

Palatability Shift of a Salt-Associated Incentive During Sodium Depletion

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Previous studies of natural palatability-sensitive reactions, elicited from rats by tastes, have indicated that the taste of concentrated NaCl becomes more palatable during states of body sodium depletion. A training procedure based upon "sensory preconditioning" or "irrelevant incentive" designs was used here to establish gustatory conditioned labels (quinine or citric acid) for either NaCl or fructose while rats were in a normal physiological state. Experiment 1 replicated demonstrations by others that gustatory conditioned labels for salt can attract and act as independent incentives during the salt appetite induced by sodium depletion. Experiment 2 used the taste reactivity measure to show that the enhanced palatability of the taste of NaCl transfers to produce enhanced palatability of the taste of the isolated conditioned label for salt in a state-dependent fashion. These results offer further support for the proposition that conditioned incentives not only predict hedonic events to follow, but themselves become attributed with the hedonic properties of their reinforcers.

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Contemporary animal learning theory stresses the informational nature of the association between a conditioned and unconditioned stimulus (CS and US) (Bolles, 1972; Mackintosh, 1983; Dickinson, Nicholas, & Adams, 1983; Holland, Holyoak, Nisbett, & Thagard, 1986; Rescorla, 1988). There are a number of ways by which a predictive association might be translated into a

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specific conditioned response. From a simple redintegrative duplication of the unconditioned response in S-R fashion, to the cognitive representation of the expected event and of anticipatory behavioural strategies, a range of possible psychological processes and production rules can be imagined for translating associations into behaviour (e.g. Mackintosh, 1983; Toates, 1986). This study examined the role of one particular psychological process in the production of behaviour guided by associations: the transfer of affect from the US to the CS, and attribution of the US's hedonic properties to the CS when the CS is subsequently encountered alone.

Recent incentive theory formulations suggested by Bolles (1975), Bindra (1976; 1978) and by Toates (1986) posit not only that hedonic attributions might occur during conditioning, but that they are an essential component of the psychological mechanism by which much goal-directed behaviour is controlled. This view is useful for explaining a variety of behavioural observations, ranging from the fact that animals may immediately return to a place where they have experienced concentrated (and normally unpalatable) salt when they are suddenly rendered sodium-deficient (Kriekhaus & Wolf, 1968; Kriekhaus, 1970; Toates, 1986), to the finding that a signal for food presentation may elicit eating from non-deprived rats (Weingarten, 1984).

There is at least suggestive evidence to support the proposition that associative predictors of significant events acquire (rather than merely signal the impending occurrence of) the hedonic properties of those events. A conditioned signal for food can elicit approach, and on its own can serve as a potent reinforcer either for new signals or instrumental actions. Signals for aversive events, on the other hand, may be avoided and can punish or suppress appetitive responses (Dickinson, 1980; Mackintosh, 1983). But even an informational model that did not assume transfer of affect to the signal might nonetheless predict that animals would work to obtain a situation that signals an impending sought-after event and to avoid one that signals an impending aversive event (e.g. Holland et al., 1986).

More convincing evidence to suggest a transfer of affective value to the CS is provided by Dickinson and Dearing's (1979) demonstration that a light signalling the omission of food could block conditioning to a tone that signalled the occurrence of shock. Such blocking can be explained by assuming that these two signals are perceived by the animal as hedonically equivalent and redundant in spite of their differences. This suggests that the signal by itself either induces an affective state or is encoded in terms of its associated affective state.

A second line of evidence for affective transfer, well suited to questions concerning whether conditioned signals elicit the specific type of affect produced by their unconditioned events, comes from measures of natural action patterns. Particular natural patterns can reflect highly specific motivational or perceptual states, and are unconditionally triggered by a narrow

range of appropriate eliciting events. Yet these patterns, and, perhaps, the psychological states that accompany them, appear to be transferable to learned elicitors. Autosshaped pecks by pigeons to a lighted key, for example, have action forms that are appropriate to the particular class of reinforcer (food or water) used to establish the pecks (Jenkins & Moore, 1973).

