Sodium Depletion Enhances Salt Palatability in Rats

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Sterotyped fixed action patterns (FAPs) are elicited in rats by oral infusions of taste solutions. These taste-elicited FAPs can be classified as either ingestive or aversive They reflect the palatability of the taste and can be modified by learning and by the physiological state of the animal. These studies demonstrated that when the physiological state of the rat is altered by sodium depletion, the pattern of FAPs elicited by oral infusions of 0.5 M NaCl shifts from a mixture of ingestive and aversive components (while sodium replete) to exclusively ingestive ones (while sodium deplete). This shift in taste reactivity occurred the first time the rats were made sodium deplete. A similar shift was not observed to accompany infusions of 0.01 M HCl, a taste solution that also elicited mixed ingestive and aversive FAPs. This result suggests that the shift in response to NaCl is not due to a general change in ingestive bias or to a general taste deficit. On the basis of the change in FAPs, it is concluded that the palatability of highly concentrated salt solutions increases in sodium-deplete rats. Such a shift in salt palatability may be instrumental in directing the appetitive behavior of the animal.

Infusions of taste solutions into the mouth elicit a pattern of highly stereotyped consummatory responses, or fixed action patterns (FAPs; this term is used to mean a modal, highly stereotyped action rather than a truly invariant one), that vary with taste palatability in rats, cats, and humans. These patterns are coded in their most basic form within the caudal brain stem, although they may be modified by descending forebrain controls in the intact animal (Grill & Norgren, 1978b; Miller & Sherrington, 1916; Steiner, 1977).

Grill and Norgren (1978a) provided a taxonomy of taste-elicited FAPs for the rat and classified each FAP as either ingestive or aversive (see Figure 1). A taste stimulus such as sucrose elicits only ingestive components: rhythmic mouth movements, tongue protrusions, lateral tongue protrusions, and paw licking. In contrast, quinine elicits only aversive components: gapes, chin rubs, head shakes, face washing, and forelimb flailing (Grill & Norgren, 1978a). Other taste stimuli may be perceived as having both positive and negative qualities (e.g., mixtures of sucrose and quinine), eliciting both sets of responses, occasionally in rapid alternation (Berridge & Grill, 1983).

These taste-elicited FAPs reflect complex central nervous decisions about taste palatability. These decisions integrate information from a variety of sources, including physiological state and conditioned associations. The FAPs elicited by a given stimulus vary with changes in satiety (Grill & Norgren, 1978b) and with classical associations involving the taste, such as

learned aversions Berridge, Grill, & Norgren, 1981; Grill, 1975). The sensitivity of this consummatory response measure makes it an excellent tool for examining how these factors can influence palatability processing, and the role of palatability in the control of ingestive behavior.

Salt appetite is an important phenomenon for the study of the control of ingestion (see Denton, 1982; Richter, 1956; Rozin, 1976, for reviews). Deficits in body sodium, or the hormonal concomitants of such deficits, drive animals (a) to ingest excessive amounts of salty solutions (e.g., Nachman, 1963; Schulkin, 1982; and see Denton, 1982), (b) to engage in instrumental responses to obtain salty solutions (Quartermain, Miller, & Wolf, 1967), and (c) to consume considerable quantities of concentrated salty solutions that are normally avoided at such high concentrations (Richter, 1936). Salt intake is thus clearly modified by physiological state.

