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Glossary

Behavioral satiety sequence A sequence of behavior that is characteristic of the transition from feeding through satiation to satiety. In rodents it is typically associated with a short period of activity followed by grooming and inactivity. A similar behavioral sequence may be observed in many other mammals, including humans.

Binge eating Rapid consumption of a large amount of food in a short period of time. In humans it is defined as a clinical disorder when associated with additional behavioral symptoms such as lack of control.

Conditioned place preference A tendency to move towards a location or contextual cues previously associated with reward through the process of Pavlovian conditioning.

Conditioned satiety A phenomenon in which sensory characteristics of a food that are consistently associated with the energy value of that food come to influence consumption during ad-libitum feeding.

Conditioned taste aversion A reduction in consumption of a food that was previously associated with illness. A wide variety of manipulations, including those that may have rewarding effects in other contexts, can lead to conditioned taste aversions.

Devaluation (of a food reward) Any process that leads to reduced motivation to consume a particular food can be said to result in devaluation of that food.

Diet-induced obesity An increase body weight, most of which can be attributed to adipose tissue, resulting from increased caloric intake. In the laboratory it may be induced by providing access to a palatable, calorically dense diet.

Hunger A motivational state in which feeding behavior is very likely, providing that an appropriate food is available.

Meal A short period of time during which feeding behavior occurs at high intensity. Meals are operationally defined using a meal criterion. The characteristics of a sequence of meals include measures of meal size, duration, inter-meal interval and feeding rate.

Meal criterion The operational definition(s) used to define a meal. The definition will usually comprise a threshold time between consumption of food items which, when exceeded, signal that the next occurrence of feeding will be part of the following meal. Optionally there may also be a requirement that a meal involves consumption of more than some minimum amount of food.

Pair feeding A behavioral paradigm that is used to determine whether the effects of a particular manipulation on body weight depend on changes in energy intake or energy expenditure.

Satiation The process that occurs during an extended period of feeding and leads to its cessation. Satiation normally develops in response to a combination of cognitive and pre-ingestive cues associated with feeding.

Satiety A state in which feeding behavior has become unlikely because of recent consumption of food. Satiety is usually maintained by a combination of post-ingestive and post-absorptive cues.

Sham feeding A surgical procedure, most usually performed on rats, in which consumed foods or liquids can be allowed to drain from the stomach through a fistula which is normally closed. This experimental paradigm can be used to eliminate post-ingestive cues associated with food intake and thus assess their role in influencing consumption. Most commonly sham feeding leads to very substantial increases in intake.

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Introduction

The amount of food eaten in a test situation is almost certainly the most widely used behavioral dependent measure in behavioral neuroscience. It is necessarily employed in the context of studies where the primary interest is the neural circuits or physiological mechanisms underlying food intake and energy balance. However, it is also often used as a "control" condition in studies of other motivational systems, especially in those that involve self-administration of drugs. Finally, food is the most frequently used positive reinforcer in studies of learning and memory. Even in such studies, the amounts that are consumed make it useful to have some appreciation of the properties of feeding behavior.

In rodents, and many other commonly used laboratory animals, feeding has a complex behavioral structure. Feeding behavior, at least when food is easily available, takes place several times a day in clearly defined meals. Small laboratory rodents, such as rats and mice, may take 10–20 such meals during a 24 h period. Feeding is also subject to strong circadian influences which can entrain other behavior as well as physiological responses, such as hormone secretion and neurotransmitter synthesis.

Feeding behavior is organized and modulated by a distributed neural network that includes structures such as the parabrachial nucleus and nucleus of the solitary tract within the brainstem, medial and lateral hypothalamic systems, as well as ventral and dorsal components of the striatum and a number of cortical areas. These different brain areas utilize a wide range of neurotransmitter systems and receive peripheral inputs that signal both short and long term correlates of energy reserves. The distinction between appetitive and consummatory components is often made for motivated behaviors such as feeding. Although it may be simplistic, it does reflect some important differences in the underlying neural and physiological systems. The distinction is followed here, with consummatory behavior referring to the behavioral processes that are engaged once an animal is in close proximity to, and consuming, food whereas appetitive behavior relates to those components which might be expressed as foraging in a natural environment.

In the laboratory, the study of appetitive behavior frequently involves behavioral responses that have been conditioned by food reward. For example, an animal may react to discrete or contextual cues that predict the presence of food (Pavlovian responses) or may be performing responses that have, in the past, led to food reward (instrumental responses). This dichotomy, although somewhat artificial, does reflect important differences in both underlying mechanisms and in the relevant behavioral paradigms.

