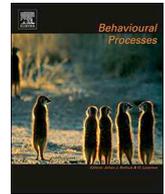




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Editorial

William Timberlake's legacy of innovation[☆]

1. A half century

This year marks a half century since William Timberlake earned his doctorate (Timberlake, 1969) and joined the Department of Psychology faculty at Indiana University, where he remained for the rest of his career. Over these fifty years, Timberlake has been an innovator and a leader, whose influence extends throughout the sciences of behaviour. With this special issue, we reconvene as a community to examine these influences critically and prospectively with a Festschrift celebrating the legacy of our cherished friend and mentor (Fig. 1).

Among Timberlake's most influential contributions to theory are his behaviour systems approach and his disequilibrium theory of reinforcement. His contributions also extend, however, to behavioural economics, circadian rhythms, contrast effects, and other areas. Timberlake has repeatedly shown a knack for identifying and finding solutions to problems that stump whole fields, through careful attention to the specifics of the apparatus and procedures, and how they interact with the species-typical characters of the animals studied.

Timberlake has consistently been a champion of cross-disciplinary integration and cooperation among sciences. He opposed the pressures that keep fields apart, and worked to bring fields together both theoretically and institutionally. Part of Timberlake's legacy is in the creation of an interdepartmental animal behaviour programme at Indiana University, which continues to provide cross-disciplinary training, and to bring allied sciences together on common aims, fostering communication among approaches. This and other of Timberlake's intellectual and professional contributions are treated in the biography provided by historian of psychology, Evan Arnet (2019).

Below we focus on a few of the ways Timberlake has strengthened our sciences—as an innovator, a maverick, a champion of integration, an animal lover, a polymath, and a leader—with attention to how these are expressed in the contributions of the special issue. The contributors hail from diverse backgrounds, take diverse perspectives, and pursue diverse research directions, but all were influenced—some as students, some as peers—by Timberlake's research and thinking, and share the belief that this influence is important to articulate in print. The result is a legacy of new ideas.

2. A builder of systems

To describe a theory or approach as a *system* means that it provides a fundamental shift in perspective that changes the way science is conducted. A short list of scholars can be said to have contributed systems.

Watson (1913); Hull (1952), Kantor (Fryling and Hayes, 2019), Skinner (1938), and Gibson (1979) each formulated systems; the Modern Synthesis of biology, a collaboration of a generation of leading biologists (Huxley, 1942), may be regarded as a system, as can the Lorenz-Tinbergen approach to ethology (Tinbergen, 1963). Contributing a system is a rare accomplishment. Timberlake contributed two, both of which remain current (and complementary, as argued by Killeen, 2019). These are outlined briefly here, and raised frequently in later sections.

2.1. A law repealed: response deprivation, behaviour regulation, molar equilibrium, disequilibrium

“Timberlake and Allison have repealed Thorndike's Law of Effect.” (attributed to George Collier; Allison, 2018, p. 1)

Response Deprivation Theory of reinforcement (Timberlake and Allison, 1974) resituates the locus of behaviour change from an unexplained, purported response strengthening power of particular stimuli, like food, to activities, like eating. Reinforcement is attributed to the animal's correcting deficits in relative activity rates. Timberlake continued to refine this view (Timberlake and Wozny, 1979; Timberlake, 1980; Hanson and Timberlake, 1983), culminating in Molar Equilibrium Theory, now commonly called the disequilibrium approach. Given the centrality of reinforcement in mainstream views, its displacement meant a shift in paradigm (Jacobs et al., 2019). Although the mainstream did not divert to follow this shift of perspective, a tributary of researchers did. Jacobs et al. (2019) describe the disequilibrium approach as “the theory of reinforcement” (p. 198) and “a general theory of behavior” (p. 197).

Kenneth Jacobs, Zachary Morford and James King (Jacobs et al., 2019) present a concrete and useful exposition of Disequilibrium theory and its applications. This is the place to start to appreciate these ideas, and what they can do. Richard McFall, James Allison, Richard Viken and Timberlake (2019) describe a new, effective treatment for obsessive-compulsive disorder based on disequilibrium theory. Killeen (2019) presents an extension of this view, embedding it within Timberlake's larger vision of behaviour systems. The result is a fit that makes one wonder why Timberlake never drew this connection between his two major theories himself.

2.2. A systems system: behaviour systems theory

Behaviour systems theory (Timberlake, 1983, 2001) may be

[☆] On the day we completed the final polishing on this introduction, the final chore for Bill's Festschrift, we learnt that Bill Timberlake had died the day before. He is missed.



