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## Behavioural factors in the regulation of food intake

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### *Introduction*

Mammalian food intake is a discontinuous process, in that feeding runs alternate with non-feeding intervals. These lifelong changes in overt behaviour indicate an underlying organization in which different needs alternately obtain priority. The way in which this channelling of needs might be realized can be investigated by analysing in detail how overt behaviour changes in time. It is of much importance to know how far food intake behaviour is influenced by the interaction processes involved.

Under *ad lib.* conditions the frequency distribution of the duration of non-feeding intervals suggests, at least in some species, the existence of meals (Le Magnen & Tallon, 1966; Thomas & Mayer, 1968; Wiepkema, 1968). In these instances food intake depends on factors that determine frequency and size of meals. Probably these meal criteria are not caused by an identical set of causal factors. For instance, food deprivation may enlarge meal size without influencing the number of daily meals (Wiepkema, 1968), whereas caloric dilution of the diet may have just the reverse effect (Le Magnen, 1969). The factors that determine exactly meal frequency will not be discussed here. They may be very difficult to unravel, since circadian processes also contribute to the distribution of meals during a 24 h period (Le Magnen & Devos, 1970).

### *Meal size*

Meal size depends on the caloric state of the animal and on sensory qualities (taste, volume, etc.) of the food (Le Magnen, 1969; Thomas & Mayer, 1968). In addition, both groups of workers found a positive relationship between meal size and duration of the meal-to-meal interval immediately following. This indicates that the start of a meal depends on when calories stemming from the foregoing meal have been metabolized up to a critical level. No relationship was found between meal size and duration of the immediately preceding meal-to-meal interval. This suggests that meal size, being very variable, is independent of the caloric deficit incurred in its pre-meal period under normal *ad lib.* conditions. Meal size, or the end of a meal may be determined by quite other causes; one group of them, largely ignored in the literature, may be taken together as 'interaction processes between feeding and non-feeding behaviour'. The significance of such interactions will be

discussed in some detail with regard to intra-meal feeding patterns in mice.

Records of food intake of mice living under *ad lib.* conditions suggested that meals were separated by non-feeding intervals of more than 5 min (Wiepkema, 1968). The same data show an interesting difference between day and night meals

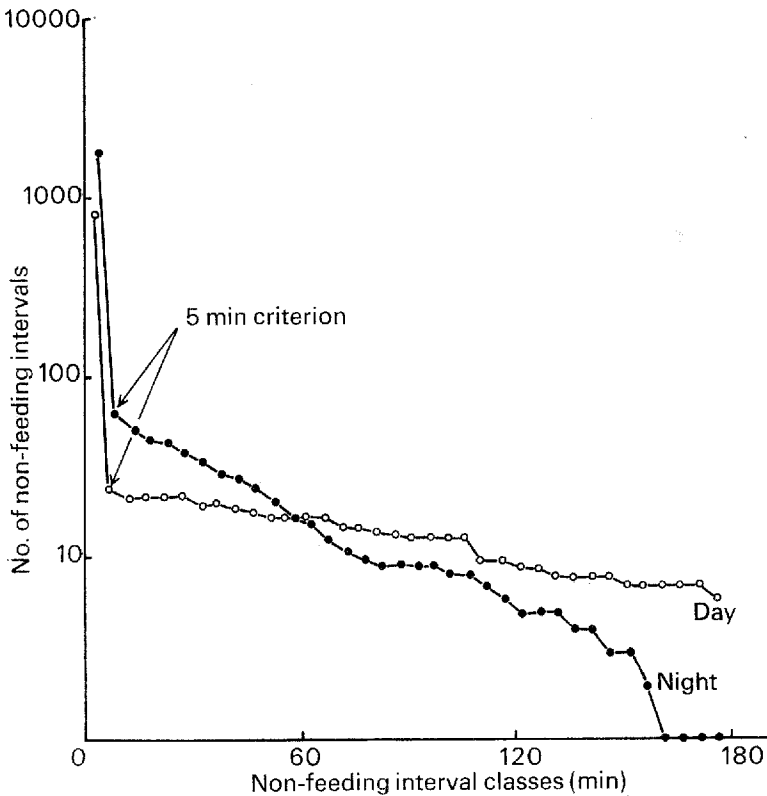


Fig. 1. Frequency distribution in mice of non-feeding interval classes occurring between feeding bouts and plotted in a cumulative way. Breadth of each class 5 min. Note the high frequency of the shortest (up to 5 min) non-feeding interval class.

