Anim. Behav., 1986, **34**, 871–880

Deterministic versus probabilistic models of behaviour: taste-elicited actions in rats as a case study

KENT C. BERRIDGE* & JOHN C. FENTRESS
Department of Psychology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

Abstract. Deterministic and probabilistic models of behavioural activation make different predictions about the relation between stimulus strength and behavioural output. This study examined the production rules that link the strength of a taste to the activation of stereotyped ingestive and aversive actions in rats. A positive correlation was found between the number of rats that showed a particular behaviour and the actual number of occurrences of that behaviour among those rats which showed it. Four models of response activation that could account for this correlation were tested. Three suggest that individual rats are governed by similar or dissimilar deterministic stimulus–response curves. The other suggests that the rules of response activation are inherently probabilistic rather than deterministic, and that a single probability controls both the likelihood that a behaviour will be shown at all by an individual and the number of responses that will be emitted, if any at all are shown. The predictions made by the probabilistic model were supported. We conclude that, over a period of minutes, rats are not governed by stable deterministic stimulus–response curves but, instead, behave in a probabilistic fashion in response to taste stimuli.

Distinct and highly stereotyped actions are elicited when solutions of different tastes are infused into the mouths of rats (Grill & Norgren 1978). These stereotyped actions, which can be elicited even after midbrain transection (Miller & Sherrington 1916; Grill & Norgren 1978), closely resemble those shown by freely drinking rats (Pelchat et al. 1983). The type and number of actions elicited depends upon the palatability of the taste. This, in turn, depends chiefly upon the composition and concentration of the stimulus itself, but is also influenced by the physiological state of the rat (e.g caloric and sodium balance) and by associations that have been formed between a taste and its post-ingestive consequences (e.g. illness; cf. Grill & Berridge 1985). The purpose of the present paper is to examine the production rules that translate a palatability evaluation into a specific pattern of observable actions.

Eleven distinct actions are recognized. Three are strongly ingestive: lateral tongue protrusions, rhythmic midline tongue protrusions, and paw licking. Two reflect neutrality or a compromise between ingestion and aversion: passive dripping of the solution, and rhythmic mouth movements. The remaining six are aversive: gaping, chin rubbing, face washing, forelimb flailing, headshaking, and rapid locomotion (Grill & Norgren 1978; Berridge & Grill 1983).

These actions provide sensitive measures of taste palatability. Using minute infusions of 50 μl (Grill & Norgren 1978) or larger volumes of 1 ml (Berridge et al. 1981), a palatability profile can be constructed for a given taste by measuring either the percentage of rats showing each ingestive and aversive action (sample incidence; Fig. 1) or the actual number of times each action is emitted (mean occurrence). Although the more detailed mean occurrence measure appears to detect some trends missed by the sample incidence measure (Berridge & Grill 1984), the agreement between the two measures is good. In a recent study employing both measures, the probability that a rat would show a given action was positively correlated with the mean number of times that action was emitted by the group as a whole ($r=0{\cdot}66$, $P<0{\cdot}01$; Berridge & Grill 1984).

The close agreement between the sample incidence and the mean occurrence measures carries implications for how we model the activation of these actions. For example, such agreement should not occur if the behaviour is controlled by a stable mechanism that (1) produces a number of responses that is proportional to the strength of the stimulus signal, and (2) is similar in response threshold and slope for all individuals (Fig. 2). This is because a stimulus of increasing strength would

* Present address for reprints: Department of Psychology, Neuroscience Building, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

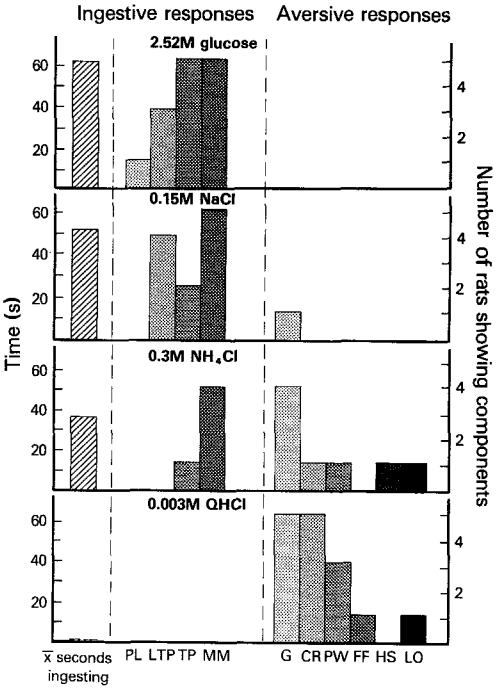

Figure 1. Palatability profiles for four tastes based on the incidence of taste elicited behaviour (except left) from Berridge et al. (1981). The tastes are in order of decreasing preference from top to bottom. Responses are paw licking (PL), lateral tongue protrusions (LTP), rhythmic tongue protrusions (TP), mouth movements (MM), gapes (G), chin rubs (CR), face washing (FW), forelimb flailing (FF), headshakes (HS) and locomotion (LO).