Taste is a crucial factor in salt appetite. Rats respond to the taste of salt with enhanced ingestion the first time they experience sodium depletion (Handal, 1965; Nachman, 1962), and gustatory reinforcement is an important factor in the maintainance of sodium chloride ingestion (Borer, 1968; Morrison & Young, 1972; Nachman & Cole, 1971). The taste of salt has been suggested to be a naturally attractive stimulus to mammals, at least up to certain concentrations (Denton, 1982; Richter, 1956), but the psychological mechanism that mediates the enhanced salt appetite during sodium depletion has remained unclear. An increase in salt preference could result from a number of different causes. Some of these causes involve changes in the way taste is processed and in the perceived palatability of the taste. Others do not. Possible mechanisms include (a) a reduction in peripheral taste sensitivity to salt of sufficient magnitude to reduce the taste intensity of normally avoided concentrations to an intensity that is normally preferred (Contreras, 1977), (b) a central change in palatability evaluation that allows normally avoided concentrations of salt to continue to be perceived as highly concentrated but nonetheless causes them to be preferred, (c) a rapid feedback

of postingestive cues following salt ingestion when the animal is sodium deplete which reinforces salt consumption independently of its palatability, or (d) any combination of these.

A mild increase in the palatability of salty foods, and reduction of salt sensitivity, during sodium deprivation has recently been suggested in humans (Bertino, Beauchamp, Riskey, & Engelman, 1981). Although it has been hypothesized that the taste of salt becomes more palatable to rats during sodium depletion (e.g., Nachman, 1962), a comparable demonstration in animals does not exist. The purpose of the present investigation was to examine whether sodium depletion induces a change in the pattern of FAPs elicited by hypertonic NaCl in rats. We consider this measure to reflect whether the palatability of concentrated NaCl solutions changes as a function of sodium depletion.

Method

Experiment 1

Five male Sprague-Dawley rats, weighing between 300 and 400 g, were preselected by a two-bottle preference test procedure (Cruz, Perelle, & Wolf, 1977) as reliable responders to sodium depletion-induced salt appetite. In order to infuse the taste solutions, rats were implanted with oral cannulas under ketamine anesthesia (Grill & Norgren, 1978a). The oral cannulas were positioned anterolateral to the first maxillary molar and anchored with dental acrylic to the top of the skull Consummatory response testing began 5 days after surgery.

To ensure that any change observed in taste-elicited FAPs was state dependent, we used an A-B-A-B design so that rats were tested in alternating states of sodium repletion and depletion. In order to verify any effect of the natrorexigenic treatment on taste-elicited FAPs, two-bottle preference tests were administered concomitantly in the home cage

Preference test and injection procedure Testing proceeded over 2 weeks. On Day 1 of each week, the Purina Rat Chow (approximately 1.0% NaCl) was removed from each rat's individual cage and replaced with 60 ml of sweetened condensed milk (approximately 0.1% NaCl) and 40 ml of 0.5 M NaCl in calibrated bottles. Rats had ad-lib access to tap water at all times. On Day 2 of each week, 24-hr intakes of 0.5 M NaCl and water were recorded, and the salt solution was removed from the cage. In this sodium-replete state, each rat was then tested for consummatory responses to 0.5 M NaCl, with the procedure described below

In order to promote natrorexigenesis, each rat was injected sc with 5 0 mg of deoxycorticosterone and 7.5
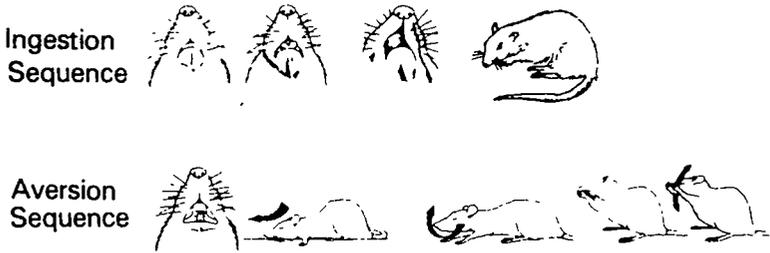
Ingestion
Sequence

Aversion
Sequence

Figure 1.   Taste-elicited consummatory responses. (Ingestive responses [top] are elicited by continuous oral infusions of glucose, sucrose, and other palatable solutions and include rhythmic mouth movements, tongue protrusions, lateral tongue protrusions, and paw licking. Aversive responses [bottom] are elicited by infusions of quinine solutions and include gapes, chin rubs, head shakes, face washing, forelimb flailing, and locomotion [not shown].