Fig. 1. A portrait of William Timberlake.

described as Timberlake's signature theoretical contribution. At its most abstract, behaviour systems is a modelling strategy by which questions about internal variables (e.g. learning, cognition, motivation) are reframed such that the animal is in the centre. Timberlake's systems approach begins by developing a theory of the animal, rather than a species-general theory of the capacity under study. This way, analyses are freer from colouring by assumptions that accompany abstractions like learning or cognition. Even more than disequilibrium theory, behaviour systems theory is a scientific system. A tidy majority of the papers in this special issue focused on behaviour systems theory. As it is such a large part of the special issue, this work is discussed further in dedicated sections below.

3. A gentleman maverick

James Allison approvingly described Timberlake's 1969 views on reinforcement, revealed during Timberlake's recruitment at Indiana University, as "subversive" (Allison, 2018). They were profoundly unlike mainstream views of reinforcement. Allison identified these subversive ideas as the seed from which their response deprivation theory of reinforcement grew (Timberlake and Allison, 1974), which matured into the disequilibrium approach to reinforcement.

Later, Timberlake (1983) put himself against the mainstream again with his behaviour systems approach. The choice of words is telling. Timberlake's (Timberlake et al., 1982) earlier name, "appetitive structure hypothesis", arguably captured the core idea of the 1983 theory more clearly than "behaviour systems". Behaviour systems, however, carries rhetorical punch: as a systems approach contrasts with an analytic approach, the term 'behaviour systems' was chosen in order to

accentuate its contrast with 'behaviour analysis', B.F. Skinner's term for the still dominant approach to animal learning.

Timberlake was certainly not alone as a critic of behaviourism, not in 1969, and even less so in 1983. A swell of dissent was growing throughout these years. Although ostensibly a part of that dissent, Timberlake's concern for the specificities of learning never moved him to join the chorus calling laboratory approaches artificial. Timberlake was deeply impressed by the acumen of the early laboratory learning researchers who developed the apparatus, procedures, and paradigms that enabled reliable behaviour, and hence became standard. These people had managed to isolate ideal conditions for reliable expression of specific forms of behaviour. Far from being disinterested, Timberlake spent his career unravelling the means by which successful laboratory preparations had managed to bring out natural behaviour so well.

What set Timberlake apart from both general-process mainstream and specific-process countercurrent is that he did not abstract the context out of behaviour. Whereas one side complained that the artificiality of laboratory apparatus and methods made them irrelevant to natural behaviour, and the other celebrated them as pure learning, both were accepting that the paradigm had succeeded, as advertised, in removing the specificities of learning from the circumstance. Timberlake showed that the specificities of learning are still present, and refocused our attention on the environment-animal system, the paradigm-subject system.

To paraphrase a popular bumper sticker, "Well-behaved people seldom make history". Among history-making scientists, however, the well-behaved are very well represented. Timberlake challenged conventional thinking throughout his career, and yet he did so with composure and from within the field. He abided the language and

acknowledged the assumptions and aims of the critiqued views. He did not exploit the presence of dissent and preach to a choir; he published his critiques specifically in journals where they would most surely reach and be assessed by proponents of the critiqued views. His arguments were supported with healthy amounts of data. And as discussed above, he gave tangible alternatives. In these several respects, Timberlake has been a well-behaved scholar, although no less of a maverick.

Timberlake is no Hegelian revolutionary, intent on overthrowing an outdated regime. Rather, his consistent message has been one of integration and cross-disciplinary communication. Although an innovator, Timberlake would have us retain hard-won insights from all perspectives and approaches, and pay close attention to how those insights were acquired. Timberlake never forgot that these sciences are all on the same side, and that whatever approach one follows, it is ultimately Mother Nature—notoriously uncooperative with scientists' aims—who calls the shots.

4. A builder of bridges

One recurrent theme throughout Timberlake's career has been unwavering dedication to cross-disciplinary integration. In theory, he led psychology back to the pioneers of ethology and systems thinking, and in practice, forward to alignment with contemporary behavioural biologists. While polarising debates divided fields, Timberlake brought fields together. Timberlake approached allied fields with humility and careful attention to how workers of different perspectives and training conduct science and what questions they address.

