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Review

# A case study in behavioral analysis, synthesis and attention to detail: Social learning of food preferences

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ABSTRACT

Philip Teitelbaum's focus on detailed description of behavior, the interplay of analysis and synthesis in experimental investigations and the importance of converging lines of evidence in testing hypotheses has proven useful in fields distant from the physiological psychology that he studied throughout his career. Here we consider the social biasing of food choice in Norway rats as an instance of the application of Teitelbaum's principles of behavioral analysis and synthesis and the usefulness of convergent evidence as well as the contributions of detailed behavioral analysis of social influences on food choice to present understanding of both sensory processes and memory.



**Contents**



## 1. Introduction: Phil Teitelbaum and me

In 1963, Phil Teitelbaum taught section three of the Proseminar that all first-year graduate students in Psychology at the University of Pennsylvania (of whom I was one) were required to attend. In addition to providing a background in the facts of Physiological Psychology, Phil devoted considerable class time to discussing the importance of: (1) combining Cartesian analysis with what he called "the method of synthesis," (2) converging lines of evidence in establishing 'facts', and (3) as close an analysis of behavior as of the nervous system for understanding of the relationship between brain and behavior.

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I still have my 50-year-old lecture notes from Phil's Proseminar classes. Although I have only the vaguest memory of the details of the experiments on the visual system and hypothalamic control of feeding that Phil used to illustrate the application of analysis and synthesis, the importance of converging lines of evidence and the power of careful study of behavior in understanding nervous system function, Phil's ideas concerning the most productive way to pursue the study of Physiological Psychology have guided my research through the decades since I wrote the following on the first page of my notes from Phil's first lecture:

> "Understanding = breaking down into simpler, more familiar things . . . . . must then synthesize to test understanding. . . if you synthesize and something is missing from the phenomenon, then you do not fully understand."

Phil's feeling for the limitations of any single method in analyzing a phenomenon and his consequent interest in using multiple techniques to establish 'facts,' though not so explicit in my notes as was his discussion of the importance of synthesis in determining whether an analysis had been successful, was implicit in the several case studies Phil provided of experimental investigations that had contributed substantially to our understanding of the nervous system. In each, including Phil's own ground breaking work on hypothalamic control of feeding behavior, careful description of behavior played a critical role in analyzing brain function.

After graduate school, although, like Phil, I became involved in studying feeding in animals, our intellectual interests increasingly diverged and our interactions became less and less frequent. In 1971, Phil visited McMaster University, where I was a young Assistant Professor, to give a departmental colloquium and we spent considerable time together during his stay in Hamilton. Phil and I spoke briefly at scattered Eastern Psychological Association meetings during the 1970s and 1980s, and we last met in Princeton at Byron Campbell's festschrift in 1997.

Despite the ever decreasing frequency and duration of our conversations, much to my benefit, I never forgot Phil's admonitions: first, that the structure of behavior deserved the same degree of careful attention as the structure of the nervous system, second, that as a safeguard against error in interpretation of isolated findings, the same phenomenon should be measured using a variety of methods, and third that synthesis following analysis could be used to ensure that analysis had provided complete understanding of a phenomenon.

In my own case, the importance of these early guidelines in experimental method were particularly important because, immediately after leaving graduate school, my research drifted into a subject matter in which I had only the most limited background (animal behavior) and became focussed on a class of behavioral phenomena (social learning in animals) that had received little prior attention from the scientific community [1]. Indeed, the sole resource that I brought to inaugurating a new area of research in a field in which I was essentially ignorant was a firm grounding in experimental method provided by both Phil's lectures and Carl Hempel's course in the philosophy of science that I had taken as a sophomore undergraduate at Princeton and which had made me a confirmed logical positivist for life [2].

## 2. Social influences on the food choices of Norway rats

When Phil visited McMaster in 1971, I was only 12 months into a research program on social biasing of food choices of rats that was to occupy my laboratory for much of the next 40 years. My students and I had just started to explore what turned out to be multiple ways in which weaning rats could use information acquired from more knowledgeable elders to decide what to eat and what to avoid eating in the world outside their home burrow. At the time, in the early 1970s, the study of taste-aversion learning was a hot topic in Psychology, so the work was focussed (I thought) on learning socially to avoid ingesting of toxic substances.

### 2.1. The phenomenon

My students and I captured Norway rats on garbage dumps in southern Ontario, brought them into the laboratory where we established them in small breeding colonies in large floor enclosures, and where we fed them powdered rat chow (Diet A) for 3 h/day.