mg of furosemide immediately after the consummatory response test and returned to its home cage; 4 hr later rats were injected with an additional 7.5 mg of furosemide (Cruz et al , 1977). On Day 3, 24 hr after the first injection, each rat was again tested for consummatory responses to 0.5 M NaCl, but this time in a sodium-depleted state. Following this test, rats were returned to their home cages for another 24-hr preference test. Ingestion of the NaCl, water, and milk diet was recorded. Rat chow was returned for the weekend, and the NaCl was removed from the cage.

Consummatory response test   Consummatory response tests were carried out in a cylindrical, clear plastic testing chamber. Each rat's oral cannulas were connected to stimulus-delivery tubes, and the rat was then allowed to habituate to the chamber for 10 min A 1-ml volume of 0.5 M NaCl was infused into the rat's mouth at a constant rate (1 ml/min) over 1 min, and the rat's taste-elicited FAPs were videotaped through a mirror positioned below the chamber for subsequent analysis. The time spent ingesting (amount consumed) during the 1-min infusion was also recorded (Berridge et al., 1981).

Consummatory response criteria   Using a slow-motion videotape analysis, we scored each rat for the occurrence of ingestive and aversive FAPs. Ingestive components (see Figure 1, top) are mouth movements—low-amplitude, rhythmic openings of the mandible (6.6 Hz); tongue protrusions—rhythmic protrusions of the tongue on the midline (8.8 Hz), with the tongue covering the upper incisors; lateral tongue protrusions—nonrhythmic extensions of the tongue on either side of the mouth, with the tongue pushing the lip laterally as it moves forward, with duration of 85–215 ms; and paw licking— persistent direction of the ingestive response toward the rat's own forepaws, with the paws held close to the mouth and lapped for some seconds. Aversive components (Figure 1, bottom) are gaping—rapid large-amplitude opening of the mandible with concomitant retraction of the corners of the mouth to reveal the internal oral labia, and retraction of the lower lip, lasting approximately 150 ms; chin rubbing—bringing the mouth into direct contact with a substrate (i.e., floor or wall) and projecting the body forward by flexion of the dorsal neck and by pectoral and forelimb musculature; head shaking—rapid side-to-side movements of the head at a

rate faster than 60 Hz; forelimb flailing—rapidly shaking both forelimbs in the horizontal plane with a frequency of greater than 60 Hz; and face washing— the unilateral downward movement of either forepaw across the face (face washing can occur as a single movement or as a group of several wipes with the same paw); fluid ejection—if the solution was not entirely consumed, then the amount of time within the minute during which the stimulus was not ingested was recorded In addition, instances of fluid ejection were classified as either passive drip or active rejection. In passive drip, fluid simply accumulated along the tip of the lower mandible and dropped off onto the floor. The rat might or might not simultaneously ingest part of the solution. In active rejection, the fluid was expelled, in conjunction with an aversive response component such as head shake, forelimb flailing, or chin rubbing

Videotape analysis   Videotapes were analyzed in slow motion for the occurrence of each FAP without knowledge of the precise experimental condition of each rat. When necessary, frame-by-frame analyses were made. Discrete FAPs such as lateral tongue protrusions, gapes, chin rubs, and bouts of face washing, forelimb flailing, head shaking, and locomotion (usually rearing) were recorded each time they occurred. Continuous responses such as paw licks, mouth movements, and passive drips were recorded in bins of 5-s duration. A rat had to perform one of these behaviors continuously for 5 s before the behavior was recorded, and every 5-s bin was counted as one occurrence; for example, a rat that showed paw licking continuously for 20 s was scored as showing four paw lick bins. Rhythmic tongue protrusions were scored in the same way but in 2-s bins. These data are presented in terms of the average number of occurrences of each FAP.

