workers in animal laboratories. The very successful methods that Rachman & Hodgson (1980) used for the treatment of obsessive-compulsive neurosis were taken over more or less directly from an animal analogue involving flooding and response prevention; it is well known that psychotherapy, psychoanalysis, and other "cognitive" methods had always failed completely with disorders of this type, whereas the new methods showed considerable success even after very short applications. Such facts are relevant to a consideration of the importance of cognitive factors and the relative priority to be given to them and to conditioning, respectively. We will only succeed in having a unified science of psychology when all sides agree to look at all the available facts, rather than merely adding small subsections with which they come into professional contact.

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On F. M. Toates (1979) Homeostasis and drinking. BBS 2:95–139.

Abstract of the original article: Drinking and thirst-motivated behaviour have traditionally been explained in terms of the rather simple concept of homeostasis. A homeostatic mechanism readily accounts for responses to acute changes in body-fluid levels. However, there are other factors regulating intake, for example, cues associated with eating, which interact with the time elapsed since last drinking and the availability of water. Future dehydration is avoided by behavioural hysteresis; a sudden reduction in fluid needs is not matched by an equivalent reduction in fluid intake. Another factor not explicable by traditional homeostasis is that, in general, drinking cannot be suppressed by water infusion. Nor are there rigid target values for body-fluid levels independent of the cost of obtaining water; when water is hard to get, a relatively low body fluid level is maintained, thus minimizing loss. On the basis of the results conflicting with traditional homeostatic theory, this paper tentatively suggests certain modifications toward a more realistic model of fluid ingestion.

by W. Tom Bourbon

Department of Psychology, Stephen F. Austin State University, Nacogdoches, Texas 75962

Anticipatory regulation: a raincoat does not feedforward make

In his target article Toates (1979) declares his intent to support and to expand control theory. In fact, as *Powers* (1979) suggests, Toates appears to abandon many principles of such a theory. This is especially true when he discusses the concept of feedforward. Toates defines feedforward as "anticipation," which is said to be a consequence of learning. Toates places feedforward in opposition to the concept of feedback. He invokes feedforward to explain drinking, which seems to anticipate water deprivation or loss. Metaphorically, he cites the example of "putting on one's coat before going out because the weather looks bad." Such behavior is said to be responding, not to

current disturbances, but to stimuli (CS's?) associated with disturbances (UC's?) in the past. In his discussion Toates seems to overlook some significant features of negative feedback in control systems.

A control system acts to maintain certain goal, or reference, perceptions of conditions. If those conditions are perceived to exist, the system acts to maintain them. If they do not exist, the system acts to produce them, or to change what it does perceive. If they exist along with perceptions that they are threatened, the system acts to prevent the threats or to make them not be perceived. In all cases the system deals with *current* perceptions by way of feedback control. Persons who don coats do so because of current perceptions of threat to the immediate goal of maintaining comfort. As a result, they stay warm and dry. The fact that a threat to their goal was perceived accounts for their behavior. To say the weather "looks bad" implies there is a reference condition, or goal, which is to continue as much as possible the feeling that the local environment of one's body is "good." If the sky does not cooperate, the coat will do the trick. If the rains do not come, the inconveniences of wearing a coat are generally minor. For a rat in a natural environment, drinking "in anticipation of deprivation" avoids dehydration, should deprivation occur, and probably has few negative consequences if deprivation does not follow.

The conclusion that anticipatory behavior is a result of feedforward, as opposed to feedback, generally results from using the wrong time intervals for one's observations of the functioning system. Persons viewed only while they are carrying a coat *before* bad weather will be seen as "anticipating" the weather. Those viewed only while they are wearing a coat *during* bad weather will be seen as "reacting to" the weather. When viewed over an appropriate interval, they are seen as maintaining their personal comfort. A rat, observed over an appropriate interval, maintains control over the many sensed variables related to fluid balances in the body.

Several commentators suggested that Toates was too quick to abandon a feedback model, and that his decision to do so resulted from an inadequate statement and assessment of such a model. Examination of more thorough presentations of such models (*cf.* Jagacinski 1977; *Powers* 1973; 1978) supports those suggestions. Drinking may relate to many variables, but an appropriately posed negative feedback model can describe such behavior both qualitatively and quantitatively.

by **John David Sinclair**

Research Laboratories of the State Alcohol Monopoly (Alko), SF-00101 Helsinki 10, Finland

Compensatory behaviors and the "rest principle"

Although the evidence that Toates (1979) presents concerning the importance of nonhomeostatic factors is rather convincing, there is another body of evidence, which neither he nor his commentators cover, that also strongly supports his views. This comes from homeostatic-like control of the intake of flavored solutions.

