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Rats learn to eat more to avoid hunger

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Short title: Rats eat instrumentally

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Abstract

Several recent experiments have provided evidence that the ingestion of a distinctive food by rats can be a learnt instrumental act as well as an associatively conditioned reaction. In the previous work, maintenance food was withheld for shorter and longer durations on different days following access to the training food. Extra eating before the longer fast was interpreted as avoidance of hunger. This interpretation was based on the evidence showing that extra eating as a result of classical conditioning comes from pairing food stimuli with the presence of little or no hunger because of repletion with energy nutrients. This theory that the extra eating arose from a response-depletion contingency was tested in the present experiment by training rats on only a long fast or only a short fast. Greater increase in intake was seen before the longer fast. The results also replicated previously seen cycles of increase, decrease and renewed increase in putative deficit-avoidant eating over about three trials, indicating that the extra eating reduces the response-reinforcing hunger and that the consequent part-extinction restores reinforcement. The shape of the learning curve was consistent with these cycles occurring from the start of training, further supporting the view that the increase in food intake before a long delay in re-feeding is hunger-reinforced instrumental behaviour.

Acknowledgements

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Introduction

Incentive motivational accounts of ingestion-related animal behaviour processes have become increasingly popular (Dickinson & Dawson, 1989; Dickinson & Balleine, 1994; Berridge, 1996, 2004). Yet there is remarkably little evidence distinguishing instrumental increases in the amounts that animals consume from the classical conditioning of sensory control of movements resulting in the consumption of a solid or liquid. It is indeed difficult to distinguish the operant from the respondent in facilitation of the motor pattern of ingestion because of the strength of sensory preference conditioning.

Nutritionally conditioned sensory characteristics have long been known to increase the amount of a food or drink consumed by a rat (Booth, Lovett & McSherry, 1972; Booth & Simson, 1971; Simson & Booth, 1973a). This conditioned preference rapidly reaches near-maximum extent while the CS-US contingency is maintained. The postingestional US produced by glucose has since been intensively investigated by Sclafani and colleagues (e.g., Sclafani, Ackroff & Schwartz, 2003; Sclafani & Nissenbaum, 1987). This contextually independent greater relative acceptance of the CS+ material is highly resistant to extinction, persisting over many trials after removal of the US (Elizalde & Sclafani, 1990).

All the evidence for facilitation of eating by contingencies between flavour and externally applied variations in hunger, *i.e.* degrees of depletion and repletion of food, is that larger intake ('preference') comes from prompt repletion and this associative effect is greatly attenuated by delay in repletion (Simson & Booth, 1973b; Sclafani & Ackroff, 1994). That is, a long delay before refeeding is not expected to increase the intake of a food with a cue signalling the subsequent hunger, and might even reduce intake by aversive conditioning. Yet several recent experiments using a discriminative paradigm have found that extra eating can be induced by protracted withholding of maintenance food. This contrast in directions of acquired responding provides strong evidence for negatively reinforced instrumental eating.

The response-reinforcement contingency is discriminative in these experiments, with the test food containing a sensory cue to a long fast, while the control condition of a brief period of deprivation conditions preference for another sensory cue in test food prior to that short fast (Jarvandi, Booth & Thibault, 2007; Thibault & Booth, 2006; White, Mok, Thibault & Booth, 2001). The result is an acquired difference in intakes of the test food between that containing the sensory cue predicting the longer fast (version L) and that cuing the shorter fast (version S), in which intake of L minus intake of S is negative when short-fast conditioned preference is expressed (Figure 1, top panel) and L - S is positive when long-fast reinforced eating is expressed (Figure 1, middle panel).

Figure 1 here

The previous experiments also showed that deficit-avoidant eating reached a peak and then declined, to an extent that depended on how long the experiment continued (Thibault & Booth, 2006). This was interpreted as the learnt extra eating reducing the negative reinforcement from the nutritional deficit induced by the long fast, *i.e.* ‘self-extinction’ of the avoidance. In addition, the most recent previous experiment showed signs of re-learning (Jarvandi, Booth & Thibault, 2007). Therefore the extent of learnt anticipatory eating is predicted to oscillate through cycles of (re-)acquisition and (partial) extinction (Figure 1, middle panel).

