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Pontine and thalamic influences on fluid rewards: III. Anticipatory contrast for sucrose and corn oil

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ABSTRACT

An anticipatory contrast effect (ACE) occurs when, across daily trials, an animal comes to respond less than normally to a first stimulus when it is followed shortly by a second, more preferred solution. Classically, ACE is studied using a low (L) concentration of saccharin or sucrose, followed by access to a higher (H) concentration of sucrose. Subjects in the control condition have two bouts of access to the weaker solution presented on the same schedule. The ACE is measured by the difference in intake of the first bout low solution between subjects in the low–low (L–L) vs. the low–high (L–H) conditions. Here we used this paradigm with sham feeding rats and determined that nutritional feedback was unnecessary for the development of ACE with two concentrations of sucrose or with two concentrations of corn oil. Next we showed that ibotenic acid lesions centered in the orosensory thalamus spared ACEs for both sucrose and corn oil. In contrast, lesions of the pontine parabrachial nuclei (PBN), the second central relay for taste in the rat, disrupted ACEs for both sucrose and corn oil. Although the sensory modalities needed for the oral detection of fats remain controversial, it appears that the PBN is involved in processing the comparison of disparate concentrations of sucrose and oil reward.

1. Introduction

In the previous two articles in this series, the results showed a dissociation in the role of the gustatory system in orosensory processing of corn oil. Rats with lesions of the parabrachial nuclei (PBN) exhibited weaker than normal operant responding for corn oil emulsions [1,2], but learned a condition aversion to corn oil [3]. Similar PBN damage disrupted responding for sucrose in both tasks. Rats with lesions of the thalamic orosensory area (TOA), on the other hand, showed no deficits in responding for sucrose or corn oil during fixed or progressive ratio tasks and they acquired a conditioned aversion to both stimuli. These results did not fully support our initial hypothesis that the gustatory PBN is important for orosensory processing of sucrose but not corn oil, and, conversely, that the TOA is necessary for processing oil but not for sucrose reward.

In the present study, we focused on reward comparison for orosensory sucrose and corn oil using the anticipatory contrast effect (ACE). The same hypothesis was tested, but with respect to relative, rather than absolute, reward value. Again, ACE previously was demonstrated only with real feeding. In order to focus on the orosensory effects of fluid rewards, Experiment 1 first demonstrated that intact sham feeding rats can exhibit ACE for sucrose and corn oil, the latter of which has never been tested. Experiment 2 tested whether PBN lesions block an ACE for sucrose and TOA damage interferes with the parallel effect for oil. A preliminary report of these results was presented at the annual meeting of the Society for the Study of Ingestive Behavior in 2009.

2. Experiment 1: anticipatory contrast effects in sham feeding rats

Ingestion of one preferred sapid stimulus is affected by the relative value of another such stimulus presented closely in time. This change in responding as a function of experience is referred to as a contrast effect [4]. An anticipatory contrast effect develops when rats suppress intake of a weak stimulus, e.g., 0.15% saccharin or 0.06 M sucrose, as it comes to predict the future availability of a stronger, more preferred, stimulus, e.g., 1.0 M sucrose. The comparison is with intake by rats that only experience two bouts of the lower concentration [5–8]. Previous studies demonstrate that this contrast effect is due to anticipation of access to the more rewarding solution, not to the memory of having received the preferred 1.0 M sucrose solution on the previous day ([9,10], but see ref. [11]). Thus, in a Pavlovian conditioning context, the first solution is considered as a conditioned stimulus (CS) and the second, more preferred solution, as an unconditioned stimulus (US) [9,12].

The caloric value of the CS plays an important role in the development of an ACE. When the interstimulus interval (ISI) is a matter of seconds, similar ACEs occur with both sucrose–sucrose and saccharin–sucrose parings. As the ISI increases from seconds to minutes

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(e.g., 5 or 10 min), the ACE diminishes in sucrose–sucrose pairings but not when saccharin serves as the CS. The difference between sucrose and saccharin pairing is not due to differences in taste, but to the caloric load of the CS. Food deprived rats are, apparently, unwilling to forgo the available calories in the first bottle while they wait for access to the more preferred stimulus. When not deprived, however, anticipatory contrast is evident, i.e. rats avoid intake of a weaker sucrose solution when waiting for access to the more preferred second solution [12].

An ACE also occurs when neither the CS nor the US contains a caloric load. Using saccharin–saccharin pairings, Flaherty and Rowan produced an ACE using 0.05%–0.15% concentrations of saccharin as the first and second solution [13]. These results suggest that an ACE could be based solely upon the relative taste intensity of the CS and the US. Accordingly, our study was designed using sham feeding to determine whether an ACE can be obtained in rats when the CS and US provide limited or no postingestive consequences. Furthermore, previous studies have always used a sweet stimulus in the ACE paradigm. This study, therefore, investigated whether disparate concentration pairs of two rewarding orosensory stimuli, sucrose and corn oil [14–16] can support an ACE in intact rats.

2.1. Materials and Methods

2.1.1. Subjects

The subjects were 36 naïve male Sprague–Dawley rats, 18 for each experiment (Charles River, Wilmington, MA), weighing 275–300 g at the start of testing. They were individually housed on a 12:12 h light: dark schedule with ad libitum access to tap water and standard laboratory diet [Rodent diet (W) 2018; Harlan Teklad, Madison, WI]. Once the experiment began, the rats were maintained on a food deprivation regimen as described in more detail below. Distilled water was available at all times, except when the rats were in the test chamber. Normal pelleted chow was weighed and provided at least one hour after the daily session.

