The covariance based law of effect: A fundamental principle of behavior

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Abstract

Building on George Price's formal account of selection, we present an abstract theoretical account of behavioral selection that integrates the domains of individual learning and evolution. From the perspective of the multilevel model of behavioral selection (MLBS), we argue that the *covariance based law of effect* (CLOE) qualifies as a fundamental principle of behavior in that it provides a general formal framework for selectionist thinking and model building. We demonstrate the feasibility of our approach by means of a covariance based model of choice behavior that explains the effects of changeover delays on operant matching.

Keywords: *behavioral selection, covariance based law of effect, multilevel model of behavioral selection, natural selection, Price equation, metatheoretical structuralism*

1 Introduction

The idea of universal principles that explain the behavioral dynamics of living organisms was once very popular among behaviorists (C. L. Hull et al., 1940; Thorndike, 1932; Tolman, 1938). This view was questioned by Skinner (1950), who argued that behavioral psychology was not ready for a general theory. Skinner's position has led to considerable skepticism towards theory among behaviorists and a tendency to adopt a pragmatist philosophy of science (Chiesa, 1994; Marr, 1983; Moore, 1998; Sidman, 1960). Today, many behavioral psychologists still work in the Skinnerian tradition: gather data, establish functional relations between observables, and so on (see, however, Staddon, 2016 for a theory-based approach).

The pragmatist strategy in behavior analysis has left the field of theory construction mainly to cognitive psychologists, who build their models around mental concepts (Anderson, 1985; Eysenck, 2001; Fodor, 1983; Neisser, 1967). Although some behaviorists have argued against the Skinnerian approach (e.g., Staddon, 2014), the majority of behavior analysts remains skeptical towards a theory driven, deductive approach to behavior (Burgos, 2007). However, the history of science shows that major progress in several scientific areas (specially the most advanced ones, e.g., physics) have occurred due to the systematization of different phenomena under common theoretical principles (Kitcher, 1993).

Notably, Skinner introduced his apparently anti-theoretical research program on purely pragmatic grounds. In his highly influential paper "Are theories of learning necessary?", Skinner argued that the ultimate goal of a science of behavior has to be a theoretical construction that is of "greater generality than any assemblage of facts" (Skinner, 1950, p. 216). Obviously, Skinner was not anti-theory per se, he was just critical about the theoretical approaches put forward by behaviorists of his time. Although still committed to the experimental approach, Skinner later revived the idea of a universal theoretical principle for the behavioral sciences by proposing "selection by consequences" as an explanatory mode that gives an ultimate causal explanation for various mechanisms of adaptive behavior, including operant conditioning, cultural adaptations and natural selection (Skinner, 1981).

In fact, the idea that learning can be characterized as a selection process had been around for quite a while (Campbell, 1956; Gilbert, 1970; Pringle, 1951; Staddon & Simmelhag, 1971; Thorndike, 1900) and is still a popular theme among behaviorists (e.g., Becker, 2019; Donahoe, 2011; D. L. Hull et al., 2001; Richerson, 2019; Simon & Hessen, 2019). However, lacking a mathematically sound theory of selection, the principle of "selection by consequences" remained an informal narrative for a long time that has been subject of substantial criticism (cf. the open peer commentaries to Skinner, 1984; also Tonneau & Sokolowski, 2000 and Burgos, 2019).

Formal models have the advantage that they enforce conceptual rigor and clarity to a much higher degree than verbally stated theories. Therefore, the full potential of the selectionist account may not yet have been revealed. However, attempts to scrutinize the selection analogy by means of formal models are rare. Donahoe et al. (1993) propose a neural model based on “selection networks” that unifies different adaptive behavioral phenomena like operant conditioning and classical conditioning. However, these neural networks are not themselves instances of selection. Instead, they are intended to provide a neural explanation for a selection process that is observed on the behavioral level (Donahoe et al., 1993). Another path is taken by McDowell (2004), who formalizes a behavioral selection process by means of an evolutionary algorithm. However, the proposed “Computational Model of Behavioral Selection” implements selection on the level of *potential* behaviors that are neither directly observable, nor do they correspond to real entities. Therefore, McDowell’s simulations do not show that reinforcement is a selection process, but rather that an evolutionary algorithm can mimic the outcome of reinforcement. Finally, there are two recent approaches to a formal selectionist theory of reinforcement that build on an abstract mathematical description of selection by means of the Price equation (Price, 1970, 1972, 1995, written ca. 1971). The first one was put forward by Baum (2017) as an attempt to state a mathematically rigorous description of reinforcement as an abstract selection process. Although Baum’s “Behavioral Price Equation” does provide a consistent conceptual framework to describe reinforcement in terms of selection, it only applies to learning scenarios where there are no other sources of behavioral change apart from reinforcement. A second application of the Price equation formalism to reinforcement was presented by Borgstede and Eggert (2021). In contrast to Baum’s approach, the proposed “Multilevel Model of Behavioral Selection (MLBS)” incorporates natural selection and reinforcement learning within a single model, thereby linking the effectiveness of reinforcers to their predictive power with regard to evolutionary fitness (Borgstede, 2020). The core of the MLBS is the *covariance based law of effect* (CLOE), which states that reinforcement is proportional to the covariance between behavior and reinforcement.

In this article, we argue that the CLOE qualifies as a *fundamental principle of behavior* that captures the essence of individual learning in terms of selection. The remainder of this paper starts with a brief introduction to the mathematical description of selection by means of the Price equation (Section 2), followed by its application to individual learning within the MLBS (Section 3). We then elaborate on the role of fundamental principles in natural science (Section 4) and show how the CLOE qualifies as a fundamental principle, in that it provides a general theoretical framework for behavior analysis (Section 5). To illustrate the value of the CLOE for theory building, we further present an exemplary application to model the effects of changeover delays on operant matching (Section 6). Finally, we discuss the results of our analysis and give an outlook on how the CLOE may unify the field of behavior analysis (Section 7).