Rats and monkeys that have had prolonged access to alcohol solutions to drink, in addition to food and water, show a large, temporary increase in their alcohol intake after being deprived of alcohol for several days (Sinclair & Senter 1968; Sinclair 1971). In addition, rats given access to alcohol only on alternate days gradually increase their consumption when it is available until they are drinking approximately twice the amount consumed per day on continual access (The intake of food and water decreases compensatorily to the increase in alcohol solution consumption).

These results resembled those with food and water both qualitatively and temporally. Consequently, it was frequently proposed that alcohol drinking is controlled by a homeostatic "alcoholstat" analogous to the classical homeostatic systems for food and water. It was then found, however, that similar results were also obtained with a variety of other flavored solutions (Wayner et al. 1972). Furthermore, the emission of nonconsummatory responses such as wheel-running and socializing is also increased by deprivation of the opportunity to make the responses. Even the simple phenomenon of choosing the right arm of a T-maze after having entered the left on the preceding trial (i.e. spontaneous alternation) can be seen as such a compensatory behavior. Finally, there was the curious series of findings that of

all species tested, one (the golden hamster) failed to compensate for deprivation of alcohol (Sinclair & Sheaff 1973), food (Silverman & Zucker 1976), saccharin, and water with large increases in consumption, and it also failed to show spontaneous alternation (Sinclair & Bender 1978).

It seems very unlikely that the similarities between these other compensatory behaviors and food and water consumption are accidental. It also seems unlikely that the other compensatory behaviors are all caused by mechanisms resembling the classical homeostatic systems. The remaining conclusion is that there is some other factor responsible for compensatory behaviors, including the deprivation-induced increases in food and water intake normally seen.

It has frequently been suggested that homeostatic factors are unimportant for short-term regulation of drinking and eating, but that they act only as emergency back-up systems. The above results suggest that the homeostatic systems are also unimportant for the additional increases produced by extending the periods of deprivation beyond a few hours.

In order to account for the similarities among the compensatory behaviors, the other factor must be common to all of them, yet they have little in common except that they are all elicited by neuronal activity. The other factor, therefore, might well be the general tendency, suggested by a large amount of recent neurophysiological research, for neuronal connections to become weaker with use and to become stronger during rest after use (see review, Sinclair 1978). According to this "rest principle," the neuronal pathways involved in, for instance, drinking would become weaker as the animal consumes water and would then slowly become stronger again when it is not drinking. As the connections become stronger with deprivation, it becomes progressively easier for stimuli to elicit drinking and for drinking to compete successfully against other responses. The size of the initial drinking bout will also increase with deprivation, since more use will be needed to reduce the strength of the drinking pathways to the point where competing responses can interrupt the activity.

It has been shown elsewhere (Sinclair 1980) that the "rest principle" can form the basis for a general theory of learning and behavior. Of relevance here is the demonstration that, given only initial random innervation between neurons excited by various stimuli and those triggering various actions, the connections will automatically become organized to produce a complex response chain for water procurement. For instance, water-licking becomes elicited by the combination of homeostatic signals: water next to the mouth, and the absence of water in the mouth; swallowing becomes elicited by the combination of homeostatic signals and the presence of water in the mouth. These connections become stronger because each response eliminates one component of its compound stimulus and also helps to eliminate the homeostatic signals, thus assuring the connections of immediate and long-term rest after use. Inhibitory connections onto the response chain would be strengthened from neurons stimulated by the combination of stomach extension (not pressure) and the taste/feel of water in the mouth, and also from those involved in competing responses. Once the complex response chain becomes established, it becomes partially autonomous: i.e., the probability that water will be obtained is influenced by the current strength of the connections within the chain, determined by when they were last used and how much they were used at that time, as well as by the excitatory and inhibitory inputs onto the chain. Homeostatic signals constitute only one of the many inputs and thus play only a complementary role in regulating drinking.

Author's Response

by **Frederick M. Toates**

Biology Department, The Open University, Milton Keynes MK7 6AA, Buckinghamshire, England

The modelling of incentive motivation processes

Introduction. The commentaries by **Bourbon** and **Sinclair** raise interesting issues. I would like to reply to both

commentaries in terms of 1) my original argument, and 2) the incentive-motivation model of Bindra (1969; 1976; 1978). My own arguments are entirely compatible with those of Bindra, and I regret that space precluded discussion of this work in the original review.

