

Taming the boojum: Being theoretical about peculiarities of learning

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Abstract

The case of the "biological constraints" movement in mid-20th-century psychology provides a reminder of the weight of psychology's reliance on theory and theory-driven methods. By 1980, a critical mass of demonstrations of the specificity of learning had eroded faith in general-process approaches. A common reaction was to call for a biological orientation. However, this proved not as straightforward as it had seemed, and much of the ostensibly biological research that followed was atheoretical. The successes in this context were due to careful theoretical work by people who appreciated the aims of the involved sciences and the interdependence of the aims with methods. Michael Domjan slowed the field's haphazard rush into ostensible biological research, and rather urged adoption of principled biological approaches. In 1982, his positive recommendation was for comparative psychology to begin to live up to its name, and adopt principled comparative methods as practised in biology. Although lauded, few followed this recommendation. Indeed, even Domjan's own subsequent research was mostly not comparative in the way he had described, but rather involved single species, guided by a behaviour systems approach. With reference to two major perspectives associated with Domjan—comparative methods and behaviour systems theory—I present Domjan's challenge not as being to make our field comparative per se, but to make it theoretical. This challenge remains current.

Keywords Behavior systems \cdot Comparative method \cdot Constraints on learning \cdot Theory \cdot Psychology-biology integration \cdot Michael Domjan

Psychology is among a bouquet of sciences that are slowly coming to recognize that the observable data with which they describe the natural world are not self-explanatory but require theoretical framing. Neuroscience has cells; genetics has molecules; ethology has behaviour; and behavioural psychology has stimuli and responses, or operants and outcomes. But despite the impressive successes of these sciences, ethology (Hinde, 1956; Tinbergen, 1963), genetics (Brendel, 2010; Gilbert, 1991), and neuroscience (Krakauer et al., 2017; Sporns, 2013) have begun to face the browfurrowing truth that observable elements do not alone make a foundation, and that there is still need to "be theoretical" and articulate principled bases for scaling up to complex patterns. The Modernist habit of eschewing theory in favour of pure description seduced these sciences (and psychology;

The present exercise will focus on a specific late-20th-century crisis in psychology: the "biological constraints on learning" movement that sputtered, then grumbled, then roared through the middle of the 20th century, leaving psychology polarized and divided. This story has a hero, which makes it easier to relate. However, the intended message is more general: psychology needs to recognize the weight of its reliance on theory, and the role of theory as a guide for methods.

A psychological wound

A wound in psychology had begun to fester in 1982 when Michael Domjan was invited to address the Midwest Psychological Association at its annual meeting (Domjan & Galef, 1983). Domjan had become known for his work on selective associations and was part of a booming research direction focused on the ways in which learning is constrained by predispositions. The thrust of his 1982 address



Skinner, 1950), with the consequence that our richness of data is matched by poverty of understanding.

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was not celebratory, but critical. He opened the wound and proceeded to clean and dress it.

Learning is specific to particular animal kinds and to particular motivational contexts (Hinde, 1973; Shettleworth, 1972). Appreciation of this simple and important truth innocuously (perhaps "softly"; cf. Beach, 1950) faded from memory over the middle decades of the 20th century. Whereas the early developers of successful apparatus and procedures had needed to confront the specificities of learning squarely (Timberlake, 1983b), later researchers inherited developed methods and apparatus designed to minimize a specific species' specificities. These later generations observed behaviour at its most reliable, in controlled environments, without having felt the growing pains of the progressive tuning process that made their measurements so germane with general-process views. It was an era of pervasive optimism and growth in animal-based psychology and increasing faith in the generality of basic psychological qualities was both a cause and consequence of much of this growth.

The 1950s saw a spattering of demonstrations that challenged this faith, various deviations from the received view that each instance of learning is like any other (e.g., Garcia et al., 1955). If these demonstrations had appeared 50 years earlier or later, most might have raised no eyebrows; if cast as problem for views of learning, this might have seemed like the battering of an unlikely straw man. But now at the peak of popularity of general-process views, they held enough theoretical punch to inspire disbelief in some and dissent in others (Garcia, 1981, gives a first-hand account of an early constraints researcher's plight). However, throughout the 1960s, this trickle became a stream, and in the 1970s, the stream became a torrent (Seligman, 1970). An increasing industry emerged of fault-finding studies designed to shine light on the insufficiency of general-process views, often in the name of "biological constraints". What were once obstacles along a rocky road to publishing had become guide stones.