Timberlake's advocacy for integration of sciences and cross-disciplinary cooperation shows most tangibly in his leadership in establishing (with distinguished biologist, Ellen Ketterson) the interdepartmental animal behaviour program at Indiana University, and the associated Center for Integrative Study of Animal Behavior (CISAB). This interdisciplinary research and training program was created to establish institutional infrastructure that would continue to support principled integration and open cross-disciplinary cooperation on problems of common interest. CISAB was designed to remain independent of any department, in order to counteract the departmental forces that keep fields separate. Timberlake was acutely aware of these pressures, and staunchly defended CISAB's independence from member departments. The early years of CISAB involved some tight Odyssean navigating between twin behemoths: Bloomington's enormous psychology and biology departments. Since its creation in 1990, CISAB has grown to include members from many disciplines (anthropology, philosophy, history/philosophy of science, cognitive science, informatics, and others). Many people continue to benefit from these bridge-building efforts, as does the maturation of our science. This aspect of Timberlake's legacy is described in greater detail in Arnet (2019).

In addition to institutional bridges, Timberlake built intellectual bridges through his empirical and theoretical work. He directed attention to helping workers of allied disciplines see the successes of each others' approaches, and to find ways of taking advantage of these successes. Crossing the psychology-biology disciplinary barrier is not easy (Domjan and Galef, 1983). Timberlake found a solution: his use of behaviour systems concepts was his attempt to connect with theory from ethology, to adapt whole-animal thinking to help address psychological questions.

In this spirit of cross-disciplinary bridge-building, a number of the Festschrift contributions drew connections with other approaches. These bridges have been built to or upon behaviour systems theory. Some drew connections with other approaches in psychology. Felipe Cabrera et al. (2019) draw a connection with Gibsonian psychology. Silva et al., 2019 highlight some parallels with Kantor's inter-behavioural psychology. Nelson and Mondloch (2019) connect with dynamical systems theory. Killeen (2019) provides a double tribute by combining behaviour systems theory with Timberlake's disequilibrium theory of reinforcement. Other bridges show how behaviour systems

theory can be put to work for the study of emotion (Burghardt, 2019), consciousness (Lucas, 2019), and timing (Freestone and Balci, 2019; Sanabria et al., 2019), and showed the benefits of bringing Markovian (Sanabria et al., 2019) or Bayesian (Freestone and Balci, 2019) mathematical tools into behaviour systems.

5. An animal lover

Timberlake's appreciation for animals shows in two tangible ways. First, his science is characterised by deep interest in the animals studied and the behavioural repertoires they bring to the laboratory. One of the core intuitions behind Timberlake's thinking is to view behaviour from the perspective of the behaving animal, a *theromorphic* approach (Timberlake, 2007). Before attempting to analyse some capacity, like learning, one first develops a theory of the animal. By Timberlake's approach, the animal is in the centre.

Second, Timberlake's admiration for animal life is visible in his leadership in and advocacy for ethical oversight of animal use in science. His work on the Bloomington Institutional Animal Care and Use Committee went well beyond standard service (discussed in Arnet, 2019).

6. A polymath

Timberlake's work was uncommonly eclectic and interdisciplinary. The breadth of work conducted in his laboratory reached the extent that, late in his career, Timberlake expressed the regret that he had spread himself too thinly. The last cohort of Timberlake's students consisted of Eduardo Fernandez (PhD 2009) studying stereotypic pacing in polar bears and walruses in the Indianapolis zoo (Fernandez, 2010), Andrea Gillman (PhD 2010) studying circadian entrainment of addictive drugs (Gillman et al., 2019), Carolina Tamara (PhD 2013) studying spatial cognition in a water maze (Tamara et al., 2010; Tamara and Timberlake, 2011), Matthew May (BA) studying defensive behaviour of rats in response to cat odours (May et al., 2012), Ceyhun Sunsay (postdoctoral student) interested in species-general modelling of learning, and Robert Bowers (PhD 2015) using behaviour systems theory to make sense of behaviour predicted by theories of causal reasoning (e.g. Bowers and Timberlake, 2017; 2018a,2018b). Such breadth of interest is also evident in this special issue, especially among the contributions of former Timberlake laboratory members.

Catherine Mondloch (PhD 1989), now professor of psychology at Brock University, whose doctoral work concerned parental feeding in pigeons, contributed current work on emotion recognition among human children. Nicole Nelson and Mondloch (2019) show how children's ability to recognise emotions is affected by presenting dynamic information—videos, rather than photographs—and discuss what this means for understanding human emotional development.