The conditioning of preference by the shorter fast and the reinforcement by the longer fast of eating that reduced the reinforcing depletion summated to produce a complex curve of learning over trials, with its detailed shape depending on the relative speeds and strengths of acquisition of preference and avoidance. Since the discriminative instrumental intake is in the opposite direction to the conditioned preference, in order for the avoidance learning to be observed, it has to be stronger than the conditioning of preference. Whether conditioned preference (a trough in L - S) appears before or after anticipatory eating (a peak in L - S) depends on as yet poorly understood differences in the experimental conditions**:** Thibault and Booth (2006) observed a trough before a peak in Experiment 1 and the first peak before a trough in Experiment 2. A theoretical case where the first peak in avoidance largely coincides with the rapid phase of acquisition of preference is shown in the bottom panel of Figure 1.

The present experiment was undertaken to extend the previous findings by giving each animal only one period of food-deprivation, preventing any contrast with the other fast on other days of training. Extra evidence on this issue was obtained by switching the lengths of fast between the groups for a second period of training, providing a sequence-balanced within-subjects test of the hypothesis.

Since the periods of fasting used in previous work (S = 3 hours; L = 10-12 hours) may be unnecessarily long, the briefer withholding of food was reduced to 2 hours and the longer to 8 hours. Also the test food was liquid in a tube, rather than solid in a jar as in previous experiments, in order to confine the cuing odours better to each food and to make it easier to measure intake. Faster digestion of a liquid food was also liable to weaken the conditioning of preference by interaction with repletion from maintenance diet, as well as to strengthen the negative reinforcement of extra eating by lengthening the period of deficit before refeeding.

We also examined variation in the strength of the learnt response, since a decline in the extra intake before the longer deprivation had been observed in the earlier experiments (Jarvandi *et al*., 2007; Thibault & Booth, 2006). This could indicate an attenuation of the imposed depletion by the extra eating in the absence of a cue after responding that the aversive contingency no longer applied – a safety signal (Seligman, 1968; Seligman, Ives, Ames & Mineka, 1970) and hence a failure of avoidance to persist. The partial extinction of the avoidance response should restore reinforcement towards the strength from the externally imposed deprivation, resulting in re-learning of extra intake.

Thus there is a complex temporal pattern of intake (Jarvandi *et al*., 2007; Thibault & Booth, 2006; White *et al*., 2001) that can be interpreted as summation of conditioning of sensory preference with cycles of discriminatively reinforced instrumental intake, its self-extinction and re-learning - for example, as in the bottom panel of Figure 1. This experiment tested the robustness of this highly specific although qualitative theory of anticipatory eating.

Method

Rats, apparatus and materials

The subjects were eight adult male Sprague-Dawley rats (Charles River, Québec, Canada), with initial mean weight of 387 g (range: 357-417 g). They were placed in individual wire-mesh cages and maintained in a climate-controlled room on a 12:12h dark/light cycle, with lights off at 08:00.

The experimental food was odourised carbohydrate (CHO) solution which consisted of maltodextrin (MD05, Manbré Sugars: a mixture of oligoglucosaccharides, low in glucose and maltose) at a concentration of 33 g/100 ml of solution, dissolved in distilled water. This solution was odourised with either grape or cherry flavour drink mix (No Name brand, Toronto, Canada) at a concentration of 0.1% (w/w) and presented in standard water bottles made of polycarbonate with metal drinking spouts. Intake of the liquid food was measured by weighing the bottles before and after presentation.

The rats were maintained on a schedule of food and water deprivation during the cycles of training and test days, as described below. The maintenance diet *ad libitum* between training trials was ground laboratory chow (Charles River rodent chow 5075, Québec, Canada).