There was something peculiar about this new research direction. It was, in essence, negative; a prior view was inadequate. It had no positive orienting theme of its own. It was atheoretical. What was common to say of biological constraints research is that it was biological in orientation. But was it meaningfully so? This was the brunt of Domjan's critical message. The constraints literature was generally not principled, neither biologically, nor otherwise.

As we approach the 40-year mark of this important turn in thinking, the present paper is an attempt to remind us of the essential insight that so few saw so clearly and so presciently as Domjan (Domjan, 1983; Domjan & Galef, 1983). While communities polarized over whether learning processes were constrained or general, or whether a focus on rats and pigeons was misleading (Beach, 1950), Domjan

recognized that the wound was not really about biology or behaviourism but primarily about an absence of theory. The challenge to adopt principled approaches, matching methods with theory, remains current.

The negative message

Biological constraint concepts did not stimulate fundamental changes in the study of animal learning; . . . they did not lead to a successful theoretical framework for systematizing knowledge about constraint phenomena. There is no reason to believe that constraints on instrumental and classical conditioning identified as exceptions to traditional principles of learning will have other common attributes. Similarly, situation-specific instances of learning and adaptive specializations may be produced by a large variety of mechanisms. (Domjan & Galef, 1983, p. 154)

Domjan's primary negative message about the constraints movement was that it was negative. It presents phenomena as exceptions to established views. It did not direct the field in positive theoretical directions, neither biological nor otherwise. The phenomena themselves may have been biological in fact, but the research surrounding them was not adoption of a principled biological approach. The appeal to evolution was post hoc. Reports of constraints phenomena would label the pattern as biological and anomalous, but the ostensible alignment with biology was only superficial and often no effort was made to provide positive interpretation (e.g., Breland & Breland, 1961). That there are predispositions in learning is banally true; attributing specificities of learning to constraints concepts takes one no closer to understanding this learning (Bowers, 2018b).

Presenting a phenomenon as an exception to theory is like putting up a broken clock. If it is set an hour behind, or if it runs too fast or slow, a free parameter or two might bring it back in line. But if you believe just that its hands are not giving the correct time, and conclude only by identifying it as an exception, it provides positive guidance on neither the time, nor anything else.

Should people not have done constraints research? To some "constraints" researchers, they were studying what they found to be "the meaty part of behavior" (Garcia et al., 1972). It warrants stressing that the critique was never directed at the study of these meaty bits, which are also in focus in other sciences, such as the vibrant field of behavioural ecology (e.g., Hollis, 2017). Behavioural ecology is not atheoretical, and it connects intimately with both of the positive solutions offered below. Rather, the critique was about how efforts to identify exceptions connect with understandings of learning more generally, and the too-common



tendency to do so atheoretically, implicitly buying into general-process assumptions.

Masquerading as a straw man

One reason that a biological constraints movement was allowed to build steam was that almost no leading learning researcher, after Pavlov, held the ostensible alternative view that all learning is the same. That was only a popular view. Differences among various forms of learning had been consistently and explicitly acknowledged throughout the 20th century. Leading behaviourists were not horrified by autoshaping or the Brelands' misbehaviour (Skinner, 1977). To show that learning processes are specific and variable might appear to challenge only a caricatured, straw-man version of the general-process views of the mainstream.

However, there are two big ways that general-process views ducked the charge rather than face it. First, the old solution to messy specificities in learning was to pack them into model parameters (e.g., Estes, 1950; Hull, 1945), where they quietly hid within neat names like alpha or beta (Rescorla & Wagner, 1972). By this strategy, the specificities of learning were conceded but considered relevant to performance, not competence, and absorbed into empirically tweaked parameters, the same grab-bag parameters that held all of the uninteresting variables, like stimulus salience.

A second way of reducing the effects of species typicalities also took inspiration from physics, designing apparatus to elicit regular learning. Through careful observation and meticulous tuning, one can design apparatus and procedures that produce very regular behaviour (e.g., Skinner, 1938; rat mazes). Although an important advance in learning research, Timberlake (1983b) noticed that this involved adapting the design to the particularities of the species; the specificities of learning are still present but incorporated into the design. Hence, to understand how such data relate to natural learning, one needs to reverse engineer the potentially powerful role of the apparatus and the thinking that went into its design (anticipating "thing knowledge"; Baird, 2004). Tweaking parameters and tweaking apparatus were both ways of looking past the specificities of learning, not looking at them and what they might mean.

