

sions of behavior proposed by Johnston and Pennypacker (1980) are latency, duration, and countability. These are characteristic of every member of a response class. Secondary dimensions such as frequency and acceleration result readily from combinations of the basic dimensions. Variability, according to this view, is not a basic dimension of behavior. Rather, it is a characterization imposed by observers upon a collection of measures of individual responses. The assertion that variability is a fundamental dimension of behavior leads readily to the assertion that it is intrinsic (Sidman 1960), a status that forecloses the search for its determinants. It also leads readily to the practice of enlisting the variability as a basis for reifying suspected causes, as Quetelet did in the 1830s and for creating relative units of measurement as Fechner and Galton did late in the nineteenth century. From here, the regression to social science methodology is almost complete.

What is the role of behavior in evolution? Much of what I know about natural selection I learned from my lifelong friend and colleague, R. Bruce Masterton (Pennypacker 1999). In particular, he taught me that although the object of natural selection is usually the adult, the product of the process is another infant. Bruce was fond of quoting Gaylord Simpson (1949): "Hens are an egg's way of begetting another egg" (Masterton 1998).

Often overlooked by biologists and behavior analysts alike is the fact that very few infants reproduce. In order to transmit its genetic material into a subsequent generation, an organism must first adapt and survive to the point where it can reproduce. For most vertebrates, at least, a major modulus of this survival is behavior. Thus, natural selection occurs with respect to behavior in a fundamental sense. Those individuals who do not behave effectively are not around to beget new infants and whatever morphological or neurological characteristics they possessed that contributed to their demise will likewise not be reproduced. Selection occurs, therefore, with respect to those characteristics (morphological and physiological) than enable successful behavior. Any efforts to isolate those mechanisms and explicate their role in the selection of operant behavior must first deal with fact that they are themselves the products of selection. Candidates for inclusion in this universe are the sensory and physiological mechanisms that come into play when reinforcement occurs, when conditioned reinforcement (likely a respondent process) is developed and when certain stimuli become discriminative for the occurrence of operant behavior.

Do some or all of these mechanisms develop ontogenetically as a result of a selection mechanism as is proposed in the case of the immune system, or are they fully developed in the genotype, awaiting expression by the right combination of environmental events?

Conclusion. This theoretical formulation, as the authors point out, offers promise for meaningful interdisciplinary research. It suggests important research questions, such as what are the details of the change in the nervous system as an operant repertoire is acquired? What is the role of private verbal behavior in adaptation to a changing social environment? Questions as complex as these may now be addressed in a formidable multidisciplinary context. The rapprochement that Skinner anticipated in 1938 and 1950 may finally be at hand and it is to these authors' credit that they will have hastened its arrival.

Selection without multiple replicators?

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Abstract: Hull et al.'s construction of operant learning as an instance of selection gives rise to problems that weaken this application of selection

theory beyond acceptable limits. We point out that most fundamental is a disregard for the need to include multiple concurrent replicators in any definition of selection and indicate how this problem may be solved.

Of the three phenomena considered in the target article, the analysis of operant learning is the most challenging and problematic. Some of the obstacles are due to our lack of knowledge. For example, it is not clear what would play the role of replicators in operant learning, or how feedback between environmental interaction and differential replication would be mediated. But an even more fundamental issue concerns the role of multiple concurrent replicators that differ in their replication rates. We will focus on this point because we believe it can be resolved in principle, without any need for further empirical studies of behavior or neurobiology.

The issue is raised by the authors in their introduction: "In operant learning, selection occurs only with respect to sequences of environmental interaction rather than with respect to numerous concurrent alternatives. Is this difference sufficient to disqualify it as a case of selection?"

The question would seem to be a matter of definition. In their general description of selection, the authors define it as "repeated cycles of replication, variation, and environmental interaction so structured that environmental interaction causes replication to be differential." The standard interpretation of the word "differential" is that in each cycle, multiple replicators differ in the extent to which they replicate. Hull et al. seem to concur with this interpretation, stating that, "variants must be linked to proliferation so that at any one time, numerous alternatives are available for selection."