2 The Price equation

The Price equation was introduced by George Price in his seminal paper "Selection and covariance" (Price, 1970). It describes the principle of selection on the most abstract level, such that it applies to any selection process. One of the most common forms of the Price equation is:

$$\bar{w}\Delta\bar{z} = \mathrm{Cov}(w_i, z_i) + \mathrm{E}(w_i\,\Delta z_i) \tag{1.}$$

Here, z_i are character values of an arbitrary set (e.g., a particular genotype). $\bar{z}$ is the arithmetic mean of z over all elements of the set (i.e., the population average). w_i designates the contribution of element i to the elements of a second set (e.g., a population of offspring) and is usually called "fitness" because it corresponds to the contribution of an individual to the future population. $\bar{w}$ is the arithmetic mean over all w_i. The Price equation partitions the difference in mean character value between two sets, $\Delta\bar{z}$, into the covariance between z_i and w_i and the expected value of fitness weighted within-elements change, $w_i\Delta z_i$. The partitioning of change into a covariance term and an expectation term corresponds to the separation of selective and non-selective sources of change. For example, if z_i designates the presence of a particular genotype in individual i, mean character value $\bar{z}$ equals the frequency of the corresponding genotype in the parent population and $\Delta\bar{z}$ is the gene frequency change from one generation to the next. Correspondingly, $\mathrm{Cov}(w_i, z_i)$ captures the effect of natural selection on gene frequency change, while $\mathrm{E}(w_i\,\Delta z_i)$ summarizes all sources of gene frequency change that are not natural selection, like mutation, recombination or environmental factors.

The Price equation is a mathematical identity and, therefore, true by definition. Consequently, the Price equation (along with all of its variants) does not provide an empirical model in any mechanistic sense. Instead, it constitutes an invaluable analytical tool that helps to disentangle different sources of change in various contexts and to identify the relevant factors that need to be studied when dealing with selection processes (Luque, 2017).

3 The multilevel model of behavioral selection

Borgstede and Eggert (2021) extend the Price equation to a multilevel model of behavioral selection (MLBS) that describes selection on different aggregate levels, thereby capturing the effects of within-individuals selection (learning) and between-individuals selection (evolution).

Formally, the MLBS consists in a multilevel extension of the Price equation applied to an arbitrary behavior b. Behavior is conceptualized on a molar level, i.e., b is not a single instance of behavior (like visiting a certain food site), but an aggregate measure that is itself extended over time (like the rate of visiting a certain food site or the time spent foraging). Like in the basic Price equation, the change in average b in a population of individuals is partitioned into a population-level covariance capturing natural selection and a population-level expectation capturing average change between parents and their offspring. To account for the comparatively small time scale at which individual learning occurs, the MLBS focuses on the survival part of evolutionary fitness, treating surviving individuals formally as their own offspring. In this setup, the change between parents and offspring expressed in the expectation term in equation 1 corresponds to the change from a parent to its own future-self, i.e., intra-individual behavioral change. The core assumption of the MLBS is that this intra-individual change is itself subject to a selection process and can be described by the same abstract principle as natural selection.

To apply the covariance principle expressed in the Price equation to the within-individual level, the individual needs to be formally partitioned into lower level elements. Since behavior takes up time, it makes sense to think of these lower level elements as behavioral episodes, which are themselves defined by recurring contextual factors (e.g., the trials in a reinforcement experiment). Within-individuals change can now be captured by recursively inserting the Price equation into the expectation term to account for behavioral variation between episodes j:

$$\begin{aligned} \bar{w}\Delta\bar{b} &= \mathrm{Cov}_i(w_i, b_i) + \mathrm{E}_i(w_i\Delta b_i) \\ w_i\Delta b_i &= \mathrm{Cov}_j(w_{ij}, b_{ij}) + \mathrm{E}_j(w_{ij}\Delta b_{ij}) \end{aligned} \tag{2.}$$

Equation 2 partitions population change of average behavior $\Delta\bar{b}$ into a population-level covariance $\mathrm{Cov}_i(w_i, b_i)$, capturing natural selection, and the expectation over intra-individual behavioral change $\mathrm{E}_i(w_i\Delta b_i)$. The expectation term is itself partitioned into a within-individuals covariance $\mathrm{Cov}_j(w_{ij}, b_{ij})$, capturing reinforcement, and a within-individuals expectation term $\mathrm{E}_j(w_{ij}\Delta b_{ij})$, capturing all sources of within-individuals behavioral change apart from reinforcement. These non-selection factors include random variation, external and internal constraints, as well as other mechanisms of behavior change. Since the MLBS focuses on reinforcement, the intra-individual expectation term is treated as a residual term and denoted δ. Dropping the indices for notational simplicity, the within-individuals part of equation 2 thus becomes:

$$w\Delta b = \mathrm{Cov}(w, b) + \delta \tag{3.}$$

Equation 3 closely mirrors Baum's behavioral Price equation (Baum, 2017). However, the MLBS does not treat behavioral selection as an isolated process where fitness is circularly defined by the observed behavioral change. Instead, "fitness", as expressed by w is taken rather literally by identifying it with the predicted evolutionary fitness of an individual, given the current behavior. Of course, the individual has no access to its actual future evolutionary fitness. Therefore, it has to adjust its behavior according to *fitness proxies* that predict the expected change in an individual's evolutionary fitness. The predictiveness of a fitness proxy with regard to evolutionary fitness constitutes its reinforcing power (Borgstede, 2020). For example, food will act as a reinforcer as long as it positively affects an individual's body weight, because in most species, body weight predicts evolutionary fitness on a population level (i.e., heavier individuals contribute more to the future population than low-weight individuals). The concept of a fitness proxy is similar to Baum's "phylogenetically important events"(PIEs) (Baum, 2018). However, it goes beyond the idea of "events" acting as reinforcers by treating *any* statistical fitness predictor as a reinforcer. This also includes behavior shown by other individuals or the individual itself, and even internal state changes (like the dopamine concentration in the brain), as long as they co-vary with evolutionary fitness on the population level.