Related to the present issue, the larger part of such views was empirically driven. Learning modellers roll with the punches. By 1982, the list of weird findings was already long, but these were described as empirical phenomena, and received more shrugged shoulders than serious efforts to make sense of them. A hyper-empirical generation habituated to the field's anomalies (Killeen, 2019) and was able to describe findings like contra-freeloading to their students in a steady voice without a bead of sweat.

Furthermore, the mere fact that mainstream views were unshaken by closets of oddities and exceptions is no

bragging point. Where a defending theory is sufficiently specific, identifying exceptions can be a helpful exercise. As it appears not to have been, the fault might be in the malleability of the general-process position.

Although the first efforts to answer the challenges posed by constraints phenomena failed, and without denying that some may have exaggerated or miscast the alternative position, somewhere hiding amongst the rhetoric and polarizing overstatements was a real challenge that warranted serious attention. To this, Domjan and Galef (1983) provided the voice of reason.

A positive message

The importance of the negative part of Domjan's critique has generally been conceded. The harder part of any critique is to provide a positive solution. The present paper will focus on two such answers that appear in Domjan's work: A comparative approach to learning, and a behaviour systems approach to learning.

Comparative approach

In 1982, Domjan's positive prescription was for comparative psychology to begin to live up to its name and adopt principled comparative methods as developed and practiced in biology. At first blush, this might have appeared as merely affirming the rallying cry of the biological constraints movement. However, the methods of biology are specific, and these methods are tied to theory in a specific way (Hodos & Campbell, 1969).

The comparative method is a powerful approach (Lorenz, 1950). It was developed to exploit what can be known about how species are related phylogenetically and the specific ecological pressures that impact their evolution. One compares a feature among a selection of species chosen to simultaneously vary ecology and phylogeny as systematically as possible. For instance, one might study the parental behaviour of several species of vole, and a similar cluster of mole species, including species that vary in each clade along a monogamy–polygamy continuum. This opens a window onto how mating systems and common ancestry affect the evolution of parenting in moles and voles.

A nice example of this strategy applied in psychology concerns the predatory behaviour of rats. Timberlake (1983a) had shown that rats will acquire a conditional response to a food-predictive prey-sized rolling ball bearing that resembles the attack and kill of prey. But apparent resemblance can be deceiving. How could he be sure that the behaviour he was observing was indeed a predatory response directed to a conditional stimulus? Timberlake and Washburne (1989) selected seven rodent species



whose feeding ecology varied in reliance on predation, ranging from predominantly herbivorous, through gradations of omnivory, to highly carnivorous. Comparison of the conditional and unconditional feeding-related response topographies of these seven species revealed that even conditional response patterns exhibited toward the food-predictive rolling ball bearing were strongly predicted by feeding ecology.

There are other good examples of the comparative method applied in psychology. The relationships among food storing, cache memory, and hippocampus size in a variety of bird species has been an area that has put comparative methods to good use (Krebs, 1990).

However, beyond just a few research areas, use of such methods remains rare in psychology. It is unlike the methods used in "constraints" research, and unlike all but a tiny fraction of psychology research involving between-species comparisons. Hodos and Campbell (1969) argued powerfully that between-species comparisons in psychology have largely failed to appreciate the principle behind the comparative method. They stressed that "much of the current research in comparative psychology seems to be based on comparisons between animals that have been selected for study according to rather arbitrary considerations and appears to be without any goal other than the comparison of animals for the sake of comparison" (p. 337), and that such research "will add little to our understanding of systematic differences and similarities among species" (p. 349). This critique has barely aged in more than half a century.

There are good reasons for the rarity of principled comparative research in psychology. Perhaps the most important reason is that its purposes are specific and its applicability is narrow. The comparative method is an evolutionary approach to the core. Biology has not only different methods to psychology but different aims as well. One can overlearn the aims of a science and limit oneself to a short list of sanctioned question forms, such as questions about function or homology. As Domjan (2015) noted, the selective association experiments from the 1960s (Garcia & Koelling, 1966), whose shock waves through psychology can still be felt, would not have even come to mind by a biological approach. Although Dobzhansky's (1973) slogan that "nothing in biology makes sense except in the light of evolution" might have been an admissible exaggeration for biology, this light illuminates only some things in psychology.

