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William Timberlake: An Ethologist's Psychologist

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ABSTRACT

William Timberlake was one of several psychologists who, in the wake of traditional learning theory, aimed to develop an improved theoretical basis for the study of learning via greater incorporation of ecology and evolution. In this short biography, I place Timberlake's varied work in historical context. Originally trained as a neoHullian behaviorist, Timberlake sought to integrate the laboratory approach and methodological rigor of behaviorism, with the ethologist's interest in the animal as such. Starting at Indiana University in 1969, he stayed there his entire professional career, where he was one of the founders of the university's internationally recognized Center for the Integrative Study of Animal Behavior. He is best known for his behavior systems theory, which characterizes animal behavior as an evolved complex hierarchically organized system. Timberlake has also made diverse contributions to the study of reinforcement, explanations of superstitious behavior and misbehavior, and the understanding of circadian rhythms and their modification, among other areas.

1. Introduction

Timberlake is one of a number of theorists who, as the hegemony of behaviorism waned, pushed for a more theoretically ambitious study of animal behavior, especially in regards to the evolved and ecological nature of organisms. To this end, Timberlake brought behavior systems thinking from ethology, in which animals are thought of as complex hierarchically organized systems, into the experimental tradition of American laboratory psychology. Timberlake is best known for his work on response deprivation and the development of a still-leading account of reinforcement (Timberlake, 1980; Timberlake and Allison, 1974), his behavior systems approach to animal learning (Timberlake, 1983a; Timberlake and Lucas, 1989), his account of superstitious behavior (Timberlake and Lucas, 1985), and, later in his career, a variety of work on temporal factors and circadian rhythms in the context of reinforcement.

While Timberlake benefited from the rise of ecological approaches in psychology, he avoided aligning himself unambiguously with a particular school or movement, and occasionally got stuck being too much a learning theorist for the biologists, and too much an ethologist for the psychologists. He maintained an eclectic perspective on the field, exemplified in both his work and his course and curriculum design. Timberlake made sure his students were historically informed, that they, like himself, knew the American learning theorists, the European ethologists, and the different methods that were used. That Timberlake is hard to pin down is not surprising for those who know him – sticking out among academics early in his career with a buckskin jacket and a guitar on his back. And his predilection to propose unorthodox experiments makes sense for someone who played in Indiana University's psychology department's rock band (Skin Deep), and spent almost the same length of time on the board of Indiana University's Theatre Circle as he did heading IU's prestigious Center for the Integrative Study of Animal Behavior (with the biologist Ellen Ketterson).

With this brief biographical introduction to Timberlake, I seek to place his thinking in context as well as to call attention to less obvious aspects of his career. The paper can broadly be divided into two sections. The first section, and the bulk of the paper, is a standard intellectual biography, focusing on the growth and development of Timberlake's theoretical aims and research program. In it, I draw a line from his training with a wide-ranging group of motivational psychology researchers at the University of Michigan, to the increasing incorporation of ethology into his learning theoretic perspective, to the development of his behavior systems approach. The second section focuses on his discipline building efforts at Indiana University Bloomington, especially his founding role in CISAB, the Center for Integrative Study of Animal Behavior.

2. The early years

William "Bill" Timberlake (1942-) was born in San Francisco. He was the eldest child of then attorney and later pastor of Sacramento's First Southern Baptist Church Dr. William B. Timberlake and Louzelle Spradling Timberlake. Long exhibiting academic excellence, he

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graduated as valedictorian from Hiram Johnson High School in Sacramento (narrowly beating out his brother), with further awards in English, liberal arts, and science, and received a full tuition scholarship to attend Pomona. While there, he began studying comparative psychology, working frequently with a graduate student at the Claremont Graduate School, William *J*. Hudspeth, who studied the effects of electric shock and strychnine on learning in rats. With the assistance of Hudspeth and his other committee members, Timberlake turned research done for a graduate level Physiological Psychology class into an undergraduate honors thesis in psychology entitled "The Effects of Strychnine and Electroconvulsive Shock on Discrimination Learning in Rats."[1] In contrast to his later integrative approach, Timberlake recalls there were few biological elements in Pomona's psychology program beyond the college's core requirements (August 23, 2018, Personal communication). After graduating from Pomona with honors in psychology in 1964, Timberlake began graduate school at the University of Michigan Anne Arbor.

3. Timberlake at Michigan

When Timberlake was accepted, Michigan was considered one of the strongest psychology programs in the country (R. G. Pachella, 2013).[2] It was most notable for its social and clinical psychology programs, but it was also very active in experimental psychology. Especially relevant for Timberlake was an innovative and eclectic group of psychologists investigating learning and motivation, including Edward Walker, John Atkinson, Joseph Veroff, and *J*. David Birch. There were generally considered to be two major ways to flesh out the study of motivation (see for instance Bindra, 1959, pp. 21–22; Birch and Veroff, 1966, p. 1). One was to do so physiologically or neurologically, by identifying the mechanistic underpinnings that mediated behaviors considered to be motivational phenomena. The other, in line with classical learning theory and the behaviorist tradition, examined motivation purely at the behavioral level, by articulating the topology of the behaviors. This was the approach that predominated at Michigan.

The study of motivation at Michigan, while still anchored in learning theory, was a hotbed for challenges to orthodox stimulus-response theories of psychology. Even the basic claim was contentious: That organisms, rather than simply responding to stimuli, had intrinsic factors that impacted their behavior and therefore additional variables would be needed to make sense of behavior. A lot of work by the motivation group at Michigan had at least a loose historical connection to Hullian behaviorism and the concept of drive. Drive theory postulated foundational "motives" such as sex, pain, hunger, and thirst that could, as the name indicated, drive, behaviors (Hull, 1943).[3] Edward Walker (who had studied somewhat acrimoniously with Kenneth Spence) and David Birch especially could be fairly described as neoHullians, but members of the group had moved well beyond drive theory. See for instance Atkinson's expectation-value theory of motivation (Atkinson, 1964) and Walker's theory of motivation based on the desire for psychological complexity (Walker, 1980, 1964).

Once at Michigan, Timberlake immediately began to work with Birch and joined his research on patterns of behaviors over time and the causes of shifts in behavior (see, for instance, Timberlake and Birch, 1967). The mere idea of a shift in behavior was deceptively radical at the time. From a traditional stimulus-response perspective, each behavior is something atomistic and separate, triggered by a particular stimulus. Birch, along with others in the Michigan motivation group, however, argued that the organism engaged in a continuous stream of activity, and the real questions of interest then concerned why an organism did one behavior rather than another (Atkinson and Birch, 1970; Birch and Veroff, 1966). Much later in his career, Birch would remark that ethologists took the same perspective on behavior (Birch, 2009). Many themes visible in Timberlake's work with Birch become characteristic features of Timberlake's approach, including a focus on motivation, a molar rather than atomistic understanding of behavior, a focus on the temporal dimension of learning and behavior, an emphasis on the organism in the generation of behavior, and an attention to behavioral coding and methodological practice. For those like Birch (and Timberlake) who interpreted behavior as a continuous stream of activity, coding and the individuation of specific behaviors was of paramount importance.

