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Evidence that appetitive responses for dehydration and food-deprivation are learned

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Abstract

Rats do not seek water when cellularly dehydrated until they are about 4 weeks of age. This lack of appetitive 'seeking' behavior in young rats differs from their precocious ingestive responses such as an increased intake of solutions infused into their mouths when they are dehydrated as young as 2 days of age. Using video analysis of appetitive behavior in a structured environment, we document this early absence of appetitive responding and the subsequent acquisition of dehydration-elicited appetitive behavior. Weaning age pups were separated into four conditions: (i) experienced, dehydrated; (ii) experienced, nondehydrated; (iii) inexperienced, dehydrated; and (iv) inexperienced, nondehydrated. 'Experienced' rats received a dehydration and drinking experience prior to the test, and 'dehydrated' rats were dehydrated (by injection of a salt load) at the time of test. At the test, all water and food was removed from the test cages, eliminating the confounding of appetitive and consummatory measures. Despite the fact that pups in all conditions had experience with water and had previously drunk, only the 'experienced' pups differentially sought water when dehydrated. Parallel experiments with food deprivation produced similar results. Pups did not exhibit food-seeking behavior when food-deprived unless they had previous experience with food deprivation and eating. The appetitive 'seeking' behavior for feeding also appears to be learned. Directed appetitive behavior in general may thus be acquired. © 2002 Elsevier Science Inc. All rights reserved.

Keywords: Thirst; Hunger; Appetite; Learning; Acquisition; Dehydration; Food-deprivation; Rat; Innate; Appetitive behavior; Motivation

1. Introduction

Weaning age rats do not seek water when dehydrated by a salt load [1–6]. This lack of appetitive behavior is in contrast to the precocious ingestive responses shown to dehydration when fluids are infused directly into their mouths. Indeed, dehydration produces increased intake of orally infused solutions in dehydrated rat pups as young as 2 days of age [7–9] without an accompanying increase in seeking behavior. Thus, early in development dehydrated rats do not seek water, but do vigorously consume water that is immediately available at their mouth. It is not until after 3 weeks of age that rats actively seek water and drink when dehydrated.

Recent experiments provide an understanding of rats' late-emerging appetitive responses, at the same time renewing support for a 90-year-old proposal that, in contrast to the consummatory responses, the appetitive components of behavior are learned, or acquired [10].[1] Without the paired experience of dehydration and drinking, rats appear unaware of the significance of dehydration and its internal and peripheral signals. That is, they do not express searching out water and drinking. With specific experience, however, rats acquire the water-seeking behavior that leads to drinking [11,12]. The earlier evidence in Refs. [11,12] used water intake as an indirect measure of water-seeking behavior, rather than measuring water-seeking behavior itself. There are two new findings reported here. First, the experiments

[1] Consummatory (two 'm's) behavior, as characterized by Craig, is the final or terminal behavior in a sequence of behaviors, whereas consumatory (one 'm') behavior is the act of mouthing and swallowing water or food. Consumatory behavior happens to also be the consummatory behavior, both confusing and fortuitous for those discussing ingestive behavior. This is a distinction consistent with Craig's initial observations dichotomizing the consummatory and appetitive components of behavior [10], and with Craig's belief that the appetitive components of behavior may be acquired or learned.

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here utilize a paradigm that allows the measurement of the appetitive seeking behavior more directly. Second, we provide evidence that food-seeking behavior when food-deprived is also learned.

2. Experiment 1

In the first experiment we report here, the emergence of learned appetitive behavior is explicitly documented using a video analysis of young rats' behavior in a structured environment that helped us isolate components of behavior for study. Because ingestive studies are typically done in a confined cage and intake is usually the experimental measure, it is difficult to unconfound the appetitive and consummatory components of ingestion and study the orientation to and search for water or food. Pups that stumble upon water when dehydrated will drink due to the precocious consumatory response, and may thus appear to already possess full appetitive responses to dehydration. The experimental design employed here allowed us to separate the appetitive components of behavior from the consummatory components.

2.1. Methods

2.1.1. Subjects

Subjects were four groups of 18-day-old ($n=6$ per group) rats of the Sprague–Dawley CD strain delivered from Charles River Laboratories. Each individual experimental run consisted of four same-sex same-litter pups, one assigned to each experimental group. Each pup was weaned from the dam at 18 days of age and housed separately in its own test chamber (Fig. 1), with milk diet as food in the food chamber and water in the water chamber. The milk diet consisted of three parts evaporated milk and one part water (plus a vitamin supplement Poly-Vi-Sol), which contained sufficient water to preclude dehydration.