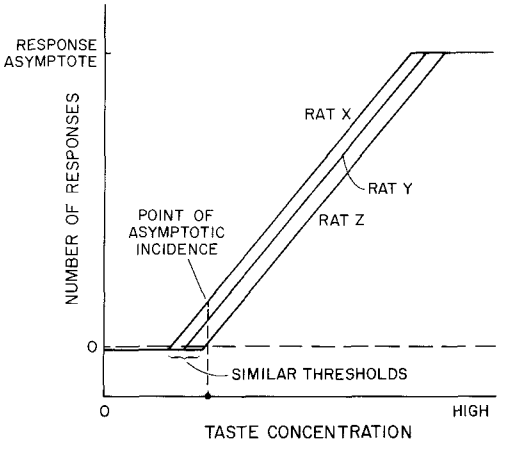

Figure 2. Similar thresholds model of activation. The response of each rat is proportional to the stimulus strength. The point at which all individuals are above threshold occurs at a relatively low concentration. Sample incidence cannot increase above this point although the mean number of responses can.

quickly surpass the similar response thresholds for nearly all individuals long before it reached an asymptote for number of actions emitted. Increases in stimulus strength beyond the group threshold point would continue to increase the mean occurrence (number of elicited responses); however, the sample incidence (percentage of rats responding) would already be asymptotic near 100% and could not increase in parallel.

A number of other activation models exist, however, that could explain a continuing correlation between these measures at high stimulus strengths. For example, it might be that the mechanism does not produce a response that is proportional to the stimulus strength, but rather a constant (or random) number of responses, with the trigger threshold for this constant response varying greatly from individual to individual (Fig. 3). This could be termed a constant-response–variable-trigger model. The mean number of responses per rat would still appear to change gradually as concentration increased. But this would be a passive statistical artefact due to the fact that an unchanging number of responses per responding (suprathreshold) individual would be 'diluted' with a decreasing number of zeros from non-responders. If this were true, one would not expect to find a significant correlation between the suprathreshold mean (mean number of responses for only those rats that did respond) and the sample incidence.

Alternatively, it could be that the mechanism

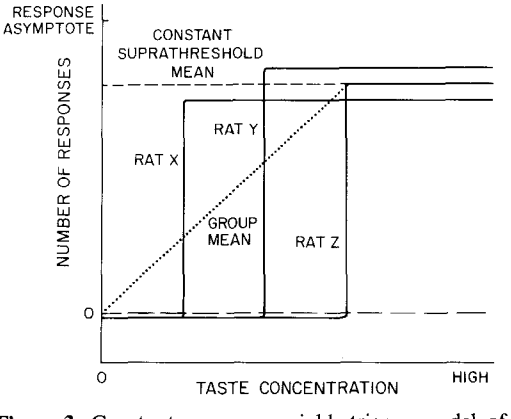

Figure 3. Constant-response–variable-trigger model of activation. Each individual contributes either zero or a constant number of responses. Individuals differ widely in threshold. This produces a group mean that increases gradually with increasing concentration even though the suprathreshold mean (for responders only) remains constant.

does produce a response proportional to the stimulus strength, but that individual thresholds nonetheless vary greatly (Fig. 4). This could be called a differing individual curves model. This model is similar to the psychophysical theory of signal detection (Green & Swets 1966). It preserves a deterministic relation between stimulus input and response output but allows different individuals to have different 'response biases'. If this were true, one would expect to find a positive correlation even between the suprathreshold mean (mean number of responses for only those rats that do respond) and sample incidence.

Finally, as Berridge & Grill (1984) have suggested, a correlation between suprathreshold mean and sample incidence is also compatible with a probabilistic decision model of activation (cf. Heiligenberg 1976; Huntingford 1984). This probabilistic model suggests that (1) the decision to activate these responses is probabilistic rather than deterministic, and (2) both the likelihood that a rat will emit a response and the number of responses it will emit, if any at all, obey the same probability (Fig. 5). Stated more formally, the model suggests that the number of emitted responses is controlled by a probabilistic rate parameter (or response–density parameter), which is an increasing function of stimulus strength. Both the sample incidence and the suprathreshold mean reflect the expression of this parameter over a given period. This model goes

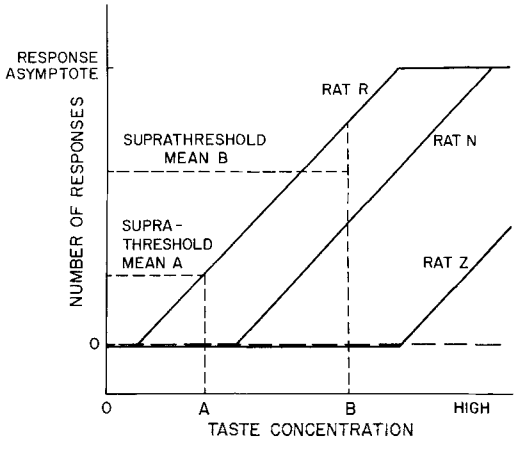

Figure 4. Differing individual curves model of activation. The response of individuals above threshold is proportional to the stimulus concentration and individuals vary greatly in threshold. The sample incidence, group mean, and suprathreshold mean all increase gradually with increasing concentration (compare low concentration A to high concentration B).