Procedure

Adaptation. The rats were adapted first to the environment for 1 week and then for another week to drinking experimental fluids: food and water were withheld for 3 h at the beginning of the dark phase, bottles of 0.1% saccharin solution were placed on the cages for 1 h and then free access to food and water was restored.

Training cycles. Each cycle consisted of a day for training and testing, including the designed period of food deprivation, and a subsequent *ad-libitum* day. During a trial (day 1 of each cycle), maintenance water and food were removed for 3 h at the start of the dark phase. Then rats were given bottles of odourised 33% CHO solution. These bottles were replaced with bottles of water after 1 h and all food was withheld, for 2 h as the short fast and for 8 h as the long fast. Half the animals had the short fast in every training/testing day (group 1 in training period 1) and the long fast was imposed on the other half (group 2). At the end of either fast, animals were given free access to maintenance chow. On the next day (day 2 of the cycle), animals had free access to water and chow and no experimental procedure was carried out. These cycles of one test day and one *ad-libitum* day were repeated 10 times to constitute one period of training and testing a particular pairing of odour and length of fast.

Training periods. Training was carried out in two periods of ten cycles in a cross-over design, balanced for sequence across two groups to which animals were randomly allocated

(Table 1). During a training period, each rat had either cherry or grape odourized test food paired with either the long (8 h) fast or the short (2 h) fast. In the first group of four rats, the short fast was tested in the first period and, after a break of four days without intervention, the long fast was evaluated in the second period. The second group of four rats had the reverse sequence of training periods. Each group was divided into two sub-groups counterbalanced for pairings of odours with lengths of fast (e.g. grape-long, cherry-short).

Table 1 here

Analysis of data

The amounts of test food intake (g) were compared between short and long fasts across trials by repeated measures ANOVA, seeking main effects of fast length (short *versus* long), sequence (1 *vs*. 2), period (1^{st} *vs*. 2^{nd}) and training day (Trials 1 to 10), and the interactions. When a main effect was significant, multiple comparisons were evaluated using Scheffé’s test. Repeated measures analysis of covariance (ANCOVA) was used to assess the effect of the shorter-fast trials on intake before the longer fast. Orthogonal polynomial contrasts were also used to test intake in each of within-subjects and between-subjects comparisons for linear, quadratic, cubic, quartic and quintic trends, with no strong quadratic trend expected because a single peak or trough is most unlikely (Figure 1).

For each trial in each training period, the mean intake of the odourised test fluid in the group receiving the long fast for that period was labeled “L”, and the mean intake before the short fast in the other group was termed “S”. Variation across trials in L minus S was evaluated for both periods (within-subjects on raw differences) and each period separately (between-subjects on trial-mean differences), using repeated measures ANOVA. This variation among trials was also tested by orthogonal contrasts, in accord with predictions of one or more phases expressing conditioned sensory preference ($L – S < 0$) or discriminative avoidance of hunger ($L – S > 0$).

Results

The intake of the test food increased over trials before both lengths of fast [Figure 2; Table 2, linear trend in both periods together (lines 1 and 2) and during each training period (lines 6 and 7)]. This indication of conditioning of preference by the nutrients in the test food itself was also seen in the earlier experiments in this series.

Figure 2 and Table 2 about here

However, this linear trend was much stronger before the long fast than it was before the short fast (Figure 2; Table 2, lines 1 and 2). Over the two training periods of 10 trials, intake of the test food increased 2.5 times before the longer fasts (from mean ± SEM = 6.6 ± 1.1 g in Trial 1 to 16.6 ± 1.1 in Trial 10), Scheffé $p < 0.001$, but only 1.6 times before the shorter fasts (from 7.4 ± 1.1 g in Trial 1 to 12.0 ± 1.1 g in Trial 10, n.s.). It follows that the longer fast by itself is reinforcing extra eating, over a delay of reinforcement greater than the duration of the shorter fast.