Although lauded, few psychologists followed this recommendation. Indeed, even Domjan's own subsequent research was mostly not comparative in the manner of his 1982 recommendation but rather involved single species in laboratory paradigms, guided by a behaviour systems approach.

Behaviour systems

In the preface to the second edition of Cybernetics, Wiener (1961) noted that around 1920, the general mode of putting the questions concerning nonlinear apparatus was to look for a direct extension of the notion of impedance which would cover linear as well as nonlinear systems. The result was that the study of non-linear electrical engineering was getting into a state comparable with that of the last stages of the Ptolemaic system of astronomy, in which epicycle was piled on epicycle, correction upon correction, until a vast patchwork structure ultimately broke down under its own weight. Just as the Copernican system arose out of the wreck of the overstrained Ptolemaic system, with a simple and natural heliocentric description of the motions of the heavenly bodies instead of the complicated and unperspicuous Ptolemaic geocentric system, so the study of non-linear structures and systems, whether electric or mechanical, whether natural or artificial, has heeded a fresh and independent point of commencement. (p. xxxvii)

The zeitgeist of systems theory and cybernetics hit ethology in the 1940s, where a small subset of systems theoretic themes enjoyed a passing popularity in the form of Tinbergen's (1942, 1950) hierarchical systems (Bowers, 2018a). However, when these themes were rediscovered in the 1980s by psychologists (Domjan, 1994, 1997; Timberlake, 1983a, 1983b, 1993, 2001) it was again a "fresh and independent point of commencement." This was timely, as this was just when the crest of the "biological constraints" wave was reaching a head, and Domjan had issued his challenge to find a better solution.

William Timberlake drew attention to one aspect of mainstream approaches to the study of learning that opened them to the kind of problem the field was facing: such approaches begin by abstracting learning, describing it in terms of a capacity, and trying to cleanse analyses of performance factors. If learning is essentially about change in behaviour, to characterize this change, one should first want to know well how the specific animal behaves prior to learning, performance variables and all (Timberlake & Silva, 1994). Timberlake saw animals behaving in many more ways than just the commonly reported dependent variables and sought to situate learning in the context of this rich repertoire. With a model of the structure of an animal's behaviour in a given context, including how behavioural forms interrelate, one can keep track of how the system changes with specific experience. This is the essence of a behaviour systems approach to learning. For instance, how a



rat's behaviour changes under a food-conditioning protocol is considered in the context of a model of the structure of the rat's native feeding behaviour (Timberlake, 1983b).

This approach displaces abstract descriptions of capacities, like learning or causal reasoning, from the centre, and refocuses on the animal studied. What feels radical about this is that it takes the very object of study out of the centre. Even if one's aim is to study learning, a behaviour systems approach begins not with a theory of learning, but a theory of the structure of the animal's behaviour. Timberlake (2007) called this an animal-centred or "theromorphic" approach (in contrast to anthropomorphic approaches). Like the shift from geocentric to heliocentric views, a theromorphic approach shifts the centre of focus.

By analogy, if one were to study combustion in a selection of differently designed engines whose inner workings were opaque, it would make sense to direct one's attention first to the engines themselves. Only equipped with a model of the outputs of those engines might one attempt to base conclusions about combustion on data collected with them.

One consequence of bumping learning from the centre is that the constructs and complex sets of assumptions that accompany any such theory suddenly become up for grabs. Typically, in addition to articulated assumptions, views of learning rely on unarticulated conjectures to fill gaps about insufficiently understood aspects of cognition, for instance, concerning the formation of representations (e.g., What is an association?). Even Pavlov's constructs of discrete stimuli and responses are open to dissolution by this perspective. By the received framing, one looks for conditional response only in the presence of the conditional stimulus, because that is how Pavlovian conditioning has been depicted (Domjan, 2021). However, if one is looking at learning as perturbations of a structured system of interrelated behavioural forms, one suddenly sees other meaningful changes happening, such as changes in responding toward the unconditional stimulus that increase its effectiveness (Domjan & Gutiérrez, 2019).