Ozlem Cevik (PhD 2000), now professor of psychology at TOBB University of Economics and Technology, whose doctoral work concerned temporal discrimination with attention to effects of methamphetamine, now studies nutrient sensing among fruit flies. Ayşe Kahraman, Afife Konyalı and Cevik (Kahraman et al., 2019) report the results of a novel method for studying short-term feeding decisions of wild-type and mutant flies on a tether, results that help narrow focus on the role of a specific genetic locus.

Francisco Silva was a postdoctoral member of the Timberlake laboratory in the 1990's, and now is professor of psychology at Redlands University. Silva (2019) reviews the extensive body of research showing that the nature of responses that develop during the course of Pavlovian conditioning depend on the nature of the conditional stimulus. Silva concludes that no stimulus is accurately described as "neutral" and that there is no way to escape considering the relation of a conditional stimulus to the ecology of the animal under investigation.

7. Behaviour systems theory today: domains, bridges, extensions

Behaviour systems theory is a very broad set of theoretical tools, and its potential to be pulled in various directions is visible in the breadth of behaviour systems-inspired work submitted to this special issue. Several of the contributions combined these ideas with other approaches, extended them, and generally tugged them in new, productive ways. This adds to the already broad collection of problems Timberlake himself set behaviour systems theory to solve.

7.1. A variety of systems

Two of the five contributors of the 1993 behaviour systems symposium held in Toronto (Timberlake and Fanselow, 1994) also contributed papers to this Festschrift: Michael Domjan (1994) and Michael Fanselow (1994). (The other three contributors were Jerry Hogan, Sara Shettleworth, and William Timberlake). Domjan and Gutiérrez (2019) provide an updated, comprehensive review of their work on sexual conditioning with Coturnix quail, in which they have taken a behaviour systems approach. They make use of Timberlake's concept of response modes, organised by temporal and spatial proximity to copulation, what they call "copulatory imminence". Domjan and Gutiérrez discuss how the behavioural and physiological outcomes of sexual conditioning depend on copulatory imminence, the nature of the conditional stimulus, and their interaction. They provide a clear and extensive review outlining how learning affects different aspects of naturally occurring behaviour and how this contributes to reproductive success.

Fanselow et al. (2019) report new data on their behaviour systems work on anti-predator defence among rats. They focus on the concept of a predatory imminence gradient, and argue that three phases of defensive behaviour (evade, freeze, strike) are organised by the imminence of attack by a predator in a way that mirrors analogous phases of the predator's behaviour. They ask whether varying the signal-shock interval produces transitions from one response mode to another in defensive behaviour as is commonly found among analogous manipulations in other conditioning paradigms. Behaviour systems thinking has been applied to conditioning in aversive contexts by other scholars as well (Bouton, 2005; Esmoris-Arranz et al., 2003), in whose hands it has become a productive research direction.

Sergio and Vivien Pellis, Amanda Pelletier and Jean-Baptiste Leca bring a behaviour systems approach to an understanding of play. Pellis et al. (2019) identify some of the challenges of studying play by a behaviour systems perspective, and some of the ways that play is unlike other behaviour systems. Despite these differences and challenges, Pellis et al. (2019) find that viewing play from a behaviour systems perspective is productive, and identify several ways in which it provides gains in understanding play, its organisation, and its diversity across animals.

7.2. New bridges to other research domains

Construction on three kinds of new bridges to behaviour systems began in this special issue. Some bridges brought the power of behaviour systems theory to new research domains. Others drew attention to parallels among approaches. A third kind of bridge brought quantitative methods to an otherwise qualitative approach.

Gordon Burghardt (this issue) discusses application of behaviour systems to the study of emotion. Plato had psychology divided into three domains: motivation, cognition, and emotion. Tinbergen (1942, 1951) applied his hierarchical systems to motivation, and Timberlake (1983, 2001) applied behaviour systems to cognition (mostly learning, but other forms of cognition as well). Now Burghardt (2019) completes the triune, to present the basis for applying an analogous approach to the study of emotion.

Gary Lucas (2019) applies these ideas to an attempt to understand consciousness. This leads him also to consider emotion, with reference

to data from affective neuroscience. The intuition that systems concepts are a good place to start to understand consciousness is compelling (see also Toates, 2006). Lucas presents a behaviour systems approach to consciousness that fits among enactive views of consciousness, which stress the embodiment and situatedness of mind.

Another bridge connects behaviour systems with the interval timing literature (Freestone and Balci, 2019; Sanabria et al., 2019), a connection hinted at with respect to the circadian timing literature as well (Kosobud, personal communication, see Gillman et al., 2019). These are discussed below.