Tastes elicit a distinct set of natural responses in rats (Grill & Norgren, 1978a). These natural responses provide a sensitive assay of food hedonics (Grill & Berridge, 1985). Preferred tastes, such as sucrose, elicit an ingestive pattern of tongue protrusions and mouth movements. Avoided quinine, on the other hand, elicits an aversive pattern of gapes, headshakes, chin rubs, and forelimb actions. But these responses reflect the rat's affective evaluation or palatability assessment of the taste rather than representing either a fixed reaction to particular sensory features (e.g., sweet, bitter, sour, salty) or necessary motor elements of ingestion (Grill & Berridge, 1985). These taste-elicited actions are often affected by changes in physiological state, by neural condition, and by pharmacological and associative manipulations in ways that parallel the changes such manipulations produce in human palatability assessments and in taste preferences of animals (see Grill & Berridge, 1985 for review). Depletion of body sodium, for example, causes the aversive reactions typically elicited by concentrated NaCl solutions to be replaced entirely by ingestive reactions (Berridge, Flynn, Schulkin, & Grill, 1984). Associative pairings of sucrose with LiCl-induced illness, on the other hand, shift the response to sucrose to an aversive pattern (Grill & Norgren, 1978b; Berridge, Grill, & Norgren, 1981; Pelchat, Grill, Rozin, & Jacobs, 1983). Manipulations that can be construed as acting on psychological processes that are separable from hedonic evaluation, however, do not affect taste reactivity, even though they may drastically alter food intake. For example, associative pairings of taste with electric shock or amphetamine, or physiological manipulations such as brain dopamine depletion or hypothalamic stimulation, may produce dramatic changes in intake without changes in hedonic taste reactivity: these manipulations have been argued to control behaviour by altering non-hedonic processes (Pelchat et al., 1983; Parker, 1988; Berridge, Venier, & Robinson, 1989; Berridge & Valenstein, 1988). Taste-elicited natural actions thus provide a specific index of food affect, unobtainable by simple intake measures, that can be applied to investigations of the role of affective transfer and attribution in incentive conditioning.

S-R Conditioning of Motor Reactions

In an animal choice or preference test, a neutral taste that has been paired with a preferred sweet taste may become more highly preferred itself (Holman, 1975; Fanselow & Birk, 1982; Boakes, Rossi-Arnaud, & Garcia-Hoz, 1987). A parallel change is seen in the taste reactivity profile elicited

from rats by a taste that has been paired with sucrose: it becomes correspondingly more ingestive and less aversive (Breslin, Davidson, & Grill, 1987), supporting the hypothesis that a conditioned hedonic reevaluation produces the preference shift. Similarly, a tone that signals food delivery can elicit approach to the food dish or even reinstate eating in a non-deprived animal (Weingarten, 1984), and a tone paired with oral infusions of sucrose causes the consummatory response elicited by neutral water to include more positive ingestive actions (whereas a tone paired with quinine shifts the response to water towards aversion), again supporting a conditioned change in affective evaluation as cause for the change in intake (Delamater, LoLordo, & Berridge, 1986).

These consummatory response shifts have been interpreted as reflecting a transfer of affect from the reinforcer to the conditioned incentive. This transfer of affect to the conditioned stimulus could partly explain the ability of the stimulus to control feeding. But another interpretation of these shifts has been possible. Conditions allowing the formation of an S-R association have existed in training procedures that paired presentation of the conditioned stimulus with direct elicitation of ingestive or aversive motor patterns by the unconditioned reinforcer. For each training trial, the CS was paired directly with the actions elicited by the unconditioned taste stimulus. For these experiments, it is difficult to rule out conclusively the possibility that a UR-paired taste or tone has elicited a consummatory response in an S-R fashion independent of the hedonic state elicited by the conditioned incentive or by the stimuli associated with it (cf. Harlow, 1937; Hull, 1943; Rizley & Rescorla, 1972).

This S-R alternative to a hedonic attribution account could be excluded from interpretations of a conditioned consummatory response shift, however, if the conditioned incentive was created using a procedure that did not pair the conditioned stimulus directly with the unconditioned motor response. Sensory preconditioning (Brogden, 1939; Lavin, 1976) and irrelevant incentive paradigms (e.g., Dickinson, 1986), which form associations between stimuli prior to their becoming activationally or hedonically potent, provide models for such a procedure. Fudim (1978) developed preference shifts in rats, using a sensory preconditioning design to give banana or almond flavours conditioned incentive properties that could be activated by deficiency-induced salt appetite. The rats received flavour-salt-taste pairings while in a normal physiological state. When the motivational value of the salt reinforcer was enhanced after conditioning, by body sodium depletion caused by formalin injections, the rats increased their preference for the flavour that had previously been paired with salt relative to the flavour that had been paired with sucrose. Similar results were obtained by Rescorla and Freberg (1978) using quinine as the conditioned taste.

Salt appetite is a useful phenomenon for the study of incentive processes

(Denton, 1982; Stellar, 1987). Without prior training, animals respond to depletion of body sodium with an increase in consumption of concentrated NaCl solutions that are normally avoided (Richter, 1956; Wolf, 1969; Denton, 1982). Animals that have previously experienced NaCl even briefly in a particular location, or as a reinforcer for an instrumental response, will return to that place, and increase anticipatory instrumental responding, upon depletion of body sodium (Dickinson, 1986; Kriekhaus, 1970; Kriekhaus & Wolf, 1968; Paulus, Eng, & Schulkin, 1984; Quartermain, Miller, & Wolf, 1967; Rosenwasser, Schulkin, & Adler, 1988; Weisinger, Woods, & Skorupski, 1970; Wirsig & Grill, 1982). The psychological target of the appetite is better characterized as the taste of salt rather than as sodium per se: consumption of salt solutions such as LiCl, which do not contain sodium but which are judged as highly salty by humans and generalized to NaCl by rats, are also enhanced by body sodium depletion (Falk, 1965; Nachman, 1963; Schulkin, 1982). Sodium depletion is accompanied by shifts in the perceived palatability of the taste of salt in humans (Bertino, Beauchamp, Risky, & Engelman, 1981) and in the taste-reactivity palatability measure in rats (Berridge et al., 1984; Grill, Schulkin, & Flynn 1986).