Experiment 2

To determine whether a sodium depletion-induced shift in FAPs occurs the first time a sodium deficit is encountered, we ran an additional group of 8 naive rats, using the same procedure except that they were not preselected to show a salt appetite and had had no experience with either salt solutions or sodium depletion. To further establish the reliability of any

shift, we arbitrarily selected 3 rats from this group and tested them for FAPs when they were sodium replete and sodium deplete every week for 4 consecutive weeks.

Control for nonspecific ingestive bias. To ensure that any change in response to the taste of salt was not a general bias induced by natrorexigenic treatment, which would apply equally to any taste whether salty or not, we ran a control group in the FAP test, using a nonsalty taste stimulus. Other work in our laboratory has shown that rats show mixed ingestive and aversive FAPs to infusions of 0.01 M HCl (Schwartz, 1983), a mildly sour solution to humans, similar to the FAP response we observed to 0.5 M NaCl Six naive rats were implanted with oral cannulas and were tested for FAPs to HCl when sodium replete and when sodium deplete, by the testing procedure described above. The only difference between the two procedures was that 0.01 M HCl was substituted for 0.05 M NaCl in the FAP test. A two-bottle preference test between 0.05 M NaCl and water was administered in the home cage as described above in order to ascertain whether a salt appetite had been induced.

Control for NaCl access. Due to the inclusion of a two-bottle preference test, a possible confound was introduced. When tested for consummatory responses in the sodium-replete state, rats had free access to the 0.5 M NaCl in their home cage during the immediately preceding 24 hr. This was not true when they were tested sodium depleted. Although the amount of NaCl consumed in this sodium-replete two-bottle test was quite small (5.9 ± 1.3 ml), this introduced the possibility that a shift could be due entirely to a rat's immediate history, rather than to its sodium state. A rat might respond more aversively in the sodium-replete test simply because it had recently had the opportunity to sate itself on NaCl. To be sure that this was not the case, we ran a third consummatory response test (Condition 3) on 8 rats 48 hr after the first sodium-depleting injection. At this time, the rats

had been allowed free access to NaCl for the preceding 24 hr and had, in fact, ingested considerably more than they had while sodium replete (30.4 ± 2.5 ml). However, a mild salt appetite can still be expected to exist at this time: Rats will continue to ingest excessive amounts of NaCl for a number of days following natrorexigenic treatment (Cruz et al., 1977). If prior salt ingestion, rather than sodium depletion, was responsible for any changes in FAPs, then the FAPs during the third consummatory test should mimic those of the first day. However, if sodium depletion was responsible for the shift in FAPs, then those of the third consummatory test should parallel those of the depletion state

Results

Experiment 1

Fixed action patterns. While the rats were sodium replete, oral infusions of 0.5 M NaCl elicited a moderate number of ingestive FAPs and a larger number of aversive FAPs (Figure 2) in both weeks of testing. In contrast, when the same infusion was delivered 24 hr following the natrorexigenic treatment, the most strongly ingestive components (paw licks, tongue protrusions, and lateral tongue protrusions; Berridge & Grill, 1983) significantly increased as a group ($p < .01$ for both weeks combined, Wilcoxon signed-rank test), while aversive FAPs showed a marked decrease ($p < .01$). Thus, there is a reciprocal shift away from aversive FAPs toward

		INGESTIVE					AVERSIVE					
		PL	LTP	TP	MM	PD	G	CR	FW	FF	HS	LO
WEEKS I	REPLETE	0.2	0.4	0.4	1.2	0.6	0.8	1.0	2.4	1.2	1.0	0.4
	DEPLETED	0	2.0	4.4	4.6	0.4	0.4	0.2	0.4	0.4	0	0.2
WEEKS II	REPLETE	0.2	0	0	0.6	2.2	0.4	1.4	5.4	6.6	2.0	0.4
	DEPLETED	2.4	3.8	5.4	4.2	0	0.2	0	0.2	0	0	0