Formally, a fitness proxy p is defined by means of a population-level linear regression $w = \beta_0 + \beta_{wp}p + \varepsilon$, where β_{wp} is the slope of the regression of individual fitness on a fitness proxy p. Substituting w in equation 3 with the predicted value from this regression and simplifying yields the fundamental principle of behavioral selection, the covariance based law of effect (CLOE):[1]

$$w\Delta b = \beta_{wp}\mathrm{Cov}(b, p) + \delta \qquad (4.)$$

The CLOE describes reinforcement on the most abstract level as the result of a covariance between behavior and reinforcement, where reinforcement is defined as any statistical predictor of evolutionary fitness. The CLOE was proposed as a fundamental principle that underlies all reinforcement based learning processes (Borgstede & Eggert, 2021). In the following sections, we will argue that the CLOE can in fact be regarded as a fundamental principle of behavior and demonstrate how it can be utilized to aid theory construction in behavior analysis.

[1] See Borgstede and Eggert (2021) for the complete derivation.

4 The role of fundamental principles in natural science

Although the history of science provides several examples of "fundamental principles" in different scientific areas, how to conceptualize them has undergone considerable debate among scientists and philosophers of science. Following the ideal of logical positivism (Carnap, 1995), early behaviorists adopted a syntactic conception of scientific theories, where fundamental principles are understood as the axioms of a theory, from which specific laws and predictions are to be derived by means of deductive reasoning.[2]

The traditional, syntactic, view of scientific theories was later questioned by philosophers of science. First, they pointed out that scientific theories are more than their axioms and theorems, in the sense that they are complemented by many other specific laws. Even the most developed scientific theories cannot be fully characterized by their axiomatic core. For example, Newtonian mechanics does not only consist of the three classical laws of motion and the law of gravitation, but also includes more specific laws with a much more restricted domain of application, for example Hooke's law, Archimedes' law, Galileo's law, etc. Moreover, classical mechanics can be stated in various syntactic forms (e.g., using the formalisms of Langrange or Hamilton). The different formalisms that have been proposed for classical mechanics over the course of time emphasize that scientific theories are not petrified structures but historical entities that can be changed and adapted in order to extend their range of applicability.

To account for these complexities, beginning in the 1960s and 1970s, several philosophers developed a semantic conception of scientific theories that views scientific theories as a collection of models, rather than axioms (Giere, 1988; Suppe, 1989; Suppes, 1970). One particularly sophisticated formulation of the semantic conception is metatheoretical structuralism (Balzer et al., 1987). The structuralist view represents scientific theories as a collection of so-called theoretical elements. Theoretical elements are connected by a hierarchical relation that specifies which theoretical

[2] A paradigmatic example of the axiomatic approach is C. L. Hull (1943).

elements are specializations of more general theoretical elements. Specializations specify subclasses of the class of phenomena described by the more abstract principles. Thus, the more specific laws are not logically deduced from the more abstract principles. Instead, they restrict the scope of the more abstract theoretical elements such they provide details about specific parts of the world that are intended to be explained by the theory.

Given the theory is sufficiently developed, these theoretical elements can be arranged in the form of a theory-net (see Figure 1). At the top of the theory-net we find the *fundamental principle* (or fundamental law) of the theory, a very general statement about how the theory accounts for a certain class of phenomena. According to the structuralist view, fundamental principles provide a definition for the general analytical concepts of the theory. However, fundamental principles buy generality at the expense of being empirically vacuous.[3] The role of fundamental principles is to serve as the guiding principles of a theory, telling us “what the theory is about” (Díez & Lorenzano, 2013). By doing so, they point us towards the relevant factors to consider when explaining a specific class of phenomena. Empirical applications of the theory require more specific laws that limit the scope of the fundamental principle. Thus, a fundamental principle provides a shared formal vocabulary for the practitioners in a scientific field.

As historical entities, scientific theories expand and adapt to explain new kinds of phenomena. For example, Newton’s second law of motion, as stated in classical particle mechanics, needed to be modified to account properly for the dynamics of fluids. This procedure is also accompanied by connecting the formal vocabulary from one theory with the formal vocabulary of another theory. Specifically, elements from different theories may be related to one another via what we may call *intertheoretical links*. Continuing from the above example, the theories of classical particle mechanics and fluid mechanics are connected by a set of intertheoretical links between Newton’s second law

[3] For a similar, non-structuralist view, on fundamental principles see Kuhn (1977) and Friedman (2001).

(the fundamental principle of classical mechanics) and the Cauchy momentum equation (the fundamental principle of fluid mechanics) (Granger, 1995).

