



Operant/Classical Conditioning: Comparisons, Intersections and Interactions

The 2014 Winter Conference on Animal Learning and Behavior Focus and Research Seminar Sessions

Stanley J. Weiss
American University, USA

Jesús Rosales-Ruiz
University of North Texas, USA

The Keynote Speaker at Winter Conference on Animal Learning and Behavior (WCALB) 2014 was Dr. Björn Brembs whose address was titled, *Pavlovian and Skinnerian Processes Are Genetically Separable*. The essence of the address, that describes the research on which Dr. Brembs based this conclusion, is described below. Articles in this issue representing the related Focus Session include: *The Many Faces of Pavlovian Conditioning* by Dr. Jozefowicz, *Pavlov + Skinner = Premack* by Dr. Killeen, *Evocation of Behavioral Change by the Reinforcer is the Critical Event in Both the Classical and Operant Procedures* by Dr. Donahoe, *On Choice and the Law of Effect* by Dr. Staddon, *Response-Outcome versus Outcome-Response Associations in Pavlovian-to-Instrumental Transfer: Effects of Instrumental Training Context* by Gilroy, Everett and Delamater, and *The Instrumentally-Derived Incentive-Motivational Function* by Dr. Weiss. As a whole, they attempt to increase our contact with, and get at the essence of, what is actually happening with these operant and classical contingencies in the laboratory and nature. The Research Seminar Session revealed the current tendency for explanations of behavior to be reduced to physiology, neuroscience, and genetics. However, anti-reductionists saw shortcomings in this approach. They recommended an interconnected holistic approach which shifts the focus away from the structure of discrete behaviors and toward examining the environment in which the behavior occurs and the consequences produced. The distinction between structural and functional analysis points to a difficulty of integrating facts about behavior with other levels of analysis that requires our attention.

Dr. Björn Brembs Professor of Neurogenetics at the Institute of Zoology at Universität Regensburg was the Keynote Speaker at the 2014 Winter Conference on Animal Learning & Behavior. The title of his address was *Pavlovian and Skinnerian Processes are Genetically Separable*. This set the stage for the Conference theme and the related Focus Session concerned with *Operant/Classical Conditioning: Comparisons, Intersections and Interactions*. Articles in this issue of the *International Journal of*

Please send correspondence to Dr. Stanley Weiss, American University, Washington, USA and Jesús Rosales-Ruiz, (Email: sweiss@american.edu and jesus.rosales-ruiz@unt.edu, respectively).

Comparative Psychology have been developed from that Focus Session. The impressive Keynote Address Dr. Brembs delivered is sketched below. For additional information, see Brembs and Plendl (2008), Brembs (2009, 2011) and Colomb and Brembs (2010). The slides from Dr. Brembs' presentation can be found at <http://www.slideshare.net/brembs/wcalb14>.

In his introduction, Brembs noted that Skinner realized in the 1930s that operant conditioning was likely composed of several processes (Konorski & Miller, 1937a, 1937b; Skinner, 1935, 1937). Brembs went on to claim that his research demonstrates that Skinner was right. He described an operant conditioning situation where a food-deprived rat was reinforced with a food pellet for every lever press (a fixed ratio or FR1), and went on to explain that, although probably there are two processes operating simultaneously here, this paradigm makes it difficult to reveal them directly. Instead, one needs to use other experiments, such as those he designed with tethered flies as subjects, organized analogously to the rats' FR1 situation, wherein he could precisely measure the direction in which they were turning.

Brembs explained that these experiments used colors instead of a lever: One color (say, blue) was associated with an aversive heat-beam – much like an unpressed lever is associated with no food. In contrast, another color (e.g., green) was associated with the heat beam being switched off when the stationary flying fly attempted a turn in the proper direction – much like a depressed lever produces food.

From the way he views these paradigms, in both experiments the stimuli were under full control of the animal. When the rat presses the lever or the fly generates a particular turning maneuver, the situation changes. For the rat, food is delivered. For the fly, heat is switched off. In both cases, the animal's behavior has produced a preferred situation. If the rat stops pressing and engages in some other behavior, food ceases to be delivered. If the fly stops attempting to turn to the right and instead attempts a left turn (coloring its environment blue), the heat is switched on.