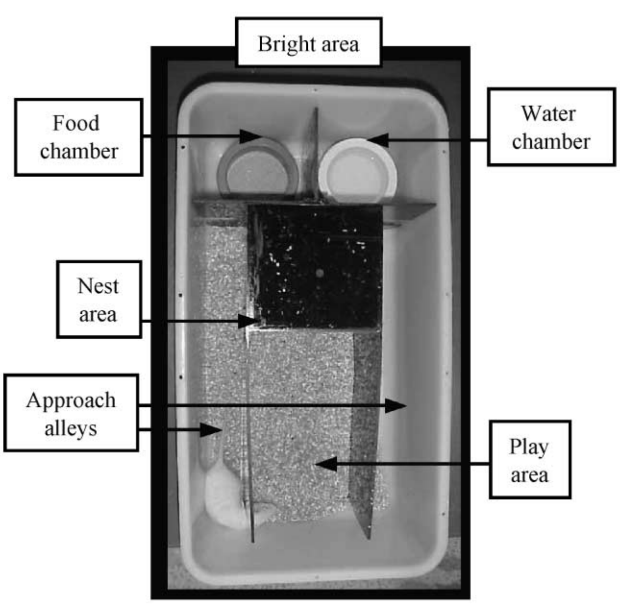

Fig. 1. An example test container used in the experiments.

2.1.2. Test apparatus

A special cage for housing and testing enclosed two lateral appetitive-approach alleys with distinct feeding and drinking chambers at the ends, as well as central play and sleep areas (Fig. 1). Because of the cage's design, getting water or food (milk diet, see above) required a rat to leave its nest and the play area, choose one of the two approach alleys, go down it, and then into the chamber at the end. Rats were discouraged from moving down the alley and into the drinking or eating chamber by the fact that these chambers were illuminated and brighter than other regions of the cage, and thus aversive to the rats. If a rat wanted water, it was necessary to explicitly seek water out by engaging in a series of observable search responses moving out of the nest and play areas, through one of the arms, and into the water chamber, responses readily scored from the videotapes. As an additional important step in separating components of behavior, at the time of the test we removed food and water from the chambers. Rats having traversed the approach alleys found the chambers in which they normally found water or food to be empty. Animals thus did not spend time in the chamber to drink or eat, nor was behavior modified or confounded by the postingestive effects of consuming fluid or food. Rather, time spent in a chamber in the absence of the ingesta served as a particularly strong indicator of interest in or orientation to the previous contents of that chamber.

2.1.3. Training and testing

An experiment began after weaning age rats had been placed in test cages for 1 day of familiarization. Then in the training or experience phase of the experiment, *experienced* rats were removed and dehydrated with a salt load, subcutaneous injection of 2 M NaCl at 2 cc/100 g body weight. They were immediately returned to their regular test containers for 1 day. *Inexperienced* rats were not dehydrated; they received injections of 0.135 M (isotonic) NaCl (also at 2 cc/100 g body weight) and were returned to their containers. Each rat in both conditions had water freely available from a water bowl in its water chamber and each drank from it. To encourage experience with drinking water, milk was removed from the food chamber for the first hour of the experience. Rats in the experienced condition drank considerably more though they typically did not drink immediately. Rather, consistent with a lack of appetitive responsiveness, they tended to drink when, several hours later, they happened to enter the water chamber. Thus, this initial experience phase of the experiment established groups of rats that had experienced dehydration and drinking, or had not experienced dehydration. Note that dehydration by injection with a salt load induces dry mouth in addition to dehydration, and our procedure cannot distinguish between which of these two stimuli or the specific nature of the internal stimulus that the experienced rat is learning about.

One day later, in the *test phase* of the experiment, half of each group was dehydrated and the other half not dehydrated. These variations in treatment resulted in four conditions: *experienced-dehydrated*, *experienced-nondehydrated*, *inexperienced-dehydrated*, and *inexperienced-nondehydrated*. Rats were returned to their test containers where all food and water had been removed (along with their bowls), and their behavior monitored by videotape recording for 1 h. The videotapes were coded over the entire videotaping period by recording the entry and exit times for each of the three areas: 'play,' 'food,' and 'water.' The alleys were coded as part of the play area. The *active time* in a chamber was the amount of awake time spent in the chamber; pups only occasionally slept outside of their nest area, but when they did, it was relatively easy for us to identify. The *total active time* is the sum of all active times in all three chambers; pups are not visible when in the nest area, and we presumed they were inactive when there. Statistical analyses (two-way analysis of variance ANOVA; post hoc tests using Tukey's HSD method) were carried out for the percentage of active time spent in the water chamber during the first 60 min; this time was long enough to get sufficient activity for results, but not so long that the dehydration would be eliminated by renal action. If dehydration-induced appetitive behavior is being expressed pups will spend more time in the water chamber. Their behavior will be differentially oriented to the site and other cues related to water. From this data, we also analyzed 'entries,' the movement from one area to another. These data were generally consistent with the measures of time in a chamber, and thus are only discussed to a limited degree below. However, note that pups of this age are quite active and that time spent in a chamber was the result of numerous entries into that chamber, not simply the result of remaining in one place (Fig. 2A and B depict the general qualitative pattern of movement for all animals in these experiments). We judged the reliability of our coding method by analyzing the same videotape twice and found high correlations for these repeated measures ($R^2=.999$). In addition, we compared our scoring of the tapes to scoring by observers completely blind to the experiments and their purpose (reliability $R^2=.983$ for 'time in chamber' measures, .987 for 'entries').