Incentive Motivation. Bindra describes the motivating and directing role of incentive stimuli. Incentive means roughly the same thing as cue strength. One might either say that body-fluid state and cue strength combine, by some rule, to give a motivational tendency, or that certain stimuli have their incentive value increased by body-fluid states (Toates 1980). Thus, water has a certain incentive value, and a relatively low body-fluid state acts as a "gate" to enhance this incentive value (Bindra 1978). A relatively high body-fluid state diminishes, or makes negative, the incentive value. In reply to **Bourbon**, this *is* negative feedback, and it is clearly present in the argument of my target article.

Control Theory. It is argued by **Bourbon** that "a control system acts to maintain certain goal, or reference, perceptions of conditions." But how? Surely not by mystical forces, but by the interdependence of biologically describable component processes. To a large extent, control theory was introduced into biology and psychology by investigators interested in human performance and vision. But rather different engineering models apply to motivational systems. To understand the performance of, say, visual tracking, one does not need to consider such details of the target object as its colour and hedonistic rating. By contrast, the performance of the control system responsible for energy intake (i.e. daily energy intake and body weight) does depend upon the food available. In rats, caloric intake is relatively high on a "sweet supermarket" diet (Wirtshafter & Davis 1977); some rats become enormous. So exactly what is the rat so carefully perceiving and defending? Bolles (1980) lucidly discusses this issue [see also Bolles & Fanselow: *BBS* 3(2) 1980]. Models must relate biologically meaningful events; they must not be abstract descriptions. If the biology is uncertain, then at least the models must be psychologically viable.

A realistic model of energy intake is of the form $c = x - k \cdot y$, where e is daily energy intake, x is some intrinsic incentive value of the food, k is a constant, and y is some measure of internal energy state. This has a negative feedback aspect, but it shows that equilibrium is dependent upon the incentive value x. Water intake can probably be fitted to a similar model, but the additional negative feedback loop of ADH (antidiuretic hormone) is present. Something looking remarkably like a set-point may emerge, and although it may then seem rather pedantic not to use the term "set-point," the strict embodiment of control is different. In other cases (e.g. feeding), to imagine a reference value for some internal energy state (Davis & Wirtshafter, 1978) seems to be stretching the concepts to the breaking point.

Consider the developmental origins of motivational control systems and take, for example, the rat-pup. It is wrong to claim that it sucks the mother's nipple because it is driven to do so by error signals in either a thirst or hunger control system. It sucks because of sensory incentive properties of the nipple and the opportunity to exercise the innate mechanical action of sucking. Only later does nutritional state exert a restraining role (Hall, Cramer, and Blass 1977). Later still, the environment provides incentives relating to distinct energy and fluid states. For a desert-adapted species such as the gerbil, in whose environment free water is unavailable, presumably distinct incentives for energy and fluid state never appear. Moist food would answer both needs. Parenthetically, it is worth relating such an incentive model to the broader issue of competition. What competes for motivational expression, inner drive states or incentives? Suppose the same incentive (e.g. moist food) applies to two "drives," hunger and thirst. These would hardly compete but would complement each other. Presumably, where competition does occur, it is between incentives stimulating different motor responses of locomotion and the like.

When we consider the mature animal, developmental history is vital, and a rather peculiar kind of control theory is needed. Thirst is aroused by water incentives accentuated by body-fluid states, but what switches thirst off? I would argue that the inhibitory signal is normally derived from a combination of partial restoration of hydrational state, stomach water contents, and water passing the mouth (Blass & Hall, 1976), the latter being inextricably associated with the actual mechanics of drinking (Hall, Cramer, and Blass 1977; Glickman & Schiff 1967). As Hall, Cramer, and Blass (1977) remind us, the animal deprived of food or water is not only deprived of chemical substances but also of the opportunity for making the mechanical responses of ingestion. This brings us near to the subject matter of **Sinclair**'s last paragraph.