Timberlake's interest in foundational questions of approach and conceptualization was readily apparent in graduate school. When asked about the classification of behaviors in relation to motivation during his preliminary examination he humorously wrote,

> "You would not believe what time it is so I won't trouble your credulity. It seems to me that last time I was confronted with a question like this[4] was in Psychology 742, as I further recall, my attempts were not hospitably received, eliciting some comment like 'It is too early for a meta-theoretical comparison, just use the theories in analysis and the comparisons will come later.' Just goes to show you how an idle comment can warp a man's whole life" (Timberlake, 1967a).

And indeed, Timberlake's experimental work would ultimately come to cover the precise behavioral implications that should be expected with different theories of motivation (which led, as his advisors predicted, to meta-theoretical comparisons.) His preliminary examination also attests to the broad intellectual reach of his committee. Timberlake was asked to discuss the work of the European ethologists Nikolaas Tinbergen, Konrad Lorenz, and Irenaeus Eibl-Eibesfeldt, as well as ethology-inflected Americans like Frank Beach and Howard Moltz.

Playing on Michigan's strengths, his proposed dissertation was "An Approximation to a Descriptive Framework of Motivational Structure (Timberlake, 1967b)." It advocated an inquiry into the intrinsic architecture underlying when and why a behavior is exhibited– in contrast to views that either did not consider motivation at all, or viewed motivation as some general force. Notwithstanding his neoHullian advisor, Timberlake framed his dissertation as a navigation between Hullian behaviorism and Edward Tolman's purposive behaviorism. Hullian behaviorism, with its emphasis on measurability and the operationalization of variables, to Timberlake, was representative of experimental and methodological rigor. But this rigor came at the cost of a narrow focus and an idealized experimental approach. On the other hand, purposive behaviorism, which emphasized the perspective of the organism and the role it played in behavior, was theoretically

[1] The other advisors on his undergraduate honors thesis committee were another graduate student, Lauren K. Gerbrandt, and two general psychologists, Paul Vitz and Aline Kidd.

[2] More historical information on the Michigan Department of Psychology can be found at "Department History | U-M LSA Department of Psychology, 2019" https://lsa.umich.edu/psych/about/department-history.html.)

[3] This is in contrast to the reinforcement theory of motivation from Skinnerian behaviorism, which aimed to be strictly empirical and therefore postulated no underlying factors (Skinner, 1938).

[4] The exact question, from January 16, 1967, is as follows: "Motivation, oriented as it is toward an explanation of the occurrence of action on the part of organisms, must necessarily embody a concern for the classification of activities. Discuss as completely as you can the problem of classifying activities from the standpoint of the topic of motivation. You will probably want to include a consideration of how activities are classed now (e.g. on what grounds do we identify eating as distinct from drinking or instrumental as distinct from consummatory?), an evaluation of the way coding is accomplished at present (e.g. are the kinds of equivalences you think are important handled satisfactorily?) and any suggestions you would make concerning procedures for attacking this problem. Calling on your knowledge of measurement, scaling and statistical theory, also write a paragraph that is directed to the interrelationships among these as they apply to the problem of coding activities."

promising, but executions thus far had been lacking in rigor. Timberlake sought a compromise. By articulating a motivational structure, he aimed to keep the theoretical focus on the animal, but he wanted to explore this structure in the tight experimental setups of the Hullian tradition of behaviorism.

His final dissertation was understandably pared down from his original ambitious proposal. Timberlake utilized continuous coding, an improvement of the time-sampling approach of the psychologist Dalbir Bindra (Bindra, 1961; Bindra and Blond, 1958), to investigate general activity in the rat. Bindra was himself a motivation researcher and had proposed a major reinterpretation several years prior (1959). Like Atkinson and Birch, Bindra rebuked the notion that motivation was a discrete clearly demarcated phenomenon which underlay only specific activities like eating and sex. He held that the organism is behaving constantly – scratching, pacing, chewing, etc. – and it is important to ask what this behavior looks like and why the animal engages in it. According to Bindra, one first needed to map out the general structure of an organism's behavior, and only then could patterns be identified that would help make sense of when an animal exhibited a specific behavior in a more rigid experimental context.

A mapping of general activity is precisely what Timberlake aimed to achieve in his dissertation. Timberlake's emphasis on general activity contrasted with the prevailing learning theoretic focus on specific instances of structured learning (Timberlake, 1970), but comports not only with Bindra, but also with the continuous stream of activity approach prominent at Michigan. In his final dissertation, Timberlake no longer explicitly described his work as balancing Hullian and purposive behaviorism, but the same dialectic is visible: procedurally focusing on rigor and detail in coding behaviors, while topically emphasizing the general activity of the animal. Ethologists, such as Frank Beach and Niko Tinbergen, are more prominent in the final dissertation than in his 1967 proposal, and he used them along with Bindra (himself influenced by ethologists), to motivate the importance of studying general activity. Indeed, ethology seemed to occupy the position that purposive behaviorism had in his proposal. However, Timberlake replaced the ethologist's usual focus on naturalistic observation with the observation of natural behaviors in the artificial context of the laboratory. He hoped that these observations would help to articulate a motivational structure which could then be used, per Bindra, as a baseline for further experimental research. In Timberlake's dissertation work, one can see the beginning of the ethology-inflected animal-centered laboratory-based comparative psychology that becomes characteristic of his approach.

In addition to David Birch, Timberlake had four other members on his committee: Edward Walker, Sachio Ashida[5] J. E. Keith Smith J.[6] and Brian Hazlett. Of particular interest are Walker and Hazlett. Walker, who as mentioned above was involved in the motivation group, co-chaired. At the time he was both a significant figure in psychology and the most popular committee member in the department (Dewsbury, 2012; Riegel, 1970). Brain Hazlett, atypical for a dissertation rooted in learning theory, but typical for Timberlake, was a behavioral ecologist. After completion of his dissertation in 1969 to receive a pH.D. with honors in Experimental Psychology and Behavior, Timberlake earned a post at Indiana University Bloomington where he remains, now as an emeritus professor of psychology.

4. Response deprivation and the early years at Indiana

At Indiana, Timberlake entered a fast-growing department with strength in the study of learning (Capshew, 2014, pp. 77–79). Irving Saltzman, a comparative psychologist, had just become department chair and would occupy the post for the next 20 years (Capshew, 2014, p. 147; Craig and Steinmetz, 2001). Timberlake joined other comparative psychologists such as James Allison, Robert B. Cairns, and (shortly thereafter) Eliot S. Hearst, to contribute to Indiana University's then excellent focus in animal behavior. (Animal behavior broadly understood is still a strength of the university, but it has largely moved outside the psychology department and veered away from learning theory.) Indiana was a transformative environment for Timberlake's career and a place where he set down both personal and professional roots. This included marrying fellow academic Holly Stocking in 1980.[7]

The most prominent project during Timberlake's early years at Indiana was his work on the response deprivation hypothesis with James Allison (another former student of David Birch). According to Allison, their work began when he overheard the not-yet-hired Timberlake discussing his views on reinforcement at a reception for prospective faculty at Allison's house (Allison, 2018). This triggered Allison to excitedly recall a paper he had read recently – Eisenberger et al., 1967 – that was along similar lines and suggest it to Timberlake. When Timberlake formally started at Indiana, he and Allison began work on the topic in Allison's lab. Response deprivation and its subsequent development into the disequilibrium account of reinforcement by Timberlake and others is one of the most important advances in the long struggle over the appropriate understanding of reinforcement (Adams, 2000).