2.2. Results and discussion

Only rats that previously had the experience of being dehydrated and drinking showed appetitive behavior by a differential orientation to the water chamber (Fig. 3; ANOVA main effect for appetitive state [$F(1,20)=14.65$, $P<.05$] with experienced-dehydrated rats spending a greater percentage of their time in the water room than experienced-nondehydrated rats ($P<.05$); difference between inexperienced-dehydrated and inexperienced-nondehydrated rats was not significant). Statistics and figures were done in terms of relative time, since this is the best indicator of differential behavior by individual rats. Yet qualitatively similar conclusions held when absolute time spent in a room was used as the measure, and in this measure experienced-dehydrated rats showed greater absolute time in the water chamber in the early time intervals than did inexperience-dehydrated rats. The same statistical tests for absolute time in the food room (i.e. nonlearning room) showed no differences. Inexperienced rats that were dehydrated showed no differential orientation to the water chamber. Indeed, they showed little change in their behavior as a result of dehydration. Internal signals produced by dehydration had no effect on these rats' behavior, despite the fact that the rats were familiar with the usual location of water, and that they do drink appropriately when they eventually encounter water [11]. The only differential behavior shown by any of the three control groups was that the inexperienced-dehydrated rats showed less relative time in the food chamber during the first 15 min. In short and consistent with previous findings [11,12], the expression of water seeking behavior in response to dehydration (i.e. 'thirsty behavior'; [13,14]) appears to require experience with the state of dehydration in the context of drinking. The appetitive component of the dehydration → drinking sequence is

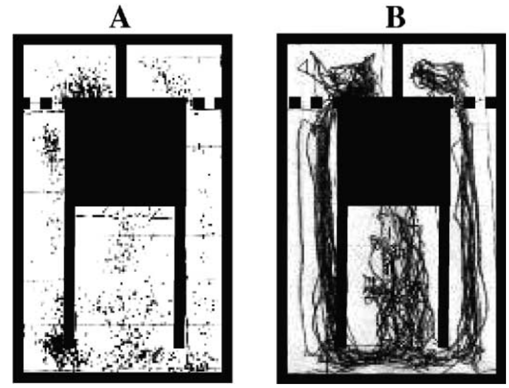

Fig. 2. Representative behavior of rats during the first 15 min of food-deprivation experiments. (A) Diagram of time spent around the test container for a rat in one representative food-restriction experiment. A point was made roughly every third of a second at whatever position the rat was at in the test container. Point clusters therefore show places at which the rat spent significant time. (B) Diagram showing paths of the same rat. In each case, the upper left chamber is the food chamber, and the upper right chamber was never occupied by water or food at any time during the entire experiment.