Superimposed on this overall increase in intake before the long fast were successive phases of variations in the strength of depletion-avoidance learning in competition with any preference conditioned by the short fast (Figure 2). This pattern was sufficiently strong to produce a cubic trend in mean intake at a Trial before food deprivation across training periods averaged across the two groups (Table 2, line 4). However, this variation in intakes differed between short and long fast groups, Fast by Trial interaction $F(9, 126) = 3.54$, $MSE = 1.06$, $p < 0.001$. As can be seen in Figure 2, in a period of trials on short fasts, the rats rapidly increased their intake of the test food, peaking at Trial 3, whereas intake before the long fasts first peaked at Trial 2 then showed a higher peak at Trial 6 and continued to increase further during Trials 9 and 10.

Comparing training periods within subjects, there are signs of a quintic contrast (Table 2, line 4), attributable to relearning of anticipatory eating after its self-extinction over Trials 7-8 and 8-9 before long and short fasts, respectively. In addition, covarying out intakes before the shorter fast left a linear trend of anticipatory eating (Table 2, line 3). That is, across trials on the long fast, the extra intake increased over successive peaks of deficit-avoidance.

The effects of longer fast in the first period of training differed from those in the second period, Period by Trial interaction $F(9, 54) = 2.22$, $MSE = 1.67$, $p < 0.05$ (Table 2, line 1). Intake before the long fast reached a peak at Trial 6 in the first training period (16.1 ± 1.7 g) and at Trial 5 in the second period (13.4 ± 1.7 g), although paired comparisons of intakes before long fasts in these trials between two periods had *p*-values no lower than 0.99 (with $df = 51.5$, $MSE = 2.36$). Moreover, between-subjects analysis gave signs of a quintic trend in intake of test food in Period 1 (Table 2, line 6), while it was far from significance in Period 2 (Table 2, line 7).

Discriminative learning of anticipatory eating was also shown by a positive value of the difference between the mean intake of test food having the odour cuing the long fast (L) and the mean intake of the odour before the short fast (S), *i.e.* L > S (as numerically from Trials 5 to 10 in Figure 2). This value varied significantly across trials, $F(9, 54) = 4.18$, $MSE = 1.38$, $p < 0.001$.

In particular, the intake of test food before the longer fast (L) increased relative to that of the shorter fast (S), which was evident as a significant L - S linear contrast (Table 2, line 5).

As to be expected with balancing between odours, the difference between test intakes before long and short fasts was around zero at the first training trial, L - S = -0.79, t(51.9) = -0.57, *MSE* = 1.38 (Figure 2). The greater intake before long fasts than before short fasts became statistically significant at Trial 6, L - S = 4.88, within-subjects *t*(51.9) = 3.52, *MSE* = 1.38, $p < 0.001$. This increase was followed by a decline in the L - S value during Trials 7 and 8, during which the amounts of test food eaten did not differ significantly between short and long fasts. A significantly positive values of L – S were observed again from Trial 9 (L – S: 5.59 and 4.54 at Trials 9 and 10, respectively), *t*(51.9) = 4.03, *MSE* = 1.38, $p < 0.01$.

In addition, comparisons of training periods between subjects showed a similar pattern of variations in L – S, although even the quintic contrast did not approach significance in these comparisons only of group mean values for each trial (Table 2, lines 8 and 9).

Discussion

Eating that avoids or reduces a deficit in supply of nutrients to tissues is learned when training is given only on long fasts, without any contrast with trials followed by short fasts. This is consistent with the hypothesis by White *et al*. (2001) that the learnt difference in intake before shorter and longer fasts arises from an increase in intake in anticipation of hunger, not from a decrease in intake in anticipation of satiety as Le Magnen (1957) originally assumed (Le Magnen, 1999).

The present results also confirmed previous observations of at least one decline in the extra eating before the longer fast (Jarvandi *et al*., 2007; Thibault & Booth, 2006). Since the investigator-applied contingencies remained, the temporary extinguishing of anticipatory eating must be a result of the animal's behaviour. That is, the negative reinforcement by signals to the brain from deficient supply of nutrients to tissues is reduced by the extra eating that the signals of large deficit have reinforced initially. This self-extinction of the extra eating should in turn create sufficient deficit again to reinforce increases in intake, as observed when training continues for enough trials. Thus this striking variation in amount of extra eating before the longer fast strengthens the evidence that the acquired ingestive responding in this paradigm is instrumental, *i.e.* under the control of response-stimulus contingencies rather than stimulus-stimulus contingencies.