Brembs claimed that if the rat case parallels the fly case such that:

- (a) the fly turning right under green light and shutting the heat off is analogous to the rat pressing the lever down and producing food, *and*
- (b) the fly turning left under blue light and turning the heat on is analogous to the rat not pressing the lever (lever up) leading to no food,

then two things happen to rats in a Skinner box. The rat learns that the lever means food (just as the fly learns that green means heat) and that lever pressing produces food. The topography of behavior (i.e., left or right paw, nose, tail, etc.) is irrelevant as long as the lever is pressed and the microswitch is closed. In this stage, (1) the behavior is still flexible, (2) any modification of the neural circuits controlling the behavior are actively suppressed and, (3) learning about the environment is dominant – what Brembs calls *world-learning*. He reports that the biochemical processes and associated molecules involved in this type of learning are those discovered in classical conditioning, e.g., adenylyl cyclases of type I, cyclic adenosine monophosphate (cAMP), and protein kinase A or PKA (Brembs & Plendl, 2008).

Brembs went on to explain that this memory of the environment is independent of the behavior that controlled the stimuli. That is, the animals can use a different, even orthogonal, behavior to press the lever (or change the color) and still keep their performance up, compared to controls (Brembs, 2009). In the case of the flies, he can test this hypothesis in a way that is impossible in the rat because if the lever is removed, there is nothing for the rat to press - if one wants to test if the behavior has been conditioned independently of the lever. In comparison, in his paradigm with flies, turning direction preference can be tested after training, with the colors turned off. At this stage, using this paradigm, the flies show no preference (Brembs, 2009).

The second thing that happens, Brembs elaborated, is that, as conditioning continues, the suppression or inhibition that keeps the behavior flexible is overcome – making the behavior more stereotyped. This means that now the behavior is not that flexible any more so a different behavior is less effective in controlling the stimuli. In the case of the flies, when Brembs removed the colors after this extended training, now they showed a preference for the previously unpunished turning direction. With this stage of conditioning having been termed *habit formation* in vertebrates, and because the fly situation appeared quite similar, Brembs co-opted this term for invertebrates as well.

In rats, after habit formation, selective devaluation of the reinforcer no longer leads to a reduction in lever pressing rate, demonstrating the behavior's inflexibility (Balleine & Dickinson, 1998; Balleine & O'Doherty, 2010; Costa, 2007, 2011; Graybiel, 2005; Yin & Knowlton, 2006). At this stage, the biochemistry underlying the recruited neuronal circuitry is completely different. However, if the type I cyclases function is blocked, then the flies can continue to learn well. Protein kinase C (PKC), instead of PKA, is important with PKC manipulations having no effect on world-learning. This type of learning modifies the behavior of the animal itself and Brembs therefore termed it *self-learning* (Colomb & Brembs, 2010).

Brembs went on to explain that, in flies, it can be showed that it is the inhibition of world-learning that slows down self-learning. Compared to learning with colors, the same experiment without colors leads to a PKC-dependent preference for turning direction requiring only half the training sessions (Brembs & Plendl, 2008).

Besides PKC, Brembs showed that the gene *FoxP* is also necessary for self-learning. He explained that this is important because the genes *FOXP1* and *FOXP2* in humans (the closest relatives to *FoxP* in flies) are associated specifically with language acquisition and other motor skills. In fact, he asserts that the *FoxP* evidence directly contradicts Chomsky's statement that language acquisition and operant learning share only superficial similarities (Mendoza et al., 2014).

Finally, Brembs described how in the marine snail *Aplysia*, he and his colleagues have isolated the neurons involved not only in learning which behavior is rewarded/punished, but also the ones controlling when the behavior is supposed to be initiated (Brembs, 2003; Brembs, Lorenzetti, Reyes, Baxter, & Byrne, 2002; Nargeot, Le Bon-Jego, & Simmers, 2009; Nargeot & Simmers, 2010, 2012; Sieling, Bédécarrats, Simmers, Prinz, & Nargeot, 2014). This research shows how operant learning modifies both the timing and the kind of behavior that will be emitted. Moreover, it provides mechanistic insight in how behavioral variability is first generated on a neuronal level and then restricted due to reinforcement. Brembs contends that these

groundbreaking findings provide a roadmap for future research on the neurobiological processes underlying all forms of operant learning in vertebrates as well as in invertebrates.