The purpose of the present study was to examine whether conditioned incentives become attributed with the affect of the hedonic event they predict. This was done by combining the hedonic sensitivity of the taste-reactivity test with the ability of the sensory preconditioning procedure to create gustatory incentives without directly pairing the conditioned taste with the unconditioned consummatory response. The first experiment replicated the ability of the sensory preconditioning/salt appetite procedure to create a learned gustatory incentive capable of controlling intake. Experiment 2 applied a taste-reactivity analysis to ask whether such a learned incentive acquires new palatability or affect as a result, in a fashion similar to that of its associated reinforcer.

EXPERIMENT 1

Method

Subjects

The subjects were 8 naive male Sprague-Dawley rats (275–350 g) housed individually on a 14:10 LD cycle. These rats had never experienced sodium depletion or NaCl solutions prior to this experiment. Rats had free access to sodium-free chow pellets and to distilled water throughout the experiment.

Training Solutions

Taste solutions were chosen on the basis of pilot studies that attempted to

assess preference for the compound solutions. Sour or bitter CS labels were paired with salty or sweet US tastes. Fructose, a moderately palatable sugar, was chosen as the second US for discriminative conditioning because it provides a gustatory incentive that is unrelated to sodium balance. CS concentrations were 0.01 *M* citric acid (0.2%) and 3×10^{-5} *M* quinine hydrochloride (0.01%). US concentrations were 0.37 *M* NaCl (2.2%) and 0.2 *M* fructose (3.6%). The CS paired with NaCl will be referred to as CS⁺ and the CS paired with fructose will be referred to as CS⁻. For half of the group of rats the CS⁺ was citric acid and the CS⁻ was quinine. For the other rats, the opposite pairing was employed.

Procedure

Preconditioning Procedure: Days 1–4. Rats had continuous access to a drinking tube containing their CS⁺-NaCl compound, in addition to food and water during Days 1–4. The CS⁻-fructose compound also was available for 24 hr on Days 2 and 4. Different exposures to the compounds were given because pilot tests had shown that rats in a normal physiological state consumed 40% less of the CS⁺-NaCl compound (6 ml) in 24 hr than of the CS⁻-fructose compound (10 ml), and because we wished to equate preconditioning *intake* of the compound solutions. Intake was recorded daily. Both compounds were removed at the end of the fourth day.

Testing and Sodium Depletion Procedure: Days 5–8. Each rat was tested in a 30-min preference test with their isolated CS⁺ and CS⁻, once while in a normal sodium-balanced state and once while sodium-depleted. Half of each group was tested first while depleted; the other half was tested first while sodium-balanced. This was intended to balance extinction and to maintain equivalent association strengths across sodium test states (but see Holland & Rescorla, 1975, concerning deprivation effects on extinction).

Rats that were tested first while depleted were injected on Day 5 with 5 mg furosemide (10 mg/ml, i.p.) and again with the same dose 2 hr later. This procedure produces significant urinary excretion of body sodium and a robust salt appetite within 24 hr (Wolf, 1982). On Day 6 these rats were given 30 min access to a tube containing 0.01 *M* citric acid and to a separate tube containing 3×10^{-5} *M* quinine HCl. The position of these tubes was switched every 5 min, and intake was recorded. The CS tubes were removed, and, in order to re-establish sodium balance, the rats received 24 hr free access to 0.5 *M* (3.0%) NaCl, in addition to food and water beginning 1 hr later. This concentration of NaCl differed from that used in training in order to minimize any loss of associative strength produced by presenting a salt US alone. On Day 8 the CS⁺/CS⁻ 30-min preference test was repeated in this rebalanced state and followed again by 24 hr access to 0.5 *M* NaCl (to allow a comparison of NaCl consumption in balanced and depleted states).

Rats that were tested first while sodium-balanced received the balanced 30-min test on Day 5, and 24 hr free access to 0.5 M NaCl over Days 5–6. They were injected with furosemide on Day 6 and re-tested with CS⁺/CS⁻ while sodium-depleted on Day 7. They were again given free access to 0.5 M NaCl over Day 8.