Finally, the results of this experiment are consistent with deficit-avoidance being acquired and partly extinguishing itself in the first few trials of training. That is, the two reliable peaks of avoidance observed here may be the second and third in an oscillation with a frequency of 2-3 trials – the theoretical minimum for acquisition, self-extinction and relearning. One of the previous experiments showed a peak of anticipatory eating at the second trial on the food that cued the longer fast (Thibault & Booth, 2006: Experiment 2), followed by a trough of conditioned preference for the cue to the shorter fast. In other experiments (Jarvandi *et al*., 2007; Thibault & Booth, 2006: Experiment 1; White *et al*., 2001), the conditioned preference has been expressed before anticipatory eating, which has appeared only at the sixth or eighth trial on food cuing the longer fast. In the present experiment on liquid test food and briefer fasts, the conditioning of preference may have been more nearly concurrent with the initial learning of avoidance and so the first expression of anticipatory eating was much attenuated. The resulting early oscillation in the difference between longer and shorter fasts was too small to be statistically reliable in this size of group.

Nevertheless, a quintic trend over trials with *p* better than 10% emerged from both within-subjects analysis of raw intakes and between-groups analysis of the first period of training, although it was negligible in the second period between subjects. The four inflections of a quintic contrast could be one trough of conditioned preference and two peaks of deficit avoidance with a trough between. Since the reliable cubic trends observed arose from a peak in L-S and a subsequent trough, *i.e.* a sequence of avoidance learning, some self-extinction and (at least a start on) relearning (the two clearest inflections), the potential quintic trends can only come from an earlier peak (initial avoidance) and a subsequent trough of preference revealed by some self-extinction. The total lack of evidence for a quintic trend in Period 2 could be the result of a reversal error causing L-S to start negative, making initial avoidance learning harder to observe than at the start of Period 1.

In short, it seems that in the present experiment the early trough of preference for short-fast odour observed in previous experiments was much attenuated by what otherwise would have been the first of three peaks of odour-discriminative avoidance of the nutritional deficits from the long fast.

Thus the details of the present data are accounted for rather precisely as the sum of two types of learnt behaviour (Figure 1, bottom panel). A readily acquired and extinction-resistant increase of acceptance is conditioned by actions of carbohydrate and protein in the maintenance diet when refed as promptly as 2 hours later, perhaps by augmenting postingestional action of carbohydrate in the test food. At the same time, there is a steady frequency of cycles of anticipatory eating, its self-extinction and its re-acquisition, as to be expected of avoidance learning without ‘safe’ places to sustain responding when it has attenuated the reinforcement that continues to be externally applied.

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Table 1. Experimental design in 8 rats of durations of food deprivation and discriminative stimulus odours of food for the two periods of training, each of 10 trials.

	Period 1	Period 2
Sequence 1	SHORT fast	LONG fast
N = 2	Cherry	Grape
N = 2	Grape	Cherry
Sequence 2	LONG fast	SHORT fast
N = 2	Cherry	Cherry
N = 2	Grape	Grape

Table 2. Strengths of orthogonal contrasts among treatments: intake of test food over 10 trials with either short fast (S) or long fast (L)