7.3. New bridges to other approaches

Felipe Cabrera, Ángel Jiménez, and Pablo Covarrubias (Cabrera et al., 2019) draw a connection between Timberlake's behaviour systems approach and Eleanor and J.J. Gibson's ecological psychology. This crossing requires guidance, given the different aims and different uses of the term 'ecological' in the two approaches. Cabrera et al. provide this guidance. The rewards of crossing this bridge include a principled connection with Gibsonian 'affordances', a term that reading Timberlake puts on the tip of one's tongue (and sometimes in one's printed word, e.g. Killeen, 2019; Burghardt and Bowers, 2017), even though Timberlake avoided using the term himself. Cabrera et al. direct attention to a correspondence between Timberlake's focus on the tuning of apparatus to support regular behaviour, and the Gibsonian notion of affordance, and thereby bring behaviour systems into contact with the Gibsons' theory of perception. Part of one's understanding of the behaviour exhibited in a given paradigm is attributable to the behaviour-supporting characteristics of the circumstance; part of the theory is worked into the procedure and apparatus. Hence, building apparatus and designing procedures are theoretical activities. For decades, Gibsonians have been embracing the effects that apparatus and context have on behaviour, while most animal learning researchers have been doing their best to reduce such effects, in the pretence of isolating 'natural' learning. Cabrera et al. make the point that Timberlake has been more like the Gibsonians in this regard, a liberating influence for future research as it has been for Timberlake and the Gibsons.

Kathleen Silva (PhD 1996), Francisco Silva and Armando Machado (Silva et al., 2019) highlight similarities between Timberlake's behaviour systems and Kantor's interbehavioural psychology. Both Timberlake and Kantor take a wholistic and organismic approach to the study of behaviour, encourage observation and measurement of multiple responses, and consider learning to involve a change in an integrated complex of behaviour rather than just a change in a single response. Both also advocate consideration of ecological factors. However, as Kantor scholars Mitch Fryling and Linda Hayes (Fryling and Hayes (2019) note in their reply, despite these apparent parallels, there may be deeper dissimilarities that become clear with careful attention to the aims of the two thinkers. These two papers together make a compelling case that a Timberlakean may have to gain from reading Kantor, and a Kantorian, from reading Timberlake.

Like Gibsonian ecological psychology and Kantorian interbehavioural psychology, there is a thematically similar point of contact among a broader set of views that stress the importance of attention to the extent that behaviour is embodied and embedded within its context, several of which also reference systems. These views include dynamical systems theory, developmental systems theory, subsumption robotics, cybernetics, general systems theory, and surely others. Despite clear overlap among these views, each has been developed in apparent isolation of the others, most targeting a constrained range of questions. In their study of emotion recognition among children, Nelson and Mondloch (2019) conceived of emotions as dynamical processes, and this led them to touch upon dynamical systems theory, while also tipping the hat to behaviour systems theory. Future bridge-building work may find value in exploring how these perspectives relate.

Killeen (2019) presents a synthesis of a different kind, between two

of Timberlake's theories, embedding Timberlake's disequilibrium theory of reinforcement within the more general framework of behaviour systems theory. This is not so unlike the above bridges, for even the disequilibrium approach has conceptual roots in systems theory, from which come the central notions of equilibria and set points. Killeen shows how a specific merger of these two theories deals neatly with a list of known empirical paradoxes.

7.4. Quantitative extensions

Although behaviour systems theory has been used on occasion to narrow focus on specific quantitative hypotheses, a strategy for making questions more precise, it is, at heart, a qualitative approach. Two contributions to this special issue took quantification of behaviour systems further, and imported Bayesian (Freestone and Balci, 2019) or Markovian (Sanabria et al., 2019) mathematical tools to model entire structures in quantitative terms, bringing the benefits of quantification while keeping the big-picture vision of behaviour systems.

David Freestone and Fuat Balci (Freestone and Balci, 2019) provide Bayesian sinews for a skeletal architecture, one showing sensitivity at lower levels to the parameters at higher levels. In this model reinforcement does not select responses, but biases a pathway through a hierarchy. The pathway is sensitive to the nature of the stimuli. The conditioning machinery is based on reinforcement learning theory (cf. Killeen, 2019). This is a very hopeful avenue to explore; but as the authors note, to condition the model with data requires substantial amounts of data involving sequences of different actions. This model now justifies collecting such data.