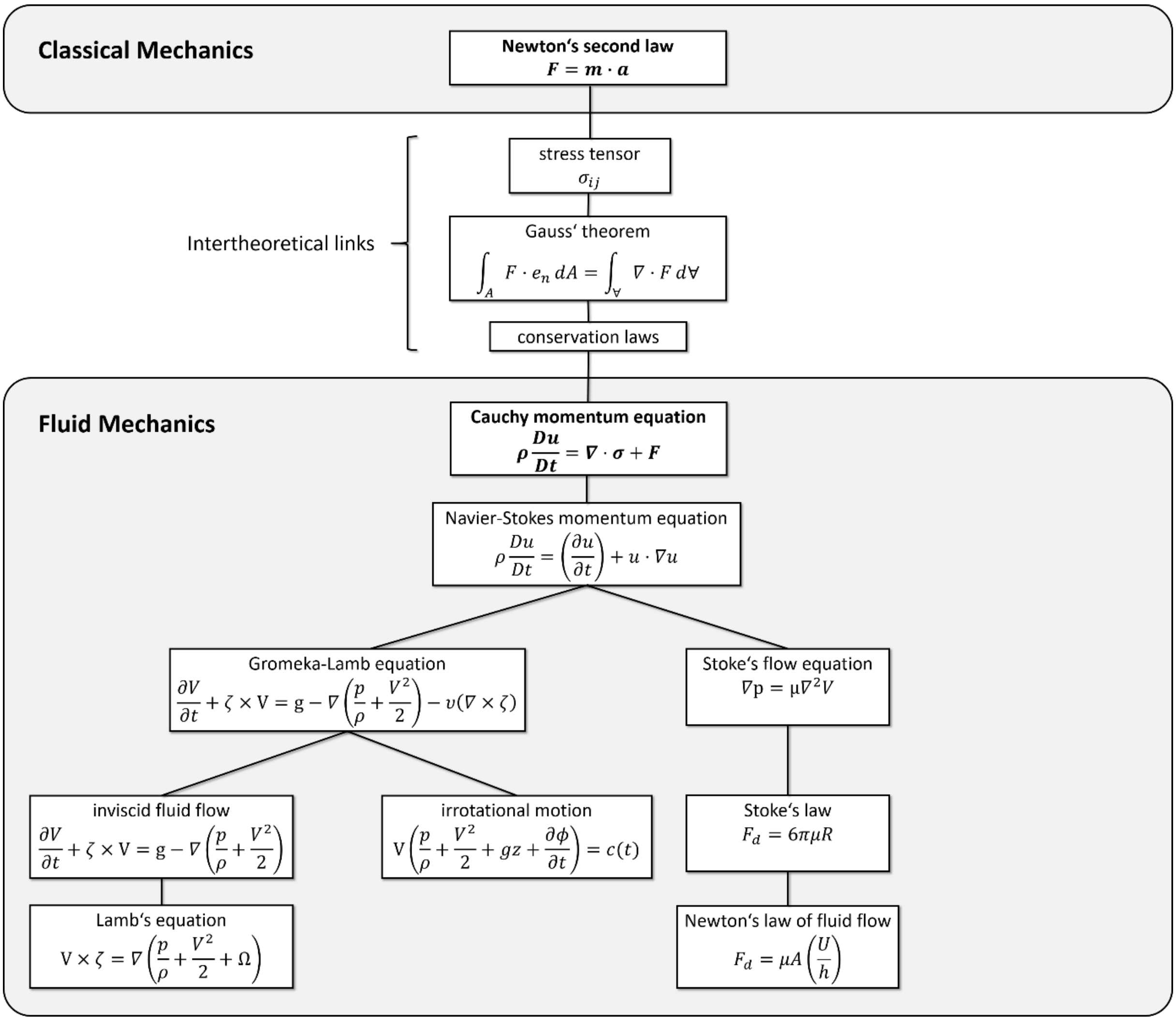

Figure 1: Theory-net depicting a subset of the theory elements from classical mechanics and fluid mechanics. The fundamental principle of classical mechanics is Newton's second law, which is connected to the fundamental principle of fluid mechanics, the Cauchy momentum equation, via a set of intertheoretical links. The Cauchy momentum equation is specialized by the Navier-Stokes equation, which then branches into the Gromeka-Lamb equation and Stoke's flow equation, etc. Each specialization narrows the scope of the above principles to a more specific subclass of phenomena.

5 The covariance based law of effect as a fundamental principle of behavior

We will now construct a tentative theory-net from several theoretical elements that have been proposed in the field of behavior analysis. Our theory-net is not intended to be final or comprehensive, but rather an attempt to demonstrate how several theoretical principles are related when pictured in the broader perspective of behavioral selection theory. Especially the lower levels of the net are far from complete and the depicted theoretical elements are best understood as illustrative examples. Our tentative theory-net for behavior analysis is depicted in Figure 2.

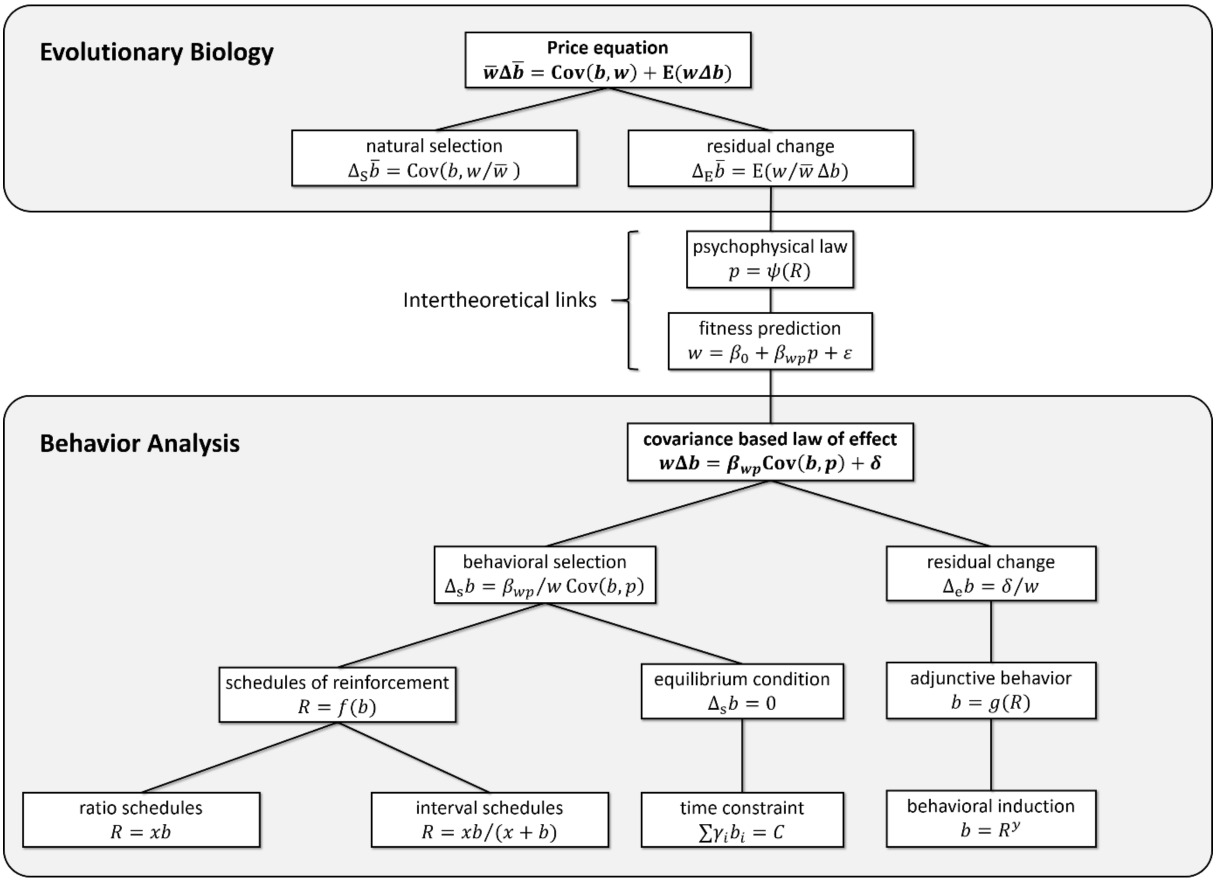

Figure 2: Tentative theory-net relating the covariance based law of effect to theoretical elements from evolutionary biology and behavior analysis.