Results

The effectiveness of furosemide injections in inducing a salt appetite was reflected in the 0.5 M NaCl intake over the 24-hr period beginning the day after the injection. Rats drank twice as much NaCl after sodium depletion as they did in sodium balance (52 ± 8 ml vs. 21 ± 6 ml), Paired- $t(7) = 11.67$, $p < 0.01$.

Relative consumption of the isolated CS⁺ and CS⁻ solutions was similarly altered by the presence of a salt appetite. A two-way (US association \times Sodium state) repeated measures ANOVA showed effects upon CS consumption by both the associative history, $F(1, 7) = 37.72$, $p < 0.01$, and the sodium state of the rat, $F(1, 7) = 19.70$, $p < 0.01$, as well as a significant Association \times State interaction between the two factors, $F(1, 7) = 17.15$, $p < 0.01$. Specifically, the effect of furosemide injections was to increase selectively the consumption of the CS⁺ solution (Figure 1). When rats were in sodium balance, consumption of the CS⁺ and CS⁻ was equivalent. After furosemide, intake of the CS⁺ was elevated with respect to the CS⁻, $p < 0.01$, Newman-Keuls, and with respect to consumption of the CS⁺ when not sodium-depleted, $p < 0.01$, Newman-Keuls. Consumption of the CS⁻ solution was not affected in the 30-min test by body sodium state.

Discussion

The selective enhancement of consumption of a taste previously paired with salt, expressed only when sodium-deficient, replicates similar findings by Fudim (1978) and by Rescorla and Freberg (1978). These results show in addition that the effect can be obtained without the use either of water deprivation in the preconditioning procedure (which may produce a small loss in body sodium itself: Weisinger, Denton, McKinley, & Nelson, 1985) or of an odorized flavour CS (which might control behaviour independent of taste).

EXPERIMENT 2

This experiment asked whether the state-dependent enhancement of preference for a salt-paired taste was also accompanied by an increase in the perceived palatability of that taste, as assessed by the taste-reactivity

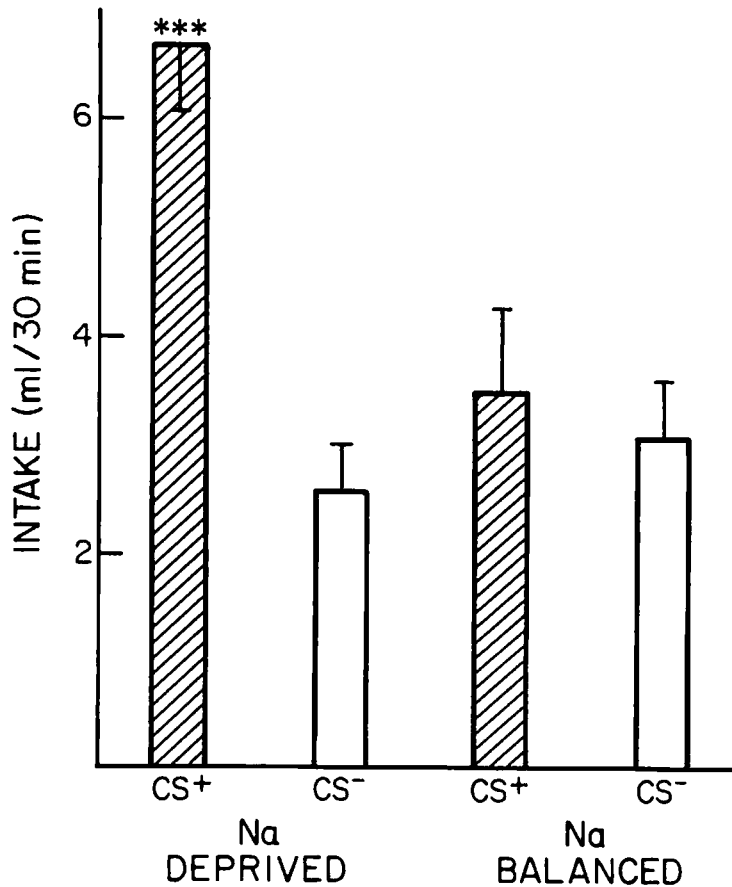


FIG. 1. Experiment 1. Mean amounts (\pm SEM) consumed of the CS⁺ (quinine or citric acid) and CS⁻ solutions in a 30-min intake test while in either a sodium-balanced or sodium-depleted physiological state. Stars denote a statistically significant elevation.

paradigm. In order to avoid a contextual shift from a free-intake training context to a delivered oral-infusion context used for taste reactivity, both the training and test phases of Experiment 2 used cannula-delivered oral infusions to administer the taste solutions.