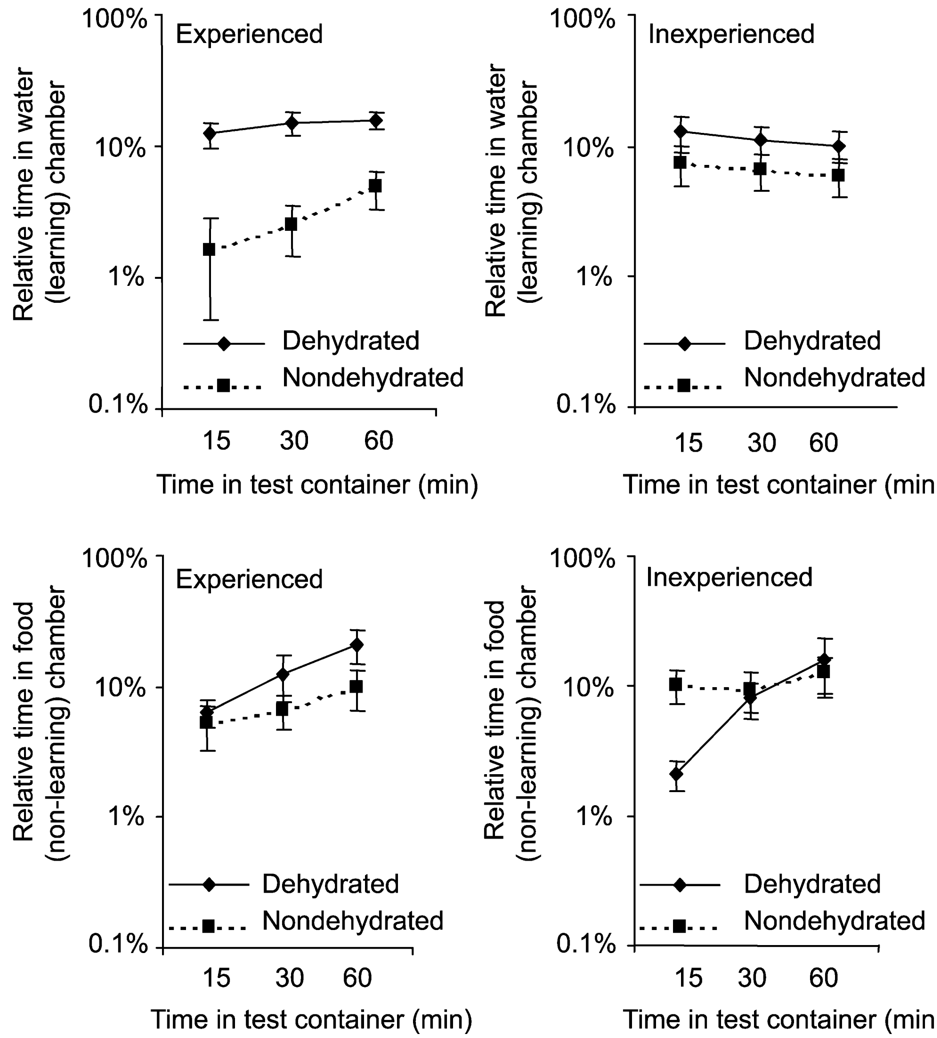

Fig. 3. Relative time spent in chamber versus the total amount of time in the test cage (minutes), for dehydration-learning experiment (Experiment 1), where the first experience of dehydration is induced via injection of salt load. Plots in the upper row are for the relative time spent in the water chamber, which is the learning chamber for this experiment; plots in the lower row are for the relative time spent in the food chamber, which is not the learning chamber, and serves as a control. Plots in the left column are for rats that had experience with dehydration paired with drinking water, and plots in the right column show results for rats that did not have such an experience. Each data point is an average of six rats. Error bars show standard error. The main observation here is that dehydrated and nondehydrated rats behave similarly in all regards except when they are experienced, and then only when they are in the room where they had their learning experience.

acquired, even though the consummatory response is present in newborns.

3. Experiment 2: Appetitive behavior for feeding

That the appetitive behavior for such a basic stimulus as dehydration is learned suggests that perhaps the same is true for other appetitive behaviors also considered biologically fundamental (e.g. Refs. [15,16], as per Ref. [10]). Nonetheless, at least at first glance, this does not appear to be the case for the feeding. At weaning age, as well as at earlier ages, rats seem willing eaters. More importantly, they respond to increasing food deprivation with increasing intake [17–19]. And, they do this in situations where they must direct and orient their behavior to food [20,21]. However, a number of redundant systems may operate to insure that animals respond to the appropriate stimuli in their environments and enhance the likelihood of encountering the appropriate ingesta. It is possible that this redundancy makes up for missing appetitive responses and obscures a broad experiential contribution to learning about being food-deprived (just as the robust consummatory drinking response can obscure that water seeking behavior is learned). In this regard, rats become more active as metabolic deficits occur (e.g. Ref. [22]). Enhanced locomotor activity to deprivation occurs very early in development, so that while the cause may not be understood, we can be relatively certain that little or no learning underlies this response to deprivation [19]. Given the tight quarters in which feeding tests are usually conducted, this deprivation-induced activity along with a disposition to consume food when it is encountered could create the appearance of food-oriented appetitive behavior in food-deprived young rats—even though their behavior may not be initially food seeking or food-oriented. For our purposes it does not matter whether the greater activity or consumatory response is, itself, learned via previous experiences, or whether it is innate [23]; in either case they can act as redundant systems in the learning of the appetitive response to deprivation, and can make it difficult to observe a learned component to food seeking, if one exists. The procedures we have described here for studying early appetitive responses to dehydration can also be used with feeding and food deprivation and allow a direct assessment of the acquired nature of feeding appetite, removing the confound of situational features which might simply insure that rats quickly stumble onto food and thus trigger a consummatory response and the appearance of food-directed appetitive behavior.

3.1. Methods

3.1.1. Subjects

Subjects were four groups of 18-day-old ($n = 11$ per group) rats of the Sprague–Dawley CD strain delivered from Charles River Laboratories. Each individual experimental run consisted of four same-sex same-litter pups, one assigned to each experimental group. Each pup was weaned from the dam at 18 days of age. The test chamber is the same as in Experiment 1 (Fig. 1), with milk diet in the food chamber and water in the water chamber. The milk diet consisted of three parts evaporated milk and one part water, which contained sufficient water to preclude dehydration.

3.1.2. Training and testing

We carried out an experiment similar to the dehydration procedure of Experiment 1 and using the same test apparatus, but we now studied appetitive behavior for feeding and used food-restriction as the experimental manipulation. In the experience phase, *experienced* rats experienced overnight food deprivation (approximately 18 h); during this period they were housed in an 'away' container different from what would be their regular test container in that it consisted of just one large cage area, rather than multiple chambers (they received water as usual). They were then returned to their regular test containers (for approximately 30 h) and allowed to eat as they encountered food. *Inexperienced* rats were not food restricted; their treatment was the same as for experienced rats, except that they received dry chow in the 'away' container, and thus did not experience food-restriction. Inexperienced rats received dry chow during this phase instead of milk in order that their total time with milk diet would not differ from that for experienced rats. Twenty-four hours later in the test phase, half of each group was food-restricted overnight (*food-deprived*) and the other half was not (*food-nondeprived*). All rats were then returned to their test containers where all food and water had been removed (along with the bowls), and their behavior monitored by videotape recording for 1 h. Statistical analyses (two-way analysis of variance ANOVA; post hoc tests using Tukey's HSD method) were carried out for the percentage of active time spent in the food chamber during the first 30 min; this time was long enough to get sufficient activity for results, but not so long that the appetitive state would be attenuated.