Consummatory Behavior

“Simple” Measures of Food Intake

The simplest paradigm that can be used to investigate feeding is to record the mass of food eaten during a fixed period of time. However, even in this apparently simple case, a host of decisions must be taken that will influence the amount of food that is eaten and modify the relative effect of any experimental manipulation that is being studied. Is the animal to be deprived of food before the test? Will it be presented with its habitual food? If a different food is to be used, will it be novel, or one to which the animal has been exposed previously? Will it be more or less palatable, or have a different macronutrient content from the regular diet?

Frequently an animal will be deprived of food for a period of time before an intake test. The chosen time period is often 24 h or greater for rats. Following withdrawal of food for such a period, animals will eat rapidly for a protracted period. The factors that determine intake in this situation will be very different from those that operate when food is freely available. Intake rate will be at close to ceiling levels, which means that the measure may be quite insensitive, especially to manipulations that tend to increase feeding behavior. Excessive periods of food withdrawal should also be avoided on welfare grounds. The motivation to feed is increased by much shorter periods of food deprivation, and can also be enhanced in a number of other ways, most obviously by supplying food that is more attractive than the maintenance diet. When it is inappropriate to vary the dietary constituents, then adding water to a standard dry laboratory diet will often be sufficient to make a palatable mash. Rats presented with a short daily period of free access to mash made in this way will consume between a third and a half of their daily caloric intake within 30–40 min, even when the mash is presented during the light phase of the photoperiod when feeding is otherwise minimal.

When increases in feeding are expected it will be common practice to use non-deprived animals. Some manipulations, such as intra-accumbens administration of GABA agonists, lead to very robust increases in intake. Other manipulations, such as administration of noradrenaline into the paraventricular nucleus of the hypothalamus, generate increases in feeding which are harder to demonstrate. For example, simply presenting “satiated” rats with a weighed, fresh supply of their maintenance diet is often sufficient to stimulate intake of a gram or two over the following 30 min. This will be quite sufficient to mask a noradrenaline-induced increase in feeding. Simply presenting the rats with fresh pellets 30 or 60 min in advance of testing and then presenting the weighed portion of these pellets after drug administration will provide a much more sensitive measure of the drug effect.

Accurate measurement of food intake will require assessment of the degree of spillage which may well be treatment dependent. In addition laboratory rodents will often respond to the presence of a more novel food with defensive burying.

There has been considerable interest in the idea that changes in some neurotransmitter systems associated with feeding, especially serotonin, may modify diet selection. Studies investigating this idea typically allow animals a choice between pure macronutrients such as casein (protein), lard (fat) and either a simple or complex carbohydrate (eg, glucose or polyose, respectively). One
important issue, which should never be ignored, is the extent to which differences in texture, water content and taste, rather than macronutrient type, are responsible for any observed changes in intake.

Responses to cues previously associated with food may also enhance the amount that is consumed during a test session (see Section Pavlovian Influences), effects that were first explored systematically by Weingarten. If hungry rats are periodically presented with food after presentation of conditioned stimulus, such a tone, they soon learn to approach the receptacle into which the food is delivered. If, at a later test session, they are given access to food when sated then they eat more if the tone is sounded during the test session. Other studies have demonstrated that the effect is selective to the stimulus associated with food delivery and not to another familiar stimulus not associated with food delivery. It is also clear that the stimulus is not simply generating an approach response to food that then leads to consumption. If the animals have learned to expect food in a different place, although this has not previously been associated with presentation of the stimulus, they will nevertheless approach and eat food. This suggests that the conditioned stimulus has a broad effect that increases the motivation to feed. It is important to be aware that effects of this kind may occur inadvertently during repeated simple tests of food intake. Cues associated with the approach of an experimenter and the opening of a cage may easily lead to such changes.

Conditioned cues can also be associated with reductions in feeding behavior. If a punishing stimulus (typically sickness) is associated with ingestion of food, especially if it is novel then a conditioned taste aversion is likely to result. Conditioning occurs most readily, often following a single CS-US pairing, when sickness follows consumption, even if the interval between the two is several hours. In contrast, brief punishing stimuli, such as electric shock, may lead to short term decreases in feeding or drinking, and provide the basis for a variety of conditioned suppression techniques.