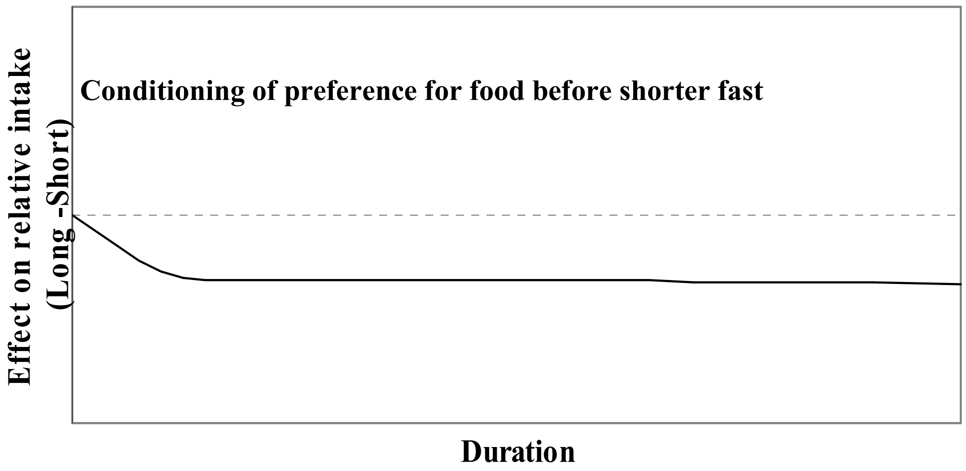
		Linear			Cubic			Quartic			Quintic		
line	Dependent variable	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
	Individuals' intake (within subjects)												
1	L	47.4	54	0.0001	3.9	54	0.05	0.18	54	0.2	1.85	54	0.2
2	S	4.8	54	0.03	17.6	54	0.0001	0.09	54	0.8	1.47	54	0.2
3	L (S as covariate)	29.3	25.8	0.0001	0.2	50.7	0.7	0.26	58.1	0.6	0.84	56.7	0.4
4	L or S, both periods	42.1	126	0.0001	13.7	126	0.0003	0.03	126	0.8	2.84	126	0.09
5	L-S, both periods	21.6	54	0.0001	0.4	54	0.5	0.27	54	0.6	0.23	54	0.6
	Group mean intake (between subjects)												
6	L or S, Period 1	42.8	54	0.0001	5.6	54	0.02	0.01	54	0.9	3.23	54	0.08
7	L or S, Period 2	10.8	54	0.002	10.4	54	0.002	0.04	54	0.8	0.57	54	0.4
8	L-S, Period 1	12.2	27	0.002	0.8	27	0.39	0.02	27	0.9	1.81	27	0.2
9	L-S, Period 2	9.4	27	0.005	0.00	27	0.99	0.38	27	0.5	0.58	27	0.4

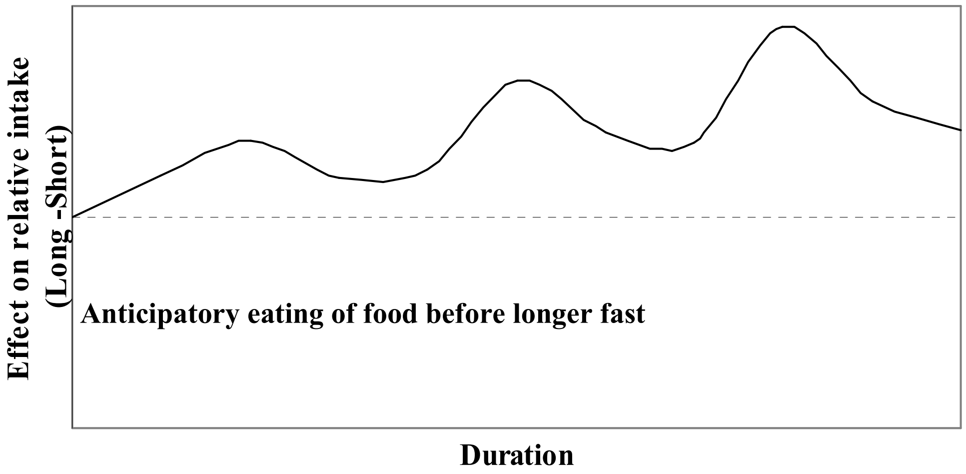
Notes. The value given as *df* is degrees of freedom of the error term. There were no grounds for examining quadratic contrasts; in the event, the only moderate *p* values observed were for lines 6 (< 0.1) and 7 (< 0.2).