The conceptual foundation of the MLBS is the abstract description of selection by means of the Price equation. The Price equation has been proposed as a unifying theoretical principle in the field of evolutionary biology that structures many subordinate general principles and specific laws, which we omit here (Luque, 2017; Rice, 2004; see also Luque & Baravalle, 2021 for a tentative theory-net for evolutionary biology). The MLBS expands the scope of the Price equation from the realm of evolutionary biology to behavior analysis. Within the MLBS framework, the CLOE relates to the basic Price equation in a similar way as the Cauchy momentum equation relates to Newton’s second law. While the Cauchy momentum equation is the fundamental principle by which Newton’s second law is applied to the field of fluid dynamics, the CLOE is the fundamental principle by which the Price equation is applied to the field of behavior analysis. The CLOE can therefore be regarded as the basic theoretical element of behavioral analysis. The CLOE is directly connected to the theory-net of evolutionary biology via an intertheoretical link. The intertheoretical link concerns the definition of reinforcers, which would be inherently circular if there were no external criterion for identifying reinforcers (apart from that they reinforce). Defining reinforcers as fitness predictors provides such an external criterion. Since the MLBS formalism requires fitness predictors to be linear, reinforcers with a nonlinear fitness function may sometimes yield unreliable fitness predictions. Therefore, given nonlinear fitness effects, organisms will achieve better fitness predictions (and thus have an average fitness advantage) if they transform the relevant physical dimensions of the reinforcer such that the fitness function becomes approximately linear. Such transformations have been studied extensively in the quantitative study of perception and are commonly called psychophysical functions (Gescheider, 2016). There is considerable evidence that many psychophysical functions can be approximated by a power function, the so-called “psychophysical law” (Stevens, 1957).

When understood as a basic theoretical element, the CLOE allows to structure several more specific laws. The behavioral selection part of the CLOE can be used to derive some general insights into the nature of reinforcement by analyzing the equilibrium condition of selection being equal to zero. For example, Borgstede and Eggert (2021) show how various empirical effects, like response deprivation, conditioned reinforcement or blocking, can be explained by the CLOE using the equilibrium condition. Borgstede (2021) further relates the CLOE to information theoretic concepts, thereby giving a non-essentialist explanation for the apparent connection between learning and information seeking. In order to apply the equilibrium condition, one has to impose constraining conditions that depend on the specific scenario. In simple choice scenarios, for example, we usually presume that the overall time spent at the different behaviors within a trial cannot exceed the trial length (note, however, that there are cases where relative time spent at different behaviors do not necessarily sum up to one, e.g., when an animal is moving and vocalizing simultaneously).

Another aspect of behavioral selection concerns the sources of covariance between behavior and reinforcement, i.e., the acting contingencies of reinforcers as expressed by the effective schedules of reinforcement. On a molar level, the feedback function of a schedule of reinforcement provides sufficient information to derive the covariance between behavior and reinforcement. Specifically, given a certain behavior rate, the first derivative of the molar feedback function returns the corresponding expected change in reinforcement per unit change in behavior. When approximated by a linear regression, the expected change in reinforcement corresponds to the slope of the regression line. For a known behavioral variance, this regression slope determines the covariance between behavior and reinforcement.[4]

Apart from behavioral selection, the CLOE separates non-selection sources of behavioral change. For example, there are instances where behavior occurs in the presence of reinforcement, although it has not been selected (Breland & Breland, 1961; Segal, 1972; Staddon & Simmelhag, 1971). Non-reinforced behavior occurring as a function of reinforcement is often summarized under the name of adjunctive behavior. A specific quantitative law governing adjunctive behavior has been proposed as the law of induction that relates reinforcement and behavior by a power function (Baum, 2018).

In the next section, we will use the analytical framework of the generalized matching law to explain various empirically demonstrated effects in the context of choice behavior by means of the more general theoretical principles proposed above. This exemplary application of the formal selectionist framework will demonstrate how the CLOE can be used to guide theory formulation in behavior analysis.

[4] For example, the reinforcement obtained from a ratio schedule is a linear function of behavior with a slope given by the average reinforcement per behavior $\beta_{Rb} = R/b$. Since, by definition of least squares regression, $\beta_{Rb} = \mathrm{Cov}(R, b,)/\mathrm{Var}(b)$, the covariance between behavior and reinforcement in a ratio schedule is $\mathrm{Var}(b)R/b$, i.e., the product of the slope of the feedback function and behavioral variance.
Note that the CLOE specifies behavioral change with regard to the effective fitness predictors p instead of R. Consequently, for real applications, we first have to apply the corresponding psychophysical function $\psi(R)$ before we calculate the covariance from a given feedback function (compare the example below).

6 Exemplary application: Effects of changeover delay on operant matching

The matching law describes the empirical relation between behavioral allocation and reinforcement under concurrent variable interval schedules when behavior has settled to a steady state (i.e., average behavioral allocation is stable). In its original form, the matching law states that the ratio of response rates between choice options equals the ratio of obtained reinforcement from the options (Herrnstein, 1961). However, the strict equality only holds if changing between options is associated with a certain delay (about 1.5 seconds) where responses do not produce reinforcement, a so-called *changeover delay* (CoD). When there is no CoD, individuals generally tend to undermatch (i.e., the response ratio is skewed towards equal responding when compared to the reinforcement ratio). When the CoD is very long (e.g., by introducing travelling costs between choice options like in Baum, 1982), overmatching is observed (i.e., the response ratio skewed towards the option with the higher response rate when compared to the reinforcement ratio). Following Baum (1982), we conceptualize CoD as an indicator of travel time between food patches. Consequently, “changing over” is not incorporated into the primary measures of response rate for the choice options but counted as a separate behavior (cf. Baum, 1974).