Once the colonies had become adjusted to life in the laboratory, we introduced a very tasty second food (Diet B) into each colony's cage during daily feeding sessions, but adulterated Diet B with a mild toxin so that adult members of our colonies would learn to avoid ingesting Diet B and would continue to avoid Diet B when subsequently offered uncontaminated samples of it. We then waited patiently until a female in each colony gave birth and reared her young to weaning age. Finally, we could watch on closed-circuit television when the weanlings made their very first excursions from the nest to eat solid food.

Rather unexpectedly, we found that for weeks young rats ate only the less palatable Diet A and totally avoided Diet B, the food that we had trained the adults of their colony to avoid. Even after we moved young to individual enclosures and offered them a choice between Diets A and B, for many days, the young continued to eat only Diet A, the food that the adults of their colony were eating and to ignore Diet B [3].

### 2.2. Exploring social biasing of rats' food choices

The first step in our analysis of this socially transmitted food aversion revealed that weaning young rats were, in fact, not learning to avoid the food that the adults of their colony were avoiding [4]. Rather, the young learned to eat the food that adults of their colony were eating. Because young wild rats are extremely reluctant to ingest unfamiliar foods [5,6] once the adults had induced them to eat Diet A, the young avoided Diet B simply because it was unfamiliar [7]. Indeed, when we tested in isolation pups raised by adults that had only Diet A to eat during colony feeding periods, these pups showed as strong an avoidance of Diet B as did pups raised in colonies where adults had access to both Diets A and B and were avoiding the latter [8].

We have subsequently provided evidence of five distinct ways in which information acquired from adult rats can bias their young to eat where and what adults of their colony are eating. I shall briefly mention four before discussing in detail the fifth because the latter provides the clearest example from my laboratory of the power of analysis coupled with synthesis to provide a thorough appreciation of the organization of a pattern of behavior. As made explicit in the final section of this article (Section 5), such detailed analysis subsequently supported substantial advances in our understanding of the physical basis of aspects of both perception and memory.

### 2.3. Four mechanisms for social biasing of food choice in rats

While suckling, neonatal rats experience flavor cues in mother's milk that influence the food choices of young at weaning [9,10]. Second, when young rats first leave their natal nest site to seek solid food, they use visual cues to locate adults at a distance from the nest site and then feed in their immediate vicinity [8]. Indeed, even an anesthetized adult rat placed near one of two identical feeding sites renders the occupied site far more attractive to pups than the unoccupied one, causing them to visit and feed there more frequently [11]. Further, adult rats do not need to be physically present at a

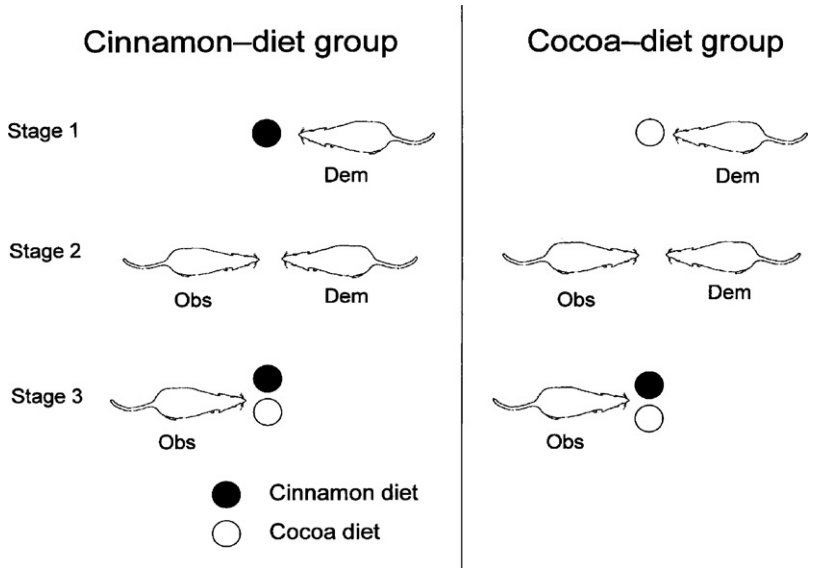


**Fig. 1.** Treatment of demonstrator and observer rats assigned to cinnamon-diet and cocoa conditions. Stage 1: A demonstrator (Dem) eats either cinnamon-or cocoa-flavored diet. Stage 2: The demonstrator interacts with a naïve observer (Obs). Stage 3: The observer chooses between cinnamon- and cocoa-flavored diets, one of which was the diet its demonstrator ate in Stage 1.