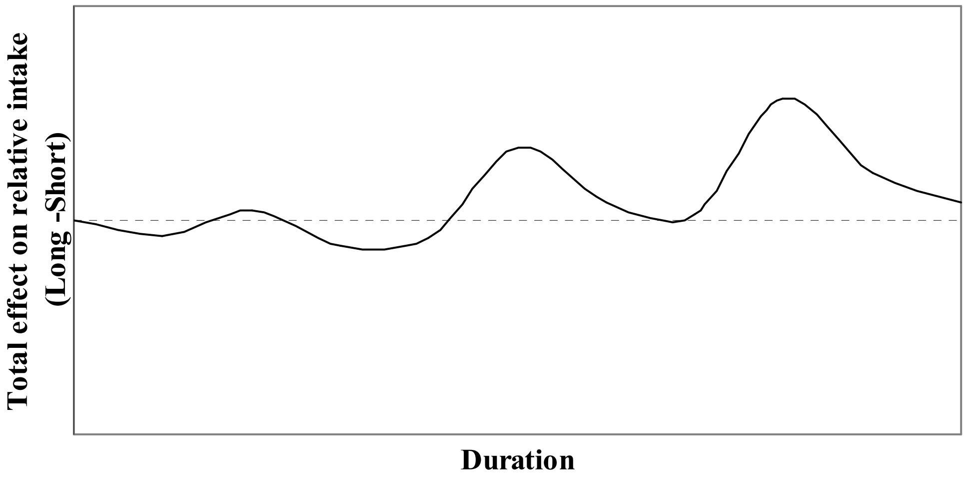
Captions to Figures

Figure 1. Theoretical graphs of effects of food deprivation on relative intakes (Long-Short) over trials. Top panel: classical conditioning of sensory preference. Middle panel: reinforcement of discriminative anticipatory eating. Bottom panel: one possible combination of the effects in the upper two panels.

Figure 2. Intake (g, mean ± SE) of test food having the odour predictive of the long fast (L: filled square) (N = 8) or odour predictive of the short fast (S: open circle) (N = 8) across two periods of training.


Conditioning of preference for food before shorter fast
Effect on relative intake
(Long -Short)
Duration


Anticipatory eating of food before longer fast
Effect on relative intake
(Long -Short)
Duration


Total effect on relative intake
(Long -Short)
Duration

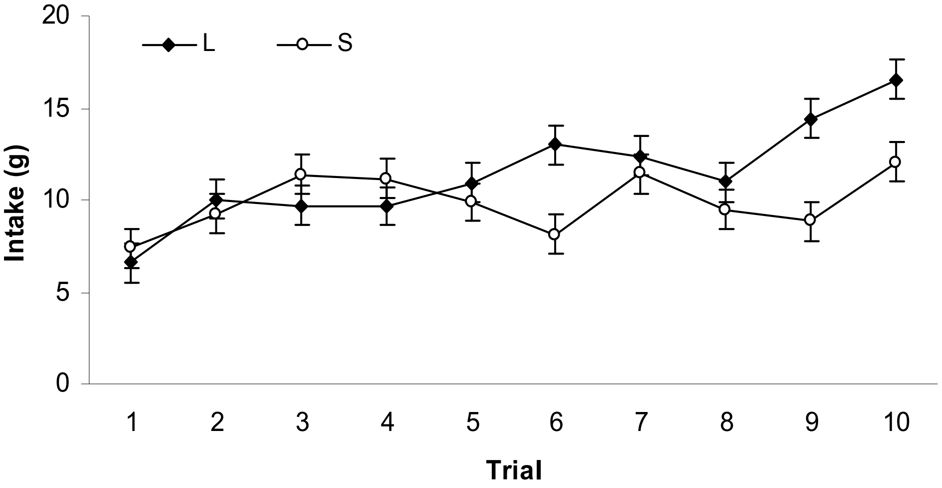


Figure 2