Special Issue Article Overview

The following articles in this issue, by highly regarded behavioral scientists concerned with conditioning and learning, contribute to a more complete appreciation of the intersections, interactions, and commonalities, as well as the differences between operant and classical conditioning processes. As a whole, they serve to increase our contact with, and get at the essence of, what is actually happening with these contingencies in the laboratory as well as in nature. Each of the articles speaks for itself, but there are some themes, objectives, consolidations and concerns represented therein that will be briefly touched on below.

Jozefowicz in *The Many Faces of Pavlovian Conditioning* shows how included under the term “Pavlovian conditioning” are: a procedure, the learning resulting from that procedure plus the process meant to explain that learning. He is concerned that this interferes with our adequately understanding these various phenomena. In fact he shows even if one focuses at only the *process* there is behavioral as well as neural evidence supporting that it is “extremely unlikely that a single Pavlovian conditioning process is responsible for learning in all procedures classified as Pavlovian conditioning.” Jozefowicz describes how the same concerns also apply to the operant conditioning situation.

Pavlovian conditioning is the name of a procedure in which a CS is paired with a US and Jozefowicz describes a wide range of preparations exemplifying this procedure. They include: Pavlov’s salivary conditioning procedure in dogs, the nictitating membrane response conditioning in rabbits, fear conditioning in rats, autoshaping in pigeons and taste aversion learning. In each case, a CS is paired with a US and the CS comes to elicit a response related to the US.

Weiss’ *Instrumentally Derived Incentive Motivational Functions* (appetitive and aversive) may add “faces” to Pavlovian conditioning as a procedure as well as a process. He proposes that these functions support the contention that environmental conditions being differentially correlated with operant-behavior-produced reinforcement could be responsible for most classical conditioning and resulting incentive-motive states.” There was no traditional Pavlovian CS – US pairing in any of his training conditions. This can be considered an example of how learning principles derived from the laboratory can be extended to help us better understand how they are likely operating in nature. These “states” are clearly learned, anticipate the future and energize behavior.

Donahoe is seeking the “essentials.” He proposes “... that the critical reinforcing event in both the classical and operant procedures is more closely correlated with the evocation of a *change in behavior* induced by the reinforcing stimulus than with the presentation of that stimulus itself.” He goes on to describe evidence at the behavioral, as well as the neurological level, that support this consolidation. This moment-to-moment conception of the conditioning process represents an insightful integration. Weiss proposes that most classical conditioning occurs outside the laboratory through the reinforcement differences that come to exist between

environmental situations as the underlying operant contingencies take hold. Might a more molar model be necessary for the “classical conditioning” produced in this manner?

In *Pavlov + Skinner = Premack*, Killeen makes Premack’s principle central to all reinforcement. Essentially, Premack translated *reinforcement* from what the operant produced *per se* to the behavior the subject engaged in, after the operant created the appropriate opportunity. According to Premack, when one’s preferred behaviors are ranked from 1 to n, a behavior is reinforced by the opportunity to engage in a lower ranked one and punished by producing conditions that require one to engage in a higher ranked behavior.

Premack originally tested his principle in rather simple laboratory situations wherein he showed, for example, that children with an initial preference for pin-ball playing over gum drops, would eat gum drops for the opportunity to play pin-ball, and vice-versa (Premack, 1959). Although confirming the process, studies of this type probably also limited and constrained its application.

Killeen takes Premack out of the laboratory and uses a hierarchy of natural action patterns, adapted from Timberlake and Lucas (1989), that applies Premack’s principle to complex behavioral repertoires of animals in nature. It is Killeen’s thesis “...that operations that move an animal into a particular subsystem or mode [e.g., predation, defense, escape] are *motivational*. When in that subsystem, the ability to engage in an action ... will reinforce actions that lie above it ... and be reinforced by actions that lie below it in that column.”