(Fig. 1). Day meals are separated by long intervals (often more than 1 h), whereas night meals may succeed each other very rapidly (intervals often less than 1 h). Although the size of both meal types does not differ very much – if anything, night meals are larger than day meals – the after-effect of both is quite different (Le Magnen & Devos, 1970; Steffens, 1969). Moreover, during night meals, spells of non-feeding behaviour are longer than during day meals. For these and other reasons it is proper to analyse both meal types separately. I shall mainly focus on behaviour patterns during night meals and their effect on meal size.

Before going into the data I must outline briefly a model that may be helpful in this analysis of meal size, see Fig. 2 (cf. De Ruiter & Wiepkema, 1969). Each meal starts with a feeding bout separated from the foregoing one by a non-feeding interval longer than some criterion. In this model,  $L$  is a level of net satiety ( $S$ )

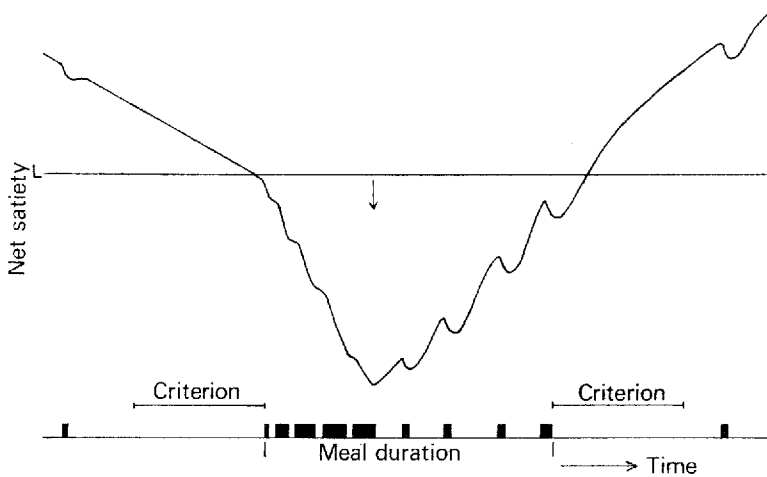


Fig. 2. Time-course of net satiety and resultant meal duration under *ad lib.* conditions. ■, feeding bout. L, level of net satiety at which feeding and non-feeding have the same probability of occurring. A meal consists of a sequence of feeding bouts and non-feeding intervals. During every feeding bout the decrease of net satiety is steepened by the evoked positive feedbacks which also operate during a short period immediately following each feeding bout. If non-feeding intervals are short, as in the first half of the meal, these positive feedbacks may enlarge successive feeding bouts and steepen the decrease of net satiety. ↓, time at which net satiety increasing signals become dominant. The rate of increase of net satiety in the second half of the meal is an arbitrary one. Feeding bouts that are separated by non-feeding intervals longer than criterion do not belong to the meal.

at which the probability of feeding ( $P_f$ ) and the probability of non-feeding ( $P_n$ ) behaviour are the same;

$$P_f = P_n = 0.5.$$

If net satiety becomes smaller than L,  $P_f$  becomes smaller than  $P_n$  and a meal may start.

Due to a sluggish start of satiety-inducing signals (see also, however, Steffens, 1969), S may decrease for some time during the opening phase of a meal. Recently, evidence has accumulated that positive feedbacks, originating from feeding itself, increase feeding tendency and steepen the decrease of S during the opening phase of a meal (De Ruiter & Wiepkema, 1969; Le Magnen, 1969; McFarland, 1970; McFarland & McFarland, 1968; Wiepkema, 1971). After some time (Fig. 2, arrow) satiety-inducing signals become dominant and S will increase. The last feeding bout of a meal is followed by a non-feeding interval longer than the same criterion used before.

Food deprivation, which increases feeding tendency as measured by amount of food ingested per time unit of a meal (including feeding and non-feeding periods) does so by increasing the length of feeding bouts and decreasing the duration of non-feeding intervals (Wiepkema, 1971). Therefore, both durations are indicators of the strength of feeding tendency when the strength of non-feeding behaviour is kept constant.