Long Term Feeding Studies

Chronic increases in food intake may be increased by modifying the diet. In rodents, and many other mammals, provision of a diet relatively rich in fat and simple, sweet tasting, sugars will increase total caloric intake, leading to diet-induced obesity. This may be accomplished by either using a pre-prepared commercial diet in place of regular chow, or by providing additional food types in a “cafeteria” style diet (eg, a separate container of lard and a bottle of sucrose solution in addition to regular chow and water). When a pre-prepared diet is used then further increase in caloric intake, and body weight, can be achieved by also giving access to a high calorie fluid such as Ensure. It is often argued that diet-induced obesity, especially when it also involves choice between dietary constituents, offers a better model of common human obesity than genetically manipulated animals such as the ob/ob mouse.

When access to such foods is only provided occasionally, perhaps every two or 3 days for an hour or two, then a different pattern of intake will emerge. Animal will eat very rapidly during the period of limited access, but will compensate for the additional energy intake by reducing intake of their standard diet on the following day. As a result there is no long term change in body weight. Such short periods of rapid intake have a provided a putative rodent model of human binge eating disorder.

In some feeding studies, a critical question will be the extent to which changes in body weight over a period of some days have resulted from changes in energy intake and energy output. Energy intake should be approximated by the energy content of the food eaten during the relevant period, although there may be changes in the efficiency of digestion and absorption, especially when intake is being restricted in some way. Energy output may be estimated directly using indirect calorimetry or other techniques. However an alternative way of tackling this question is to use a pair feeding paradigm.

A typical experiment of this type might use three groups: the first receives the manipulation in question, which might be a drug treatment, such an antipsychotic compound with weight gain as an established side effect, a second group receives the same manipulation but has its food intake restricted to that of a third control group which receives no active treatment. Such an experiment can have a number of potential outcomes. One possibility is that the degree of weight increase in the two experimental groups is very similar and higher than that seen in the control group. This would indicate that the mechanism underlying weight increase is one that depends on a reduction in energy output. It might reflect a lowering of metabolic rate, but it is also possible that reductions in voluntary activity, perhaps induced by a sedative or muscle relaxant effect of a drug, might be responsible for such an outcome. Direct behavioral observations will help to separate these options. An alternative outcome might be that the weight of the pair fed and control groups is similar, and lower than that of the experimental group given unrestricted access to food. This would strongly suggest that increased food intake is responsible for the increase in body weight produced by this manipulation.

The same kind of design can be applied to a treatment that is associated with a reduction in body weight. In such cases there will be a single drug treatment group and two control groups, one of which receives ad-libitum access to food and the other of which has its food intake matched to that of the drug treated group. Although the paradigm may seem ideal for separating the effects of energy intake and output, the results from a particular experiment may be ambiguous in several ways. If the experiment is underpowered and the data of the pair fed group is intermediate between the treatment and control groups, then the conclusion drawn will depend on which of the (non-significant) paired comparisons is judged to be more important. A frequent outcome, especially when the experiment is conducted over a longer time period, is that there may be differences between the pair fed and unrestricted group which become less evident with time. Several points are relevant in interpreting such an outcome. First, energy intake cumulated over the study period may remain substantially different and sufficient to explain the observed weight differences. Second, there may be gradually emerging adaptive changes to perceived energy deficits that occur at either a behavioral or physiological level.
These may be exacerbated by the very different daily intake patterns that emerge in the restricted and control groups as the experiment progresses.

**Detailed Measures of Consummatory Behavior**

The consummatory phase of eating may be studied at several levels. Observations at the macro-level often involve recording some variant of the behavioral satiety sequence. This technique, which originated with Richter in the 1930s, and was refined by Bolles and Antin in the 1960s before the development of the present form of analysis, is especially useful for distinguishing the development of normal satiety from reductions of eating as a result of illness, pain or stress induced by an experimental manipulation. For rodents, the method utilizes relatively broad behavioral categories, such as feed, groom, inactive and rear. These may be recorded continuously, typically from prior recording of the experimental sessions. An alternative method, which provides very similar data, is to utilize live sequential one-zero recording from a complete experimental cohort of subjects. Although the sequence will be variable from one individual to another, common features include an initial period of intense eating followed by increased activity (both locomotion around the cage and rearing), grooming and, provided the observation period is long enough, a period of inactivity. One conventional, though arbitrary, indication of the onset of satiety is the point at which the proportion of time devoted to eating is less than that spent in inactive behavior.

A second, macro-level technique is the recording of free running meal patterns. Again this may be achieved in several ways. One method, deriving from Kissileff’s development of a pellet delivering eatometer, allows a rodent to take standard, grain based pellets (rat: 45 mg; mouse: 10 or 20 mg). Intake of pellets and water should be monitored with good temporal resolution (at least to a fraction of a second). Such a system will allow accurate assessment of instantaneous feeding rate as well as the microstructure of feeding and drinking bouts. However it will be less easy to manipulate dietary constituents, and if this is required then it may be better to use a recording system that depends on repeated automatic weighing (usually via built in strain gauges) of food and water containers. Temporal resolution will be significantly worse with such systems and estimation of instantaneous feeding rate is not possible.