Federico Sanabria and colleagues (2019) build another quantitative behaviour systems model using Markovian mathematics in which the current state determines the probability of subsequent states, and responses are modelled as the output of unobserved states, with a dynamic sequential order. They consider a series of elaborations on the basic Markov model, evaluations of which lead to their apex model: a nonlinear, partially hidden Markov model. The result is a quantitative behaviour systems model, one that may be synthesized with that of Freestone and Balci (2019) for a formidable theory of behaviour.

7.5. Conceptual maintenance work

Amid all the forward-looking contributions highlighted above, Bowers (2019) looked back to examine several conceptual fine points of behaviour systems theory and precursors. Notions of consummation and general search, the place of prediction of response form, the role of hierarchies, directedness, and behavioural spontaneity are disassembled and soaked, as one might do with a sticky carburettor, with attention to theoretical and historical context, and the intentions of the architects. A general outcome of this exercise is reaffirmation of the openness of behaviour systems theory to new research directions, an openness demonstrated by several innovative contributions to this special issue. Innovators may find this piece helpful in relating their use of systems to Timberlake's, and to some extent Tinbergen's and Craig's views as well.

8. Time

Time was a point of focus at the 1993 behaviour systems symposium (Timberlake and Fanselow, 1994). Timberlake (1994) discussed data showing that conditional response form was sensitive to the duration of the interval between presentation of a predictive cue and food. Domjan (1994) discussed analogous data with sexual conditioning among male quail (for an updated review, see Domjan and Gutiérrez, 2019), and Fanselow (1994) did similarly with rat defensive behaviour. Fanselow et al. (2019) revisit this aspect with new data, manipulating the signal-shock duration. Consideration of temporal aspects of behaviour organisation continued to produce returns for Timberlake (2001), and it

featured prominently in his behaviour systems models.

This prominence of attention to time suggests that behaviour systems theory may function as a theory of timing. Timberlake did not do this, but two contributions to the special issue (Freestone and Balci, 2019; Sanabria et al., 2019) extended behaviour systems theory in a way that unpacks its relevance to timing. Interestingly, they did this in different ways, to produce two behaviour systems-based theories that deal squarely with timing. A behaviour systems theory of timing carries the advantage of a clear connection with a theory of performance, bringing the study of timing back into the study of embodied animal behaviour. Freestone and Balci (2019) and Sanabria et al. (2019) raise the bar for theories of timing.

8.1. Circadian timing

One research focus of Timberlake concerned temporal discriminations involved in day-length (circadian) cycles. Circadian rhythms must be kept in phase with the environment, and organisms do this with special sensitivity to environmental cues. Ambient light, which changes with the positioning of the sun, is the most obvious of such cues, but there are other circadian cues, including temperature and food. Timberlake and colleagues made important contributions to our understanding of circadian entrainment by food and drugs of abuse. Four of those colleagues, Andrea Gillman, George Rebec, Norman Pecoraro (PhD 2001) and Ann Kosobud (Gillman et al., 2019) describe work unravelling how drugs affect circadian rhythms, and how the subsequent use of those drugs is affected by those changes. Commenting on this work, Ann Kosobud noted that "the addictive power of drugs of abuse is at least in part due to their action on a biologically-based behavior system", and suggested that fuller understanding the broad range of effects of drugs of abuse may benefit from attention to how related suites of behaviour and their determinants interact. This suggests movement toward application of behaviour systems theory to the study of drug abuse.

9. Adjunctive begging in the 'superstition' paradigm

Pigeons in conditioning chambers presented with periodic food often exhibit wall-directed behaviour, including various bumps and bobs, steps and stoops. Skinner (1948) described such behaviour in the case in which pigeons were automatically presented food at fixed times. His explanation was intuitive: accidental juxtaposition of response and food presentation. Although the pigeons did not need to act to receive food, behaviours that happened by chance to occur immediately prior to food delivery might be reinforced, with positive feedback producing a contingency. Skinner compared this with superstition, which became the label for the related body of research. Despite the intuitive appeal of this explanation, when researchers looked closer, they found that it was not so simple (Staddon and Simmelhag, 1971, carefully critiqued Skinner's, 1948, analysis; Killeen and Pellón, 2013, returned the favour, critiquing Staddon & Simmelhag's analysis with equal care. Together, these three studies provide a fascinating success story for dialectics in science).