If all the other actions an animal performs are relevant to understanding learning, it suddenly feels daunting. Like the comparative method, behaviour systems was another tough way to start. However, there have been some striking generalities that behaviour systems research has been able to make good starts with. Notably, Timberlake (1983b) stressed that predatory behaviour of rats could be divided into three distinct subproblems. Hunting is not a singular action, nor is it sufficient to produce the conditions for eating. To eat a cockroach, the predator must exercise a very specific set of actions involved in handling and killing the prey. Before this, however, the predator must engage in a second set of actions involved in the capture of prey. And to put oneself in the situation where prey is available to be captured involves a third set of actions with the goal of finding prey. The hunting

rat thus has to solve three problems, each with a distinct cluster of actions: general search, focal search, and handling. Remarkably, an analogous three-cluster analysis worked for the predator avoidance behaviour of the rat (Esmorís-Arranz et al., 2003; Fanselow, 1994; Fanselow et al., 2019) and the sexual behaviour of the male Coturnix quail (Akins et al., 1994; Domjan, 1994; Domjan & Gutiérrez, 2019). Although the specific actions involved are obviously very different in these three cases, all involve three very clear general search, focal search, and consummatory/imminent components, related to the proximity of the event (felling prey, copulating, or facing the predator's strike; Bowers, 2020), and all have been shown to be sensitive to conditioning techniques. An analogous distinction between exploration (general search) and exploitation (focal search) has been similarly productive for such unlikely extensions as searching for information or searching through memory (Hills et al., 2015). Domjan and Gutiérrez (2019) provide a recent review of the rich and novel research directions where a behaviour systems perspective has led the study of sexual conditioning among quail.

Behaviour systems approaches are again evolutionary at heart, consistent with the commonly held intuition that the solution to "biological constraints" would be a biological approach. The structure of behaviour is assumed to be affected by evolutionary pressures to achieve the familiar goals of feeding, mating, and avoiding dangers. More than this, a behaviour systems view permits the unpacking of big blunt functional constructs. It may be vacuous to talk about selection for big things like feeding or sex (or learning!), but statements about the structure of a system or a behavioural interaction are always more specific than statements just concerning the parts (p (AopB) < pA). Behaviour systems theory provides a principled way of connecting evolution with data about specificities in learning, which is what Domjan had been challenging the field to produce (Domjan & Galef, 1983). Other thinkers have developed efforts to close the same gap, strategies for retaining the benefits of specificprocess approaches in ways that specifically suit the study of learning (Davey, 1989; Johnston, 1981; Suboski, 1990). Among these, behaviour systems theory has been the most productive and has had the greatest impact on contemporary views of learning, providing a general framework for interpreting species- and system-specific learning phenomena that had appeared awkward for older views of learning.

Alas, learning is not the only functional capacity that suffers from an impoverished view of performance. Analysis of any cognitive capacity—whether to reason about cause and effect (Bowers & Timberlake, 2018), or to time intervals—stands to benefit from a behaviour systems approach that situates the capacity of interest in the context of the possessor's circumstance and permits interpretation of a



wider array of behavioural forms (for further reading, see Bowers, 2019, 2020; Burghardt & Bowers, 2017; Cabrera et al., 2019; Hogan, 1994).

Combining the comparative method with behaviour systems

Chemistry is enviable for having just one periodic table. Like the periodic table, a behaviour systems model depicts some of the relations among the parts. But unlike the kinds of chemistry, the kinds of biology each have their own structured ways of behaving. There is not just one scheme for all life, but one for every kind of animal. Biology will never catch up with chemistry, and evolution is to blame. Knowing the culprit, however, gives us a good place to look for solutions; methods developed for understanding differences among related things, such as the comparative method.

These two approaches are complementary. Behaviour systems models now exist for a number of species. With not just a theory about the digger wasp's behaviour (Baerends, 1941), but also one about the stickleback fish (Tinbergen, 1942) and the herring gull (Baerends et al., 1970) and other animals and systems besides, the field begins to have a basis for comparison. If one were to produce behaviour systems models of reproduction in a selection of teleost fish, or of predatory feeding in a selection of rodents, or so forth, comparative methods could be used to address questions related to the evolution of the structure of behaviour, the generalities of motivational systems, and what is basic to cognition or motivation.

Epilogue

One of the best predictors of the views one holds is what views one knows. There are theories that are held by almost everyone who knows them. Students become enthusiastic converts of theories they study, and typically hesitate to revise their views in light of discrepant data. Hence, psychology students from different universities often sound like they come from different planets, despite having the same access to data. If just knowing a theory is sufficient for holding it, what theories students learn about may be critical to the state and future of our science. If psychology curricula just cover the empirical highlights, this might produce a conservative and atheoretical generation of future scientists.