Method

Subjects

Eight naive male Sprague-Dawley rats (275–325 g), which had not experienced sodium depletion or salt solutions before, were anaesthetized and

implanted with chronic oral cannulae (Grill & Norgren, 1978a). Each cannula entered the roof of the mouth lateral to the first maxillary molar, ascended lateral to the skull, where it was anchored with skull screws and acrylic cement, and exited the head dorsally. These cannulae lie flat against the roof of the mouth and do not disturb normal eating by the rat, but do allow solutions to be directly infused into the mouth when connected to delivery tubes. Preconditioning began after 5 days recovery from surgery. All rats had free access to sodium-free food and to distilled water throughout the experiment.

Training Solutions

The same taste stimuli and compounds were used as in Experiment 1. For half of the group of rats, 0.01 M citric acid was the CS⁺ paired with 0.37 M NaCl. For the other rats, the NaCl-paired CS⁺ was 3×10^{-5} M quinine HCl. The CS⁻ taste for each group (quinine or citric acid) was paired with 0.2 M fructose.

Procedure

Preconditioning Procedure: Days 1-4. Each rat received one 10-min preconditioning exposure per day to the CS⁺-NaCl compound and one exposure per day to the CS⁻-fructose compound, spaced 4 hr apart, on Days 1 to 4. The order of compound presentation was reversed each day. On a preconditioning trial, a stimulus delivery tube (PE 10 nozzle within a PE 160 sheath) was connected to the cannula of a rat, and the rat was placed in an observation chamber for 5 min habituation. A 2-ml volume of the compound solution was infused by syringe pump into the mouth over a 10-min period. Each rat thus received four 10-min controlled exposures to its CS⁺-NaCl compound taste mixture and an equal number of controlled exposures to its CS⁻-fructose mixture. The behaviour of rats during preconditioning exposure trials was recorded by an observer each minute on a check-off basis. This analysis did not reveal differences in the reactions to the preconditioning exposures.

Taste-Reactivity Test: Days 4-6. Each rat was tested twice for taste reactivity to its separate CS⁺ and to its separate CS⁻, once while in sodium balance and once after depletion of body sodium. Half of the group of rats was tested first while in balance, and half was tested first while depleted. In order to check the effectiveness of the sodium-depletion procedure and to replicate the unconditioned shift in salt palatability during sodium depletion, taste reactivity to 0.5 M NaCl was also tested in each sodium state condition.

Rats that were tested first while depleted were injected with furosemide as in Experiment 1 in the late afternoon of Day 4. On Day 5 they were tested in

the morning for taste-reactivity to citric acid (which was the CS⁺ for 1/2; CS⁻ for 1/2). In a taste-reactivity test, a rat's cannula was connected and the rat was allowed to habituate as during preconditioning. A 1-ml volume of the taste solution was infused at a constant rate over 1 min. A mirror positioned beneath the transparent floor reflected a view of the face and mouth into the close-up lens of a videocamera, and behaviour was recorded for later slow-motion analysis. Four hours later each rat was tested for reactivity to quinine, and 1 hr after that for reactivity to NaCl. Each rat was allowed free access overnight to 0.5 M NaCl in addition to food and water, in order to re-establish sodium balance. On Day 6, they were tested for taste reactivity again with quinine, citric acid, and NaCl, in that order, in this re-balanced state.

Rats that were tested first while in sodium balance were tested with NaCl in the afternoon of Day 4 (to avoid delivering NaCl immediately prior to furosemide injections). They were tested sequentially with citric acid and with quinine on Day 5 and injected with furosemide that afternoon. On Day 6, they were again tested with quinine, citric acid, and NaCl, in that order.

Taste-Reactivity Analysis. Each rat was scored for the occurrence of natural ingestive and aversive actions. Strongly ingestive actions are paw licking; lateral tongue protrusion (non-rhythmic) past the lip followed by forward extension, lasting about 160 msec; and rhythmic tongue protrusions along the midline, with a cycle length of roughly 160 msec. Strongly aversive actions are: gapes (large openings of the mandible and retraction of the lower lips lasting about 125 msec); chin rubbing (bringing the mouth in direct contact with the floor and projecting the body forward); face washing (either a single wipe with the paws or a bout of several wipes); forelimb flails (shaking of the forelimb with a frequency of greater than 60 Hz); headshaking (at greater than 60 Hz); paw treading (planting of the forelimbs on the floor and alternating forceful strokes forward and back); and rapid locomotion about the chamber (see Grill & Berridge, 1985, for a discussion of taste-reactivity analysis and palatability).

Videotape Scoring. Videotapes were scored at 1/30 to 1/10 speed by an observer blind to the conditioning history and physiological condition of the rats. For the purpose of quantifying the number of responses emitted, discrete actions such as lateral tongue protrusions, gapes, chin rubs, and bursts of face washing, forelimb flailing, headshakes, paw treading, and locomotion were recorded each time they occurred. Continuous actions that typically persist for relatively long periods were recorded as follows: paw licks, mouth movements, and passive dripping were recorded in 5-sec bins (any occurrence of these behaviours up to 5 sec duration was counted as a single occurrence). Rhythmic tongue protrusions were scored in the same way in 2-sec bins.