It was found that feeding-bout length increases during the opening phase of a meal,

whereas the origin of the processes enhancing food intake appeared to be oral (Wiepkema, 1971). However, in this same opening phase, there is no concomitant decrease of the duration of non-feeding intervals. On the contrary, non-feeding behaviour occurs in short bouts at first followed by some increase in bout length later on in the meal. To analyse this unexpected phenomenon, feeding patterns were recorded in two situations that activate non-feeding behaviour differentially.

#### *Interaction processes*

Feeding patterns of twenty-five male mice were recorded either in the home cage or in a strange cage after 0 h, 24 h or 48 h of food deprivation. In all instances feeding behaviour was recorded during the first 5 min of the first night meal. The mean lengths of the first six successive feeding bouts and non-feeding intervals are given in Figs. 3 and 4 respectively.

In the home cage, feeding tendency, as measured by feeding-bout length, increases strikingly during the opening phase of the meal whereas, in the strange environment, feeding tendency only increases in the most deprived animals. Since in the home cage the increase of feeding tendency is the same for all three types of

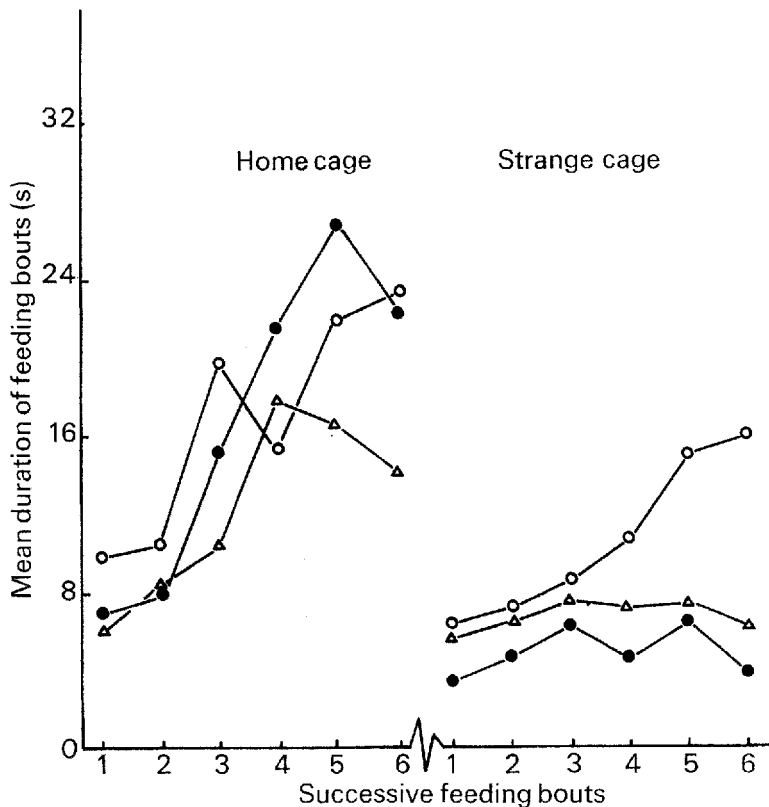


Fig. 3. Mean duration of the first successive feeding bouts of a meal in twenty-five male mice in home and strange cages. Feeding behaviour was recorded during the first 5 min of the first night meal after a period of ●—● 0 h; △—△ 24 h; ○—○ 48 h of food deprivation.