The contentious history of theories of reinforcement is reviewed by Adams (2000), however, Timberlake and Allison were, in particular, responding to David Premack's influential relativity theory of reinforcement, sometimes called the Premack principle. Rather than define reinforcers operationally in the context of how they functioned in specific experiments (as per Skinner, 1938, p. 62), or search for stimuli that functioned to reinforce behavior across situations (as per Meehl, 1950), Premack shifted the focus to responses. This entailed, for example, focusing on eating as an activity rather than just the food. He argued, "any response A will reinforce any other response B, only if the independent rate of A is greater than B" (Premack, 1959, p. 220). Independent rate refers to the rate of a response when an animal is allowed to engage in that behavior freely. For instance, if, when unconstrained, a rat spends 40% of its time eating, and 10% running on a wheel, then eating can be used to reinforce running. Crucially, reinforcement is relational in Premack's account, dependent on the relevant independent rates, rather than the nature of the activities.

Timberlake and Allison experimentally refuted key details of Premack's account. They found, for instance, that in a schedule in which rats were required to lick a 0.4% saccharin solution for 80 s to get 10 s of access to a 0.3% solution, that licking the 0.4% saccharin increased. This was surprising because during an unconstrainted baseline, rats will spend more time licking the 0.4% solution. Contra Premack's theory then, a behavior with a lower independent baseline was shown to reinforce a behavior with a higher independent baseline (Allison and Timberlake, 1974, 1973). These departures from Premack led to the development of the response deprivation hypothesis. Timberlake and Allison argued that as long as the animal had a non-zero baseline probability of engaging in a behavior, if deprived of that behavior, then the opportunity to engage in that behavior could serve as a reinforcer. Even if at baseline a rat spends 30% of its time eating and only 3% running, if it is required to eat more than its baseline preference to get any access to the wheel at all, that is what the rat will do. Following Premack, the animal and its preferences are critical in understanding the reinforcement relation. However, moving beyond Premack,

[5] Ashida was a psychologist working on the social behavior of rats. He is now better known as a masterful practitioner and teacher of Judo.

[6] Keith Smith, a psychologist and statistician, was one of several respected mathematical psychologists at Michigan. Timberlake unsurprisingly credits him with greatly aiding in his data analysis.

[7] Technically, I should say "married for the first time." Like many things, Timberlake and Stocking have done marriage in their own way. In this case, on a five-year renewing basis.

Timberlake's and Allison's account included an understanding of how the relative preferences of the organism would shift in different schedules (that is, the interaction between the relative schedules and the baseline conditions accounts for patterns of reinforcement).

In their view, a reinforcer is not only indexed to the organism, but also to the particular state of the organism. Considering the perspective of the animal, this makes intuitive sense – the possibility of eating will motivate a starving animal and a full animal very differently. Timberlake homed in on a central problem while at Michigan – the need to articulate a larger motivational structure that can make sense of the relationship between stimulus and response in different experimental setups. The response deprivation hypothesis marks his first attempt at a solution and the early stirrings of his animal-centered approach to learning theory.

Despite experimentally confronting Premack's theory, dialectically, Timberlake and Allison placed their work in opposition to Skinner's operationalization approach to reinforcement. Skinner had held reinforcers were whatever served the role of reinforcement in an experimental setup (1938 p. 62). Psychologists were increasingly aware of the difficulties of radical behaviorism (see, for instance, Breland and Breland, 1961; Hinde, 1966; Shettleworth, 1972), but no broadly accepted solution had yet crystallized in the animal learning community. Timberlake and Allison explicitly referred to the Skinnerian reinforcement model, somewhat disparagingly, as a Kuhnian paradigm (Kuhn and Hacking, 2012), claiming it was a "model which directs experimentation and interpretation but cannot itself be tested" (Timberlake and Allison, 1974, p. 149). Response deprivation marked Timberlake's membership in the cadre of comparative psychologists proposing and testing new theoretical orientations in the wake of Skinner and traditional learning theory.

Timberlake further developed and supported the response deprivation account in a number of papers during the late 1970s (Timberlake, 1979; Timberlake and Wozny, 1979), culminating in his disequilibrium approach in which an organism's unconstrained behavior is viewed as a system at equilibrium (Timberlake, 1984, 1980; Timberlake and Farmer-Dougan, 1991). Behavior can then be modified by pushing the system into disequilibrium, e.g. food deprivation, and requiring a response, e.g. running on a wheel, for the animal to return to equilibrium. Timberlake's disequilibrium account is still a leading interpretation of reinforcement. Disequilibrium models are employed in applied behavior analysis and also show considerable promise for therapeutic applications (Jacobs et al., 2017; W. Timberlake and Farmer-Dougan, 1991; Viken and McFall, 1994). The clinical research of fellow Indiana researchers Dick McFall and Rick Viken is especially notable in this regard. In forthcoming work together with Timberlake and Allison, they document success using therapeutic methods rooted in disequilibrium theory in several cases of obsessive compulsive disorder (McFall et al., 2019).

5. Skinner's shadow and Timberlake's biological behaviorism

Response deprivation was merely the first of many tangles Timberlake had with B. F. Skinner and the legacy of radical behaviorism. Given Timberlake's desire to explore the organizational structure underlying behavior, something iconically *verboten* in Skinner's program, the conflict is unsurprising. Arguably his most direct confrontation was in 1985, over "superstitious" behavior (Skinner, 1948; Timberlake and Lucas, 1985).

Skinner had described and explained superstitious behavior in a famous paper in 1947 (1948). He observed that if pigeons were fed at regular intervals independent of their behavior, they developed structured repetitive responses, called "superstitious" behavior by analogy to our own tendency towards stereotyped but useless superstitious behaviors (1948). For Skinner, superstitious behavior was essentially arbitrary. As an organism is engaging in some motions or one behavior or another, it, by chance, gets rewarded. The organism then engages in that behavior more often, because it got rewarded, which makes it more likely that (by chance) it will get rewarded again. The feedback cycle continues and soon the organism is knocking three times and not stepping on cracks. The explanation was simple, intuitive, and fit well with prevailing theory. However, subsequent research revealed that superstitious behaviors usually had the form of purposive behaviors, rather than arbitrary movements, and therefore left the door open for evolutionary and ecological insights (Jenkins and Moore, 1973; Woodruff and Williams, 1976).

In an important precursor to Timberlake's work on superstitious behavior, Staddon and Simmelhag (1971) argued that superstitious behaviors were actually formed from components of the animal's unconditioned responses – feeding behavior in most studied cases – which were elicited by the periodic presentation of the reward. Staddon and Simmelhag held that this explained why pecking in pigeons was being elicited. Timberlake and Lucas, in several experiments, found data broadly concordant with Staddon and Simmelhag and discordant with Skinner (Timberlake and Lucas, 1985). Although, contra Staddon and Simmelhag, they observed it was not simply the isolated behavior of pecking that was being elicited, but rather a whole suite of behaviors associated with feeding.