Figure 2 Taste-elicited fixed action patterns of 5 rats to 0.5 M NaCl when either sodium replete or sodium deplete. (Values represent the mean number of responses per rat. Ingestive responses are paw licking [PL], lateral tongue protrusions [LTP], tongue protrusions [TP], and mouth movements [MM]. Failure to show any consummatory response, either ingestive or aversive, results in the passive drip of fluid from the mouth [PD]. Aversive responses are gapes [G], chin rubs [CR], face washing [FW], forelimb flailing [FF], head shakes [HS], and locomotion [LO].)
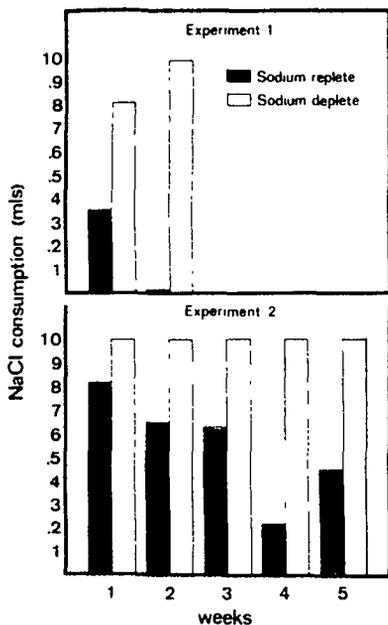
Figure 3 Mean NaCl consumption during the oral infusion test when either sodium replete or sodium deplete. (A maximum of 1 ml could be consumed in this test. Experiments 1 [5 rats] and 2 [3 rats] occupy the upper and lower portion of the figure, respectively.)

ingestive FAPs following natrorexigenic treatment.

Infusion and home cage NaCl consumption. During the infusion tests, rats reliably ingested more NaCl while sodium deplete than while sodium replete, $F(1, 4) = 48.1, p < .01$ (Figure 3). The natrorexigenic treatment likewise produced a salt appetite as measured by home cage consumption (Figure 4), $F(1, 4) = 76.6, p < .01$. Consumption of NaCl during the second week of depletion was greater than that during the first week of depletion, $F(1, 4) = 13.4, p < .05$. There were no reliable differences between weeks in consumption of NaCl while sodium replete.

Experiment 2

Fixed action patterns. The first natrorexigenic treatment produced a marked change in the FAPs elicited by NaCl in the 8 naive rats. Tongue protrusions by themselves increased significantly during depletion, from 0.9 ± 1.2 to 5.4 ± 1.9 ($p < .02$, Wilcoxon signed-rank test), and ingestive
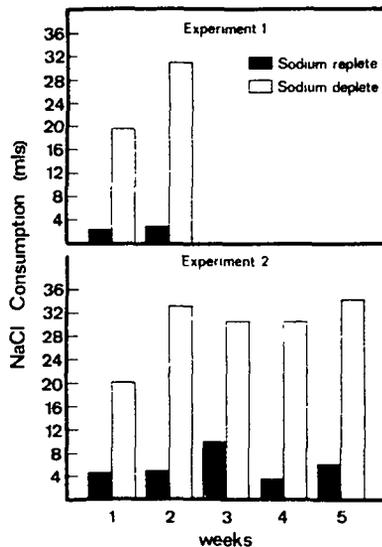

Figure 4. Mean NaCl consumption during the 24-hr preference test in the home cage when either sodium replete or sodium deplete. (Experiments 1 [5 rats] and 2 [3 rats] occupy the upper and lower portion of the figure, respectively.)

responses pooled together (paw licks, tongue protrusions, and lateral tongue protrusions) also increased from 3.0 ± 1.8 to 11.6 ± 3.4 ($p < .01$). In contrast, aversive responses (6.4 ± 2.1) were eliminated by the natrorexigenic treatment ($p < .01$).