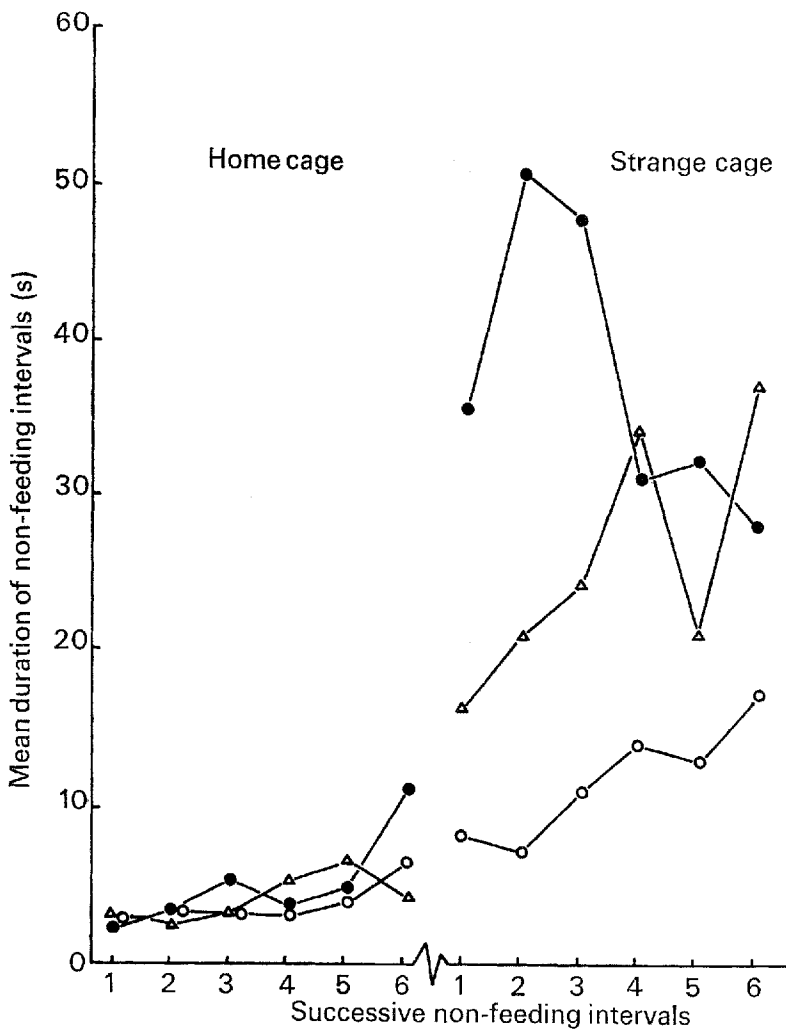


Fig. 4. Mean duration of the first six successive non-feeding intervals of a meal in twenty-five male mice in home and strange cages. Feeding behaviour was recorded during the first 5 min of the first night meal after a period of ●—● 0 h; △—△ 24 h; ○—○ 48 h of food deprivation.

food deprivation, it is concluded that in the strange environment also the increase in feeding tendency, as shown after 48 h of food deprivation, is not a direct result of the caloric deficit involved.

Non-feeding behaviour also differs strikingly in both situations. In the home cage, feeding is interrupted for only short periods just allowing the animal to perform some scratching, digging, climbing, etc. The mean length of these non-feeding intervals is about 5 s, which contrasts sharply with the duration of the same intervals in the strange environment. In this latter situation the animal performs intensive exploratory behaviour and may become very aggressive. This non-feeding behaviour is strongly reduced when feeding tendency is high as is the case after 48 h of food deprivation.

These results suggest that the increase of feeding tendency depends in some way on the strength of non-feeding behaviour. It may be that non-feeding behaviour when activated produces non-feeding intervals longer than the decay-time of the positive after-effects of feeding. This is supported by the fact that, after 48 h of food deprivation in the strange environment, feeding tendency does increase slightly, but in this instance non-feeding intervals are only somewhat longer than in the home cage (10–20 s). From these results it is concluded that positive feedbacks may be effective for up to about 15 s.

As stated before, these positive feedbacks set up by feeding increase feeding tendency and guarantee a substantial meal size (Fig. 2). However, when this increasing effect of feeding tendency is cancelled out by long non-feeding intervals, the initial slope of  $S$  during a meal will be smaller than in Fig. 2 and, assuming that satiety-inducing signals become dominant at the same time as in Fig. 2,  $S$  will decrease not as far as in Fig. 2 and may cross  $L$  relatively soon after the start of the meal (Fig. 5). Pilot observations on complete meals under conditions that activate non-feeding behaviour differentially support this expectation.