He goes on to describe how through selective breeding the English Pointer is trapped in one link of an action chain and perpetually unable to consummate the nominal goal of that action – and is concerned that our laboratory animals have regularly been stuck at local minima. Killeen clearly helps us appreciate how (a) operant conditioning, (b) naturally occurring sequences of behavior related to particular situations and conditions plus, (c) Pavlovian conditioning can be effectively integrated for a more complete understanding of-going behavior.

Staddon, in his *On Choice and the Law of Effect* (LOE), presents a simple dynamic analysis of the molar matching law and related research. He begins with cumulative records which show behavior of individual subjects in real time – rather than thousands of aggregated responses as most “matching” experiments do. His simple law-of-effect (LOE) model easily reproduces the post-reinforcement “burst” of responses that reliably occur when animals are first exposed to intermittent reinforcement. He shows how much can be explained just by this elementary, non-temporal process.

He goes on to explain how concurrent variable-interval schedules tend to produce alternation because of the strong negative feedback that VI schedules provide – the longer one choice is neglected, the higher its payoff probability becomes. It is perhaps not surprising that a changeover delay is usually needed to get the matching relation: “The precise correspondence between relative frequency of responding and relative frequency of reinforcement broke down when the COD was omitted.” (Herrnstein, 1961, p. 271).

Staddon points out that concurrent random-ratio schedules have no such feedback. Data from random-ratio schedules suggest a law-of-effect-based cumulative-effects model which assumes: (a) that reinforcement-

linked response tendencies compete; (b) that the highest-strength response is the one that occurs; (c) other responses are “silent,” their strength unchanged until they occur; and (d) response strengths depend on relatively long-term reinforcement history. He shows that LOE models make several interesting predictions where matching either fails or does not apply.

Staddon’s discussion of VI schedules in the matching research led the author (SJW) to recall that some years ago he ran a few undergraduates on a VI schedule for several 30-min sessions as a baseline for an anticipated subsequent manipulation. When interviewed after these sessions, every student said, to the effect, “Well Professor Weiss, you stumped me. A few times I thought I figured out the sequence, like two fast and three spaced responses, but ultimately I couldn’t.” That humans are accustomed to solving problems could severely limit the application of findings based on paradigms without a “logical solution”.

Gilroy, Everett and Delamater, in their *Response-Outcome versus Outcome-Response Associations in Pavlovian-to-Instrumental Transfer: Effects of Instrumental Training Context*, report that training two instrumental Response-Outcome (R-O) relations in distinct contexts disrupted the ability of those responses to be modulated by Pavlovian stimuli in a sophisticated multiple response, outcome and context Pavlovian-to-Instrumental (PIT) paradigm. They interpret this to support the view that instrumental learning results in the development of highly specific Response-Outcome (R-O) associations that are used in the backward direction during a specific PIT test.

Gilroy et al. go on to discuss their results in the context of the potential associations that could be learned (context-outcome, response-outcome, and outcome-response) during instrumental learning and caution that although “... we have emphasized associative mechanisms at the intersection of Pavlovian and instrumental learning that would permit for an interaction at the levels of learning and performance, it is important to realize that there very well may be important differences, as well, in the underlying associative circuitries of Pavlovian and instrumental learning that may prevent interactions from taking place in some circumstances.” (It should be noted that PIT is the current manner of describing what has traditionally been referred to as the transfer-of-control (TOC) paradigm. See Weiss’ article in this issue for a functional analysis of the single response, outcome and context TOC design.)

Research Seminar Session: Conditioning, Learning, Behavior and Levels of Explanation

The status of behavioral research as a scientific subject matter is well established. Yet, even though behavioral analysis is a prominent feature of various disciplines (e.g., behavioral genetics, behavioral neuroscience, behavioral biology and behavioral pharmacology), it too often continues to be regarded as relevant only because of what it tells us about other processes considered, more important such as physiology and brain function. Skinner (1938) wrote, “Facts about behavior are not treated in their own right, but are regarded as something to be explained or even explained away by the prior facts of the nervous system.” (p. 4). This reductionistic tradition continues to be favored today. West and King (2001) summarized it well when they said, “... the study of behavior seems to be something someone does to get to somewhere else. Behavior affords a gateway to physiology, neuroscience, and genetics.” (p. 587).