Once a record of intake has been obtained, it will require further analysis to extract meal patterns. An initial choice of a bout or meal criterion is required to define individual meals (Fig. 1). The meals can then be characterized in terms of their size, duration, intra-meal feeding rate and inter-meal interval. Although time based meal criterions are most commonly used, some experimenters also impose a minimum size for a meal. A combination of meal pattern analysis in free feeding animals with the recording of the behavioral satiety sequence has confirmed that the sequence is not an artefact of regularly presenting animals with a palatable, easily eaten food. Such studies have also suggested that the most appropriate criterion for meal termination should include consideration of both feeding and drinking responses.

Microstructural analysis of licking patterns is frequently used when a liquid food has been provided. These techniques, especially as developed by Davis, Smith and colleagues, are conceptually similar to meal pattern analysis, although they operate at a finer level of analysis. Changes in palatability and caloric load produce distinct patterns of change in the resulting licking bout analysis.

Another technique which holds out the promise of distinguishing between hedonic and reward-related effects of a manipulation is the taste reactivity task. This paradigm, developed by Grill and Berridge, is best known for its supportive role in the incentive sensitization theory of addiction. Animals, typically rats, are prepared with an intra-oral catheter through which more or less palatable solutions can be introduced in measured volumes. The animal’s responses are scored and can be divided into negative and positive hedonic components. This relatively pure measure of hedonic responses to food-related stimuli can then be compared with the reward related aspects that are measured using more conventional instrumental tasks (Section Instrumental Tasks).

While such observational methods can give additional information that may be difficult to collect using automated methods, it is important to ensure that inadvertent observer bias is avoided. As in many other domains, randomization and blinding during data collection and analysis are important components of good experimental design.

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**Figure 1** Applying meal criterions to a series of individual feeding responses (short vertical lines). In this case, the process would generate three meals of size 7, 6 and 4. The single feeding response between meals 2 and 3 is excluded as not reaching a meal size criterion.
Appetitive Behavior

Pavlovian Influences

A variety of Pavlovian procedures may be used to study appetitive components of feeding behavior. They share the common feature that, during training, food is presented in combination with a conditioned stimulus without regard to the animal’s current behavior. When the conditioned stimulus is discrete and signals the imminent availability of a small reward, animals will usually display an orienting reflex to the stimulus before moving towards the likely source of food (the “magazine” in an operant conditioning chamber). As training proceeds, the orienting reflex will often become less pronounced, especially when the relationship between stimulus and food is entirely predictable. An animal may also direct behavioral responses towards the conditioned stimulus. These are usually referred to as autoshaped responses and their form is strongly related to the relevant consummatory behavior. Under some circumstances these responses may be easily measured, as when the stimulus is a lever inserted briefly into the cage and is pressed, or a light is illuminated in an aperture where the animal may make a nose poke. If there is a short interval between presentation of the stimulus and the availability of food in the magazine, strong individual differences in behavior may arise. Some animals may predominantly direct responses before the reward is delivered toward the lever or light, whereas others may immediately direct their investigatory responses towards the magazine. Animals showing the first type of behavior are referred to as sign trackers, as opposed to the goal trackers of the second group. However, at least in some studies, there will also be individuals showing a mixture of the two types of responding, suggesting that a binary classification of individuals may be inappropriate.

Contextual stimuli may also be used to condition approach responses. One classic version is the conditioned place task. It uses a two-compartment chamber, each with distinct contextual cues. During training animals are confined to one of the two chambers (Fig. 2). Food is made available in one and not in the other. During test sessions animals are free to enter either compartment. They are likely to spend a greater proportion of time in the food associated chamber. This learned preference is susceptible to both reversible revaluation (eg, the preference increases with an increasing level of food deprivation) and to more permanent devaluation (eg, the preference decreases after the induction of a conditioned taste aversion to the particular food reward associated with the reinforced chamber). Testing is always carried out in the absence of food. One consequence is that the response is susceptible to extinction both within and across test trials. Place preference tasks are susceptible to differences in initial preferences for the different compartments and the decision as to whether to fully randomize the assignment of animals to possible training conditions, or to train against any initial preference is an important one.

Instrumental Tasks

Food is a potent reinforcer and many different instrumental responses have been used to estimate components of feeding motivation. In most of these paradigms food is provided, so they do not provide pure measures of appetitive responding during the test session.