Feedforward. According to **Bourbon**, Toates is supposed to "place feedforward in opposition to the concept of feedback." In fact, they are two aspects of the same system. It is a question of whether we talk about distinct systems or merely aspects of one system. The feedback aspect refers to the potentiation of the incentive value of water by relatively low hydrational levels. Potentiation of incentive, and hence ingestion, by association with cues (e.g. eating) predictive of future fluid states is feedforward. According to my argument, the subsequent effects of the feedforward mode of action on physiological state may adjust the future strength of feedforward. If I put a coat on because I am cold, it is feedback. If I put it on, despite being thermally comfortable, because I am about to enter a colder environment, it is feedforward. If I adjust future feedforward behaviour on the basis of the outcome of past feedforward experience, it is adaptive control. All these modes of control serve the same end – to minimise departures of temperature from optimum. To pursue Bourbon's example, people carrying a coat may be showing anticipation, but they are not showing feedforward. They show either feedback or feedforward, as the case may be, only when they put the coat on. Nothing that Powers or Jagacinski have written makes this distinction less valid.

The "rest-principle." I was familiar with **Sinclair**'s work and was fascinated to read about what is apparently a rodent model of Eysenckian (Eysenck 1977) introversion (hamsters) and extraversion (rats, and everybody else). When Sinclair's book becomes available, it will make it much easier for me to consider this work in depth. My initial reaction is one of some surprise that events at the level of the individual cell and its synapse can apparently be so easily translated to explanations of gross behavioural events. Similarly, one wonders, for example, how useful the synaptic basis of habituation, investigated in invertebrates such as *Aplysia*, will be as a model of complex vertebrate behaviour. To take another example, some animals are strongly aroused sexually by replacing a familiar partner by a novel partner having different characteristics – a phenomenon known as the Coolidge effect. It seems to make functional sense, in that it is most apparent in animals having the most to gain by a promiscuous strategy (Schein & Hale 1965), but at what level in the nervous system can we explain it? [See also Symons: "The Evolution of Human Sexuality" *BBS* 3(2) 1980].

In terms of ingestive behaviour, one can see the advantages to an animal of showing what could loosely be called sensory adaptation to particular taste stimuli. Recovery would increase the effectiveness of the stimulus in inducing ingestion. Time will tell whether **Sinclair** has produced a convincing neural model of such processes. Take, for example, an

animal that is able to obtain essential nutrients (e.g. vitamins and amino acids) only by sampling from each of three distinct foods. It may show temporary satiety to food 1 due to sensory adaptation (loss of incentive) but be "hungry" for foods 2 and 3. Such a mechanism would deliver a balanced diet, and there is evidence that rats do behave rather like this (LeMagnen 1971). In the extreme, if a single diet were to be deficient, then an aversion to it would develop (Rozin & Kalat 1971; Booth & Simson 1971), but that probably reflects an emergency mechanism. There is evidence that spiders forage optimally in terms of a balanced diet (Greenstone 1979), though the mechanism by which this is achieved is, as yet, obscure.

Sensory adaptation avoids some of the problems inherent in proliferating drives to account for the variety shown in the animal's ingestive habits. We do not envisage an array of bodily deficiency states corresponding to different dietary components and giving rise to distinct drives. With one or two notable exceptions (e.g. sodium), it would be difficult to see how a deficiency state would make itself felt in such a specific way. Taste could more easily record recently ingested substances and give a balance to the diet.

The results of Wayner and associates, to which **Sinclair** refers, may be explicable, up to a point, in terms of sensory adaptation to specific chemical substances and their associated taste. This might partly explain how intake is enhanced by short periods of alcohol deprivation, and it would thus be compatible with Sinclair's model. In addition, though, we imagine that an associative factor will be present; drinking alcohol will have either advantageous or adverse consequences, which will potentiate or diminish its incentive value. Given the presence of other caloric and fluid sources, it is not clear as to how the rat might assess the consequences of ingestion. Neither is it clear as to how the various deprivation schedules would enable the rat to change the strength of associative factors.

I am not sure whether **Sinclair** would predict a long-term potentiation of ingestion by a single period of deprivation. In terms of his model, I can't see why he should. But this does occur in the case of 0.05% saccharin solution, as shown in Figure 23 of the article by Wayner et al. to which Sinclair refers. To my knowledge, it has never been shown to occur for normal food and water deprivation. In the case of wild rats brought into captivity, a water-restriction schedule is followed by a massive, but only transient, increase in daily water intake (Boice 1971).

In addition to the "rest principle" being applicable to the induction of ingestion by specific sensory inputs, it might also apply to the general mechanics of drinking (see earlier). Hence, if a rat is infused subliminally with water, this might not normally reduce drinking to the expected extent, simply because any reduction in motor output allows recovery of the neuromotor side of drinking. This reminds us of the Lorenz model of motivation (see Lorenz & Leyhausen 1973).

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