Timberlake and Lucas (1985) approached such results as the expression of species-typical feeding behaviour. One puzzle that remained was what the frequent occurrence of wall-directed behaviour had to do with feeding. Timberlake and Lucas (1985) proposed the hypothesis that wall-directed behaviour in such circumstances is an expression of begging (p. 298). Timberlake pursued this hypothesis with a further series of experiments:

"In the superstition paradigm discussed above, the female pigeons almost exclusively showed wall-directed behavior, including bumping, pressing, head bobbing, and stepping, often with wings half-drawn. Despite over 20 experiments examining determinants of this behavior, its functional context remained mystifying until we

observed similar behavior in young (10–20 days) squabs begging from their parents (Mondloch & Timberlake, 1991) and in mature females begging from males in courtship. Although these observations did not prove that wall-directed behavior in adult pigeons was related to food-begging behavior, they did directly lead to further experiments that provided evidence supporting this view.

In this last series of (unpublished) experiments, the female pigeons engaged in more wall-directed nonpecking behavior than the males—an effect expected if this behavior is related to a food-begging function because adult females show more begging than males. Ring doves, a member of the same genus as pigeons, showed similar wall-directed behavior, but chickens, a different genus, showed only scratching and pecking. This was predicted from a consideration of differences in the feeding systems of the two species. Parent-young feeding in ring doves is similar to that of pigeons, but hatchling chickens are precocial, almost immediately feeding on their own by pecking and scratching at food on the ground.” (Timberlake and Silva, 1994, pp. 77–78).

Earlier this year, one of us (RIB) went looking for a report of those experiments, only to find that they had still not been published. Luckily, Timberlake had years earlier entrusted those data to his student, Eduardo Fernandez (PhD 2009), in whose thesis work he saw a connection (Timberlake, 2010). Fernandez prepared a report of those old data for the special issue (Fernandez and Timberlake, 2019c). Wall-directed behaviour of pigeons in conditioning chambers is an expression of begging, a conclusion with potentially far-ranging implications given its prevalence in operant work with pigeons.

10. Choice

Among the major paradigms in laboratory animal learning research on which Timberlake has left his mark, choice paradigms do not come immediately to mind. Yet, two of the contributions to this special issue (Zentall et al., 2019; Killeen, 2019) focused on how Timberlake’s theories help make sense of the data of a particular choice paradigm: the Kendall (1974) effect. Of the many curious sub-optimality in behaviour, this one has appeared so saliently suboptimal that it often goes by the sub-optimal rubric of “sub-optimal choice”. In the Kendall effect, an animal with two response options in a concurrent chain schedule will preferentially work a poorer alternative that dispenses signalled food at a moderate rate (typically 20%), over a richer one that dispenses un-signalled food at a higher rate (typically 50%). This is among the empirical paradoxes treated by Killeen (2019), who shows how the Kendall effect makes sense in light of disequilibrium views on reinforcement.

Thomas Zentall, et al. (2019) describe results of sub-optimal choice experiments inspired by behaviour systems theory. Pigeons, the most frequent subjects in such studies, show the effect with uncanny consistency. Rats, however, most often choose the richer option. This apparent species difference led Zentall et al. (2019) to behaviour systems theory. They present the hypothesis that the difference lies in how the stimuli used elicit focal versus general search response forms. They describe data from some initial experiments that motivate this hypothesis. As a good start, they have isolated specific manipulations of stimuli that produce the Kendall effect in rats.

What would Timberlake say about the Kendall effect? Timberlake (1988) discussed how thinking in terms of behaviour systems might help to understand a very similar self-control paradigm, involving pigeon subjects in Skinner boxes with two keys in a choice paradigm, very much like in Kendall’s setup. He argued that “the current self-control paradigms for pigeons appear designed to produce impulsiveness because they predict a very proximate reward with a punctate cue suitable for controlling focal search” (p. 695). Note that these same features Timberlake suggested were bringing out focal search in self-control studies are present in the suboptimal choice paradigm, and like the impulsive outcome displayed by pigeons under such conditions,

pigeons choose the light that gives an immediate signal, even when this produces poorer overall returns. Under this circumstance, taking the richer choice involves “a disruption of the search, capture, and handling sequence”. Timberlake (1988) presented a clear hypothesis: “Impulsiveness should be decreased by increasing the delay to the first reward or by requiring pigeons to locomote to particular locations in response to diffuse cues to obtain access to food”, or by “any procedure that de-emphasizes the relative proximity of the nearest reward or directly decreases the strength of the focal search mode” (p. 695). We suspect Timberlake would have a similar answer for exerting experimental control over the Kendall effect¹.