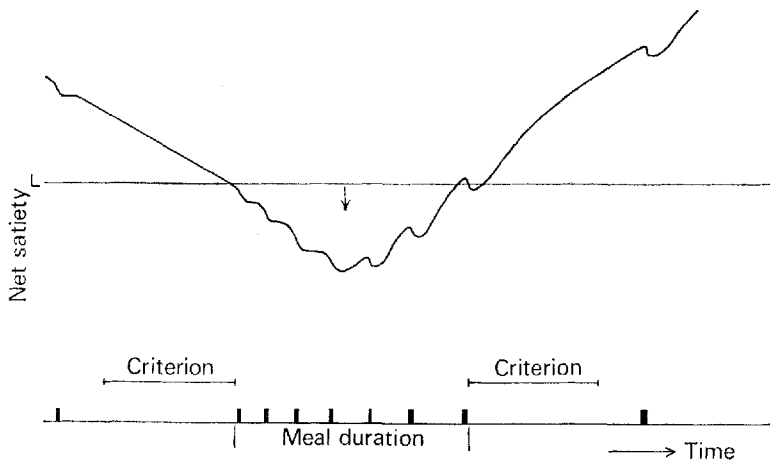


Fig. 5. Time-course of net satiety and resultant meal duration under *ad lib.* conditions. For explanation see Fig. 2. In this figure non-feeding intervals are long and cancel out the positive feedbacks stemming from each feeding bout. Therefore, decrease of net satiety will not steepen in the first half of the meal. If net-satiety increasing signals become dominant at the same time as in Fig. 2, meal duration will be shortened very much as compared to the meal of Fig. 2. Rate of increase of net satiety in second half of the meal is an arbitrary one.

As can be seen in Fig. 3, the strength of non-feeding behaviour reduces feeding-bout length as is suggested by the shorter duration of the very first feeding bout in the strange cage as compared to the same bout in the home cage. In both these instances positive feedbacks presumably have the same influence.

These results suggest an alternative explanation for the absence of any increase in feeding-bout length as observed in the strange cage after 0 h and 24 h of food deprivation (Fig. 3). It may be that a strong activation of non-feeding behaviour reduces the slope of  $S$  in such a way that during a long period  $S$  more or less equals

L. In that instance feeding-bout length will not increase, whereas the meal in itself disappears; the animal becomes a nibbler.

What has to be examined in much more detail is how feeding and non-feeding behaviour alternate during long periods and whether the characteristics of these behavioural changes support the idea either of meal-eating or of nibbling. It is quite possible that the answer will depend on the circumstances under which the experiments have been done.

In this paper, the meal-eating pattern has been assumed, since this probably holds good for at least the home cage situation. In these instances it is of much importance to know how feeding tendency (or *S*) changes during the end phase of the meal. If *S* increases gradually towards the end of a meal, it will equal *L* over a relatively long period and, from this, it has to be expected that the end of the meal will vary considerably. This may explain the high variability observed in meal size and the lack of correlation between pre-meal interval and meal size (Le Magnen & Devos, 1970; Thomas & Mayer, 1968).

On the other hand, the occurrence of positive feedbacks in the opening phase of the meal shortens the period during which *S* may equal *L*, which may result in a relatively well-defined start for a meal. This may be one of the reasons why a positive correlation between meal size and post-meal interval could be found by Le Magnen & Devos (1970) and Thomas & Mayer (1968).

I have to come back now to the question why non-feeding intervals are so short during the opening phase of a meal as compared with their average length as calculated from later parts of meals (Wiepkema, 1971).

The results presented in this paper show that the length of non-feeding intervals is determined by external signals that activate non-feeding behaviour and by the strength of food deprivation (Fig. 4). A tentative explanation is that during the opening phase of the meal there is a 'minimum duration' of non-feeding behaviour. By this is meant that if for some reason non-feeding behaviour does occur, it always needs at least 3–4 s. In the course of the meal, non-feeding behaviour may increase in duration thanks to changes in net satiety (*S*). To what degree the duration of non-feeding intervals may increase depends on total caloric deficits determined by foregoing periods of 24–48 h of food deprivation. Positive feedbacks stemming from feeding primarily influence feeding tendency itself and do not affect overt non-feeding behaviour or only a little.

Of course, these explanations have to be tested in many more ways than has been done hitherto.

Finally, a remark on the difference between day and night meals. Since night meals differ from day meals in having longer intervals of non-feeding behaviour one could expect that these meals are shorter than day meals. However, this is not so, since both types of meals have about the same duration. This may be explained by the fact that, during the day, feeding tendency is much lower than during the night (Le Magnen & Devos, 1970). How this difference is brought about in the details of meal patterns has to be examined in future research.

Obviously, meal size and pattern are determined by a very complicated inter-

action between behaviour systems, which are related to different needs of the animals. A very much better knowledge of these interaction processes is needed in order to understand what causal factors determine whether or not an animal will eat at a certain moment. Detailed analyses of behaviour are very helpful towards the solution of this problem.

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