2.1.2. Surgery

For Experiments 1A and 1B, the rats were divided into low–low (L–L) and low–high (L–H) groups (n = 9/each). They were treated with atropine sulfate (0.15 mg/kg ip) and, 20 min later, anesthetized with pentobarbital sodium (50 mg/kg ip) for the gastric fistula surgery. Details for the design and implantation of the gastric fistulas are described elsewhere [17]. The rats had at least two weeks to recover before starting the experiment.

2.1.3. Apparatus

Testing occurred in 6 identical modular operant chambers measuring 30.5 cm × 24.1 cm × 29.2 cm. Each chamber was equipped with a house light, a white noise generator, and 3 sipper tubes that could be programmed to advance and retract depending on the testing schedule; only 2 tubes were used for this experiment. These sipper tubes could enter the chamber through 1.3-cm holes, spaced 16.4-cm apart from left to right of one aluminum wall. The house light and white noise generator were located on the wall opposite to the sipper tubes. The white noise generator provided a background noise level of 75 dB. Three chambers served as L–L chambers where only low concentration pairs were presented. The other three served as L–H chambers where both the low and the high concentration pairs were presented. Spout licking was recorded using a triple lickometer circuit. Each test chamber was located in a sound attenuating cubicle that was fitted with a ventilation fan. This set up for ACE tasks and online data collection was operated by a PC computer and an interface (MedPC; MED Associates Inc. St. Albans, VT).

2.1.4. Procedure

The rats were run in squads of 6, with 3 rats placed in the L–L chambers and the other 3 placed in the L–H chambers. Before each rat was placed in a chamber, its stomach was flushed with lukewarm water as described in the companion articles. Testing was preceded by one 5-min habituation trial, in which the rats were placed in the chamber with the house light and white noise on. Food was removed from the home cage the day before the habituation trial. Thereafter, normal pelleted chow was weighed (20–25 g) and given to the rats in their home cage at least one hour after they finished their daily trial. The body weight was maintained at 90% of free feeding. During testing, the rats were given 3 min access to 0.06 M sucrose in bottle 1 (B1). Immediately after that, B1 retracted and bottle 2 (B2) advanced. Rats in the L–L condition were then given 3 min access to the same 0.06 M sucrose solution in B2. Rats in the L–H condition, on the other hand, were given 3 min access to the 1.0 M sucrose solution in B2. There was one such pairing a day for 14 days in succession.

After a week off, the L–L and L–H groups were reversed and tested for ACE using corn oil concentration pairs. During the first 7 trials, 1% corn oil served as the L concentration and 25% corn oil served as the H concentration. Thereafter, the L concentration was increased to 2.5% corn oil for another 8 trials. This design failed to support the development of an oil ACE in rats with open fistulas and a history of experience with sucrose. Experiment 1B addressed the same question, but with rats that were naïve to sucrose.

In Experiment 1B, 18 new rats were first trained for 14 days using 1.5% corn oil followed by a second 1.5% corn oil as the L–L condition or 1.5% followed by 25% corn oil as the L–H condition. After 14 trials, it became clear that even sucrose naïve rats did not lick the 1.5% corn oil emulsions consistently when tested at 90% of free feeding body weight. Given the low intake of the L concentration by rats in the L–L control group, it was not possible to assess contrast (i.e., suppressed intake of the L concentration when paired with the future availability of the H concentration) due to a floor effect. Consequently, the rats were placed back in a free feeding condition for two weeks and then began training with the 2.5% vs. 25% condition using the same L–L and L–H groups. The rats licked 2.5% corn oil consistently after 10 trials. After the 10th trial, more pellet chow (3–5 g) was given to the rats for the rest of 8 trials in order to reduce the deprivation level from 90% to 95% of free feeding body weight. Although the fistula was open and postingestive feedback should have been nil, it was thought that rats may be more likely to forego intake of the lesser corn oil cue in anticipation of the more concentrated emulsion if they were less food deprived. At 95% of free feeding body weight, the rats did develop an ACE with corn oil using 2.5% as the L stimulus and 25% as the H stimulus. The rats were then given two weeks of free feeding without training and placed back on the food deprivation regimen with a target of 95% of their free feeding body weight. The L–L and L–H groups were reversed and the L concentration was increased to 5% corn oil. There were 8 more such trials.

2.1.5. Solutions

The sucrose solutions were made with distilled water and the corn oil emulsions were blended with distilled water and Tween-80 [100 ml corn oil–water mixture with 0.75 ml Tween-80 (Sigma-Aldrich, St. Louis, MO)]. All procedures in this experiment were approved by the Institutional Animal Care and Use Committee of the Pennsylvania State University College of Medicine.

2.1.6. Statistical analysis

It took the rats 6–8 days to begin licking consistently. Only rats that licked consistently thereafter contributed data to the analysis. In Experiment 1A, all rats contributed data to the analyses. In Experiment 1B, data from three rats were omitted. One rat died after surgery and one rat from each L–L and L–H group did not lick throughout training. The data included daily 3-min sham licks on B1 and B2 and the latency to start licking each bottle. The lick and latency data were averaged into 2-day blocks and were analyzed by mixed