This issue of reductionism was raised at the WCALB 2014 Research Seminar Session. In many ways, the points discussed paralleled current debate in the scientific community. For some participants, it was already all said and done that behavioral phenomena could be explained completely by physiology, neuroscience, and genetics and by reducing behavior to neural networks. The behavioral explanation was questioned, since it was assumed that the more complete explanation of behavior must be found inside the black box. This position was opposed by some who asserted instead that an explanation outside the black box at the behavioral level was valid and the way to go.

However, those who have searched for explanations at the behavioral level have been accused of focusing only on behavior and ignoring the role of physiology, neuroscience, and genetics. This is unfortunate, because without those behavioral facts, physiology, neuroscience, and genetics would not have much to study. As Skinner said, “Valid facts about behavior are not invalidated by discoveries concerning the nervous system, nor are facts about the nervous system invalidated by facts about behavior. Both sets of facts are part of the same enterprise, and I have always looked forward to the time when neurology would fill in the temporal and spatial gaps which are inevitable in a behavioral analysis.” (1988, p. 128). Thus, physiology, neuroscience and genetics supplement a behavioral analysis at the level of the whole organism interacting with the environment. From this perspective, facts about the organism (i.e., physiology, brain and genes) are considered part of the conditions necessary for the occurrence of behavior rather than explanations of behavior on their own. The explanation lies in the environmental contingencies, but facts from neuroscience and physiology help fill in the physical details that connect behavior to biology.

One alternative to reductionism discussed at WCALB 2014 was to acknowledge that there are different causes of behavior as proposed by Aristotle (triggers, functions, substrate and formal representation), all valid in their own right. In this view, the understanding of any phenomenon requires the understanding of all of its causes and how they interconnect. This position is in keeping with the modern anti-reductionism stance. For instance, in recent years biological scientists have moved away from the idea that biological systems can be fully explained by molecular biology and have instead favored some sort of holism or interconnected system (Van Regenmortel, 2004).

In the study of development, West and King (2001) have also recommended a systems approach that integrates the molecular and the non-molecular. Similarly, in recognition that drug-taking cannot be reduced to drug actions, those who study addictions have also called for a systems approach (see Kalant, 2009; and commentaries). A systems approach, while not easy, has the advantage of letting different disciplines pursue explanations at different levels as parts of a bigger picture. Complete understanding of behavior then comes from the coordination of all of these explanations (see, Killeen, 2001). An integrative science of behavior depends, of course, on the integrity of the levels. Errors at one level would necessarily produce errors in the explanatory system (Ruff, 2003).

West and King (2001) caution that the linkage between levels is compromised when the behavioral phenomena linked are devoid of important ecological and social variables relevant to the occurrence of the behavior in question. For example, they found that despite an elegant and thorough analysis of song-related neural structures, this analysis alone could not predict copulatory success. Instead, they discussed that they

“... have taken a more direct approach to understanding the task of song development by focusing on its goal, successful courtship.” (p. 597). As researchers move toward looking at behavior in its ecology, the focus is shifting away from the structure of discrete behaviors and instead toward examining the environment in which the behavior occurs and the consequences produced.

The distinction between structural and functional analysis points to one difficulty of integrating facts about behavior with other levels of analysis. Before behavior can be linked to other levels of observation or even reduced to one of those levels, there needs to be agreement about what is being reduced or integrated. Physiology, neuroscience and genetics have traditionally relied on a structural analysis of behavior rather than a functional one. A bird's song no doubt has a biological structure that can be mapped to other structures and functions of the nervous system. However, focusing only on structure takes away from the environmental variables that are part of the behavior. For example, a bird song could be one behavior when it is directed toward females, yet the same song could be a different behavior when directed toward males or when emitted in the absence of conspecifics. Although the song remains the same, the interaction with the environment produces different consequences. From a behavior analytic point of view, explanations are concerned with stating functional relations between behavior change and changes in the antecedent and consequent environment. These functional relations between behavior and environment create analytic units that make possible the study of behavior.