In this section, we will demonstrate how the effects of CoD on under- and overmatching can be explained in the broader context of behavioral selection theory, making explicit use of the theoretical elements proposed above. For the sake of simplicity, we limit our formal analysis to the selection part of behavior change (for an explicit treatment of adjunctive behavior by the law of induction see Baum, 2015).

6.1 Model

Let b_1 and b_2 be the number of lever presses for levers 1 and 2 in an experimental trial, with R_1 and R_2 being the corresponding obtained reinforcements (number of food pellets). The fitness function of food intake is generally a monotone increasing function with diminishing slope (i.e., the fitness gain per food pellet is higher when the animal is food deprived when compared to the same animal having access to a high amount of food). Therefore, the animal can approximately linearize the fitness function if it applies a power transformation. The corresponding psychophysical function yields a linear fitness predictor $p = R^s$ with $0 < s < 1$.

The covariance between behaviors b_i and fitness predictors p_i is derived from the molar feedback function of the underlying schedules of reinforcement. For variable interval schedules, a reasonable feedback function is given by $R = xb/(x + b)$. Figure 3a depicts the corresponding feedback functions for a VI 2 schedule. Depending on the steepness parameter of the psychophysical law, the effective feedback function with regard to the linear fitness predictor p (i.e., after the psychophysical transformation) changes accordingly (Figure 3a, dashed and dotted lines).

To predict steady state behavior, we apply the equilibrium condition for behavioral selection, thereby setting behavioral change equal to zero for each lever pressing rate b_i. If each behavior was treated separately, the equilibrium condition would imply that $\mathrm{Cov}(p, b_i) = 0$. However, because the feedback function in a variable interval schedule is monotone increasing, the resulting covariance between behavior and reinforcement would always be positive and the equilibrium condition could never be reached. Therefore, individuals would increase their lever pressing rate indefinitely. This is where behavioral constraints become relevant. Since in our experimental setup the two choice options are mutually exclusive, the sum of all responses can never exceed the maximum number of responses in a trial. In the simplest case where the complete time is divided between the two choice options, the response rate at one lever determines the response rate at the second lever. Consequently, positive selection acting on one behavior implies negative selection on the other behavior. It can be shown that, at the point of equilibrium, the amount of negative selection equals the amount of positive selection, resulting in a linear function with a slope of -1 (see Figure 3b, solid line). The equilibrium condition then becomes:[5]

[5] See Appendix A1 for a formal derivation.

$$\mathrm{Cov}(p, b_1) = \mathrm{Cov}(p, b_2) \tag{5.}$$

At the point of equilibrium, the covariances in Equation 5 are completely determined by the slopes of the feedback functions for b_1 and b_2. Therefore, Equation 5 basically states that behavior is in a steady state if and only if the marginal returns of the two choice options are equal. It has been shown that under concurrent variable interval schedules, equalizing marginal returns coincides with maximizing reinforcement and with strict matching (Baum, 1981). However, if the number of reinforcements is transformed according to a psychophysical power function, the equilibrium condition becomes skewed towards the less frequent behavior, resulting in undermatching (see left column of Figure 4).

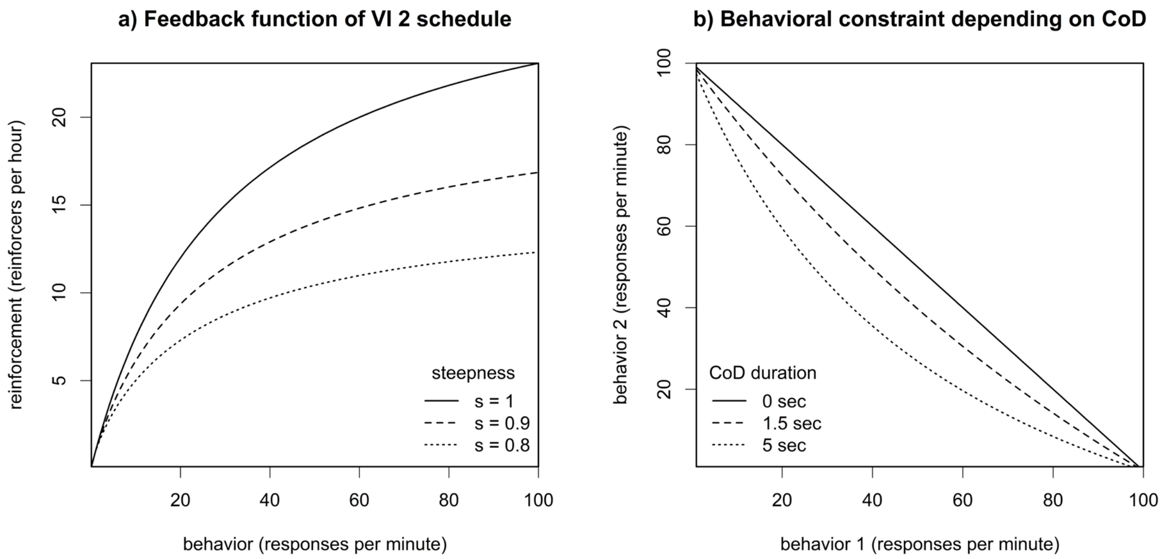

Figure 3: Effects of the parameter s (steepness of psychophysical function) on feedback (a) and duration of CoD on the behavioral constraint in a concurrent VI/VI schedule (b).

To model the effects of CoD on matching performance, we change the constraining condition to explicitly account for the duration of CoD. Hunter and Davison (1978) showed that the total time spent changing between two behavioral options is approximately proportional to the product of the numbers of responses on the corresponding options. Treating “changing over” as an additional behavior that competes for the available time, we can specify a corresponding constraint (see Figure 3b). [6]

Like before, additional responses at one option tend to decrease the number of responses at the other option. However, if there is a CoD, the slope of the function is no longer constant but depends on the value of b_1. Moreover, for higher CoD, the function becomes more convex, with a slope of -1 if both behaviors are equally frequent (i.e., $b_1 = b_2$), a slope steeper than -1 if b_1 is the less frequent behavior, and a slope flatter than -1 if b_1 is the more frequent behavior (see Figure 3b). Consequently, the amount of indirect selection now depends on the relative allocation of behavior, thereby skewing behavioral allocation towards the more frequent response. Therefore, for large durations of CoD, the model predicts that the more frequent behavior will be preferred over the less frequent behavior, resulting in overmatching for high durations of CoD. Taken together with undermatching being the default in the absence of CoD, there will be a specific value for the duration of CoD where the constraining effect and the effect of nonlinear fitness functions cancel each other out and produce strict matching CoD.