Results

The effectiveness of sodium depletion in enhancing salt palatability was demonstrated by a change in taste-reactivity to 0.5 M NaCl (Figure 2, top). Ingestive actions (paw licks, lateral tongue protrusions, and rhythmic tongue protrusions) as a group were increased to NaCl after furosemide injections compared to when sodium-balanced (11.8 ± 1.4 vs. 5.7 ± 1.4), Wilcoxon matched pairs $T(8) = 0$, $p < 0.01$. Aversive responses (gapes, chin rubs, headshakes, paw treads, face washes, and forelimb flails) to NaCl were reciprocally diminished after furosemide injections compared to when sodium-balanced (2.0 ± 1.2 vs. 18.3 ± 4.4), Wilcoxon $T(8) = 0$, $p < 0.01$.

The pattern of ingestive actions elicited by the CS⁺ (citric acid or quinine) that had been paired with salt was also changed by furosemide injections (Figure 3). The effect of sodium depletion on ingestive taste-reactivity to CSs directly paralleled the effects on intake found in Experiment 1, Friedman ANOVA $\chi^2(3) = 9.56$, $p < 0.05$. Specifically, ingestive actions to the CS⁺ were selectively enhanced after body sodium depletion. Total ingestive actions were elevated to the CS⁺ (13.8 ± 2.1) relative to the CS⁻ (7.6 ± 1.2) when rats were sodium-depleted, Wilcoxon matched-pairs $T(8) = 4.00$, $p < 0.05$, while no difference existed between CS⁺ and CS⁻ when rats were in sodium balance (8.4 ± 2.0 vs. 7.8 ± 1.9). Total ingestive reactivity to the CS⁺ when depleted was also elevated marginally above reactivity to the same stimulus when in balance, Wilcoxon $T(8) = 1.00$, $p = 0.06$, and ingestive tongue protrusions as a specific action were significantly more frequent to the CS⁺ when depleted than when in balance (6.5 ± 2.1 vs. 2.1 ± 1.10), Wilcoxon $T(8) = 1.00$, $p = 0.03$.

In contrast to the effect on unconditioned salt reactivity, aversive actions to the CS⁺ and CS⁻ were not affected by sodium depletion (Friedman ANOVA $\chi^2(3) = 4.38$, $p > 0.1$) (see Figure 4). Positive and negative evaluations of palatability have been proposed to be separately controlled (Berridge & Grill, 1984), and these results could possibly indicate a selective change in the positive hedonics of the acquired gustatory incentives. An alternative explanation for this asymmetrical effect might be that the variance of aversive reactions to the CS tastes was relatively high in this study, which would have obscured other effects.

DISCUSSION

Ingestive palatability-dependent responses to an arbitrary incentive taste, which previously had been paired with the taste of salt, were increased specifically during a rat's first experience of sodium deficiency. When sodium-depleted, rats emitted more ingestive actions to the quinine or citric acid CS⁺ than to the CS⁻. This was not the case when the rats were in sodium

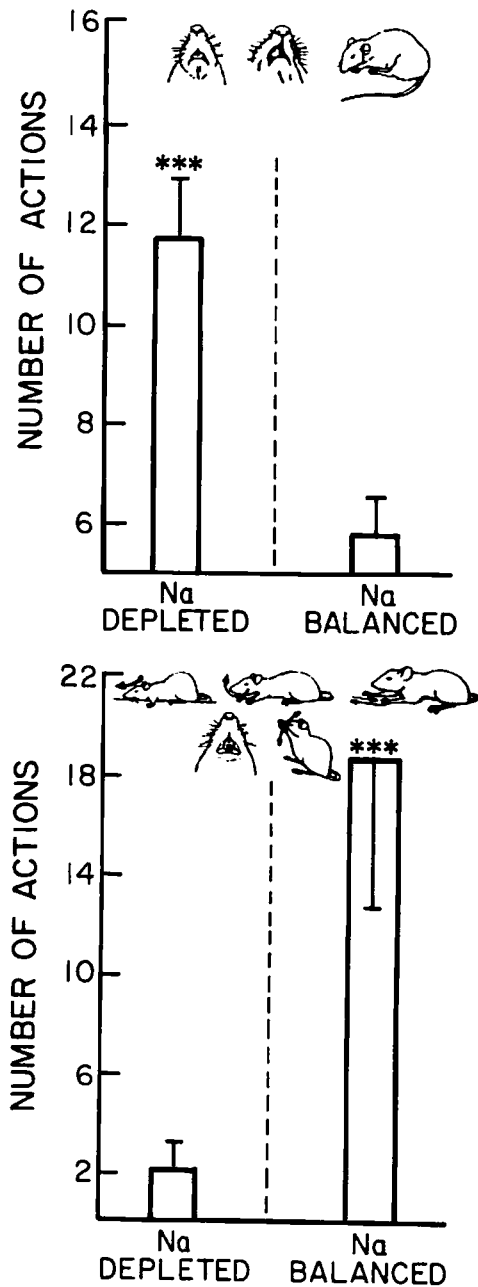


FIG. 2. Experiment 2. Taste reactivity profile to 0.5 M NaCl while in either a sodium-balanced or -depleted physiological state. Top: combined mean (\pm SEM) number of ingestive actions (rhythmic tongue protrusions, nonrhythmic lateral tongue protrusions, and paw licks). Bottom: combined mean (\pm SEM) number of aversive actions (chin rubs, head shakes, paw treads, gapes, face washes, and forelimb flails).