Thus it would seem clear that selection requires multiple replicators by definition. When the authors discuss operant learning, however, they frame the theory in terms of a single replicator at any given time. They clearly recognize the problem this raises: "If the environment must have multiple and differing copies of a replicator concurrently available for selection to occur, operant behaviors seems definitionally excluded." However, they go on to conclude rather surprisingly that this requirement does not apply. They reason that, "there appears to be no reason to assume that all replication processes involve concurrently existing events or objects." That is certainly true, but replication is not the same as selection. With little further discussion of the problem, they decide in their conclusion that, "replicators that do not proliferate in this way also count as instances of selection."

This leaves unresolved contradictions between the authors' general definition of selection and their specific conclusion about operant learning. This new interpretation of selection also includes a much wider range of phenomena than the original definition. For example, imagine a bird that molts its feathers each year, then produces a new "generation" of feathers that is similar but not identical to the previous year's. This would fit the description of a process that retains features of an object across generations, with a mechanism of variation to introduce novelty. But surely we would not want to call this selection. Indeed this seems a clear example of the mere persistence of patterns, which the authors in their introduction explicitly exclude. Even if the sequence of plumages showed "improvement" over time by some criterion, it would not be by means of differential replication, and it would not be through a process of selection.

Is the definition of selection ultimately a matter of taste or semantics, with one answer being as good as another? It is not, in part because the theory of selection has developed beyond mere verbal argument. A tradition of rigorous mathematical description of the selection process in biology provides a foundation for developing a general theory. All formal representations of selection are quite explicit about the requirement for variation among multiple concurrent alternatives. This includes Fisher's "fundamental theorem of natural selection" (Fisher 1958), the Price equation (Price 1970), and the replicator equation (Schuster & Sigmund 1983). Here the role of variation is not just qualitative, but appears

as a quantitative expression of the rate of change as a function of the genetic or phenotypic variance present at a given point in time.

To pursue the biological analogy, imagine an organism that consistently produces a single offspring and then dies. If we allow for heritability and mutation, and analyze this situation using the mathematics of selection theory we will inevitably conclude, quite correctly, that natural selection does not occur because there are no variants to select among. The lineage either persists or ends, but it will not generate adaptation. The same reasoning applies to operant behavior, for the same reasons.

Does this mean that the project of explaining operant learning as a selective process is doomed to failure? We do not believe so, because there is no need to envision the process as involving only a single replicator at any given time. If replicators consist of specific neural configurations that produce tendencies or proclivities for certain behaviors, it is not hard to imagine a population of such replicators that compete for the opportunity to be expressed as behaviors (interactors), and to be thereby strengthened or weakened according to their relative "success" (e.g., in eliciting positive affect). It is also not hard to envision that stronger neural configurations would be more likely both to persist and to spawn variants.

The formal structure of selection theory can be applied to such a scenario without any major conceptual obstacles. We could even envision the possibility that selection occurs among a set of concurrent alternatives previously generated in sequential order. Given a straightforward conceptual solution, what remains is only that the empirical aspects be clarified and tested. Indeed, a start has already been made on developing the quantitative selection theory developed in biology into a broader account of selection in general (Price 1995), and of learning in particular (Frank 1997). We think this approach holds considerable promise, and we urge the authors as well as other workers to forge ahead on this exciting endeavor.

Activity anorexia: Biological, behavioral, and neural levels of selection

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Abstract: Activity anorexia illustrates selection of behavior at the biological, behavioral, and neural levels. Based on evolutionary history, food depletion increases the reinforcement value of physical activity that, in turn, decreases the reinforcement effectiveness of eating – resulting in activity anorexia. Neural opiates participate in the selection of physical activity during periods of food depletion.

Selection of operant behavior by contingencies of reinforcement involves changes in an organism's neurophysiology and neurochemistry. Neural changes, in turn, participate as part of the contingencies of reinforcement selecting operant behavior. As Hull et al. point out, "the first step in operant selection occurs at the behavioral level [at the interface between the organism and environment] . . . And the second step occurs inside the organism at the neural level." The target article, therefore, raises the fascinating problem of the interplay of events outside and within the organism (see Skinner 1969, pp. 282–84 on behavior, and the nervous system). In this commentary, I explore the interrelationships between the biological, behavioral, and neural levels as illustrated by a biobehavioral analysis of activity anorexia.