3.2. Results and discussion

Rats that had previous experience with food deprivation and feeding showed differential orientation to the food chamber, while inexperienced rats did not (Fig. 4; ANOVA main effect for appetitive state [$F(1,37) = 10.57$, $P < .05$] with experienced-food-deprived rats spending a greater percentage of their time in the food room than experienced-food-nondeprived rats ($P < .05$); difference between inexperienced-food and inexperienced-food-nondeprived rats was not significant). Qualitatively similar conclusions held when absolute time spent in a room was used as the measure. The same statistical tests for the water (i.e. non-learning) room showed no differences. Inexperienced-food-deprived rats did not show increased seeking behavior compared to inexperienced-food-nondeprived rats despite their familiarity with food and despite their food restriction the night before.

Yet, in contrast to the findings with dehydration, deprived rats in both groups did show general changes in behavior. Both experienced and inexperienced rats showed increased activity (the total amount of time active in the three areas) when deprived (cf. Refs. [22,24]). In addition, our measure of 'entries' indicated that deprived pups in both groups passed from one chamber to another at a higher rate than did nondeprived pups (food-deprived entries for first 30 min = 35.9 [2.05 S.E.M.]; nondeprived entries = 27.32 [1.49 S.E.M.]). That is, locomotor activity was higher in deprived pups. Specific deprivation-induced food-oriented behavior required experience, but deprivation-induced increased activity did not. In a smaller cage and with food present, such increased activity could clearly contribute to an enhanced likelihood of encountering food and triggering ingestion. Increased activity might be considered an appetitive response (and 'general agitation' was actually another feature of the appetitive component as described by Craig [10]). However, increased activity is not the same thing as directed food seeking and is clearly separable.

Interestingly, the deprivation-mediated increased activity does not appear to be influenced or guided by odor signals: although the ingesta were removed at the time of the test, the residual odors remained from spillage. Yet, inexperienced, deprived rats did not increase their time spent near the odor. Preferential orientation to odor