feeding site to make it more attractive to pups than alternatives. When leaving a feeding site and returning to their burrows, adult rats deposit scent trails [12,13] that their young follow when seeking food [14] and while feeding, deposit olfactory cues both in the vicinity of a feeding site [11,15–17] and on foods that they are eating [18] that cause young rats to visit and eat more frequently at marked than at unmarked sites. Fifth, and perhaps most interesting, in Norway rats as in honey bees [19], interaction of naive individuals with successful foragers at a distance from a feeding site profoundly influences the subsequent food choices of the naive.

### *2.4. Social transmission of information concerning distant foods*

We developed an experimental paradigm intended to provide a laboratory analogue of a situation that free-living Norway rats should experience with some frequency; an individual rat leaves the burrow that it shares with others of its species, finds food, eats and then returns to its burrow where it interacts with other burrow residents. Our question was whether such interaction at a distance from a feeding site could influence the subsequent food choices of individuals with whom the returning successful forager interacted [20].

### *2.5. Exploring the effects of social interactions far from a feeding site*

In our three-stage laboratory protocol (See Fig. 1) we: first, fed a "demonstrator" rat one of two foods (Stage 1), then placed the demonstrator together with a naïve "observer" rat for a few minutes (Stage 2), and finally (Stage 3) offered the observer rat a choice for 24 h between cinnamon- and cocoa-flavored diets, one of which was the diet that its demonstrator had eaten during Stage 1 [21]. Invariably, after interacting with a demonstrator rat, an observer rat shows a significantly enhanced preference for whichever food its demonstrator had eaten (e.g. [20,22,23]).

Such effects of demonstrator rats on their observers' food preferences are unexpectedly powerful. For example, in one experiment, after we fed 'focal' rat subjects a highly palatable diet and injected them with a mild toxin to induce nearly complete aversion to that diet, we allowed these focal subjects to interact with demonstrator rats that had just eaten the diet the focal subjects had learned to avoid [24]. When we then offered the focal subjects a choice between the highly palatable diet to which they had learned an aversion and laboratory chow, half of the focal subjects ate as much of the palatable diet to which they had previously learned an aversion as did naive animals simply offered a choice between the highly palatable diet and laboratory chow [24].

Effects of demonstrator rats on their observers' food choices are also surprisingly long lasting and resistant to interference. When we introduced delays of either 7 or 30 days between when an observer interacted with its demonstrator (Stage 2) and Stage 3, when we offered observers a choice between cinnamon and cocoa-flavored diets, even a month after interacting with their demonstrators, observers still showed a profound influence of demonstrators' diet during Stage 1 on observers' food choices in Stage 3 [25,26]. Others have extended the period between Stages 2 and 3 in our standard protocol to 3 months and still found an effect of the food eaten by demonstrators in Stage 1 on observers' food choices in Stage 3 [27].

Of course in the real world, a rat that has interacted with a first successful forager might both interact with other successful foragers and eat other foods itself before encountering whatever food the first successful forager with which it interacted had eaten. So, we undertook a series of studies to examine the effects on a food preference acquired as a result of interacting with a first demonstrator of subsequently eating other foods and interacting with other demonstrators.

We fed demonstrators cinnamon-flavored diet and introduced a 6-day delay between Stages 2 and 3. During that 6-day interval we maintained subjects assigned to each of three control groups on their normal rat-chow diet, whereas observers randomly assigned to three experimental groups either: (1) ate four unfamiliar foods, (2) interacted with demonstrators that had eaten four unfamiliar foods, or (3) both ate four unfamiliar foods and interacted with demonstrators that had eaten those four foods. None of these three manipulations had any effect on observers' preferences for their focal demonstrators' diets [28–30].

## 3. Analysis

To explore the behavioral processes supporting effects of demonstrators on their observers' food choices, we had to gain

some control over the interaction of demonstrator and observer rats. We used a procedure identical to that described in Fig. 1 except that during Stage 2, we separated demonstrator and observer with a screen partition [20].

Separating demonstrator and observer with a screen during Stage 2 did not interfere with communication between them, whereas separating them with a transparent Plexiglas barrier blocked any effect of demonstrators on their observers' diet choices in Stage 3. Clearly, cues in some modality other than visual, perhaps auditory, perhaps gustatory or olfactory carry the message passing from demonstrator to observer [20].