Articulating how Timberlake, beyond simply his work on superstitious behavior, engaged with and critiqued Skinnerian behaviorism would take a full article (for that, see Timberlake, 1988a), but there is another specific instance that tells us something about both Timberlake the scientist and Timberlake the person. The year was 1988, the 50th anniversary of Skinner's *The Behavior of Organisms,* and Timberlake had been invited to give a paper at a symposium at a convention of the American Psychological Association (APA) celebrating the contributions of Skinner. Skinner himself was in attendance, still a willing and able defender of his own work. And there, at the conference to celebrate Skinner's first major work, in front of the man himself, Timberlake delivered a respectful but no holds barred critique of the behaviorist program. He opened his talk with, "typically historical figures [[Skinner]] are either praised or buried. I have come neither to praise nor to bury, but rather to consider what he's done, both conceptually and empirically" (Timberlake, 1988b). Timberlake now asserts his problem was never with Skinner, but the people who had gotten ahold of his work (August 23, 2018, Personal communication.) Nonetheless, Timberlake took the opportunity to engage in a dense multipronged critique of Skinner's theoretical approach.

Timberlake saw Skinner's project as important and brilliantly executed, but also problematically limited. At radical behaviorism's introduction, it encouraged needed epistemic work by demanding rigor and skepticism from a field that had been far too lenient in its accepted explanations. However, Skinner's network of interdefined terms and concepts (often strictly operationalizations) left no room for growth. Timberlake contended that Skinner had achieved precision the wrong way – with exact, but stipulative, definitions – rather than engage in the grueling work of sharpening theoretical terms against nature until they are precise (Timberlake, 1988a). By way of illustration, this would be tantamount to confusing a precisely measured amount of medication, with the appropriate dose for a specific patient. Consequently, investigation within a Skinnerian framework would tell one what to call certain observations – how to slot observations into a previously defined vocabulary – but not necessarily more than that. The concepts, stipulative and inelastic as they were, could not serve as scaffolding for further theoretical insight. The evident success of Skinner's program, according to Timberlake, was not based on its theoretical soundness, but rather, on the tacit knowledge of animal behavior that was being built into instruments and schedules (more on this later), as well as the selection of the right organisms for the right tasks.

Nonetheless, Timberlake was not an unalloyed opponent of Skinner. His complicated relationship with behaviorism is on display in a 1999 book chapter he wrote on "Biological Behaviorism" (Timberlake, 1999). There Timberlake clarifies his respect for the methodological rigor and

"manipulationist" approaches of the behaviorist but argues that behaviorism needed to be theoretically reformed with an ethological focus on the animal. For example, one could replicate the natural environment of the animal in the laboratory for more careful observation and control. Such a framing broadly aligned Timberlake with other trained psychologists exploring the value of a more ecological perspective like Sara Shettleworth and Bennett Galef. Crucially, Timberlake never sought to dismiss the findings of learning theory, but rather to provide a thicker more theoretically informative explanation for observed experimental phenomena.

6. Investigations of auto-shaping and misbehavior

Timberlake's re-evaluation of elements of traditional learning theory using the idea that the animal exhibits general behaviors which are then modified to specific schedules and circumstances was not limited to reinforcement and Skinner. A now classic 1975 paper on auto-shaping, done together with an undergraduate honors student, Douglas L. Grant, brought Timberlake's theoretical orientation to bear on Pavlovian conditioning. Auto-shaping was a phenomenon which had only been discovered a few years before (Brown and Jenkins, 1968; Hearst and Jenkins, 1974). The original example of auto-shaping was with pigeons. A key light was reliably paired with food, such that regardless of the pigeon's behaviors, the food would still be presented. Contrary to the expectation that the pigeons would simply wait by their feeding dish for food after being signaled, the pigeons instead pecked at the key light as if it itself were the food. A leading explanation for this was based on the Pavlovian stimulus substitution hypothesis. Coming from classical conditioning, the hypothesis posited that the stimuli which evoked a reflex, in this case, food, would be substituted by the predictive stimulus (the key light) and the pigeon would begin to treat the predictive stimulus as food.

Timberlake and Grant tested the stimulus substitution hypothesis by using a live rat on a platform as the predictive stimulus. They wrote, "if the stimulus substitution hypothesis is correct, subject rats should treat the predictive rat as food, gnawing or biting it" (Timberlake and Grant, 1975, p. 690). Despite the dry tone, Timberlake and Grant took this possibility extremely seriously and were standing by to intervene (Robert Bowers, December 30, 2018, Personal communication). However, building on contemporary experimental challenges to the stimulus substitution hypothesis, they hypothesized that a rat might explore and sniff the predictive rat – the social behaviors normally paired with food acquisition for rats – rather than simply treat it as food. Fortunately for the predictive rat, this was indeed the behavior Timberlake and Grant observed. Their unique experimental setup with the live rat allowed them to isolate the role of the predictive stimulus in shaping behavior and presented a major challenge to the stimulus substitution hypothesis.

As an alternative explanation, Timberlake and Grant posited that "auto-shaped behavior reflects the conditioning of a system of species-typical behaviors commonly related to the reward. The form of behavior in the presence of the predictive stimulus will depend on which behaviors in the conditioned system are elicited and supported by the predictive stimulus" (Timberlake and Grant, 1975, p. 692). In other words, the rat has a range of behaviors associated with food, and which specific behaviors are induced depends on the stimulus that signals the food. With their experiment, the live rat stimulus elicited social feeding behaviors. They aligned their results with the ethologist Konrad Lorenz's suggestion that "an entire behavior system was conditioned by the procedures of classical conditioning, not just an isolated reflex" (Timberlake and Grant, 1975, p. 692). Their approach contrasted starkly with the perspective of traditional learning theory. They challenged the idea of a neutral predictive stimulus whose relation to the unconditioned stimulus is defined purely by the experimental context. Instead, the nature of the predictive stimulus and how it interacts with the general behavior of the animal being studied matters greatly, determining the form of the conditioned behavior that comes to be elicited by the predictive stimulus (also see Silva, 2018).

Throughout the 1970s and into the 80 s, Timberlake continued to leverage an ethological perspective, which emphasized natural behavior, to explore classical and instrumental conditioning. Especially prominent was work with honors undergraduate students Glenda Wahl and Deborah King on so-called misbehavior (Timberlake et al., 1982). "Misbehavior," that is unwanted or inexplicable behavior under reinforcement regimes, e.g. a pig choosing to root about rather than perform a task for food even when food deprived, had haunted psychology since Breland's and Breland's wryly titled report of these phenomena, "The Misbehavior of Organisms" (1961). In their extensive experience training animals using operant methods with food as a reward, the Brelands found that behavior was inclined to "drift" towards instinctive food-gathering behaviors. From this, they argued that misbehavior was not idiosyncratic, but rather reflected the irrepressibility of animal instincts, which distorted trained behaviors in predictable ways. Others advocated for a classical conditioning based explanation of misbehavior, in which during the course of operant conditioning the animal would make unintended associations between the reward and arbitrary actions. However, there was little rigorous experimental data on the matter and Timberlake and his undergraduate co-authors were among the first to study misbehavior in a laboratory setting (also see Boakes et al., 1978). From their investigations, they staked out an "appetitive structure" view which combined elements of both the instinctive view favored by the Brelands and the Pavlovian view. The term "appetitive" is a clear acquisition from ethology, and "structure" aligns with Timberlake's longstanding emphasis on underlying motivational structure.[8] The view held that misbehavior was the unintended elicitation of species-typical behavior based on the similarity of the stimulus to natural cues (i.e. it had both unintended association and instinctive behavior.)