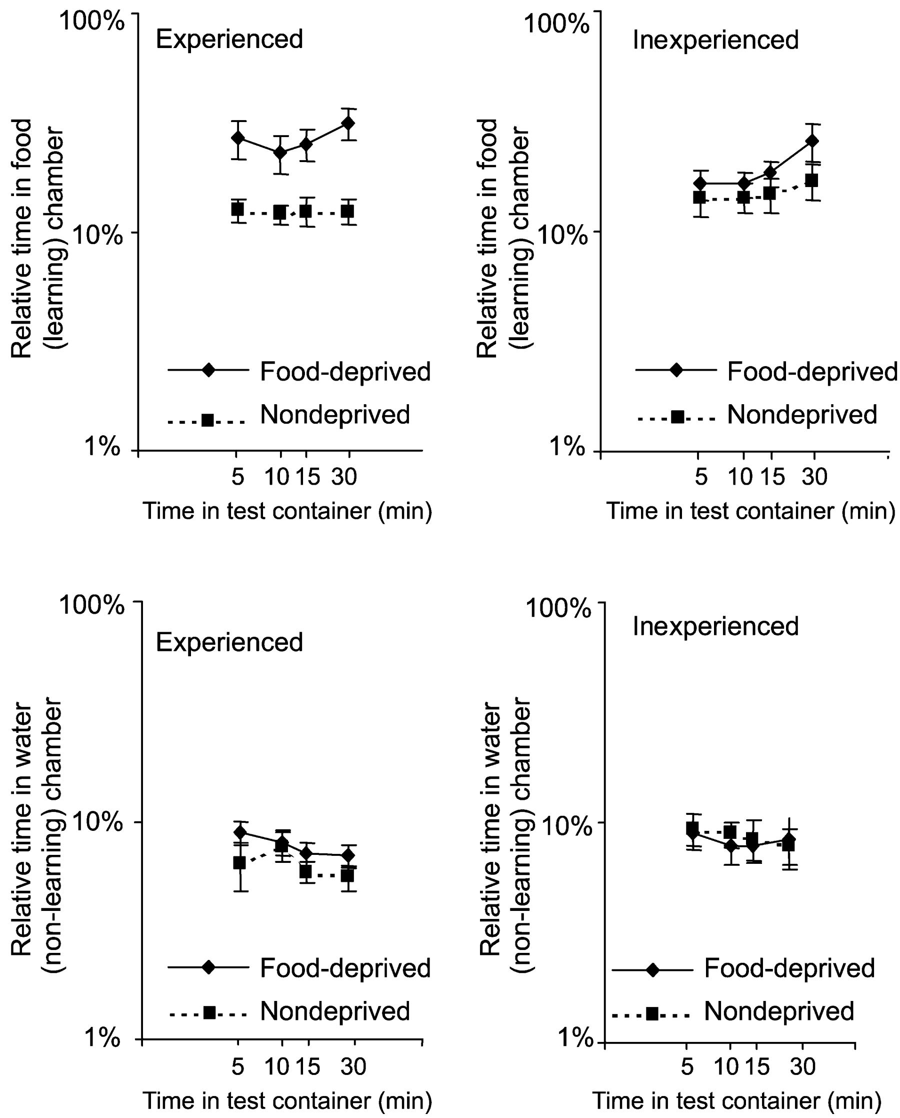

Fig. 4. Relative time spent in chamber versus the total amount of time in the test cage (minutes), for food-seeking behavior experiment (Experiment 2). Plots in the upper row are for the relative time spent in the food chamber, which is the learning chamber for this experiment; plots in the lower row are for the relative time spent in the water chamber, which is not the learning chamber, and serves as a control. Plots in the left column are for rats that had experience with food-deprivation paired with eating food (a milk diet), and plots in the right column show results for rats that did not have such an experience. Each data point is an average of 11 rats. Error bars show standard error. The main observation here is that food-deprived and food-nondeprived rats behave similarly in all regards except when they are experienced, and then only when they are in the room where they had their learning experience.

appears to require pairing that odor with previous deprivation experience. In fact, in experiments in which the odor was moved to the other chamber on test day (unpublished results), experienced rats differentially oriented to the room with the odor signals, not to the previous location of the food, though the inexperienced rats did not show this orientation.

Based on the interpretation we have presented with regard to appetitive learning, it is easy to imagine how the important contribution of experience to providing the guidance and orientation to food when food-deprived can be obscured by the normal course of experience and laboratory testing of feeding in rats. Because young rats are typically food-deprived and tested in an environment in which food is nearby, their enhanced activity and avid ingestion once food is contacted insures that they almost instantly feed—they simply respond to the proximate eliciting stimuli with the consummatory response. (In casual observation we have noted that the rats in our *experienced* training condition ate relatively soon after being placed back in their cages compared to the relatively delayed drinking of dehydrated rats on their first experience.) This initial experience also provides rats with their first training about food and the experience of deprivation. In a more natural setting, young rats' initial feeding is also strongly influenced by the presence of their parents (e.g. Ref. [25]). Redundant systems are thus in place to insure that in early development young rats find themselves in the proximity of food when they are in metabolic need. Nonetheless, the present experimental paradigm reveals that these young rats are probably not initially seeking food or showing behavior that differentially favors food sites or the approach to food.

4. Experiment 3: Normal stimuli for learning about appetitive behavior

Similar to the above explanation for the normal learning about food appetite, with dehydration and drinking there are natural contingencies which help insure that the appropriate appetitive behavior is acquired. In the laboratory setting, early experience with dry chow regularly creates a situation in which rats may dehydrate themselves from eating and then learn about drinking. Such learning may be related to dealing with the dry mouth created by eating or with food's systemic dehydrating effects [26]. These processes might contribute to insuring that rats learn, from early on, to direct their activity towards water when they are dehydrated. The importance of such normal contingencies (in nature rats may also experience both dry and wet foods) in the natural development of appetitive behavior is confirmed by an additional experiment.

4.1. Methods

4.1.1. Subjects

Subjects were four groups of 18-day-old ($n = 10$ per group) rats of the Sprague–Dawley CD strain delivered from Charles River Laboratories. Each individual experimental run consisted of four same-sex same-litter pups, one assigned to each experimental group. Each pup was weaned from the dam at 18 days of age and housed in its own test chamber (Fig. 1).

4.1.2. Training and testing

We repeated the dehydration paradigm described in Experiment 1, but rather than using a salt load to produce the dehydration, we fed pups dry chow. This experiment began when weaning-age rats were placed in their test cages for 4 days. During this time *experienced* rats received dry, powdered chow as their food (which was intrinsically dehydrating, and, being powdered, stayed in the food chamber) and *inexperienced* rats received evaporated milk as their food (which contained sufficient water to preclude dehydration). It is possible but unlikely that, prior to weaning, pups had experience with chow since that was the dam's food: the chow was in nuggets suspended over the cage that only the mother could reach, thereby minimizing the contact of chow with the pups, and pups could not reach the water bottle in the mother's cage, and so could not acquire experience orienting to water even if they happened to ingest some chow. From the beginning of the experiment, each rat had water freely available from a water bowl in its water chamber and each drank from it, although the rats in the experienced condition drank considerably more. In the course of this *experience phase* of the experiment, the experienced rats would become dehydrated by eating chow, would eventually enter the drinking chamber, encounter their water bowl and drink, over time repairing their fluid deficit [11]. Four days later, in the *test phase* of the experiment, half of each group was dehydrated and the other half not dehydrated by injection, as in Experiment 1.

4.2. Results and discussion

As with experience produced by a salt load, when rats that had experienced the chow diet were subsequently dehydrated, they showed differential water-seeking behavior and the inexperienced rats did not (Fig. 5; see also Ref. [11]; ANOVA main effect for appetitive state [$F(1,36) = 8.01$, $P < .05$] with experienced-dehydrated rats spending a greater percentage of their time in the water room than experienced-nondehydrated rats ($P < .05$); difference between inexperienced-dehydrated and inexperienced-nondehydrated rats was not significant). Qualitatively similar conclusions held when absolute time spent in a room was used as the measure. The same statistical tests for the food room (i.e. nonlearning room) showed no differences.