### 3.1. Converging lines of evidence

We developed several converging lines of evidence, each consistent with the hypothesis that olfactory cues support transmission of flavor preference. First, if after a demonstrator has eaten and before it interacts with an observer, the demonstrator is anesthetized and its nose placed 5 cm from a screen partition separating it from its observer, thus making direct physical contact between demonstrator and observer impossible, demonstrators still profoundly influence the food choice of their observers [20].

This rather simple finding has several important implications. First, we can infer that the message passing from demonstrator to observer is passively emitted by the anesthetized demonstrator, not produced in response to its detecting the presence of an observer. Second, the Plexiglas-barrier experiment shows that the important cue is not visual, yet it can be transmitted over some distance, hence it is not gustatory. We are left with only olfactory or auditory cues to carry the message from demonstrator rats to their observers, and auditory cues emitted by an unconscious rat that identify the flavor of the diet it has been eating seem extremely unlikely.

Second, and more directly, if before observers interact with demonstrators in Stage 2, we flush observers' nasal cavities with Zinc sulfate solution to produce a transient anosmia [31], observers fail to exhibit a preference for their demonstrators' diets during testing in Stage 3. Control observer rats whose nasal passages are rinsed with saline solution show an undiminished tendency to eat the same diet as their respective demonstrators [20]. Last, but not least, not only rats but also humans can use olfactory cues emitted by recently fed rats to determine what diet a rat has been eating. When we asked human observers to sniff the breath of rats recently fed either cinnamon- or cocoa-flavored diet, they could, with 85–90% accuracy, tell which rat has eaten which diet [32]. We did not, however, notice any particular craving for cinnamon- or cocoa-flavored rat diet in our human observers, which brings me to the next issue that needs to be addressed.

### 3.2. Detailed analysis

It's not surprising that an observer, whether human or rodent who sniffs a rat's mouth can tell which of two foods the rat has recently eaten. Both particles of food clinging to the fur and vibrissae of rats and the odor of foods emerging from the digestive tract of recently fed rats carry information identifying the food that a rat has recently eaten [33,34].

The more difficult question is why, in a proximal sense, after an observer rat has determined that a conspecific demonstrator has just eaten say cinnamon-flavored food, the observer should exhibit an enhanced preference for cinnamon-flavored food.

As mentioned above (Section 2.2), rats, particularly wild rats, are often extremely hesitant to eat unfamiliar foods [5,6] and, at least under some circumstances, simple exposure to a food will increase a rat's subsequent intake of it. Observer rats might, therefore, develop an enhanced preference for their respective demonstrators' diets as the result of simple exposure to the smell of a diet carried on a demonstrator, in which case demonstrator rats would be acting as simple carriers of food particles and food odors.

However, results of a number of studies offer no support for the hypothesis that socially induced changes in observer rats' food preferences result from simple exposure to the smell or taste of a diet. For example, when we maintained rats *ad libitum* on both cinnamon- and cocoa-flavored food and for 1 week before giving them 30 min/day to interact with demonstrator rats fed either cinnamon- or cocoa-flavored food, we still saw massive effects of the food fed to demonstrators on the food choices of their observers. Changes in observers' food preferences seem to result from exposure to food-related cues in the social context provided by the presence of a demonstrator [35].

To identify the nature of the contextual cues rendering demonstrators effective in altering their observers' food preferences, we exposed observers to demonstrators treated in four different ways: (1) we anesthetized *powdered-face demonstrators*, rolled their faces in either cinnamon- or cocoa-flavored diet and then presented their faces to observers. (2) We treated *dead powdered face demonstrators* just as we had treated powdered-face demonstrators except that we sacrificed dead-powdered-face demonstrators by anesthetic overdose immediately before we placed the dead-powdered face demonstrators with observers. (3) We anesthetized demonstrators assigned to the *powdered-rear condition*, just as we had treated demonstrators assigned to the powdered-face condition, but rolled their rear-ends, rather than their head ends, in cinnamon- or cocoa-flavored diet before allowing observers to interact with the rear-ends rather than the heads of these demonstrators. (4) To control for effects of simple exposure to a diet, we used *Surrogate demonstrators*, rat-sized pieces of cotton batting one end of which was rolled in cinnamon- or cocoa-flavored diet and presented to observers.