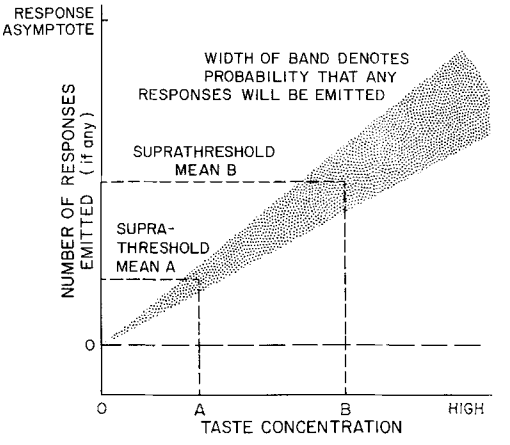

Figure 5. Probabilistic model of activation. For each individual both the probability that a behaviour will be shown at all, and the number of occurrences of that behaviour emitted (if any at all are shown), increase with concentration. However, there is no threshold above which an individual can be counted on to respond because each trial is independent. Sample incidence, group mean, and suprathreshold mean all increase gradually with increasing concentration.

further than standard signal detection theory (Green & Swets 1966) in that it rejects the possibility of an absolute threshold set by deterministic causes. This lack of a threshold is not simply due to noise within the central nervous decision system, but rather reflects the probabilistic nature of the decision mechanism itself.

The probabilistic decision model agrees with the prediction of the differing individual curves model that one would expect to find a positive correlation between the suprathreshold mean and the sample incidence. The differing individual curves model, however, also predicts that individuals show a deterministic consistency across trials; rats that responded to weak stimuli (i.e. that have low thresholds or are biased to respond) would be expected to show more responses at high concentrations than rats that had been weak-stimulus non-responders (i.e. that have high thresholds or are biased against responding). This is because rats with low thresholds would be at a higher point along their individual curves, when presented with a strong stimulus, than rats with high thresholds. The probabilistic model, on the other hand, considers each trial independent and does not expect individual consistency; response to a weak stimulus would not be a good predictor of an individual's response to a strong stimulus.

The present investigation was designed to choose the best model from among these alternatives. The results of these experiments suggest that there is a significant positive correlation between the suprathreshold mean number of an action and its sample incidence, thus ruling out the constant-response–variable-trigger model. They further suggest that an individual's response to a weak stimulus cannot be used to predict the response to a stronger stimulus, and that the mechanism of response production operates in a probabilistic, rather than in a deterministic fashion.

The first experiment examines the correlation between the suprathreshold mean and the population incidence of behaviour elicited by 1-ml oral infusions of tastes of differing concentrations. It also examines whether the behaviour of individuals to high concentrations can be predicted from their behaviour to low concentrations. Two groups of rats were run in separate analyses, in order to establish the replicability of the conclusions.

EXPERIMENT 1

Methods

Part A

Eleven adult male Sprague–Dawley rats were maintained on ad libitum food and water throughout the experiment. In order to allow precise control of the volume and timing of stimulus presentation, the rats were anaesthetized with ketamine and acepromazine and implanted permanently with two oral cannulae using the method of Grill & Norgren (1978). These cannulae enter the mouth anterolateral to the first maxillary molar, are anchored to dorsal skull screws, and exit from the top of the head. After recovery from surgery, the cannulae do not disrupt feeding nor do they disturb the rat in any detectable way; in every respect, the rats behave as though unaware of the cannulae.

After recovery, the rats were presented with two concentrations of three taste stimuli: 1·0 and 0·03 M sucrose, which elicit primarily ingestive actions; 0·1 and 0·01 M hydrochloric acid, HCl (HCl at this concentration is sour tasting to humans and has no irritative effect), which elicit both ingestive and aversive actions; and 3×10^{-4} and 3×10^{-5} M quinine HCl, which elicit primarily aversive actions.

Rats received one stimulus per day in balanced order. At the time of testing, a rat's oral cannulae were connected to stimulus delivery tubes. The rats were allowed to habituate to the cylindrical clear plastic test chamber for 5 min prior to testing. A 1-ml volume of the taste solution was then infused into the mouth over 1 min at a constant rate. Responses occurring within the 1-min trial were videotaped, using a mirror positioned beneath the transparent floor of the test chamber, for subsequent analysis.