Figure 4 presents the results of a numerical simulation with a programmed reinforcer ratio of 3:1 (concurrent VI 2 / VI 6 schedule). The simulation was carried out for three different values of the steepness of the psychophysical function and three different CoD durations. The panels show the amount of behavioral selection (as calculated from the CLOE) from various starting points (i.e., different combinations of response rates) as arrows indicating direction and relative strength of selection. Stable state behavior was calculated using the corresponding equilibrium condition for each combination of parameters (see Appendices A1 and A2 for formal details).

[6] See Appendix A2.

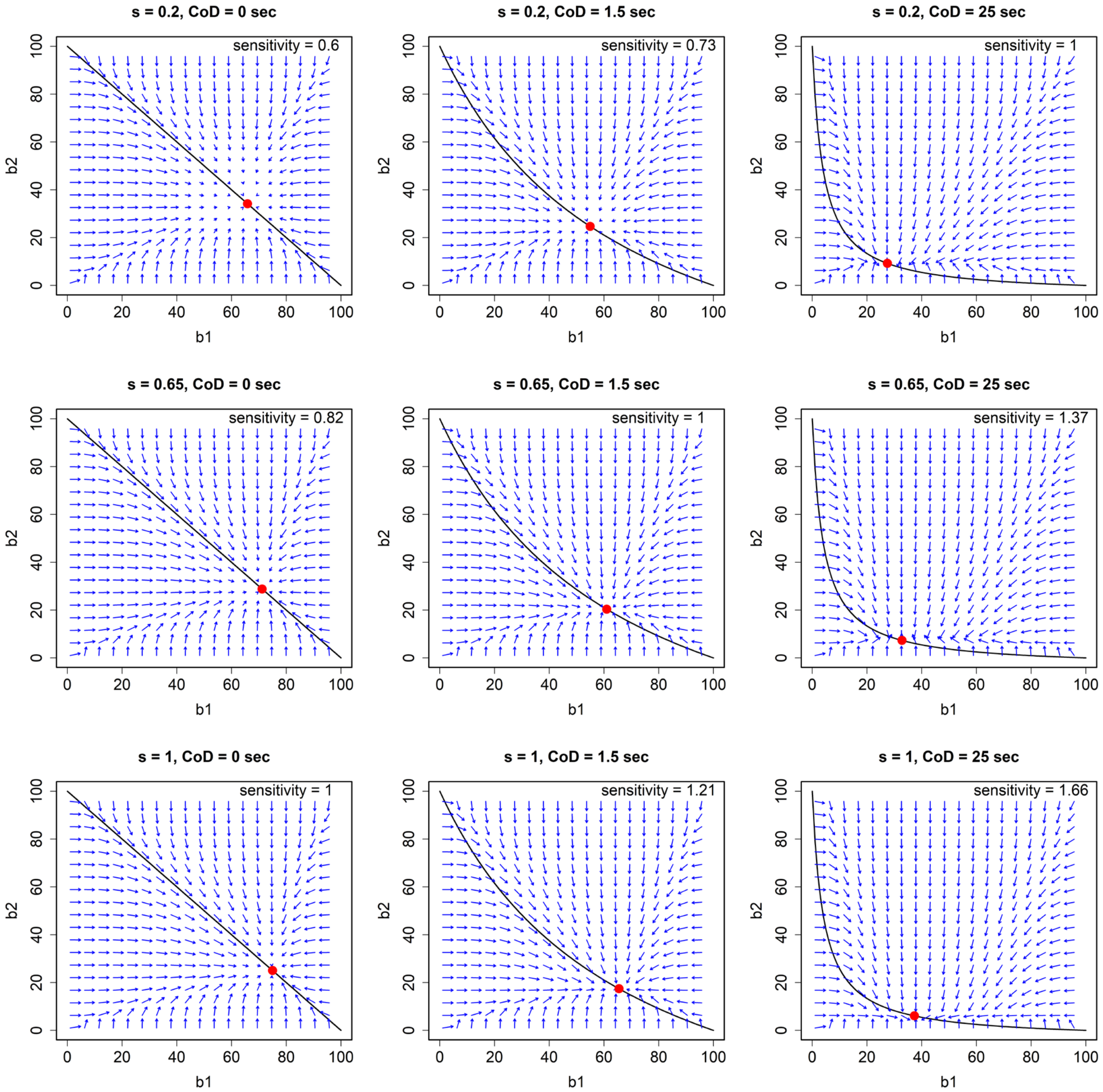

Figure 4: Vector field plots for different combinations of the parameters s (steepness of psychophysical function) and γ_2 (duration of CoD). The plots were generated using a numerical simulation of two mutually exclusive behaviors under a concurrent variable interval schedule (VI 2 / VI 6), yielding a programmed reinforcer ratio of 3:1, with $z = 0.5$ and $C = 100$ (see Appendices A1 and A2 for formal details). The red dots mark the equilibrium points derived from the CLOE (i.e., stable state behavior). The solid lines correspond to the constraining condition. The sensitivity values of the fitted matching equation for each condition reveal that strict matching is a special case where the undermatching tendency that results from the psychophysical function is counterbalanced by the overmatching tendency that results from CoD.

7 Discussion

In this article, we have argued that the field of behavior analysis would benefit from an abstract theoretical perspective that guides experimental research as well as model construction. In our view, “selection by consequences” can provide such a theoretical perspective if presented within a consistent formal selectionist framework like the MLBS. We have sketched how the covariance based law of effect (CLOE) can be understood as a fundamental theoretical element underlying all specific laws of behavior. The feasibility of our approach was demonstrated by an exemplary application of the CLOE to explain the effects of changeover delays on operant matching.