Timberlake, Wahl, and King observed (and filmed) that in response to a moving ball bearing which predicted the delivery of food, a rat will invest time attending to and pursuing the ball bearing like prey. Moreover, upon capturing the ball bearing other aspects of the rats feeding systems would unspool, such as investigation, manipulation, and chewing. This contrasted with an operant perspective in which the rat should acquire the actual food as efficiently as possible. From the appetitive structure perspective, the problem was not the animal's but the experimenter's, who naively assumed a pairing could be made between any arbitrary atomic behaviors without any other behaviors being pulled alongside. In contrast to this, Timberlake argued, behaviors were not atomic but interconnected and reflected an underlying organization concordant with the animal's evolution and ecology. The exhibition of species-typical behavior in the misbehavior research became a dramatic representation of Timberlake's behavior systems framework. Video demonstrations of rats suddenly focusing on and scrambling after ball-bearings like prey were a huge hit at conferences (August 23, 2018, Personal communication), and provided an engaging demonstration of the importance of the animal in laboratory studies of learning. (As it happens, Timberlake does an excellent impression of the rat being transfixed by the moving ball-bearing. His student, Robert Bowers, recalls that re-enactments were a frequent feature of Timberlake's courses (December 30, 2018, Personal communication).)

While Timberlake's direct application of ethology's theoretical tools to problems in classical and instrumental conditioning was somewhat unusual, his research nonetheless fit well with contemporary currents in psychology. His work blended with both those seeking a more ecological perspective on learning and those increasingly emboldened to look for systems and structures underlying observed patterns of

[8] Appetitive behavior refers to exploratory goal-seeking behavior. The term comes from the American psychologist Wallace Craig (1918), but it was co-opted and expanded by ethology.

behavior.[9] Throughout the 1970s and into the early 1980s we see Timberlake occupying a complex position in relation to animal learning. He bucked the sparseness and atomism of behaviorist approaches but aimed to keep much of their skepticism and methodological rigor. He brought in the ecological and evolutionary orientation of ethology but anchored himself within the laboratory approach that dominated American psychology. A quote from a 1983 review exemplifies Timberlake's balancing act:

> Animal learning has a long history of carefully expunging mentalism and instincts from its worldview; it is now in the odd position of attempting to integrate aspects of these viewpoints into a coherent whole. This time around, these viewpoints are much more solidly based on research and theory, but we should not forget entirely the excesses and foibles of their origins. Ultimately, we cannot ground psychology in common sense, hedonisms, cognitions, instincts, or enlightened rational behavior. All of the mechanisms referred to by these concepts must operate within evolved structures related to stimulus sensitivity, decisions, and amount and type of behavior. It is these structures that we are after (Timberlake, 1983b).

From this position arises Timberlake's best known theoretical contribution: behavior systems.

7. The development of Timberlake's behavior systems approach

For Timberlake, his behavior systems perspective was a natural development of his work on appetitive structure. Behavior systems approaches more generally are rooted in the ethological insight that organisms can be understood as hierarchically organized systems of interconnected behaviors (Bowers, 2018). Timberlake was of one the main psychologists to develop this insight and bring it into laboratory-based learning theoretic psychology. In contrast to the frequent ethological contention that laboratory behavior is artificial and therefore unrevealing of natural behavior, he held that the same behavior system was at play and that laboratory investigation could be extraordinarily revealing provided one was aware of both the general behavior of the animal and the specific way the experimental setup was channeling the animal's behavior. The interrogation of well-accepted practices and protocols for hidden assumptions was concomitant with Timberlake's behavior systems research program, and he frequently contended that when unacknowledged assumptions were cleared away, the importance of evolved structured systems of behavior became obvious. Nowhere was this more apparent than in Timberlake's investigations of scientific instruments in psychology, which was a central line of development for his behavior systems framework.

Timberlake had long worried that the highly structured experimental approaches and instruments of Hullian and Skinnerian behaviorism were masking important phenomena. The most direct antecedent of behavior systems for Timberlake – the "appetitive structure" view found in his work with Wahl and King – explicitly tested the assumption that stimuli were neutral. Moreover, the first prolonged discussion of his behavior systems perspective, the 1983 book chapter, "Appetitive Structure and Straight Alley Running," is paired with an analysis of the instrumentation used to study behavior (Timberlake, 1983c). Timberlake, in a series of straight alley running experiments with rats, had found that rats will learn straight alley running even in the absence of an explicit reward. Consequently, he contended that a major assumption of learning research, that food was doing all the reinforcing in straight-alley maze experiments, was apparently false – unacknowledged ecological factors were playing an important role. (Timberlake along with members of his lab later made a similar methodological critique of the popular radial arm maze (Hoffman et al., 1999; Timberlake, 2002; Timberlake et al., 1999).

Through his investigation of straight alley running, Timberlake sought to make a larger argument that would both account for the remarkable success of traditional learning theory and the surprising (to Timberlake) inattention to ecological factors. Particularly, Timberlake denied that learning theorists, even those steeped in radical behaviorism, were ignorant as to the importance of species-typical behavior. He held that "this awareness is expressed in the design of apparatuses and procedures, rather than acknowledged in theoretical concepts" (Timberlake, 1983c, p. 165). Early designers of scientific instruments had sculpted them, intentionally or otherwise, to work with species-typical behaviors (no one expects pigeons to bar press or rats to peck at key lights) (Small, 1900; Timberlake, 1983c). However, absent that historical information, and given the general nature of prevailing learning theory where the instrument was not supposed to matter, experimental instruments were instead concealing the motivations and behavioral pattern of the animal. Consequently, the fit between animals and instruments had to be investigated to uncover the ecological information contained within.

Timberlake relied upon his nascent behavior systems theory to explain just how rats did learn straight-alley running in the absence of a reinforcer. Specifically, he held from his findings that learning was a matter of how the appetitive structure of the animal interacted with the environment, which in this particular case meant that a rat's natural tendency to follow trails and edges led to them learning straight-alley running. For someone broadly using the terminology and investigatory techniques of traditional learning theory, such claims were far afield from the idea that reinforcers mold behaviors out of random movements.

The project matched well with broader currents within psychology that had been exploring the role of ecology and biological constraints in learning (Domjan, 1983; Domjan and Galef, 1983; Shettleworth, 1972), and Timberlake explicitly connected his work with this movement. In a section of the chapter called "The Ecological Approach: Behavior Systems and Appetitive Structure" (p. 167) Timberlake introduced behavior systems and contextualized it with a lengthy description of the features of the ecological approach:

> (1) Learning occurs against the backdrop of the complex and sophisticated organization of response elements, stimulus sensitivities and motivational hierarchies which underlie an animal's behavior. (2) Any learning that occurs is not automatic but is dependent on and mediated by the organization underlying the animal's behavior. (3) Learning is not limited to circumstances in which a reinforcer closely follows a particular response or stimulus. Learning occurs whenever and however there has been selection for efficient local adaptations of behavior to deal with predictable variation (W. Timberlake, 1983a, p. 167).

Drawing from both ethology (e.g. Baerends, 1976; Tinbergen, 1951) and evolution-inflected comparative psychology (e.g. Galef and Clark, 1972), Timberlake embraced a systems approach to ecological learning, in which an organism possesses a pre-existing batch of structured behavior systems, for example, a feeding system or a parenting system. While Timberlake's behavior systems view is comparatively well known, he was always careful to acknowledge that his was one behavior systems view among many, rather than a privileged perspective (for an overview of different behavior systems theories, see Bowers, 2018; Burghardt and Bowers, 2017).