The videotapes were scored for the occurrence of each action at one-tenth actual speed. A microcomputer was calibrated to this speed, and each action corresponded to a key on the computer keyboard. As each action occurred, its key was pressed, creating a transcript of the number, timing and order of each action. Scored ingestive actions were paw licking; non-rhythmic lateral tongue protrusions past the lip, followed by forward extension, with a total duration of 164 ± 9 ms (mean ± SEM); and rhythmic tongue protrusions along the midline with a cycle length of 166 ± 7 ms. Scored aversive actions were gapes (large opening of the jaw and retraction of the lips lasting 124 ± 8 ms), face washing (either a single wipe with the paw(s) or a bout of many), forelimb flailing (shaking of the forelimbs in the horizontal plane with a frequency of greater than 60 Hz) and headshaking (at greater than 60 Hz). For the purpose of analysis, lateral tongue protrusions, rhythmic tongue protrusions and gapes were counted in terms of the number of occurrences; face washing, forelimb flailing, and headshaking were counted in terms of the number of bouts; paw licking was counted in terms of the integrated seconds of time spent performing.

Part B

Six naive rats were run in an identical procedure except that three concentrations of sucrose, HCl, and quinine were used. In addition, two concentrations of ammonium chloride (NH_4Cl) were used. This stimulus elicits both ingestive and aversive actions in rats (and tastes salty and metallic to humans). Stimulus concentrations were: 1·0, 0·3, and 0·03 M sucrose; 0·1, 0·03, and 0·003 M HCl; 3×10^{-4}, 3×10^{-5}, and 3×10^{-6} M quinine HCl; and 0·15 and 0·05 M NH_4Cl. Stimulus concentrations for both experiments were chosen to elicit different levels of responding, based upon pilot observations.

Results and Discussion

Part A

Only those individuals that showed a given behaviour to a particular taste stimulus were used to calculate the suprathreshold mean for that behaviour. Each taste stimulus and concentration was considered separately. The suprathreshold mean for a given action and taste concentration was paired with the percentage of rats showing the action for the same taste (only ingestive actions were considered for sucrose concentrations and only aversive actions for quinine concentrations; for HCl, both ingestive and aversive actions were considered). The correlation for each set of six pairs was then calculated. With a maximum of six pairs there is a maximum of four degrees of freedom possible. If no rat showed an action to a particular taste (i.e. no rat was suprathreshold), then that taste was excluded from the analysis. For this reason, the degrees of freedom vary for certain actions.

In addition to the calculations performed for each action, a separate correlation was obtained for all ingestive actions combined and for all aversive actions combined. For this analysis, the mean number of total ingestive actions was paired with the mean incidence of ingestive actions, i.e. the sum of the percentages of rats that showed each action, divided by three (the number of ingestive action categories). The same was done for aversive actions. Such an analysis does not attempt to compare 'apples' to 'oranges' but rather compares 'fruit' to 'fruit' without assigning weights to different actions.

Table Ia shows that the suprathreshold mean is positively correlated with sample incidence for both individual actions and for combined ingestive and combined aversive actions. The correlation varies between 0·45 and 0·95. For $df=4$, these correlations are statistically significant for two separate ingestive actions (lateral tongue protrusions and rhythmic tongue protrusions; $P<0·01$ and 0·05 respectively); for the same df, the aversive suprathreshold mean is significantly correlated with incidence when actions are combined ($P<0·05$).

Part B

The same analyses were performed upon the responses to 11 taste stimuli in experiment 1B (Table Ib). Two out of three ingestive actions showed a significant positive correlation between suprathreshold mean and sample incidence (rhythmic tongue protrusions and paw licking; $P<0·05$); the same was true for three of four aversive actions (gapes, forelimb flailing and headshakes; $P<0·05$). Both ingestive and aversive actions showed a significant correlation when combined ($P<0·05$ and 0·01).

These results suggest that a positive correlation between the mean number of a taste-elicited action shown by a group and the percentage of individuals within a group showing the action at all is not due to a changing number of constant-response contributors. Instead the mean number of responses,

Table I. Correlation of suprathreshold mean to sample incidence

	Ingestive actions							Combined ingestive actions	Combined aversive actions
	LTP†	TP	PL	G	FW	FF	HS		
(a) Experiment 1A (six taste stimuli, eleven rats)									
	**	*							*
Spearman's r	0·95	0·85	0·78	0·42	0·80	0·61	0·59	0·75	0·86
(df)	(4)	(4)	(4)	(3)	(4)	(4)	(3)	(4)	(4)
(b) Experiment 1B (eleven taste stimuli, six rats)									
		*	*	*		*	*	*	**
Spearman's r	0·44	0·64	0·71	0·61	0·22	0·77	0·72	0·69	0·89
(df)	(8)	(8)	(8)	(9)	(9)	(8)	(7)	(8)	(9)

* $P<0·05$, **$P<0·01$.