The consummatory responses of the 3 rats that were tested for 5 consecutive weeks are shown in Figure 5. A consistent pattern of results emerged during the consecutive weekly tests: Ingestive FAPs to 0.5 M NaCl were increased by the treatment, whereas aversive FAPs were eliminated. A change in the response to NaCl when the rat was sodium replete was also noted over repeated experiences. The rats had never tasted an NaCl solution prior to the first week shown in Figure 5. The number of ingestive responses elicited in the sodium-replete state decreased from the early (3.5 ± 1.3) to later (0.0 ± 0) weeks ($p < .05$, comparison of the first 2 weeks (6 scores) and the last 2 weeks (6 scores), Wilcoxon signed-rank test). The occurrence of aversive FAPs remained unchanged.

Infusion and home cage consumption. All rats consumed the entire 1.0-ml infusion when sodium deplete but only an average of 0.5 ± 0.1 ml when replete. A sig-

		INGESTIVE					AVERSIVE				
		PL	LTP	TP	MM	PD	G	CR	FW	FF	HS	LO

WEEKS		PL	LTP	TP	MM	PD	G	CR	FW	FF	HS	LO
I	REPLETE	0.6	2.6	1.6	5.3	2.0	3.3	0	0	0.3	1.6	0
	DEPLETED	3.6	3.3	7.6	3.0	0	0	0	0	0	0	0
II	REPLETE	0.3	0.6	1.0	4.3	3.0	0	0	1.0	1.6	3.0	0.6
	DEPLETED	4.3	3.0	7.6	5.3	0	0	0	0	0	0	0
III	REPLETE	0	0.3	2.3	4.6	4.0	0	0	0	0	2.0	0.3
	DEPLETED	2.3	1.0	13.0	1.3	0	0	0	0	0	0	0
IV	REPLETE	0	0	0	2.3	4.0	0.6	0	0	0	3.0	0
	DEPLETED	3.3	0.6	8.3	4.0	0	0	0	0	0	0	0
V	REPLETE	0	0	0	4.0	4.3	0	0	0.6	0.6	3.3	0
	DEPLETED	4.0	1.0	9.3	3.6	0	0	0	0	0	0	0

Figure 5 Taste-elicited fixed action patterns of 3 rats to NaCl when either sodium replete or sodium deplete (Ingestive responses are paw licking [PL], lateral tongue protrusions [LTP], tongue protrusions [TP], and mouth movements [MM]. Failure to show any consummatory responses, either ingestive or aversive, results in the passive drip of fluid from the mouth [PD]. Aversive responses are gapes [G], chin rubs [CR], face washing [FW], forelimb flailing [FF], head shakes [HS], and locomotion [LO].)

nificant effect of weeks, $F(4, 8) = 6.8$, $p < .05$, and Weeks × Replete/Deplete interaction, $F(4, 8) = 6.3$, $p < .05$, reflected a decrease in infusion consumption in the sodium-replete state over the 5 weeks of testing (see Figure 3).

Salt ingestion in the 24-hr test was significantly elevated by sodium depletion during the first week, $t(7) = 4.8$, $p < .05$. The two-bottle NaCl consumption of the 3 rats tested for 5 weeks was also significantly greater while sodium deplete than while sodium replete, $F(1, 2) = 53.9$, $p < .05$. Likewise, water consumption in the home cage was elevated in the sodium-deplete state (42.7 ± 3.5 ml) compared with that in the sodium-replete state (22.2 ± 3.5 ml), $F(1, 2) = 327.1$, $p < .01$, presumably because of the diuretic effects of the furosemide (Cruz et al., 1977) and the osmotic effects of hypertonic NaCl. Repeated experience did not effect the consumption of NaCl in the home cage regardless of whether the rat was sodium replete or sodium deplete.