Although Timberlake’s research was led in different directions, his first published paper was all about choice. Timberlake and Birch (1967) showed that the latency of shifts from an ongoing to an alternative behaviour was a function of the relative attractiveness of those behaviours. Characteristically for Timberlake, it involved a non-standard apparatus, concerned affordances, and mixed exploratory and consummatory responses.

11. Omissions and additions

While we surely missed some potential papers that might have been included, the Festschrift has been a success in highlighting Timberlake’s theoretical influences. Generations of psychology students have encountered Timberlake’s theories in course curricula, and his research has received plentiful attention. However, Timberlake did much more for our science than a Festschrift special issue can capture. Among the influences not represented are those embedded in the tireless work behind the scenes: Timberlake’s building institutional infrastructure for the benefit of cross-disciplinary communication, his leadership in setting ethical standards for animal use, and his establishment of a long-standing research experience program for undergraduate education. There are many more people who benefited from Timberlake’s service efforts than those who were prepared to write a scholarly article about a specific influence. While preparing the special issue, we heard from many people who wanted to contribute, but this format favours recognition of only a small part of Timberlake’s contributions. Some of these gaps are patched in Arnet’s (2019) biographical contribution.

In addition to the papers in the Festschrift, Timberlake’s influence is immediately apparent in several other works published this year and last. For instance, Burghardt and Burkhardt’s, 2018 one-century review of Craig’s (1918) theory of appetitive behaviour acknowledged Timberlake’s behaviour systems as an especially productive descendant of Craig’s theory. Timberlake’s former post-doctoral student, Ceyhun Sunsay (2018) presented results of a Pavlovian study using a restrained rat as a stimulus to a subject rat, reminiscent of Timberlake’s (1983) work using conspecifics as conditional stimuli. And Timberlake’s name graces multiple papers published this year, including a clinical case study led by department colleague Richard McFall (McFall et al., 2019), and zoo enrichment work with former student, Eduardo Fernandez (Fernandez and Timberlake, 2019a,2019b).

12. A misnomer?

Timberlake did not claim behaviour systems theory as his own, neither the principle, nor the phrase. Rather, he said that he was taking a behaviour systems approach, and credited others who had taken behaviour systems approaches before, primarily Tinbergen (1942, 1951), and to some extent also Baerends (1976); Hogan (1971); Fentress

¹ One of us (RIB) began to explore this, conducting two (unpublished) sub-optimal choice experiments with pigeons in a 1-meter long box, one involving diffuse stimuli that had to be approached rather than pecked; the other that separated stimuli from food spatially. Four of four subjects showed the sub-optimal pattern, contra hypothesis.

(1983), and Lorenz (1969). However, these uses were all quite different from each other, and Timberlake was taking this perspective in new directions. In Timberlake's hands, behaviour systems theory matured into a general framework (Timberlake, 1983; Arnet, 2019, notes that the seed was evident in Timberlake's 1967 dissertation proposal—16 years of gestation). The resultant theory has thus come to be known by this name, entering textbooks as "behavior systems theory" or "the behavior systems approach". The name stuck. As a consequence, behaviour systems theory now refers to two related sets of ideas: Timberlake's theory, and the views from ethology he was building upon.²

Late in his career, Timberlake expressed dissatisfaction with this name (personal communication), letting an old designation stand for a new set of ideas. A common name permitted confusion among ideas that were actually very different, and the sense that it was nothing new, while Timberlake's theory was far from tired or overused. Now may be a good moment to correct this old mistake, and give Timberlake's theory a name that differentiates it from its predecessors, while retaining the connection with those views Timberlake stressed. Cabrera et al. (2019) have proposed "TBS", for "Timberlake's Behavior System". One might also return to "appetitive structure hypothesis" (Timberlake et al., 1982). Now that Timberlake has retired in earnest, with concerns of modesty out of the way, we suggest "Timberlakean Systems Theory".

13. Closing

As Baerends (1976) said of Tinbergen's legacy, so we can say of Timberlake's: "the best way we can give further tribute to this stimulating pioneer work is to develop and modify it further, with an always critical, but positive attitude." (p. 737). Even the small part of Timberlake's legacy that we were able to capture with this special issue is a vibrant body of remarkably fresh ideas.

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²This was not the first theory Timberlake left without a unique name. Extensions of Response Deprivation Theory have appeared variously as equilibrium, molar equilibrium, disequilibrium, behaviour regulation, or just response deprivation. He sometimes referred to this set of ideas as a theory, sometimes as an approach. The motive may have been the same, a will to connect with and acknowledge related views that came before.

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