† Ingestive actions are: lateral tongue protrusions (LTP), rhythmic tongue protrusions (TP) and paw licks (PL). Aversive actions are: gapes (G), face washing (FW), forelimb flailing (FF) and headshakes (HS).

even for responders only, changes in parallel with the incidence of that response throughout the population. The constant-response–variable-trigger model is clearly incorrect for taste-elicited responses.

Two alternatives remain that could account for this correlation: the differing individual curves model and the probabilistic decision model. According to the differing curves model (Fig. 4), the response threshold and response asymptote for each individual occur at different stimulus strengths. Concentration point A in Fig. 4 elicits a small number of responses from rat R alone. Concentration point B elicits a larger number of responses from rat R and it also elicits responses from rat N, though not as many as from rat R. If we were to separate rats into categories R and N based upon whether or not they responded at low concentrations, then we should also expect to find a difference between the suprathreshold means of R rats (weak-stimulus responders) and N rats (weak-stimulus non-responders) at high concentrations; the suprathreshold means should be higher for R rats (weak-stimulus responders). The probabilistic decision model, on the other hand, would predict that the response at a high concentration is independent of the individual's response at the low. It would predict that there is no difference at the high concentration between weak-stimulus responders and weak-stimulus non-responders.

For each action and taste, the rats in experiment 1 were classified as either weak-stimulus responders or as weak-stimulus non-responders. For each action and taste, the suprathreshold mean of the weak-stimulus responders for the high concentration of the same taste was calculated and compared to the high-concentration suprathreshold mean of the weak-stimulus non-responders (in order for a comparison to be made, an action must have had at least one responder and one non-responder at the low concentration, and there must have been at least one responder in both groups at the high concentration). Nine comparisons were thus obtained for experiment 1A. Eighteen comparisons (comparing lowest concentration to highest concentration) were obtained for experiment 1B.

Table II shows that weak-stimulus responders were not likely to show more responses at high concentrations than weak-stimulus non-responders. Combining experiments 1A and 1B, in 44% of 27 comparisons, the weak-stimulus responders showed more responses at high concentrations than weak-stimulus non-responders. The opposite was found in 52% of the comparisons (in 4% there was no difference between the groups). These data appear to confirm the prediction of the probabilistic decision activation model, that the groups' high-concentration means do not differ. The prediction of the differing individual curves model, that weak-stimulus responders would show more responses at high concentrations than weak-stimulus non-responders, was not confirmed.

One difficulty with these data, however, is the possibility that a response ceiling effect may exist. It could be that the differing individual curves model is correct, but that the reason the two groups do not differ at high concentrations is that both groups have reached a response asymptote. In other words, is the high concentration too high? Fortunately, this can be tested in experiment 1B, where a middle concentration exists for three tastes. These middle concentrations elicit responses at a level well below asymptote. Eleven comparisons of the responses to middle concentrations of weak-stimulus responders and weak-stimulus non-responders were obtained for experiment 1B (Table II). As in the earlier comparisons, weak-stimulus responders were not likely to show more responses than weak-

Table II. Comparison of high-concentration responses of low-stimulus (L-S) responders and non-responders

Experiment	Comparisons in which the greater number of actions was shown by L-S responders	Comparisons in which the greater number of actions was shown by L-S non-responders	Number of comparisons
1A	33%	67%	9
1B (highest concentration)	50%	44%	18
1B (middle concentration)	45%	55%	11

stimulus non-responders at the middle concentration (45% for weak-stimulus responders versus 55% for weak-stimulus non-responders). The probabilistic prediction was again confirmed.

It should be noted that the differing individual curves portrayed in Fig. 4 show a linear relation between stimulus strength and response number. Would deviations from linearity change the deterministic prediction concerning weak-stimulus responders and non-responders? Within broad limits, it would not: whether the actual stimulus–response relation is linear or curvilinear (either concave up or concave down), the prediction of the deterministic model remains the same so long as the slopes of individual curves are roughly similar. The prediction would not hold true, however, if individuals that were relatively insensitive to stimulus intensity in terms of threshold (i.e. weak-stimulus non-responders) were nonetheless extremely sensitive to intensity above that threshold (i.e. had steeper slopes or higher levels of initial suprathreshold responding than most other individuals). If this were true, then the expected results of a high stimulus comparison would resemble what we have found. There are two lines of evidence, however, against this possibility. First, threshold and slope measures of sensitivity tend to vary in parallel when sensitivity is altered by manipulations of the physiological state of the rat or by changes in the associative significance of the taste (Berridge et al. 1984; Berridge & Grill 1984; personal observations). Second, an inspection of the curves of individual rats, in the experiment in which a three point curve can be plotted for each rat (1B), does not support the hypothesis that either slope or the initial level of responding varies systematically between weak-stimulus responders and non-responders. We therefore regard this possibility as unlikely.