An oddly recurrent theme in animal learning papers has been how lay presentations and even introductory textbooks misrepresent the field (e.g., Domjan, 2021; Rescorla, 1988). Perhaps the field's hyper-empirical orientation is to blame for this. Perhaps the pretense that our data are appropriately taken at face value has permitted the noted distortions. Amid fluxing Zeitgeists in psychology, cognitive science and biology, students have effectively lost access to whole

generations of research and progress, much of which is important to grasp in order to understand the movements that occurred within these theoretical contexts.

The happy truth is that the field of animal learning is sophisticated and theoretically rich. This richness includes theories of a list of kinds, including frameworks (sometimes called "systems"; e.g., Darwin, 1859; Hull, 1952; Skinner, 1938), functional theories (e.g., Rescorla & Solomon, 1967), law-style descriptive theories (e.g., Rescorla & Wagner, 1972; Herrnstein's matching law), mechanistic theories (e.g., Skinner's, 1938, reflex reserve; Killeen, 1988), the theromorphic theories-within-theories described above (Timberlake, 2007), normative theories (e.g., Bayesian networks: Pearl, 2000; optimal foraging theory), and impressive thinking in the ample space between (e.g., Rescorla, 1967) and within these theories (e.g., Domjan & Gutiérrez, 2019).

Just as methods need theory, theory needs methods. A useful theory provides structure that limits a science, telling the practitioner what to measure, what the numbers mean, where to look, and in some cases, how different levels of analysis affect each other. Darwin's theory of natural selection has been so productive not because of any matter of fact in focus in popular debates, but because of the methodological advances that followed it, not least of which is the comparative method. Behaviour systems theory, likewise, is valuable not because of any matter of fact about whether animals are control systems, but how that view directs research. No degree of success with this framework would justify treating one's friends like control systems.

Michael Domjan is now known for several impactful contributions to the field of animal learning, but perhaps the most important of these was his pulling on the reins of a field heading too haphazardly into ostensibly biological approaches. Domjan agreed with the emerging consensus that there was value in aligning with biology but navigated this way with care, seeing that some of the most trodden paths were dead ends. Those who heeded were led to principled approaches to the study of learning.

In a 1949 address, Frank Beach (1950) evoked an analogy with the *boojum*, an imaginary beast from a Lewis Carroll poem. Sparing Carroll's quirky sense of humour and excessive artistic licence, Beach (1950) warned that comparative psychology was pursuing a quarry that, like the boojum, would doom its catcher to obsolescence. Tamed with theory, however, the boojum was a prize snark!

References

Akins, C. A., Domjan, M., & Gutiérrez, G. (1994). Topography of sexually conditioned behavior in male Japanese quail (*Coturnix japonica*) depends on the CS–US interval. *Journal of Experimental Psychology: Animal Behavior Processes*, 20, 199–209.