At WCALB the issue of structural and functional analysis of behavior was also discussed but at a more basic level: The level of the stimulus and response. Participants debated whether it is possible to talk about a stimulus without reference to a response or a response without reference to a stimulus. This question was new to the neuroscientists in the discussion, who were more familiar with defining stimuli and responses with respect to their structural and physical characteristics only. From this approach, the properties of the response can be defined completely by the field of biology and the properties of the stimulus by the field of physics. For the behavior scientists, however, the stimulus and response are two factors that interact to make up their subject matter: behavior. The response by itself does not constitute a behavioral event, even though it can be defined as a more or less fixed pattern of neural, muscular and glandular events all the way down to its molecules. The stimulus must also enter into the definition of behavior and it is this connection between stimulus and response that gives rise to behavioral phenomena. While behavior scientists begin with the physical description of the stimulus and response, just as biologists and physicists do, these descriptions are insufficient to characterize the interactions that behavior scientists study.

Another question raised during the discussion was what to call a stimulus that is not connected to a response or a response that is not connected to a stimulus. It was suggested to call a response not connected with a stimulus an *action*. This led to the next question, is there such a thing as a response without a stimulus? For the determinists in the room, that could not be the case. If there was a response, they would search for the stimulus. This was considered an error by the neuroscientists because it would prevent the search for internal mechanisms of action. However, the determinists objected to dissecting the stimulus from the response. Behavioral phenomena are continuous. A response leads to a stimulus which in turn leads to another response and so on, as Killeen's article in this issue describes. This continuous nature of behavior is central to the analysis of behavior.

The discussions at WCALB were very productive and stimulating. They reflected the scientific scene in general, in that an integration of the various disciplines is a continuous and ongoing challenge. It became clear that in order to have an integrative science of behavior more discussions are needed regarding the basic assumptions of the various disciplines concerned with explaining behavior. What is a stimulus, what is a response, what is the nature of the interactions that the different disciplines consider important? The mingling of behavior scientists and neuroscientists at WCALB was a good step toward addressing these questions. The meeting ended with a reminder that “criteria” is plural. We all need to be mindful of the other’s perspective.

The video of the Research Seminar Session can be found at

<https://www.youtube.com/watch?v=usCYJy9PI9Q&list=UUIq9EAG5h9yc25rYSjywNMw>.

References

- Balleine, B. W., & Dickinson, A. (1998). Goal-directed instrumental action: contingency and incentive learning and their cortical substrates. *Neuropharmacology*, *37*, 407-419.
- Balleine, B. W., & O’Doherty, J. P. (2010). Human and rodent homologies in action control: corticostriatal determinants of goal-directed and habitual action. *Neuropsychopharmacology*, *35*, 48–69. doi:10.1038/npp.2009.131
- Brembs, B. (2003). Operant reward learning in aplysia. *Current Directions in Psychological Science*, *12*, 218–221. doi:10.1046/j.0963-7214.2003.01265.x
- Brembs, B. (2009). Mushroom bodies regulate habit formation in *Drosophila*. *Current Biology*, *19*, 1351–1355. doi:10.1016/j.cub.2009.06.014
- Brembs, B. (2011). Spontaneous decisions and operant conditioning in fruit flies. *Behavioural Processes*, *87*, 157–164. doi:10.1016/j.beproc.2011.02.005
- Brembs, B., Lorenzetti, F. D., Reyes, F. D., Baxter, D. A., & Byrne, J. H. (2002). Operant reward learning in *Aplysia*: neuronal correlates and mechanisms. *Science*, *296*, 1706–1709. doi:10.1126/science.1069434
- Brembs, B., & Plendl, W. (2008). Double dissociation of *pkc* and *ac* manipulations on operant and classical learning in *drosophila*. *Current Biology*, *18*, 1168–1171. doi:10.1016/j.cub.2008.07.041
- Colomb, J., & Brembs, B. (2010). The biology of psychology: Simple conditioning? *Communicative & Integrative Biology*, *3*, 142–145. doi:10.4161/cib.3.2.10334
- Costa, R. M. (2007). Plastic corticostriatal circuits for action learning: what’s dopamine got to do with it? *Annals of the New York Academy of Sciences*, *1104*, 172–91. doi:10.1196/annals.1390.015
- Costa, R. M. (2011). A selectionist account of *de novo* action learning. *Current Opinion in Neurobiology*, *21*, 579–86. doi:10.1016/j.conb.2011.05.004
- Graybiel, A. (2005). The basal ganglia: learning new tricks and loving it. *Current Opinion in Neurobiology*, *15*, 638–644. doi:10.1016/j.conb.2005.10.006
- Herrnstein, R. J. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior*, *4*, 267-272.
- Kalant, H. (2009). What neurobiology cannot tell us about addiction. *Addiction*, *105*, 780–789
- Killeen, P. (2001). The four causes of behavior. *Current Directions in Psychological Science*, *10*, 136-140.