These results suggest that the differing individual curves model portrayed by Fig. 4 is incorrect. Individual rats are not governed by stable deterministic stimulus–response curves. It might be, however, that they are governed by unstable deterministic curves. The comparisons of experiment 1 used tests conducted on separate days. We know that the response to tastes is influenced by physiological state, etc., as well as by the taste stimulus itself. It might be that, in spite of our attempt to maintain controlled conditions, individuals were not in fact tested in similar states on separate days. This could have had the effect of shifting an individual's curve (or response bias) from day to day. It might be possible to confirm the deterministic prediction if the response to different concentrations were examined on the same day, within the same hour.

EXPERIMENT 2

Eight naive rats were equipped with cannulae as in experiment 1. Some changes in the procedure from experiment 1 were required in order to test multiple stimuli in close temporal proximity. Within a test day an A–B–B–A order of presentation was used, where A and B corresponded to different concentrations of the same taste. In order that the response to a stimulus be unaffected by a preceding stimulus, two water rinses preceded and followed each taste stimulus. It was also necessary to reduce the stimulus volume from 1 ml to 50 μl, to avoid presenting the rats with the relatively large volume that a series of four 1-ml stimuli plus rinses would entail. A large volume could produce post-ingestive consequences (e.g. osmotic, caloric) that could affect the responses to later stimuli. A 50-μl volume is approximately equivalent to the volume ingested by a rat over 10 licks (Halpern 1975). Even with four taste stimuli and 10 water rinses, a rat received only 0·7 ml of fluid over the course of a test series. Use of this stimulus size eliminated the problem of post-ingestive effects while preserving behavioural sensitivity to different tastes (Grill & Norgren 1978).

Two concentrations of sucrose (1·0 and 0·03 M) and of quinine HCl (6×10^{-4} and 3×10^{-5} M) were used. Because of the minute volume and short duration of the infusion, ceiling effects were unlikely to obtain and no intermediate concentration was used. The order of high and low concentrations was balanced across rats. A rat received both sucrose stimuli on one day and both quinine stimuli on another day; this order was also balanced across rats.

At testing, a rat's two cannulae were both connected to stimulus delivery tubes; one contained the first taste stimulus and the other contained distilled water. After a 5-min period, two 50-μl water rinses were delivered 30 s apart. Thirty seconds after the second rinse, the first taste stimulus was delivered, followed again by two rinses 30 s later. Without touching the rat or its cannulae, the delivery tube for the first taste stimulus was replaced by one for the second (the

delivery tube actually comprised an outer sheath surrounding an inner fluid-filled tube; the inner tube could be drawn up and a new tube inserted from outside the test chamber). This procedure was continued for the remainder of the series. The entire series of four taste stimuli and 10 water rinses was administered in less than 20 min for each rat. Responses to taste solutions were videotaped and analysed as in experiment 1. Behaviour was scored starting at the beginning of the stimulus and ending when the rat ceased to respond.

Results and Discussion

Table III shows that the correlation between suprathreshold mean and sample incidence was replicated using this procedure. Correlations were calculated using the responses to the four taste stimuli and to the water rinses; water trials on sucrose days were considered separately from water on quinine days in case a contrast effect on the palatability of water was produced by preceding stimuli. Although the correlation for each action alone appeared somewhat lower in certain instances than in experiment 1 (Table III), the combined ingestive actions showed a very strong correlation between suprathreshold mean and incidence (0·91, $P<0·05$), as did combined aversive actions (0·90, $P<0·05$).

The primary purpose of this experiment was to compare the response of low-stimulus responders and non-responders to high concentrations when the two concentrations were presented in close temporal proximity. Seven comparisons were obtained using the analytic procedure of experiment 1. In two comparisons (29%), weak-stimulus responders showed more responses to the high concentration than weak-stimulus non-responders. The opposite was true in four comparisons (57%). The groups were equal in one comparison (14%). Thus, as in experiment 1, there was no indication that the response to a weak stimulus could be used to predict an individual's response to a stronger one in the way that the differing curves model would have suggested.

GENERAL DISCUSSION

These experiments demonstrate that the probability that a rat will show a given taste-elicited action (sample incidence) and the number of times that it will show that action if it shows any at all (suprathreshold mean) increase in parallel with stimulus strength. This parallelism, however, does not occur because a stronger stimulus more strongly activates a greater number of stable individual stimulus–response curves. Our results are not explained by positing that individuals have different thresholds above which they can be counted on to respond in a deterministic fashion. Instead our results suggest that, whether an individual rat is examined over successive days or successive minutes, the response is related to stimulus strength in a probabilistic fashion. A change in the stimulus strength changes both the probability of response and the number of responses that will be shown (if any at all). This is not simply an artefact of examining animals in groups, as a stable differing curves model would suggest, but is also a property of the individual.

It is worth considering how such a probabilistic system of behavioural activation could arise out of a deterministic nervous system. There are at least

Table III. Experiment 2 (four tests plus two water rinses): correlation of suprathreshold mean to sample incidence for a 50-μl volume

	Ingestive actions							Combined ingestive actions	Combined aversive actions
	LTP†	TP	PL	G	FW		HS		
		*						*	*
Spearman's *r*	0·28	0·85	0·49	0·87	0·76	0·02	0·61	0·91	0·90
(*df*)	(4)	(4)	(3)	(3)	(3)	(2)	(3)	(4)	(3)

* $P<0·05$.