- Baerends, G. P. (1941). On the life history of *Ammophila campestris*. *Jur. Nederl. Akademie van Wetenschappen*, 44, 483–488.
- Baerends, G. P., Drent, R. H., Glas, P., & Groenewold, H. (1970). An ethological analysis of incubation behaviour in the herring gull. *Behaviour*, Suppl., 17, 135–235.
- Baird, D. (2004). Thing knowledge: A philosophy of scientific instruments. University of California Press.
- Beach, F. A. (1950). The snark was a boojum. *American Psychologist*, 5, 115–124.
- Bowers, R. I. (2018a). A common heritage of behaviour systems. *Behaviour*, 155, 415–442. https://doi.org/10.1163/1568539X-00003497
- Bowers, R. I. (2018b). Constraints on learning. In J. Vonk & T. K. Shackelford (Eds.), Encyclopedia of animal cognition and behavior. Springer. https://doi.org/10.1007/978-3-319-47829-6_1265-1
- Bowers, R. I. (2019). Behavior systems. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior*. Springer. https://doi.org/10.1007/978-3-319-47829-6_1232-2
- Bowers, R. I. (2020). Six clarifications for behaviour systems. *Behavioural Processes*, 170, Article 103987. https://doi.org/10.1016/j.beproc.2019.103987
- Bowers, R. I., & Timberlake, W. (2018). Causal reasoning in rats' behaviour systems. *Royal Society open. Science*, 5, Article 171448. https://doi.org/10.1098/rsos.171448
- Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*, 16, 681–684.
- Brendel, V. (2010). Continuing the paradigm shift in biology: Advances towards characterization, modeling, and prediction of the plant transcriptome. Seminar presented at Indiana University.
- Burghardt, G. M., & Bowers, R. I. (2017). From instinct to behavior systems: An integrated approach to ethological psychology. In J. Call (Ed.), G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Assoc. Eds.), APA handbook of comparative psychology (Vol. 1, pp. 333–364). American Psychological Association.
- Cabrera, F., Jiménez, Á. A., & Covarrubias, P. (2019). Timber-lake's behavior systems: A paradigm shift toward an ecological approach. *Behavioural Processes*, 167, Article 103892. https://doi.org/10.1016/j.beproc.2019.103892
- Darwin, C. (1859). On the origin of species. Appleton.
- Davey, G. C. L. (1989). Ecological learning theory. Routledge.
- Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, *35*, 125–129.
- Domjan, M. (1983). Biological constraints on instrumental and classical conditioning: Implications for general process theory. *Psychology of Learning & Motivation*, 17, 215–277.
- Domjan, M. (1994). Formulation of a behavior system for sexual conditioning. *Psychonomic Bulletin & Review, 1*(4), 421–428.
- Domjan, M. (1997). Behavior systems and the demise of equipotentiality: Historical antecedents and evidence from sexual conditioning.
 In M. E. Bouton & M. S. Fanselow (Eds.), Learning, motivation, and cognition: The functional behaviorism of Robert C. Bolles (pp. 31–51). American Psychological Association.
- Domjan, M. (2015). The Garcia-Koelling selective association effect: A historical and personal perspective. *International Journal of Comparative Psychology*, 28.
- Domjan, M. (2021). Revisiting how we depict Pavlovian conditioning. APS Observer, 34, 86–87.
- Domjan, M., & Galef, B. G. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Animal Learning & Behavior*, 11, 151–161.
- Domjan, M., & Gutiérrez, G. (2019). The behavior system for sexual learning. *Behavioural Processes*, 162, 184–196. https://doi.org/10.1016/j.beproc.2019.01.013
- Esmorís-Arranz, F. J., Pardo-Vázquez, J. L., & Vázquez-Garcia, G. A. (2003). Differential effects of forward or simultaneous conditioned stimulus–unconditioned stimulus intervals on the defensive

- behavior system of the Norway rat (*Rattus norvegicus*). *Journal of Experimental Psychology: Animal Behavior Processes*, 29, 334–340. https://doi.org/10.1037/0097-7403.29.4.334
- Estes, W. K. (1950). Toward a statistical theory of learning. *Psychological Review*, *57*, 94–107.
- Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin & Review*, 1, 429–438.
- Fanselow, M. S., Hoffman, A. N., & Zhuravka, I. (2019). Timing and the transition between modes in the defensive behavior system. *Behavioural Processes*, 166, Article 103890. https://doi.org/10. 1016/j.beproc.2019.103890
- Garcia, J. (1981). Tilting at the paper mills of academe. *American Psychologist*, 36, 149–158.
- Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. *Science*, 122, 157–158.
- Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, *4*, 123–124.
- Garcia, J., McGowan, B. K., & Green, K. F. (1972). Biological constraints on conditioning. In A. H. Black & W. F. Prokasy (Eds.), Classical conditioning II: Current research and theory. Appleton-Century-Crofts.
- Gilbert, W. (1991). Towards a paradigm shift in biology. *Nature*, 349, 99.
 Hills, T. T., Todd, P. M., Lazer, D., Redish, A. D., Couzin, I. D., & the Cognitive Search Research Group. (2015). Exploration versus exploitation in space, mind, and society. *Trends in Cognitive Sciences*, 19, 46–54. https://doi.org/10.1016/j.tics.2014.10.004
- Hinde, R. A. (1973). Constraints on learning: An introduction to the problems. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning* (pp. 1–19). Academic Press.
- Hinde, R. A. (1956). Ethological models and the concept of 'drive'. The British Journal for the Philosophy of Science, 6, 321–331.
- Hodos, W., & Campbell, C. B. G. (1969). Scala Naturae: Why there is no theory in comparative psychology. *Psychological Review*, *76*, 337–350.
- Hogan, J. A. (1994). Structure and development of behavior systems. *Psychonomic Bulletin & Review, 1*(4), 439–450.
- Hollis, K. L. (2017). Ants and antlions: The impact of ecology, coevolution and learning on an insect predator–prey relationship. Behavioural Processes, 139, 4–11. https://doi.org/10.1016/j.beproc.2016.12.002
- Hull, C. L. (1945). The place of innate individual and species differences in a natural-science theory of behavior. *Psychological Review*, 52, 55–60.
- Hull, C. L. (1952). A behavior system: An introduction to behavior theory concerning the individual organism. Yale University Press.
- Johnston, T. D. (1981). An ecological approach to a theory of learning. Behavioral and Brain Sciences, 4(1), 162–173. https://doi.org/10. 1017/S0140525X00008220
- Killeen, P. R. (1988). The reflex reserve. *Journal of the Experimental Analysis of Behavior*, 50, 319–331.
- Killeen, P. R. (2019). Timberlake's theories dissolve anomalies. Behavioural Processes, 166, Article 103894. https://doi.org/10.1016/j.beproc.2019.103894
- Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience needs behavior: Correcting a reductionist bias. *Neuron*, 93, 480–490. https://doi.org/10.1016/j. neuron.2016.12.041
- Krebs, J. R. (1990). Food-storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions of the Royal Society-Biological Sciences*, 329, 153–160.
- Lorenz, K. Z. (1950). The comparative method in studying innate behaviour patterns. Symposia of the Society for Experimental Biology, 4, 221–268.