The appetitive behavior for drinking thus emerged after the standard experience of feeding on rat chow and was presumably mediated by a process similar to that for the salt-load-dehydration and the food-deprivation previously described. Such learning allows for the possibility that animals may flexibly identify sources of water and calories in items and locations available in and appropriate to a particular environment. That learning can make a contribution to the consummatory component of ingestion is well appreciated (e.g. Refs. [27,28]). 'What' animals are willing to consume (e.g. their learned preferences and aversions) and 'how' they consume (e.g. the motor topography of feeding behavior) is subject to learning. Further, it is known that the stimuli guiding appetitive responses can also be learned. Indeed, emphasis has been given [29] to the traditional argument that such learning is the sine qua non for 'motivation.' What we have additionally shown and summarized in this report is that expression of appetitive behavior by water or energy imbalance is itself acquired—that without appropriate initial experience an animal does not seek water or food when it should. To state this in a shorthand manner: An inexperienced, dehydrated rat does not appear to appreciate that it should seek water or that it needs fluid. Its behavior does not, in fact, indicate that it is experiencing any signal indicating that it should change its behavior (unless it has fluid in or near its mouth which then evokes a heightened consummatory response). An inexperienced, food-deprived rat is more generally active, but it does not seem to appreciate that it should seek food or needs nutrient (unless it has food in or

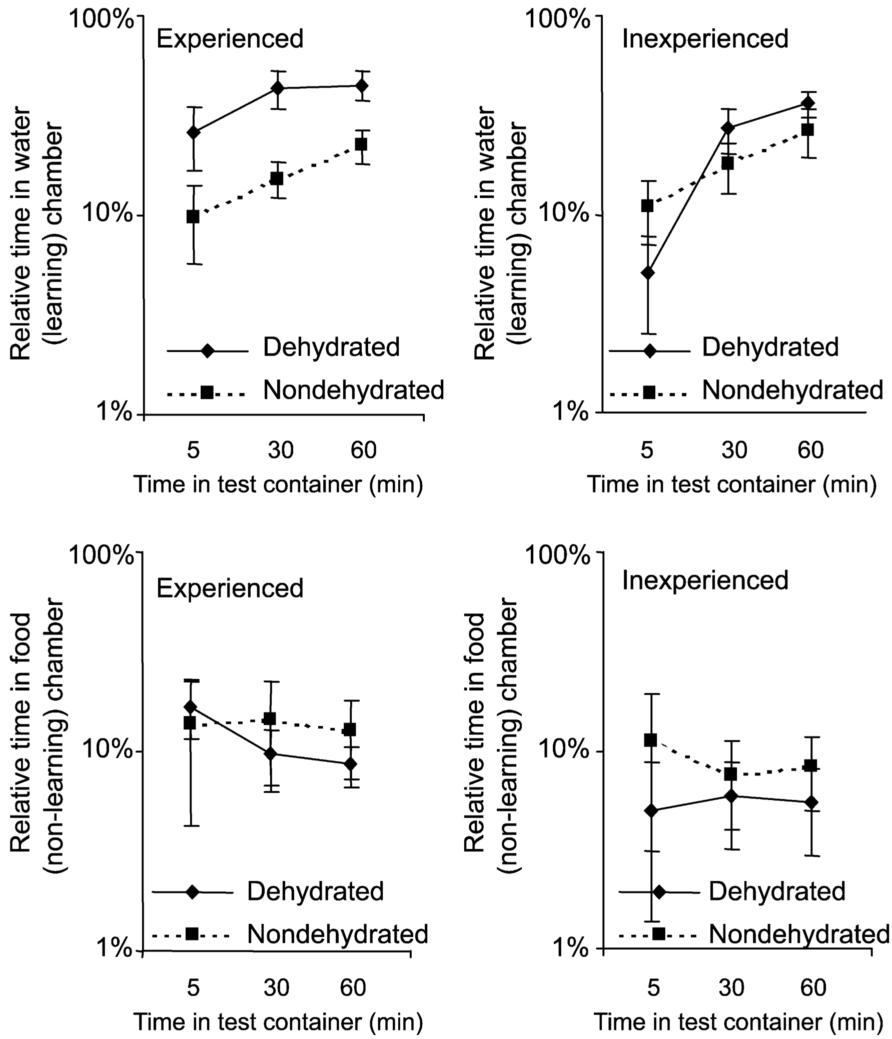

Fig. 5. Relative time spent in chamber versus the total amount of time in the test cage (minutes), for dehydration-learning experiment, where the first experience of dehydration is naturally induced via chow diet (Experiment 3). Plots in the upper row are for the relative time spent in the water chamber, which is the learning chamber for this experiment; plots in the lower row are for the relative time spent in the food chamber, which is not the learning chamber, and serves as a control. Plots in the left column are for rats that had experience with dehydration paired with drinking water, and plots in the right column show results for rats that did not have such an experience. Each data point is an average of 10 rats. Error bars show standard error. The main observation here is that dehydrated and nondehydrated rats behave similarly in all regards except when they are experienced, and then only when they are in the room where they had their learning experience.

near its mouth which then evokes a heightened consummatory response).