One example, historically important, and still current technique, is running speed to a food reward at the end of a straight alley. Running speeds are sensitive to the value of the reward that is provided. For example, providing a larger than expected food reward will produce a clear increase in running speed on the next few trials, while a smaller than expected reward will have the opposite effect (the Crespi effect, originally described in 1942). The decrease in running speed over a series of trials can provide a sensitive index of satiation. For example, a drug treatment that decreases satiation will have little effect on running speed in early trials but enhance it, relative to a control condition, later in the session.

Lever press, or nose poke, operant responses also provide useful measures of feeding motivation. The great majority of studies use animals that are mildly food deprived and tested in short sessions. Ratio or interval schedules may be used. Fixed or variable

Figure 2  A typical two chamber conditioned place preference chamber. During the training the doors are left in place. They are removed during testing and the animal can then move from one chamber to the other through the central corridor. The food container is also removed during testing. Preference is usually measured as a ratio measure derived from time spent in the two main chambers of the apparatus.
ratio schedules will tend to produce high response rates that are sensitive to feeding motivation whereas interval schedules are less useful in this regard. However response rate on a ratio schedule will also be sensitive to other factors such as motor impairment or sedation induced by a particular experimental manipulation. An alternative approach is one in which the number of responses required for reward gradually escalates during the session. Animals on such progressive ratio schedules will eventually stop responding. The ratio at which they stop is termed the breakpoint, and will be less sensitive to extraneous effects of an experimental manipulation than response rate. The operant requirement may escalate through either an arithmetic or a geometric series. An arithmetic series will escalate more slowly later in the test session. As a result food consumption prior to the breakpoint is likely to be higher than with a geometric sequence, and hence the potentially confounding effects of satiation may be greater.

Any of the schedules described so far will result in food consumption and hence initiate satiation. A purer measure of appetitive behavior may be obtained by using a modified second order schedule. Responding can be sustained for an extended period, especially at the beginning of a test session, if a conditioned stimulus is associated with food delivery and lever pressing is initially only rewarded with presentation of this stimulus. Schedules of this kind can be used with rats and mice and can easily provide a measure of responses rate, over an initial non food-reinforced period of 5 min in a 30 min test, which remains stable from one test session to another. This allows comparison of the effects of a several related manipulations (eg, different drug doses) using a within subject design.

Several other paradigms, including conditioned reinforcement and Pavlovian to instrumental transfer, deserve consideration if the research question concerns the extent to which conditioned stimuli may energize a feeding response. For example, in Pavlovian to instrumental transfer animals undergo a two component training process in which, separately, they acquire a Pavlovian association between a stimulus and food delivery and also learn to perform an instrumental response for that food. In the test sessions, which may be carried out in extinction or with food reward provided, instrumental response rates are measured in alternating periods during which the conditioned stimulus either is, or is not, present. Pavlovian to instrumental transfer (PIT) is measured as the extent to which responding is facilitated in the presence of the conditioned stimulus.

PIT may be of two types, usually known as “specific” and “general”. They can be distinguished operationally by training animals on three separate CS-reward relationships. In the subsequent instrumental training sessions two responses are associated with two of the rewards used in the earlier Pavlovian phase of the experiment. If selective revaluation of one or other of these rewards leads to a selective change in instrumental responding (normally tested in extinction) then selective PIT is demonstrated. If revaluation of the third reward leads to a change in the level of both instrumental responses then general PIT is demonstrated. The general form of PIT is thought to arise through non-specific motivational effects on instrumental responding. By contrast specific PIT must involve retrieval of the specific CS-reward and reward-response relationships in order that only responding of the relevant type is affected.

**Conclusion: Choosing an Appropriate Model**

A number of factors will determine the appropriate animal models of feeding for a particular study. Only rarely will the results from a single test paradigm be sufficient to determine the behavioral mechanism of action of a manipulation that affects food intake. The better approach is to choose a test battery which reflects the neural and behavioral mechanisms of interest. Detailed behavioral analysis is likely to be rewarding in many circumstances. In addition to maximizing scientific utility, it will be important to consider how animal welfare can be enhanced by considering the principles of refinement and reduction. For example, long periods of food deprivation are ethically inappropriate, may also be scientifically undesirable, and should be avoided. Within subject designs will frequently be more powerful than a between subject approach and will also minimize the number of animals that are required for a particular study.

Models will also frequently be chosen for their translational utility in relation to a particular human clinical condition. Individual models can be assessed in relation to their predictive, face and construct validity. However reliance on a single model may be unwise and it is preferable to use several independent models that will help to triangulate the clinical condition of interest.

**Further Reading**