- Pearl, J. (2000). Causality. Cambridge University Press.
- Rescorla, R. A. (1967). Pavlovian conditioning and its proper control procedures. *Psychological Review*, 74, 71–80.
- Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *The American Psychologist*, 43, 151–160.
- Rescorla, R. A., & Solomon, R. L. (1967). Two-process learning theory: Relationships between Pavlovian conditioning and instrumental learning. *Psychological Review*, 74, 151–182.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), Classical conditioning II: Current research and theory (pp. 64–99). Appleton-Century-Crofts.
- Seligman, M. E. P. (1970). On the generality of the laws of learning. *Psychological Review*, 77, 406–418.
- Shettleworth, S. J. (1972). Constraints on learning. *Advances in the Study of Behavior*, 4, 1–68.
- Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis*. Appleton-Century-Crofts.
- Skinner, B. F. (1950). Are theories of learning necessary? Psychological Review, 57, 193–216.
- Skinner, B. F. (1977). Herrnstein and the evolution of behaviorism. *American Psychologist*, *32*, 1006–1012.
- Sporns, O. (2013). The human connectome: Origins and challenges. NeuroImage, 80, 53–61. https://doi.org/10.1016/j.neuroimage.
- Suboski, M. D. (1990). Releaser-induced recognition learning. Psychological Review, 97, 271–284.
- Timberlake, W. (1983a). Rats responses to a moving object related to food or water: A behavior systems analysis. *Animal Learning & Behavior*, 11, 309–320.

- Timberlake, W. (1983b). The functional organization of appetitive behavior: Behavior systems and learning. In M. Zeiler & P. Harzem (Eds.), *Advances in analysis of behaviour* (Vol. 3, pp. 177–221). John Wiley & Sons.
- Timberlake, W. (1993). Animal behavior: A continuing synthesis. *Annual Review of Psychology*, 44, 675–708.
- Timberlake, W. (2001). Motivational modes in behavior systems. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 155–209). Erlbaum.
- Timberlake, W. (2007). Anthropomorphism revisited. *Comparative Cognition and Behavior Reviews*, 2, 139–144.
- Timberlake, W., & Silva, F. J. (1994). Observation of behavior, inference of function, and the study of learning. *Psychonomic Bulletin & Review*, 1, 73–88.
- Timberlake, W., & Washburne, D. L. (1989). Feeding ecology and laboratory predatory behavior toward live and artificial moving prey in seven rodent species. *Animal Learning & Behavior*, 17, 1–10.
- Tinbergen, N. (1942). An objectivistic study of the innate behaviour of animals. *Brill*.
- Tinbergen, N. (1950). The hierarchical organization of nervous mechanisms underlying instinctive behaviour. *Symposia of the Society for Experimental Biology*, *4*, 305–312.
- Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift fur Tierpsychologie*, 20, 410–433.
- Wiener, N. (1961). Cybernetics ((2nd ed.). ed.). MIT Press.

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