We found, that powdered-face demonstrators had significant influence on their observers' food preferences whereas surrogate, dead-powdered-face and powdered-rear demonstrators did not. The significantly greater effect of powdered-face than of surrogate demonstrators indicates again that simple exposure to a diet is not sufficient to alter observers' subsequent food choices. Some contextual cue provided by the presence of the head end of a living rat seems necessary [34].

One possibly important difference between live and dead rats is that live rats are breathing, while dead rats are not. Similarly, the anterior end of a live rat emits rat breath, while their posterior end does not. So, it seemed reasonable to ask whether some constituent of rat breath might provide the contextual cue that makes the diet-identifying cues carried by demonstrator rats effective in changing their observers' food preferences. Gas chromatograms of sulfur compounds in rat breath provided evidence of the presence of relatively large amounts of carbon disulfide (CS2) [36].

## 4. Synthesis

We subsequently found that by adding a few drops of a very dilute solution of CS2 to a cotton-batting surrogate rat rolled in cinnamon- or cocoa-flavored diet, we could make that surrogate rat almost as effective as an anesthetized demonstrator rat in altering observer rats' food preferences. CS2 is thus identified as an important component of the social context that allows demonstrator rats to alter the food preferences of their rat observers [36].

Human beings also have trace amounts of CS2 on their breaths, so one might expect that if the combination of food odor and very small amounts of CS2 is sufficient to produce a change in the flavor preferences of rats, human demonstrators who ate a food and

then breathed on a rat should increase rats' preferences for the foods that the human demonstrators have eaten. In fact, we have found that observer rats offered a choice between cinnamon- and cocoa-flavored diets after interacting with a human demonstrator that has eaten one or the other show an enhanced preference for the diet that their human demonstrator has eaten as great as that which they show after interacting with demonstrator rats fed either cinnamon- or cocoa-flavored diet [37].

## 5. The nervous system

After 10 years of behavioral analysis, we had reached the limits of understanding of olfactory control of social transmission of food preference in rats that such methods could provide. However, the careful analysis and synthesis that we had provided allowed others to gain insights into the functioning of the nervous system that might not otherwise have been possible.

### 5.1. The olfactory system

Roughly 1% of the main population of olfactory-receptor neurons in the olfactory epithelium of mice (the GC-D receptors) express guanylyl cyclase. However, neither the olfactory stimulus triggering a response in these receptors nor their function was known.

Munger et al. [38] have recently used gene-targeted mice with disruptions in the transduction cascade of GC-D receptors in response to stimulation with CS2 to show: not only that the GC-D olfactory subsystem in mice responds to stimulation with biologically relevant concentrations of CS2, but also that the GC-D olfactory subsystem must be intact for observer mice to acquire socially transmitted food preferences.

Further, field potential recordings of electro-olfactory responses to CS2 in the main olfactory epithelium showed sensitivity to CS2 at concentrations far lower than those found in rat breath as well as substantially reduced responses to CS2 in homozygous gene-targeted mice that fail to express GC-D. Consistent with the results of these field-potential recordings, single GC-D receptor cells in the main olfactory epithelium of control mice respond vigorously to stimulation with CS2 whereas homozygous transgenic mice with expression of guanylyl cyclase inhibited show greatly reduced response to CS2.

As would be expected if expression of GC-D and normal activity in the other two parts of the molecular transduction cascade that Munger et al. [38] explored provide a necessary substrate for socially mediated enhancement of food preferences, homozygous gene-targeted observer mice fail to show a preference for their demonstrators' diets that heterozygous mice with intact olfactory systems show. Further, intact observer mice that interact with a cotton-batting surrogate demonstrator dusted with either cinnamon- or cocoa-flavored diet and moistened with CS2 preferred the diet that they had experienced together with CS2, whereas homozygous gene-targeted mice did not, and control experiments for effects of gene targeting on both general olfactory sensitivity and the memory and learning necessary for observers to show effects of interaction with a demonstrator on their observers' subsequent food preference showed no effect of genetic lesions on performance. The GC-D olfactory subsystem seems to be a necessary substrate not only for response to CS2, but also for social influence on food choice.

A carefully analyzed behavioral phenomenon led to both discovery of a previously unknown function for an olfactory receptor and a means of exploring a molecular pathway linking reception to behavior.