5. General discussion

Although the general phenomena of the acquisition of appetite for drinking has been previously reported [11], the present experiments explicitly tracked *appetitive behavior* rather than inferring the appetitive behavior from the measurement of intake. In doing so, they confirm the learned change in orienting or appetitive responses that occur when dehydration is paired with consumption of water. Furthermore, they have revealed that the same process occurs in learning the appetitive responses for feeding.

Our description of the emergence of appetitive behavior is consistent with an emerging perspective on the control of appetitive behavior derived from research on Pavlovian conditioning. From this perspective, changes in physiological state are perceived as a special type of conditioned stimuli (CSs) referred to as 'occasion setters' [30] that set the occasion for or modulate the action of other stimuli or CSs. The condition of dehydration or deprivation generates internal stimuli that can be sensed by the nervous system. [What the internal stimuli are that might regulate food intake (e.g. Ref. [31]) has been harder to uncover than for liquid (e.g. Ref. [14]).] After conditioning, some portion or component of these stimuli becomes the signal that is linked to the stimuli related to an animal's experience with food or fluid and thus allows these external stimuli to become effective or evocative in guiding an animal towards food or fluid (e.g. Refs. [32,33]). That is, after being paired with feeding or drinking, the internal stimuli produced by dehydration or deprivation 'set the occasion' for signals related to food or water to elicit a conditioned orienting or appetitive response. It is the case, and consistent with a more traditional view, that the efficacy of this internal permissive stimulus need not be learned—it could represent an inborn modulatory process. But an acquired effectiveness fits with our data on the learned nature of appetitive behavior, now for both feeding and drinking. It provides a framework for further analysis of what it is that is being acquired, and why it happens.

An alternate and also potentially applicable understanding relates to current analysis of learning about the relationship between physiological state and consummatory responses in the context of operant conditioning (e.g. Ref. [34]). By this account, animals must learn that when they experience a change in a particular physiological state, the value of certain incentive stimuli (such as signals related to food or water) has also changed. In this way, animals do not know what to do with food until it has been experienced in both deprived and nondeprived conditions. The incentive value must be acquired in the context of a particular state.

Both of these learning perspectives point to the essential acquired nature of appetitive responding and suggest that the great flexibility and adaptiveness of the sequence of appetitive responses may be related to the degree to which an animal's orientations and appetites are tuned from the outset to its specific experiences. Nonetheless, one may ask whether the finding that 'learning to seek something' is acquired is of particular interest, given the degree to which redundancies in the behavioral system and the natural exposure to appropriate stimuli will invariably assure that animals show characteristic and similar 'seeking' behavior. But note that it is exactly the identification and analysis of the fundamental operation of individual components in the behavioral sequence that will allow us to appreciate how coherent sequences of behavior are ultimately assembled and controlled [35]. It is certainly the case that such a response system is built up of highly evolved elements that are organized to insure a relatively reliable and robust repertoire of behaviors for any species [36,37]. Yet appreciating how the behaviors are produced requires recognition of the individual elements and components of the behavioral stream. What appears to the observer as a coherent string of behavior may depend on a number of discrete and independent neurobehavioral elements whose operation must be individually understood if we are to relate behavioral function to controlling physiology or neural organization.

The existence of ubiquitous appetitive elements that typically must be acquired raises two specific significant issues: (1) what is it that makes the learning happen; and (2) what is actually being learned. With respect to the production of learning, we do know that a consummatory response must occur, and that the response must be initiated by the animal [12]. For example, just infusing water into an animal's mouth when it is dehydrated does not result in appetitive learning. However, it is not known whether the learning requires just the oral stimulation from water or food, or depends on the postingestive effects of consumption. The present experiments provide a beginning description of what it is that animals are learning. There is a distinct change in appetitive behavior with animals spending more time approaching the previous sites of food or water. What remains of interest is why this is happening. Are animals now just more responsive to the stimuli in one arm and thus spending more time there, or is there now a goal orientation in their behavior? These first acquired behaviors may afford an opportunity to identify core components of appetitive organization.

In the last half-century we have learned a lot about the emerging physiology of consummatory behavior, but little about the seeking, orienting, or appetitive side of behavioral systems. The basic behavior components in an appetitive response sequence—such as consummatory responses of dehydrated or food-deprived rats, and the increased level of activity of food-deprived rats—are so effective at encouraging the learning required for seeking behavior that they have tended to conceal the existence of this necessary learning step. We show here that 'seeking' behavior related to the two ingestive appetites—those for water and food—is acquired only after, respectively, the pairing of dehydration with water experience and the pairing of food restriction with food experience. Without these experiences, dehydrated rats will not seek water even though they have experience drinking water when not dehydrated, and food-restricted rats will not seek food even though they have experience eating when not food-restricted.

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