† Ingestive actions are: lateral tongue protrusions (LTP), rhythmic tongue protrusions (TP) and paw licks (PL). Aversive actions are: gapes (G), face washing (FW), forelimb flailing (FF) and headshakes (HS).

two possibilities. The first, which might be called a 'flickering determinism', is that individual rats do in fact behave in a purely deterministic fashion but that their stimulus–response curves are extremely unstable (cf. Ludlow 1982 for a similar model). From moment to moment the rat may be expected to behave deterministically; however, its curve shifts or flickers so rapidly that tests spaced minutes apart are effectively testing differing curves. This is essentially a signal detection account, if one assumes that noise varies rapidly within individuals and that the magnitude of this variation is sufficiently great to cause individuals to completely overlap one another over a matter of minutes.

The second possibility is that the response production mechanism itself is probabilistic. All that would be required would be to have an approximation of a random number generator within the nervous system. This random event generator could operate within an otherwise completely deterministic system. It is easy to imagine a software analogue for such a system that would produce the data we have observed. In three steps: (1) randomly pick a number from 0 to 10; (2) set a value X, where X also varies between 0 and 10 and is proportional to the strength of a taste stimulus; (3) if the random number is less than or equal to X, then emit X number of the appropriate action; if the random number is greater than X, then emit none. Of course, the algorithm by which a computer generates a random number may itself be entirely deterministic and it is equally possible that the nervous system generates a random output via a deterministic mechanism. The point, however, is that the output of this neural mechanism is random or chaotic, and this random output constitutes an essential component of each response generation.

Students of animal behaviour have long been aware that it is sometimes useful to speak of behaviour in probabilistic terms. But the probabilistic appearance of behaviour has generally been taken simply to reflect its multicausal nature; there are other factors, internal and external, in addition to the stimulus, which act upon the mechanism of production. For example, external stimuli may combine in space and time (Sherrington 1947). Central excitatory and inhibitory states may combine (von Holst & von St. Paul 1963; Teitelbaum, in press) and impose their summed effects upon external stimuli (Lorenz 1970; Houston et al. 1977; Davis 1980; Toates 1980; Fentress 1983). Multiple internal contributing processes arise and decay at separate rates (Heiligenberg 1976). Processes arising from ongoing behaviour feed back to control the response to the next stimulus (Fentress 1968). There may also be hierarchical interactions between stimuli and states (Tinbergen 1951; Baerends 1970), and between stimuli, oscillators, and servomechanisms (von Holst 1973; Gallistel 1980). These myriad causes all contribute to the inconstancy of the stimulus–response relation. But all of these factors are presumed to act deterministically; it is only the complexity of their interaction that produces the illusion of randomness (although Heiligenberg (1976) suggests that certain internal processes may actually fluctuate randomly; however, these then combine with other, conventional causes to influence behaviour in the deterministic fashion suggested by signal detection theory). The probabilistic model described above differs from these existing conceptions of behaviour by incorporating a random element as an essential feature of the mechanism of behaviour production.

Our data do not allow us to choose between the flickering deterministic and the truly probabilistic mechanisms. In order to decide between them, behavioural or neural experiments of a finer degree of temporal resolution than we have attained here will be required. A flickering deterministic model would predict that, regardless of the number of inputs (e.g. gustatory stimuli, physiological state cues, etc.) into the deterministic decison and of the speed with which they change, there must, at any moment, be some interval (however short) during which two equivalent stimuli would elicit equivalent responses. The probabilistic decision, which incorporates a random element into every stimulus–response decision, would not predict this. In any case, our data suggest that the probabilistic model may be most useful for predicting the behaviour of individuals from minute to minute, even under highly controlled conditions. They also raise the possibility that the neural mechanism of response production may itself operate in a truly probabilistic fashion.

ACKNOWLEDGMENTS

We are grateful to C.R. Gallistel, H.J. Grill, V.M. LoLordo, A.R. Ludlow and D. Treit for their helpful comments on this manuscript. We are especially indebted to C.R. Gallistel and A.R. Ludlow for instruction in the statistics of beha-

vioural modelling. We also thank W.G. Danilchuck and H. Parr for assistance with the behavioural analysis and computer programming. This work was supported by fellowships from the Killam Foundation and from NATO to K.C.B. and by grants from the Canadian MRC and NSERC to J.C.F.

An appendix of the original data used in this analysis (e.g. incidence and suprathreshold mean responses to taste infusions, individual response curves) is available from the authors upon request.

REFERENCES

Baerends, G. P. 1970. A model of the functional organisation of incubation behaviour in the herring gull. *Behav. Suppl.*, **17**, 261–312.