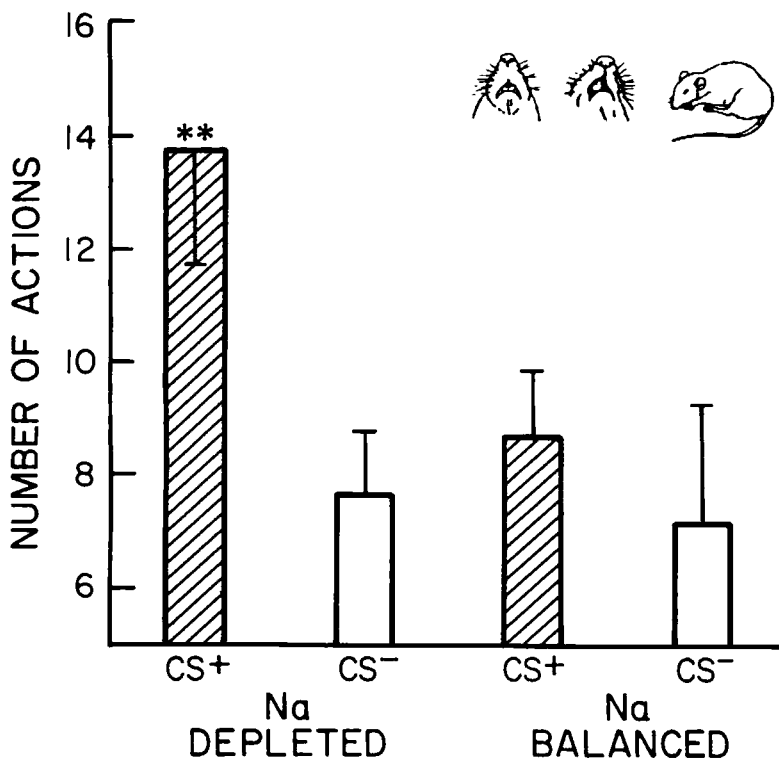


FIG. 3. Experiment 2. Ingestive taste reactivity to conditioned tastes. Mean (\pm SEM) number of combined ingestive actions emitted to the CS⁺ (quinine or citric acid) and CS⁻ while either sodium-depleted or -balanced. Stars denote a statistically significant elevation.

balance. The enhancement of positive reactivity to the CS⁺ occurred in spite of the elimination of the possibility of S-R explanations. S-R hypotheses would have predicted that a CS for concentrated NaCl should always elicit taste-reactivity components similar to those that had been elicited by NaCl itself during sodium-balanced training (i.e. predominantly aversive responses), and that this aversive CR should be independent of sodium state during testing. The S-R predictions clearly are wrong in both cases. These results demonstrate a state-dependent associative shift in the palatability of a gustatory conditioned signal, which occurs in parallel to the shift in palatability of the associated unconditioned salt stimulus.

The present experiments support the view that acquired incentives are attributed with new hedonic properties as a function of conditioning (Bindra, 1976; 1978; Toates, 1986). A conditioned signal for a reinforcer may well generate an expectancy for that impending reinforcer and the future affect it will carry. Yet these and other results (Dickinson & Dearing, 1979) suggest that, in a real sense, when a conditioned incentive is gained, the animal may