In this early 1983 iteration of Timberlake's behavior systems approach, systems are hierarchically decomposed into functional patterns (of actions) and sensitivities to stimuli that Timberlake refers to as perceptual-motor modules. Perceptual-motor modules, in turn, are decomposable into structured actions (with precise characteristics depending on the stimulus). His chief example was the feeding system of the rat. Timberlake analyzed the feeding system in terms of three

[9] A special issue of the journal *Learning and Motivation* came out in 1984 focused on learning in ecological context – Timberlake wrote the introductory article.

response modes: a search mode, a capture mode, and a food handling mode. The search mode was composed of individual foraging and social approach/following, the capture mode of investigation and predation, and the food handling mode of hoarding, ingestion, and rejection (Timberlake, 1983c, p. 168). Importantly, the feeding system was an articulation of motivational structure. As a rat runs through its feeding system, the precise behavioral instantiation of the motivational structure depends on the environment.

A detailed discussion of behavior systems followed shortly thereafter in another 1983 book chapter (Timberlake, 1983a), as well as articles that applied it explicitly (Timberlake, 1983d). Other prominent presentations of the view include a book chapter in 1989 and then a greatly updated book chapter in 2000 (Timberlake, 2000; Timberlake and Lucas, 1989).[10] Throughout his career, Timberlake continued to increase the nuance and sophistication of the behavior systems approach. By 1989, he had expanded the nested hierarchy to include system (e.g. feeding), subsystem (e.g. predation), mode (e.g. focal search), module (e.g. socialize), and action (e.g. sniff), and greatly fleshed out each level in the hierarchy (also see Timberlake, 2000).

Timberlake emphasized that the behavior system was not absolute, but was instead a framework that guided the organism's behavior. Rather than constituting a complete description of an organism's behavior, it is precisely a behavior system's openness to the environment that leads to learning and adaptive behavior. However, what learning is, is completely redefined in the behavior systems approach. Instead of learning being the application of some general processing capacity, learning instead proceeds by modification of an existing behavior system, with any way to modify a system constituting learning.

Revealingly, behavior systems play the precise role of the envisioned "motivational structure" from Timberlake's original ambitious dissertation proposal in graduate school. Following in the footsteps of the motivation group at Michigan, a behavior systems approach takes for granted that the relationship between stimulus and reinforcer is complicated and importantly shaped by the organism. As mentioned above, there were two broad ways to proceed from this stance. One strategy would be to identify mediating factors. That is, to identify how neurologically, hormonally, cognitively, etc., the relationship between stimulus and reinforcer (and behavior more generally) is mediated. The other, which Timberlake chose, was to the map more carefully the contours of this motivational system without necessarily getting into the mechanistic details. This is what behavior systems does. However, while Timberlake may have pulled the broader notion of a motivational structure from motivational psychology and learning theory, it was from ethology he got the idea that the specific structure of the motivational structure could be detailed by attending to how ecological and evolutionary factors would actually shape the system underlying species-specific behavior. Hypothetically, the system articulated by the behavior systems approach could be integrated with neural, cognitive, and hormonal findings detailing the mechanistic structure and processes associated with the production and modification of behavior, and these could even be checked against each other for coherence (Timberlake, 1997, 1995, 1993).

Despite this ambitious vision, behavior systems's original purchase among experimenters was somewhat limited. While behavior systems could, in theory, be filled out with mechanistic details, it was less clear how the approach would help those researchers interested in neurological, hormonal, and developmental factors in their on-the-ground research. Conversely, for researchers anchored in the more field-work oriented tradition of ethology, the relevance of Timberlake's lab-based program was also far from clear. Finally, while it provides a general theory in the sense that behavior systems at the more abstract level would be shared across species, the details of each system would be organism specific and therefore still demanded species-specific research. For example, rats and pigeons would both have feeding systems, but the specific component modules and actions would be very different – no pecking for food for rats. This meant that in practice behavior systems, even for those who were sympathetic to it, functioned more as a guiding approach than as a stereotypical physics-style theory with clear predictions derived from general laws (Michael Domjan, August 28, 2018, Personal communication).

Domjan, who has done extensive work rooted in a behavior systems approach, further notes that the experimental efficacy of behavior systems shows up primarily at the boundaries of approaches (Timberlake's experimental oeuvre bears this point out). Even accepting that it provides compelling explanations of phenomena like "misbehavior" or auto-shaping, one had to find these cases sufficiently important to dictate theory choice. Generally, when it came time to convince those in the Skinnerian, Pavlovian, and Ecological camps to embrace the behavior systems approach, as Domjan puts it, "each camp could retreat to areas that didn't involve the boundary" (August 28, 2018, Personal communication). Nonetheless, despite these occasional difficulties proving its practical relevance, many of the more theoretically-oriented members of the community paid attention to Timberlake's behavior systems approach and his associated critiques of classical learning theoretic approaches.

8. Behavior systems going forward and the timberlake lab

Timberlake was hardly a lone theorist penning book chapters at his desk, and throughout the 1980s and 90 s he found himself running an increasingly busy and diverse lab. Timberlake embraced a very open laboratory culture, and diverse postdocs, graduate students, and interested undergraduate students contributed to the eclectic reach of the Timberlake lab. A wide array of projects (too wide according to some friends and lab members) were going on in the lab at all times. This was reflected in the physical space of the lab. While generally a rat researcher, at one time or another various other species of rodents, as well as pigeons were in residence (William Timberlake, August 23, 2018, personal communication). Different areas would have different activity spaces for different animals, from aquatic mazes, to radial arm mazes, to modified Skinner boxes, and there was often a scattering of both old and new computer equipment about the lab. (The sheer density of stuff related to research is a trait that extended to Timberlake's office.)

Former students of Timberlake point to the dialectical style of working with him, where work was often a sort of conversation between themselves and Timberlake rather than a hierarchical affair (Francisco Silva, September 9, 2018, personal communication, Robert Bowers, August 28, 2018, personal communication, Gary Lucas, September 7th, 2018, personal communication). His peer Peter Killeen commented on the importance of graduate and undergraduate students to Timberlake's work (August 24, 2018, personal communication). Many of his most noted papers, in fact, were written in collaboration with honors undergraduate students. Generally, Timberlake found it tremendously helpful to have other interested people on hand to help him develop his own, often slightly jumbled, ideas. Nonetheless, despite the varied paths taken by members of his lab, Timberlake's broader research program continued to focus on the development of the behavior systems approach.

It needs to be remembered that the meat of behavior systems is not in the abstract formulation of a behavior systems perspective, but rather in the articulation of specific behavior systems of organisms and how they interact with the environment to generate behaviors.

[10] A history of Timberlake's behavior systems approach specifically, albeit in comparison with Kantor's interbehaviorism, can be found in Silva, Silva, and Machado (Silva et al., 2019). Bowers provides a broader history of behavior systems approaches, with special attention to their anchoring in ethology, as well as an up-to-date summary in the *Encyclopedia of Animal Cognition and Behavior* (Bowers, 2018, 2017; also see Burghardt and Bowers, 2017).