Our approach builds on the most abstract formal description of selection by means of the Price equation (Price, 1970). The Price equation applies to all selection processes, biological and non-biological. Therefore, if behavior analysis can be coherently subsumed under the principle of selection at all, any formal account of behavioral selection needs to be consistent with the Price equation. However, “recognition of covariance [...] is of no advantage for numerical calculation, but of much advantage for evolutionary reasoning and mathematical model building” (Price, 1970, p. 521). Consequently, taken on its own, the CLOE is almost empirically vacuous. Like all other fundamental theoretical principles, it is not a “capture it all” law, but rather a statement of *what the theory is about*. As such, it helps to structure theoretical and empirical thinking by pointing us to the factors that are relevant to our research. In the case of the CLOE, the basic theoretical statement is: *behavior analysis is essentially concerned with a Darwinian process*. If we accept this basic statement, the formalization in terms of the CLOE is straightforward. Applying the formal framework of the MLBS, one can then construct specific models for various scenarios by identifying the relevant sources of selection, as well as external and internal constraints on behavior (e.g., Strand et al., 2021). Moreover, a formalized selectionist approach provides a general theoretical framework to make sense of otherwise puzzling empirical findings (like the effects of CoD on operant matching). Therefore, the MLBS may bear the potential to formulate a unified account of learning and behavior in general.

Since the MLBS provides an explicit link between behavioral selection and natural selection, biological constraints of behavior naturally arise. For example, the mechanisms for the detection of fitness predictors certainly vary between different species and may range from simple temporal integrators in bacteria to complex neural processing, which some might want to call “cognitive”.[7] Depending on the specific biological mechanisms that realize adaptive behavioral responses to changing environments, learning may take very different forms. However, if we understand learning as a selection process that is functionally linked to natural selection, we will always see the more general pattern behind apparently distinct processes.

When Skinner (1950) claimed that the quest for a general theory of behavior was premature, he was certainly right with regard to the theoretical programs put forward by Hull, Tolman and others. These approaches were ambitious but ultimately failed to capture the general structure of behavioral dynamics. It was not until the 1970s, when George Price wrote his seminal papers on the nature of selection, that psychology could possibly come up with a general theory of behavior that is of “greater generality than any assemblage of facts” (Skinner, 1950, p.216). The MLBS might be considered as the type of theory that Skinner envisioned. It goes “beyond the collection of uniform relationships” (Skinner, 1950, p. 215) in such a way that all regularities of adaptive behavior are taken to be special instances of the fundamental principle of behavioral selection: the covariance based law of effect.

The experimental analysis of behavior has produced a vast amount of data and a considerable amount of stable effects that have withstood decades of empirical tests. What is needed now is a theoretical integration of these effects from an overarching theoretical perspective. We believe that behavioral selection is the key to such a unifying account of behavior.

8 Appendix: Calculating behavioral equilibria using the CLOE

8.1 A1: Equilibrium without CoD

In experimental settings with mutually exclusive behaviors, behaviors compete for the available time during an experimental trial. An appropriate constraint is given by a weighted sum over all mutually

[7] The same holds for mechanisms regulating adjunctive behavior.

exclusive behaviors in a trial, $\sum \gamma_i b_i = C$, with C being the trial duration and γ_i being the average duration of a single instance of each behavior b_i. Given such a behavioral constraint, selection on each behavior can be partitioned into a direct selection component (obtained from the feedback function of the corresponding behavior) and an indirect component (obtained from the feedback functions of the competing behaviors).

We can analyze the amount of indirect selection of b_1 via the competing behavior b_2 if we weigh the selection on b_2 by the expected change in b_2 per unit change in b_1 (i.e., the partial derivative of b_2 with respect to b_1, which is given by $\frac{\partial b_2}{\partial b_1}$). Hence, the overall selection on $b_1$is:

$$\Delta_s b_1 = \beta_{wp}\mathrm{Cov}(p, b_1) + \frac{\partial b_2}{\partial b_1}\beta_{wp}\mathrm{Cov}(p, b_2) \tag{S1}$$

In the absence of CoD, at the point of equilibrium, we would expect each increase in response rate at b_1 to result in an equal decrease in response rate at b_2. Therefore, $\frac{\partial b_2}{\partial b_1}$ would be constant with a value of -1, resulting in the following equilibrium condition:

$$\mathrm{Cov}(p, b_1) = \mathrm{Cov}(p, b_2) \tag{S2}$$

8.2 A2: Equilibrium with CoD

Like above, we start with the general time constraint for mutually exclusive behaviors, $\sum \gamma_i b_i = C$. However, we need to account for the additional time spent changing between the options. Let $\gamma_1$be the duration of a single response and γ_2 the time needed to change from option 1 to option 2. Adapting the findings from Hunter and Davison (1978), we can express the total number of changeovers between options as zb_1b_2, with z being a parameter expressing the general tendency to change between options. Given that the animal does not engage in any other behaviors during the experiment, the total duration of an experimental trial can now be partitioned into one part describing the time spent responding, $\gamma_1(b_1 + b_2)$, and the time spent changing from one response option to the other, $\gamma_2 zb_1b_2$. Hence, the constraining condition becomes:

$$\gamma_1(b_1 + b_2) + \gamma_2 z b_1 b_2 = C \tag{S3}$$

The rate of change in b_2 per unit change in b_1 due to this constraint can be obtained by solving S3 for b_2 and calculating the first derivative of b_2 with respect to b_1, which yields:

$$\frac{\partial b_2}{\partial b_1} = -\frac{\gamma_1^2 + \gamma_2 z C}{(\gamma_1 + \gamma_2 z b_1)^2} \tag{S4}$$

The equilibrium condition thus becomes:

$$\mathrm{Cov}(p, b_1) = \frac{\gamma_1^2 + \gamma_2 z C}{(\gamma_1 + \gamma_2 z b_1)^2} \mathrm{Cov}(p, b_2) \tag{S5}$$

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10 Conflicts of interests

The authors declare no competing interests.

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