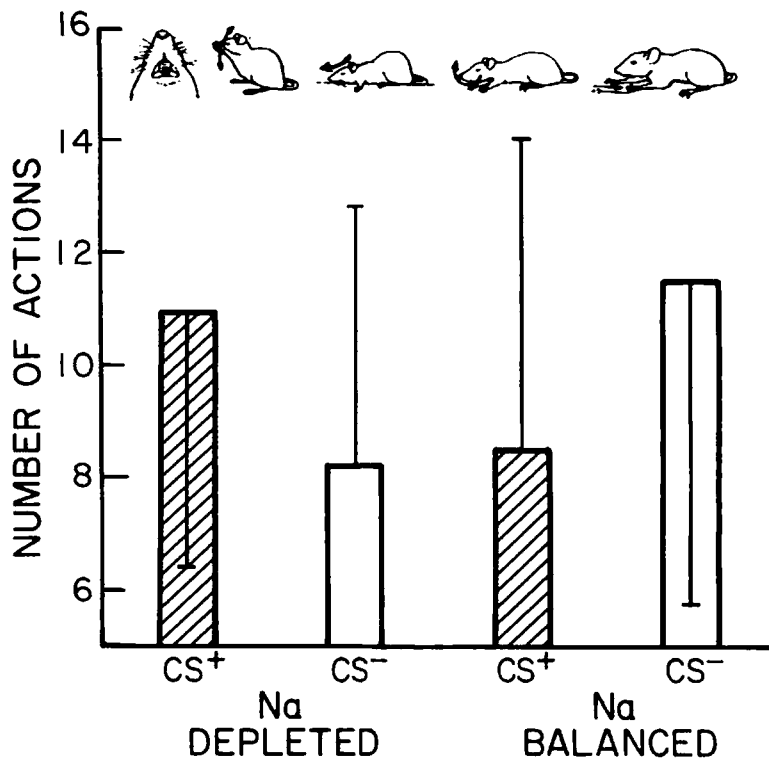


FIG. 4. Experiment 2. Aversive taste reactivity to conditioned tastes. Mean (\pm SEM) number of combined aversive actions emitted to the CS⁺ and CS⁻ while either sodium-depleted or -balanced.

already be hedonically rewarded. As yet, it is not possible to distinguish whether the CS elicits affect by activating an explicit representation of the sensory properties of the US, which carry an hedonic value, or whether the CS has become directly attributed with its own hedonic value, independent of a mediating US representation (i.e. whether the CS-US association operates as a "declarative" or a "procedural" knowledge function in controlling hedonics [e.g. Boden, 1988]). It is clear that the CS becomes capable of acting as a potent hedonic elicitor, however, rather than simply as an informational signal. This is not to deny the potential validity of expectancy theories of associative learning (Holland et al., 1986; Rescorla, 1988); hedonic elicitation is, rather, a particular performance generating rule by which associative representations may be integrated with other psychological systems to control behaviour.

There is some reason to believe that a CS might serve alternatively either

as a predictive signal or as a hedonic target under different conditions. For instance, devaluation of a reinforcer by pre-feeding or by conditioning of an aversion should reduce appetitive responding in extinction if a representation of the devalued reinforcer is accessible to the animal, and in many cases this is what happens (Colwill & Rescorla, 1985; Dickinson 1987; Dickinson et al., 1983). But in other studies animals continue to respond in extinction after reinforcer devaluation (Harlow, 1937; Holman, 1975; Dickinson, 1987), as might be predicted if conditioned incentive stimuli have gained their own hedonic value which can sustain responding in certain situations independent of an expectation of the reinforcer. Hedonic analyses of devalued reinforcers and their conditioned stimuli might provide a way of asking whether CS-elicited affect is always mediated by a US representation. In any case, Pavlovian incentive representations have been argued to be a major component even of apparently instrumental behaviour (Dickinson & Dawson, 1987; 1988) and the "CS as hedonic target" could play an important role in directing such behaviour (see also Berridge et al., 1989).

Finally, the palatability enhancement of a taste previously paired with salt, found only when a rat is depleted of sodium, may highlight a difficulty involved in maintaining a clear conceptual distinction between consummatory and emotional conditioned responses (e.g. Konorski, 1967, pp. 394-395, in which the former is held to arise from CS activation of a "US gnostic unit," whereas the second is held to arise from separate CS activation of a "limbic unit"). As has been pointed out before (Gallistel, 1978; Wong, 1978; Toates, 1986), it was not the palatability engendered by salt during sodium-balanced training trials that became associated with the conditioned quinine and citric acid tastes. The palatability of hypertonic salt when a rat is sodium balanced is relatively aversive, as shown by Figure 2. The shift in reactivity to the CS⁺ that occurred after sodium depletion reflected the palatability that salt *would have had if it had been delivered then*, rather than the actual palatability it had when experienced previously. This indicates that the content of the associative representation triggered by the conditioned taste was more closely of the "pre-evaluation sensory" characteristics of salt, as suggested by Konorski's "sensory-consummatory" versus "affective-preparatory" distinction (1967). Yet to identify the consummatory response with purely sensory properties of the stimulus is clearly impossible: the consummatory response shifted markedly to different presentations of the same taste, for salt, citric acid, and quinine. The taste-elicited consummatory response reflects sensory-appropriate affect, as Toates's (1986) incentive analysis would suggest, rather than sensory quality *per se* (see also Mackintosh, 1983). This affect was shifted appropriately in this experiment by an integration of physiological and associative factors.

In summary, these experiments indicate that neutral stimuli are actively imbued or attributed with affect as a function of associative conditioning.

They support the proposition that conditioned incentives may control behaviour in part by acting directly as hedonic targets, quite in addition to acting as a signal for hedonic reinforcers to come.

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