In our laboratory, rats placed on food restriction and provided with a running wheel die of self-starvation (Epling et al. 1983; see also Routtenberg 1968). The wheel running of these animals increases exponentially over days. At the same time, the rats give up eating and their body weights plummet. Control animals, given the same food restriction but prevented from running, adapt to the reduced food supply and survive as healthy individuals. The

laboratory model shows that food restriction induces physical activity that, in turn, suppresses eating. Epling and Pierce (1991) called this process activity anorexia.

A biobehavioral analysis of activity anorexia involves evolution and natural selection (i.e., the fit between phenotypes and environment as discussed by Hull et al.). For organisms faced with sporadic reductions in food supply (e.g., unpredictable famines), natural selection would have favored increased physical activity (see Mrosovsky & Barnes 1974 for cyclic reductions in food supply, hibernation, and anorexia; also see Mrosovsky & Sherry 1980 for a review of natural anorexias). That is, animals that traveled or migrated under conditions of food depletion contacted food, survived, and reproduced. Natural selection also would have favored anorexia during times of food-related travel. Under famine conditions, there would be a net negative energy balance between foraging for small, difficult to obtain food items and traveling to a more abundant food source. Animals that stopped to eat along the way would use up their energy stores and die. Those animals that gave up eating, and kept on going, often would have contacted a stable and abundant food source – increasing their reproductive success (see Epling & Pierce 1991; Pierce & Epling 1996).

For animals with this evolutionary history, we predicted that food depletion increases the reinforcement value of physical activity and that intense physical activity decreases the reinforcement effectiveness of eating. Pierce et al. (1986; Experiment 1) used male and female rats to test the reinforcement effectiveness of wheel running under different levels of food deprivation (see also Belke 1996). Animals were trained to press a retractable lever for 60 sec of wheel running. Next, we tested each animal at free feeding weight (100%) and at 75% of *ad libitum* weight on a progressive fixed-ratio schedule of reinforcement (an increasing fixed number of lever presses) for 60 sec of wheel running. The point at which the rats gave up lever pressing for an opportunity to run in a wheel was used as a measure of reinforcement effectiveness. Results indicated that, for each animal tested, wheel running sustained larger fixed ratios at 75% compared with 100% body weight. In terms of behavioral selection, our research shows that reductions in feeding enhanced the reinforcement value of physical activity. Additional research (Pierce et al. 1986; Exp. 2) indicates that increases in physical activity reduced the reinforcement value of eating (measured as the "give up" point on a progressive fixed ratio schedule of food reinforcement). These changes in reinforcement effectiveness insure that, during periods of food depletion, animals engage in physical activity rather than eating (i.e., activity anorexia).

At the neural level, endogenous opiates may function as part of the contingencies of food-related travel or physical activity. One possibility is that physical activity is partly maintained on a schedule of endogenous opiate release that requires more and more amounts of physical exertion (see Radosevich et al. 1989 on dose-response between intensity of physical activity and level of plasma β -endorphin). The endogenous reinforcement hypothesis suggests that injection of an opiate antagonist will decrease the level of wheel running of food-restricted animals. We tested the effects of the opiate antagonist, naloxone, on the wheel running of hungry rats (Pierce & Epling 1996). Rats were made hyperactive by restricting their feeding and providing a running wheel. Once wheel running stabilized, each rat was given injections of naloxone (50 mg/kg in saline) or saline (0.5 mL) on alternate days. Figure 1 shows wheel turns (1.1 meter per turn) for the one-hour period following the injection of the drug. For each animal, wheel running is reduced on days of naloxone compared with days of saline (control) injections. These findings suggest that the wheel running of food-restricted rats is increased by release of endogenous opiates – indicating that neurochemical changes are part of the contingencies regulating travel during periods of food depletion.

An important part of selection by consequences occurs during the lifetime of the individual. Our research on activity anorexia illustrates how environmental contingencies at the biological level (e.g., unpredictable food depletion) resulted in the motivational