Control for general ingestive bias. Infusions of 0.01 M HCl evoked a mixture of ingestive (2.1 ± 3.8) and aversive (7.6 ± 2.4) FAPs in sodium-replete rats. This response to HCl was not changed by natrorexigenic treatment, even though the treatment produced a significant salt appetite, $t(5) = 4.9$, $p < .01$, as measured by the two-bottle preference test in the home cage. Similarly, the amount of the HCl infusion that was consumed remained unchanged by this treatment. The FAP shift that was observed to salt during sodium depletion apparently does not extend to all tastes that elicit mixed FAPs.

Control for NaCl access. The FAPs to NaCl in the third test condition, 48 hr after treatment and following 24 hr of free access to salt in the home cage, were significantly different from those in the sodium-replete state (Figure 6). Combining across all

	INGESTIVE					AVERSIVE				
PL	LTP	TP	MM	PD	G	CR	FW	FF	HS	LO
SODIUM REPLETE										
0	0.2	0.2	2.3	2.4	0.5	0.5	1.2	0.7	2.2	0.2
CONDITION III										
0	1.2	0.9	4.2	1.3	0	0	0.5	0.6	1.0	0.2

Figure 6   Taste-elicited fixed action pattern of 5 rats to NaCl while either sodium replete or in Condition 3. (In Condition 3, rats were tested 48 hr after natrorexigenic treatment and following 24 hr of free access to NaCl in the home cage. Ingestive responses are paw licking [PL], lateral tongue protrusions [LTP], tongue protrusions [TP], and mouth movements [MM]. Failure to show any consummatory response, either ingestive or aversive, results in the passive drip of fluid from the mouth [PD]. Aversive responses are gapes [G], chin rubs [CR], face washing [FW], forelimb flailing [FF], head shakes [HS], and locomotion [LO].)

weeks in both experiments, significantly more ingestive FAPs were elicited by salt infusions in the third condition than in the replete state ($p < .05$, Wilcoxon signed-rank test). Similarly, significantly fewer aversive responses were elicited in the third condition than in the sodium-replete state ($p < .01$). Thus, the FAP shift to NaCl was clearly a function of the rat's physiological state. The amount of the NaCl infusion ingested during this third condition did not differ significantly from that consumed on the preceding sodium-deplete test day. Overall, the amount ingested in the third condition remained significantly greater than that ingested when the rat was sodium deplete ($p < .05$).

Discussion

There is some evidence that humans who chronically lose sodium may display a craving for salt (Wilkins & Richter, 1940). Recently, some data have been gathered which suggest that humans placed on a sodium-deficient diet may initially find salty foods to taste less salty and more pleasant; the converse holds when they are on a sodium-rich diet (Bertino et al., 1981; Bertino, Beauchamp, & Engelman, 1982). Taken together, these data suggest that humans in a state of sodium deficiency tend to ingest more salt and that a mechanism underlying this increased ingestion might be an increase in the perceived pleasantness of salt.

The possibility of a hedonic shift in the taste of salt during sodium deficiency is clearly supported by the present results in the rat. These results demonstrate that the FAPs elicited by the taste of a salty solution change concomitantly with the internal state of the rat. Sodium-replete rats displayed aversive consummatory responses, together with partial ingestion. By contrast, when a state of sodium need was induced by the natrorexigenic treatment, only ingestive FAPs were elicited, and the infused NaCl was entirely consumed. This shift in the palatability of salt is a robust phenomenon, occurring every time in every rat. These results provide further support, within the domain of sodium homeostasis, for the phenomenon of alliesthesia, or hedonic shifts related to internal state (Booth, 1980; Cabanac, 1971). The palatability of salt appears to be controlled by the rat's natrorexigenic state.

