consistent with that of Booth (1972). The higher preference for the flavour which had been paired with a small meal demonstrated in the present study could be attributed to a difference in the speed of onset of the suppression of intake in the later stages of the meal. This might suggest that an acquired oral and/or olfactory factor contributed to the development of the satiety which ended the meal to which the flavour previously associated with the large meal was added. When faced with a choice between flavour cues previously associated with large and small meals during conditioning, a satiety signal switched off eating immediately after the animal had perceived that the flavour was previously correlated with a large meal which was too satiating. However, there was no such satiety signal forthcoming from flavour correlated with less satiating small meals and consequently, rats consumed significantly more food with a flavour which was previously associated with a small, less satiating meal. Hence, satiety had no positive reinforcing effects and might have been aversive. As was mentioned earlier, such a conclusion is consistent with that of Van Vort and Smith's (1983) who found that satiety had no positive reinforcing effects on flavour preferences at all whilst using sham feeding techniques and a similar flavour tracking procedure.

An alternative explanation is that when rats were exposed to flavours correlated with large meals, they developed slightly stronger aversions to them than when exposed to flavours correlated with small meals. However, since Experiments 2 - 4 controlled for the amount of flavour exposure, this hypothesis is highly improbable. Furthermore, the mere fact that all groups in Experiment 1 ate in excess of 60% vanilla-flavoured food during choice tests further weakens this argument.

The conditioning of flavour preferences based on meal size demonstrated in the present research does not in any way contradict Le Magnen's (1969) findings of conditioned appetite at all. Conditioned discriminative (also referred to as selective or differential) appetite induced during conditioning causes a rat to eat more of the reinforced, and hence beneficial food, and less of the non reinforced food in the final choice test. As Bolles et al. (1981) pointed out, conditioned satiety and conditioned appetite merely represent complementary aspects of intake regulation. Whereas the phenomenon proposed by Le Magnen (which Bolles et al. later failed to demonstrate) was basically concerned with food selection through learning about the caloric potential of different foods, the phenomenon demonstrated in the present study more likely operates after the selection of the diet offering optimum caloric consequences has been completed. Hence, the animal learns to eat less of that diet on a day-after-day basis under conditions in which constraints are put on the timing of meals.

According to Capaldi et al. (1987), shifts in preferences such as those demonstrated in the present study can be viewed within either a classical conditioning or an instrumental learning paradigm. In a classical conditioning framework, the flavours are the conditioned stimuli (CSs) and they are being associated with some unconditioned stimulus (US) that is produced by consumption of meals of different sizes made from the same diet. In an instrumental learning paradigm, the flavours are the discriminatory stimuli (SDs) signalling the reinforcement produced by the instrumental response of consuming meals of different sizes. The important question therefore concerns what is the US or reinforcer in either paradigm.

One of the best candidates for the US or reinforcer in the type of learning demonstrated in the present study is the post-ingestive consequences of ingesting meals such as calories. Supporting evidence for flavour-calorie learning in rats has been reported elsewhere (e.g., Capaldi et al., 1987; Deems et al., 1986; Hayward, 1983; Holman, 1975; Mehiel and Bolles, 1984; Sherman, Hickis, Rice, Rusiniak & Garcia, 1983). Another possible candidate for the US or reinforcer is some oral stimulus such as flavour (or taste). However, this is very unlikely because the different sized meals in each experiment in the present study consisted of exactly the same diet, which meant that the flavour of the food contained in the two meals was identical. Thus, the flavour-meal size conditioning effects demonstrated in the present research were most probably the result of flavour-calorie rather than flavour-flavour associations.

Finally, it must be noted here that although only four experiments are reported in the present paper, six additional experiments were also carried out which consistently failed to yield any significant effects. However, preferences were mainly in the direction which is predicted by the conditioned satiety hypothesis, that is, the small meal flavour was relatively more preferred. These findings also suggest that the flavour-meal size conditioning effect definitely occurs but we have not yet been able to identify all the conditions which enable consistently reliable effects.

In conclusion, both mature and weanling rats appear to be capable of learning about flavour-meal size associations. In particular, they acquired conditioned satiety, albeit very weakly, rather than conditioned appetite as previously demonstrated by both Bolles et al. (1981) and Hayward (1983) in their similar studies. These conditioned satiety effects, which are most probably due to flavour-calorie rather than flavour-flavour (or tastes) associations, are also distinctly elusive.

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