- Konorski, J., & Miller, S. (1937a). Further remarks on two types of conditioned reflex. *Journal of General Psychology*, *17*, 405–407.
- Konorski, J., & Miller, S. (1937b). On two types of conditioned reflex. *Journal of General Psychology*, *16*, 264–272.
- Mendoza, E., Colomb, J., Rybak, J., Pflüger, H.-J., Zars, T., Scharff, C., & Brembs, B. (2014). Drosophila FoxP mutants are deficient in operant self-learning. *PloS One*, *9*, e100648. doi:10.1371/journal.pone.0100648
- Nargeot, R., Le Bon-Jego, M., & Simmers, J. (2009). Cellular and network mechanisms of operant learning-induced compulsive behavior in Aplysia. *Current Biology*, *19*, 975–84. doi:10.1016/j.cub.2009.05.030
- Nargeot, R., & Simmers, J. (2010). Neural mechanisms of operant conditioning and learning-induced behavioral plasticity in Aplysia. *Cellular and Molecular Life Sciences*, *68*, 803–816. doi:10.1007/s00018-010-0570-9
- Nargeot, R., & Simmers, J. (2012). Functional organization and adaptability of a decision-making network in aplysia. *Frontiers in Neuroscience*, *6*, 113. doi:10.3389/fnins.2012.00113
- Premack, D. (1959). Toward empirical behavior laws: I. Positive reinforcement. *Psychological Review*, *66*, 219–233.
- Ruff, R. M. (2003). A friendly critique of neuropsychology: facing the challenges of our future. *Archives of Clinical Neuropsychology*, *18*, 847–864
- Sieling, F., Bédécarrats, A., Simmers, J., Prinz, A. A., & Nargeot, R. (2014). Differential roles of nonsynaptic and synaptic plasticity in operant reward learning-induced compulsive behavior. *Current Biology*, *24*, 941–950. doi:10.1016/j.cub.2014.03.004
- Skinner, B. F. (1935). Two types of conditioned reflex and a pseudo type. *Journal of General Psychology*, *12*, 66–77.
- Skinner, B. F. (1937). Two types of conditioned reflex: A reply to Konorski and Miller. *Journal of General Psychology*, *16*, 272–279.
- Skinner (1938). *The behavior of organisms*. New York, NY: Appleton-Century-Crofts.
- Skinner (1988). Reply to Marc N. Richelle. In A. C. Catania & S. Harnad (Eds.), *The selection of behavior. The operant behaviorism of B. F. Skinner: Comments and consequences* (p. 128). New York, NY: Cambridge University Press.
- Timberlake, W., & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of constraints on learning* (pp. 237–275). Hillsdale, NJ: Erlbaum.
- Van Regenmortel, M. H. V. (2004). Reductionism and complexity in molecular biology. *EMBO Reports*, *5*, 1016–1020.
- West, M. J., & King, A. P. (2001). Science lies its way to the truth ... really. In E. M. Blass (Ed.), *Developmental Psychobiology: Handbook of Behavioral Neurology*, (Vol. 13, pp. 587–614). New York, NY: Kluwer Academic/Plenum Publishers
- Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience*, *7*, 464–476. doi:10.1038/nrn1919

Financial Support: Preparation of this work was supported in part by NIDA Award R01-DA008651. It is solely the authors' responsibility and doesn't necessarily represent official views of NIDA/NIH.

Conflict of Interest: The authors declare no conflict of interest.