One factor that could contribute to this shift in response is the peripheral reduction of taste sensitivity to concentrated salt that occurs during sodium depletion (Contreras, 1977). Behavioral evidence from both rats and humans supports the suggestion that tastes are perceived as less salty during sodium deprivation (Bertino et al., 1981; Morrison, 1980). However, the evidence on whether the magnitude of this sensory reduction is sufficient to reduce the intensity of a normally avoided 0.5 M NaCl solution to that of a preferred solution is somewhat

mixed. Contreras and Frank (1979) reported a reduction in the firing rate of "salt-best" chorda tympani fibers following sodium deprivation, sufficient to shift the response to nonpreferred 0.3 M NaCl to what would normally be elicited by preferred 0.07 M NaCl. On the other hand, although human renal patients do report salty solutions to taste less intense than do normal persons, the reported reduction in intensity is insufficient to account for the reported increase in palatability of the same solutions (see Moskowitz & Abramson cited in Contreras, 1978). The most prudent course is to assume that reduced peripheral sensitivity may contribute to the shift in palatability of concentrated salt but that a central change in the evaluation of tastes that continue to be perceived as highly salty must also occur. The assumption of a change in central palatability processing is supported by the finding that sodium depletion does not alter the taste reactivity of decerebrate rats to NaCl (Grill & Schulkin, 1984; personal unpublished observations, 1984). Decerebration should not disrupt the reduction of peripheral nerve sensitivity produced by natrorexigenic treatment. Fudim's (1978) report that flavors paired with NaCl become preferred following sodium depletion is also consonant with a central change in palatability processing.

The enhanced ingestion of salt in omnivores like rats and humans, and in herbivores like sheep, has been shown to be independent of specific associations between taste and postingestive consequences: The enhancement occurs the first time sodium need is encountered (see Denton, 1982; Rozin, 1976; Wolf, 1969, for reviews). Our results on the shift in the palatability of NaCl support this hypothesis, because the rats displayed this shift in taste reactivity the first time they were made sodium deficient. Moreover, the number of ingestive FAPs elicited by the NaCl when the rats were sodium deficient remained constant throughout the successive trials and weeks. This is compatible with earlier reports that the motivation for salt when sodium deficient remains constant over repeated trials, as measured by operant re-

sponding for salt in rats (Quartermain et al., 1967).

Although ingestive FAPs to salt when the rat was sodium deficient appeared to remain constant, ingestive responses when it was sodium replete did not. A sodium-replete rat's first infusion of NaCl evoked both ingestive and aversive FAPs. However, the number of strong ingestive FAPs (paw licks, tongue protrusions, and lateral tongue protrusions) to salt in the sodium-replete state gradually declined over repeated experiences with the NaCl. During the fourth and fifth weeks these responses completely disappeared. This response shift may reflect the development of a discriminative classical association between the taste of salt and its consequences in the two different states. This discriminative association could arise due to experience with the differentially reinforcing consequences of ingesting salt when sodium replete and when sodium deplete. In addition, because the number of aversive FAPs remained constant in the 5-week replication whereas ingestive FAPs declined, it also shows that ingestive and aversive FAPs can be independently controlled. Changes in ingestive FAPs need not be accompanied by reciprocal changes in aversion. This supports the hypothesis that the positive and negative aspects of palatability are separately processed in the production of taste-elicited FAPs (Berridge & Grill, 1983), because it shows that the decision to produce ingestive responses does not have to vary inversely with the decision to produce aversive responses.

Finally, as we have indicated, the motivation to ingest salt may be related to its variable hedonic value. In the wild, rabbits and elk have been reported to search for salt when their food sources were low in sodium. In the laboratory, sheep, cows, and rats will work for salt when sodium deficient (see Denton, 1982, for review). These goal-directed, motivated behaviors might be attributable to the enhanced hedonic value of salt as an ingestive stimulus as well as to the drive properties of the hunger for salt. Our results support the view that salt appetite is mediated by a change in salt palatability, because they show that sodium

deficiency renders the taste of salt more palatable. Shifts in the hedonic value of tastes may thus be important in motivating adaptive behavior.

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