Building on the initial development of the behavior systems approach in the 1970s and 80 s, in the 1990s, when the Timberlake lab was at its most productive, we see an experimental program detailing the organizational architecture that undergirds behavior down to the species level. Some of the behavioral systems work consisted of trying to elucidate the ecology of the animal in the lab, through foraging studies and investigations of predatory capture across different species of rodent (Roche et al., 1998; Roche and Timberlake, 1998; Timberlake and Washburne, 1989). Relatedly, the lab continued Timberlake's graduate school tradition of monitoring behavior over relatively long periods (often 24 h), under various schedules of feeding and drinking, to provide the background upon which the interpretation of isolated behaviors should occur (Lucas et al., 1988b; Timberlake and Lucas, 1991). The Timberlake lab often deployed the ethological behavior systems perspective to target behaviors that were either unexplainable or explainable only in an *ad hoc* way by traditional approaches. For example, backward conditioning, in which an organism appears to link a "reward" to a stimulus that was presented afterward, was accounted for by Timberlake and Silva through the relevance of post-food search behavior to the larger feeding system (Silva et al., 1998, 1996; Silva and Timberlake, 2000, 1994a).

Especially prominent were applications of instrumental and Pavlovian approaches geared towards revealing the precise structure of the behavioral system. From a systems perspective, change in behavior at one point in the system would have impacts elsewhere, and the effects of interventions would depend on the background state of the animal (e.g. if the animal is food deprived). With this in mind, the Timberlake lab studied such topics as the laboratory elicitation of conflict between different aspects of a behavioral system (Timberlake, 1986), anticipatory behaviors (Lucas et al., 1988a; White and Timberlake, 1994), and the use of time by animals (Lucas et al., 1988a; Timberlake et al., 1987). The Timberlake lab's intersecting interest in time and the underlying structure of behavior led to several contributions to the study of circadian rhythms in the late 1990s and early 2000s (Kosobud et al., 2007; Pecoraro et al., 2000; White and Timberlake, 1998). In fact, work on how drugs of abuse influence the entraining of circadian rhythms, done in partnership with the neighboring Rebec lab, is one of the few realizations of the hypothetical integration of the behavior systems perspective with a neurophysiological approach.

9. Timberlake's institutional contributions at indiana university

Timberlake participated in Indiana University campus life in a myriad of ways, from organizing Animal Behavior lunches, to supporting theater, to engaging in REU (research experiences for undergraduates) mentorship. Most significant from a career perspective are his involvement in research ethics on campus, especially co-chairing the Bloomington Institutional Animal Care and Use Committee (BIACUC) from 1985 to 1989, and helping to found IU's prestigious Center for the Integrative Study of Animal Behavior (CISAB).

Timberlake had a career-long interest in ethics. He was on the board of fellows for Indiana University's Poynter Center for the Study of Ethics and American Institutions for over 10 years, including participating in a seminar led by the center that resulted in a volume on research ethics (Penslar, 1995). Timberlake provided occasional commentary on works on animal welfare (see Timberlake, 1990, commenting on Dawkins, 1990), and, at Indiana University, he was instrumental in folding courses on research ethics into the undergraduate curriculum in animal behavior, including being part of the Campus Committee on Teaching Ethics in Science from 1989-1991. As someone with both an ethologist's appreciation of animals and a laboratory psychologists need to do interventionist experiments, he occupied a complicated position with respect to animal research ethics. From 1985–1989, when he was co-chair of Indiana University Bloomington's inaugural institutional animal care and use committee with the biologist Jim Holland,[11] Timberlake helped guide the university through an especially fraught time for animal ethics. During the early 1980s, the school had come under fire from the federal government for not fully meeting its animal care obligations (Moore and May, 1980; Pinnell, 1980). With the advent of the federal policy changes in the 1980s that demanded greater accountability for research and the rise of the animal rights movement, the university was under pressure to do right by its research animals.

Timberlake, as the co-chair of the Bloomington Institutional Animal Care and Use Committee (BIACUC), was often in the line of fire. In 1988 he found himself linked in the media to alleged university efforts to restrict viewing of the animal rights film *Hidden Crimes* and branded as an opponent of free speech after a memo of his was leaked to the Humane Society and then the media (Timberlake, 1988c). As accusations against Timberlake and other psychologists at IU continued to intensify, claiming that they mutilated animals and stole research funds, among other cruelties, Timberlake in his capacity as co-chair of BIACUC had to partner up with the university's public relations office to help resolve the situation (Timberlake, 1988c). This was an ironic position for Timberlake as most of his own research was very mild to animals and he himself advocated for ethical treatment. Nonetheless, the more radical animal liberation activists were constant bugbears to animal researchers at the time. It got to the point where the IU psychologists infiltrated the meetings of animal rights radicals (Cokinos, 1988), and Timberlake needed to request heightened security measures for labs which used animals for World Laboratory Animal Liberation Week, April 18–24, 1988 (Timberlake, 1988d, 1988e). Perhaps because of the unexpectedly extreme demands of the position, Timberlake stepped down as co-chair of BIACUC in 1989.

Better known are Timberlake's efforts as a founding member of Indiana University's Center for the Integrative Study of Animal Behavior. The Center, or CISAB as it is generally known, is now considered one of the best integrative programs for animal behavior in the world. CISAB has roots in an early informal group of professors throughout biology and psychology at Indiana University who were interested in providing an interdisciplinary perspective to their students studying animal behavior and pushing back against growing specialization and isolation. The professors included Timberlake, Jeffrey Alberts (psychology), Ellen Ketterson (Biology), Val Noland (Biology), William Rowland (Biology), and Roderick Suthers (Physiology and Biophysics).

The biologist Ellen Ketterson and Timberlake (as principal investigators) applied for an research training grant from the National Science Foundation (NSF) in 1990, along with 11 other people who signed onto the grant application.[12] The grant application was organized around the four questions approach of the ethologist Niko Tinbergen, which encouraged investigators of animal behavior to address issues of survival, evolution, ontogeny, and causation. For the grant, these topics were then mapped broadly onto three disciplines for the proposed center: evolutionary biology (survival/evolution), neuroscience (ontogeny), and animal learning (causation) (Ellen Ketterson, October 26, 2018, personal communication, (Center for the Integrative

[11] Then known as BARC (Bloomington Animal Research Committee) and later BIACUC (Bloomington Institutional Animal Care and Use Committee). The "Bloomington" appellation is important, as Indiana University, a multi-campus university, had separate committees for each campus as well as an all-campus committee. This two-tiered system led to no small measure of confusion during the 1980s. In fact, Indiana University almost squelched the Bloomington campus committee entirely, and occasionally overruled it at the university level, despite the fact that Bloomington researchers had far more engagement with live animal research than those at other campuses. See for instance a memo by Timberlake (1989).

[12] The full list of people on the research training grant is Jeffrey Alberts, Joseph Farley, Ellen Ketterson, Andrew King, Val Nolan, John Phillips, William Rowland, Dale Sengelaub, Samuel Skinner, Joseph Steinmetz, Roderick Suthers, William Timberlake, and Meredith West.

Study of Animal Behavior (1991)). Per the interdisciplinary orientation of the center, these disciplines served as areas of study that had to be fulfilled for participants earning an undergraduate minor in the program ("Handbook for the Program in Animal Behavior and the Research Training Group in Animal Behavior," 1996). Additionally, the initial grant specified five major research programs for CISAB: (1) communication, (2) sexual behavior in mate choice, (3) orientation/migration, (4) learning mechanisms, ecology, and behavioral plasticity, and (5) parental behavior and ontogenetic transitions. Timberlake and Ketterson were successful on their first attempt, securing one of 10 awards from around 600 applications (Timberlake, 1994b). This marked the formal beginning of CISAB.