Berridge, K. C., Flynn, F. W., Schulkin, J. & Grill, H. J. 1984. Sodium depletion enhances salt palatability in rats. *Behav. Neurosci.*, **98**, 652–660.

Berridge, K. C. & Grill, H. J. 1983. Alternating ingestive and aversive consummatory responses suggest a two-dimensional analysis of palatability in rats. *Behav. Neurosci.*, **97**, 563–573.

Berridge, K. C. & Grill, H. G. 1984. Isohedonic tastes support a two-dimensional hypothesis of palatability. *Appetite*, **5**, 221–231.

Berridge, K. C., Grill, H. J. & Norgren, R. 1981. Relation of consummatory responses and preabsorptive insulin release to palatability and learned taste aversions. *J. comp. physiol. Psychol.*, **95**, 363–382.

Davis, J. D. 1980. Homeostasis, feedback and motivation. In: *Analysis of Motivational Processes* (Ed. by F.M. Toates & T.R. Halliday), pp. 23–37. London: Academic Press.

Fentress, J. C. 1968. Interrupted ongoing behaviour in two species of vole (*Microtus agrestis* and *Clethrionomys britanicus*). *Anim. Behav.*, **16**, 154–167.

Fentress, J. C. 1983. Ethological models of hierarchy and patterning of species-specific behavior. In: *Handbook of Behavioral Neurobiology, 6* (Ed. by E. Satinoff & P. Teitelbaum). New York: Plenum Press.

Gallistel, C. R. 1980. *The Organization of Action: A New Synthesis*. Hillsdale: Lawrence Erlbaum.

Green, D. M. & Swets, J. A. 1966. *Signal Detection Theory and Psychophysics*. New York: Wiley.

Grill, H. J. & Berridge, K. C. 1985. Taste reactivity as a measure of the neural control of palatability. In: *Progress in Psychobiology and Physiological Psychology, Vol. 11* (Ed. by J.M. Sprague & A.N. Epstein). New York: Academic Press.

Grill, H. J. & Norgren, R. 1978. The taste reactivity test: I and II. *Brain Res.*, **143**, 263–297.

Halpern, B. 1975. Temporal patterns of liquid intake and gustatory neural responses. In: *Olfaction and Taste V* (Ed. by D.A. Denton & J.P. Coghlan), pp. 47–52. New York: Academic Press.

Heiligenberg, W. 1976. A probabilistic approach to the motivation of behavior. In: *Simpler Networks and Behavior* (Ed. by J.C. Fentress), pp. 301–313. Sunderland: Sinauer.

von Holst, E. 1973. Relative coordination as a phenomenon and as a method of analysis of central nervous functions. In: *The Behavioral Physiology of Animals and Man: Selected Papers of Eric von Holst* (translated by Robert Martin), pp. 33–135. Coral Gables: University of Miami Press.

von Holst, E. & von St. Paul, U. 1963. On the functional organization of drives. *Anim. Behav.*, **11**, 1–20.

Houston, A. I., Halliday, T. R. & McFarland, D. J. 1977. Towards a model of the courtship of the smooth newt, *Triturus vulgaris*. *Med. Biol. Eng. Comp.*, **15**, 49–61.

Huntingford, F. 1984. *The Study of Animal Behaviour*. London: Chapman & Hall.

Lorenz, K. 1970. The establishment of the instinct concept. In: *Studies in Animal and Human Behaviour, Vol. 1* (translated by Robert Martin), pp. 259–315. Cambridge, Massachusetts: Harvard University Press.

Ludlow, A. R. 1982. Towards a theory of thresholds. *Anim. Behav.*, **30**, 253–267.

Miller, F. R. & Sherrington, C. S. 1916. Some observations on the buccopharyngeal stage of reflex deglutition in the cat. *Q. J. exp. Physiol.*, **9**, 147–186.

Pelchat, M. L., Grill, H. J., Rozin, P. & Jacobs, J. 1983. Quality of acquired responses to taste by *Rattus norvegicus* depends upon type of associated discomfort. *J. comp. Psychol.*, **97**, 140–153.

Sherrington, C. S. 1947. *The Integrative Action of the Nervous System*. New Haven: Yale University Press.

Teitelbaum, P. In press. The lateral hypothalamic double-disconnection syndrome: a reappraisal and a new theory for recovery of function. In: *100 Years of Psychology in America: G. Stanley Hall and the Johns Hopkins Tradition* (Ed. by S.H. Hulse & B.F. Green). Baltimore: Johns Hopkins Press.

Tinbergen, N. 1951. *The Study of Instinct*. Oxford: Clarendon Press.

Toates, F. M. 1980. A systems approach to sexual behaviour. In: *Analysis of Motivational Processes* (Ed. by F.M. Toates & T.R. Halliday), pp. 319–338. London: Academic Press.

(Received 7 January 1985; revised 3 May 1985; MS. number: A4459)