### 5.2. Learning and memory

Several of the unusual features of social influence on food choice in rats – its occurrence in a single trial, its strength, duration and resistance to interfering experience – make the phenomenon particularly promising for studying the neuroanatomical, neurochemical and genetic substrates of learning and memory [25].

In the years since discovery of the phenomenon, work in several laboratories has provided evidence that the hippocampus plays an important role in early processing of memory of a socially induced food preference [26,39,40]. The finding that, as with the memory of spatial relations, retrograde amnesia after hippocampal damage was temporally graded, with lesions occurring shortly after learning having far greater impact on subsequent memory than more delayed lesions, suggests that the hippocampal region plays a critical role in memory consolidation, but that once a memory is firmly established, the hippocampus is no longer important for either storage or retrieval [27,41]. Again, as in long-term memory for other types of information [42], evidence suggested that long-term memories of socially acquired information about foods resides in the orbitofrontal cortex (OFC) [43].

Winocur et al. [44] used both social learning about food and conditioned fear paradigms to examine the hypothesis that memories transferred from hippocampal to neocortical structures do not maintain their original form [45]. The authors suggest that memories stored in the hippocampus become less detailed and context dependent over time and that it is this degraded, relatively context-free memory that is transferred to and stored in extra-hippocampal structures.

Although the experiments described above have used the social learning paradigm to extend understanding of memory processes, they took relatively limited advantage of the unique properties of social learning about foods (other than the relative ease of training subjects), to explore the relationship between brain function and memory [25]. Indeed, it wasn't until quite recently that Lesburgueres et al. [46] took full advantage of the unique features of the social learning paradigm to explore the formation and storage of long-term memories.

In a first study of an extended series examining the interplay between the hippocampus and the OFC during the initial processing and subsequent storage of social influences on food choice, Lesbergueres et al. [46] found, consistent with previous work, that: (1) 30 days after interacting with a demonstrator rat, memory of a food experienced during interaction depends on a functioning OFC, whereas (2) 24 h after training, the same memory is independent of the OFC.

However, unexpectedly, given the prevailing view that the hippocampus is responsible for early processing of memories and extra-hippocampal structures for long-term storage, Lesbergueres et al. [46] also found that an observer rat's long–term memory of a socially experienced food odor was blocked by disruption of the OFC during the first week after interaction of an observer with a demonstrator.

To explain this novel result, Lesburgueres et al. [46] hypothesized a "tagging" process in which specific neurons in the hippocampus and OFC are allocated to a specific memory when an observer subject interacts with a demonstrator and that this subset of tagged neurons is subsequently important in the dialogue between hippocampus and OFC that produces long-term memory.

In the experiment testing this hypothesis that took greatest advantage of previous behavioral analysis of social influence on food preference, Lesburgueres et al. [46] allowed individual observer rats to interact with two demonstrator rats each fed one of two flavored diets. Intact observer rats experienced cocoa on the breath of a demonstrator and had their OFC inactivated 1 week later, just before experiencing cumin on the breath of a second

demonstrator. The observer rats thus needed to develop two independent memories, one for cocoa and one for cumin, both residing in the OFC. Disruption was found only of memory for cumin, experienced with the OFC blocked during the early processing of the memory in the hippocampus, while the proposed tagging and initial dialogue between hippocampus and OFC had been hypothesized to occur. Lesberguers et al. [46] went on to explore the molecular basis of the hypothesized tagging process, finding that the formation and strength of memories for foods experienced in a social context is associated with acetylation of protein.

Sweatt [47] has suggested that Lesbergueres et al.'s [46] work provides empirical demonstrations consistent with two hypotheses. First, synaptic cortical tagging is involved in remote memory consolidation in the cortex on a time-scale orders of magnitude different from that seen in the tagging that is a component of long-term potentiation (a cellular mechanism previously known to play a role in the molecular basis of memory in the hippocampus). Second, epigenetic molecular mechanisms contribute to formation of tags and consequently to memory consolidation in extra-hippocampal areas.

### 5.3. Discussion

The point, of course, is not that exploration in depth of the characteristics of social learning of flavor preference in rats was a necessary antecedent to discovery of the neural-tagging process that Lesbergueres et al. [46] have proposed to explain memory processing in the cortex, but that such behavioral exploration providentially provided a paradigm that facilitated such discovery. As Phil Teitelbaum taught me and so many others, "If meaningful correlations are to be made between brain mechanisms and behavior, then the analysis of behavior will require as much sophistication and attention to detail as the analysis of the brain [[48], p. 358]."

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