CISAB involved a careful balancing act between getting money from the NSF and getting money from the university. And it almost certainly would have failed without the strategic support of key members of the university administration. George Walker, then Vice President for Research as well another College of Arts and Sciences dean, Morton Lowengrub, committed university backing, which together with the dedication of the founding members, helped to grow CISAB into the large permanent institution it is today (Ellen Ketterson October 26, 2018, Personal communication). Both Walker and Lowengrub proved to be long-term supporters of CISAB, helping it secure needed resources on several occasions (Ketterson and Sengelaub, 1995).

How the center, despite the initial grant being only for five years (and then renewed for less money for five more), became such a fixture of Indiana University is in large part due to the early guidance of Timberlake (Ellen Ketterson October 26, 2018, Personal communication). Timberlake demanded from the beginning that the center be given an actual physical space rather than exist as an abstract network of individuals, especially given that biology and psychology, the two main departments faculty were joining from, occupied opposite sides of the campus (Timberlake, 1991). Other members of the research training group were apparently somewhat skeptical about the necessity of a concrete location, but the current director of the center, Cara Wellman, notes it ended up being a key decision for the longevity of CISAB (October 31, 2018, Personal communication). Despite some financial difficulties in acquiring a home (Timberlake, 2019), CISAB's initial physical location at 402 N Park St provided a space for the intermixing of researchers, as well as core offerings of the center such as its seminar series, which focused on providing students with information about different methodologies. CISAB also managed to secure its own lab, providing an explicit place for interdisciplinary research.

Timberlake sought to infuse every aspect of the center with an integrative ethos from its inception, and designed protocols which ensured that awarded money went to truly integrative interdisciplinary projects. Although some of his elaborate protocols were changed by later reforms, there is little doubt that the initial integrative vision has been at least broadly realized by the center, if perhaps not exactly as Timberlake intended. The current director of CISAB, Cara Wellman points to a large amount of collaboration between labs that may have never occurred without the structure of the Center (Cara Wellman, October 31, 2018, Personal communication). Additionally, in 1995, Timberlake and the biologist Bill Rowlands successfully applied to NSF for funds for a Research Experiences for Undergraduates (REU) site grant (Rowland and Timberlake, 1996). They took approximately 10 undergraduates every summer, and using the resources of CISAB, brought them into the world of the interdisciplinary study of animal behavior. Timberlake co-directed the REU until 2009 and it continues on, making it one of the longest-running REU sites.

The investigation of animal behavior has changed since the founding of CISAB, and its once radical aim of interdisciplinarity is now increasingly demanded,[13] and yet CISAB is still seen as the exemplar for how to do it right ("CISAB Five-Year Review," 2017). Since its founding, CISAB has continued to grow both larger and intellectually broader. The NSF grant was renewed in 1995 (Ketterson and Sengelaub, 1995), and in 1999 CISAB had its first major expansion outside of psychology, biology, and neuroscience (Walker, 1999). As of 2019, it has grown from the 13 original faculty to over 50, with faculty in fields as diverse as anthropology, zoology, computer science, and optometry. Much of the growth of CISAB is due to the leadership of the biologist Emília Martins, who greatly expanded on the initial vision after taking over for Ketterson and Timberlake in 2002. Presently, the dominant department in both CISAB and the associated REU is biology, and a commensurate role for the psychological study of animal learning, as per Timberlake's vision, never quite fully materialized. Nonetheless, the general commitment to exposing students to diverse perspectives and teaching them a range of methodological skills remains.

Timberlake's and Ketterson's initial push for permanence shows clearly in other aspects of the center's legacy. For instance, a small local meeting for graduate students seeking support from the grant to share work has since grown into a regional animal behavior conference. It would, of course, be a mistake to attribute the success of CISAB to Timberlake alone. Major cooperative achievements like the Center for Integrative Study of Animal Behavior demanded major cooperative efforts from faculty. Nonetheless, the initial push by Timberlake and Ketterson – from spearheading the grant application, to securing administrator support – as well as years of their leadership was critical to the establishment and enduring integrity of the program. The parallels between Timberlake's work and vision for CISAB are striking, including the express integration of ethology and learning theory, the menagerie of research projects in the lab, and the focus on methodology. For Timberlake, CISAB represented a desired intellectual and theoretical transformation of the study of animal behavior by institutional means, even if the current iteration, with its dearth of learning theoretic approaches, may not fully represent his initial vision.

10. The legacy of william timberlake

From his experiments, to his theoretical contributions, to his discipline building at Indiana University, Timberlake combined a psychologist's interest in learning with an ethological conception of animals as complex behaving systems. Methodologically, Timberlake sought to study animals as natural systems through "artificial" methods. In doing so, he retained many of the insights and rigor of the experimental tradition in learning theory. However, for Timberlake, instrumental and classical conditioning, are not constitutive of learning, but instead experimental practices that modify behavior systems in relatively predictable ways. Rather than learning being something singular and abstract (with different animals being better or worse at learning), learning is indexed ecologically for Timberlake, rooted in the structure of an animal's behavior system and the ways it can be modified. He rebuked the notion that true understanding could be found in careful operationalization and precise definitions without going through the work of honing one's concepts against the ecological world of the organism. Throughout his career, Timberlake pushed for a more theoretically ambitious program, both intellectually and institutionally, that seeks to understand behavior on the animal's terms– not, to be clear, in an anthropomorphic sense, but rather with an eye to the known motivational structure, ecology, and perceptual capacities of the animal under investigation. (Timberlake would occasionally call this view of his "theromorphic" (2007, 1997)).

It was this overall goal, embodied by the behavior systems approach, that underpinned his many specific experimental contributions, from the disequilibrium theory of reinforcement to his ecological accounts of superstitious behavior and misbehavior. It is a well-known irony of early comparative psychology that it was not particularly comparative (Beach, 1950). Animals were treated as interchangeable exemplars of a general learning theory. Timberlake was among those

[13] Although demanding integration is a far cry from actually achieving it, as an anonymous reviewer reminded me.

psychologists who sought generality in a different place. Not in the abstract nature of learning, but rather in the nature of organisms as evolved systems that need to maintain themselves in environments by the fulfillment of specific functions. Unlike some ethologically-minded thinkers who wanted to disregard laboratory work as artificial, Timberlake emphasized that a behavior systems exists regardless of context and can be investigated both in natural and in experimental settings (although it should not be expected to be static and unchanged between contexts). Timberlake's later work aimed to demonstrate the flexibility of such a mindset as the Timberlake lab took on circadian rhythm modification, stereotypies, and foraging behaviors among other projects.

In many ways, the behavior systems approach makes the study of animal behavior hard, not easy. Learning is no longer something simple and uniform, but rather involves a plurality of modifications to a behavioral system based on evolutionary history, ecological context, and present state of the animal. Behaviors themselves, rather than being concrete actions that are reliably induced by specific stimuli, are dependent upon an interrelated system, making causal attribution and explanation messy and complicated. This places new demands on those who wish to study animal behavior as well. An integrative and multidisciplinary background is needed for students of animal behavior to apply something like behavior systems. Likewise, there is no easy experimentalism, where one simply plugs the research into overarching theory and existing instruments. Instead, scientists must consider the particular behavior systems of the organism they are working with, in the context in which the behavior occurs. For Timberlake, these difficulties are simply the price of understanding behavior.

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