ON THE CURRENT STATUS OF THE EVOLUTIONARY THEORY OF BEHAVIOR DYNAMICS

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The evolutionary theory of behavior dynamics is a complexity theory that instantiates the Darwinian principles of selection, reproduction, and mutation in a genetic algorithm. The algorithm is used to animate artificial organisms that behave continuously in time and can be placed in any experimental environment. The present paper is an update on the status of the theory. It includes a summary of the evidence supporting the theory, a list of the theory's untested predictions, and a discussion of how the algorithmic operations of the theory may correspond to material reality. Based on the evidence reviewed here, the evolutionary theory appears to be a strong candidate for a comprehensive theory of adaptive behavior.

Key words: adaptive behavior, behavior dynamics, complexity theory, evolutionary dynamics, neural Darwinism, selection by consequences

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At least two approaches to mathematical theorizing can be identified in modern behavior analysis. One consists of building mathematical models from detailed empirical observations for the purpose of reproducing those observations algorithmically (McDowell, 2017). Because specific observations are essentially built into these models, their broader applicability is usually limited. An example of this type of theory is Staddon's (2016) response-strengthening, winner-take-all, model of responding on concurrent ratio schedules (McDowell, 2017). This model produces a near-exclusive preference for the alternative with the smaller ratio, which is what is typically observed on these schedules. An inevitable consequence of this approach to mathematical theorizing is that many models are developed to accommodate the many specific phenomena of interest. John Staddon (2001, 2016) is a prominent proponent of this many-models approach, and refers to the models as simple sketches that capture various aspects of learning. According to Staddon (2016), "[b]iology is not like physics. There is no grand 'standard model' that underlies all…historical principles (p. 202)."

A second approach to mathematical theorizing entails building theories on the basis of first, or prior, principles (McDowell, 2017). From the outset, this approach is intended to produce theories that are applicable to a range of phenomena. Reflex reserve theory (e.g., Catania, 2005; Killeen, 1988) is an example of a prior principle theory. The reflex reserve operates according to rules that are specified *a priori*, without reference to empirical observations. Once a prior-principle theory is developed, it is typically tested in various experimental environments to determine how broadly it may be applied. Finding that a theory accounts for a specific phenomenon or set of observations constitutes evidence supporting the theory. In contrast to the many-models approach, this second approach to mathematical theorizing implies that there may in fact be a single model or theory that can account for most, or perhaps all, adaptive behavior. Evidently, a crucial feature of the single-theory approach is the effort to show that a candidate theory accounts for a wide range of phenomena. Prior-principle theories may be compared to each other by comparing the ranges of phenomena to which they apply. Theories that apply to wider ranges of phenomena are better theories.

The topic of the present paper is the evolutionary theory of behavior dynamics (ETBD), which is a prior-principle theory. The prior principle it instantiates is the idea that behavior evolves in ontogenetic time under the selection pressure of consequences from the environment. Five years ago, McDowell (2013b) discussed some of the evidence

supporting this theory in a lengthy paper that was written for a general audience. Since then, new supporting evidence has been reported, and there have been advances in the material interpretation of the theory. In addition, predictions of the theory were not discussed in the earlier paper. Consequently, the present paper is an update and extension of the earlier paper, and also serves as a guide to the current literature on the evolutionary theory. It is written specifically for a behavior-analytic audience, and consists of accessible summaries of evidence and predictions rather than detailed descriptions, which were provided in the original articles. The objective of the present paper is to answer the following four questions in an accessible way. What is the evolutionary theory? What is the evidence supporting it? What are its predictions? How is it related to material reality?

The Evolutionary Theory of Behavior Dynamics

The evolutionary theory is a complexity theory (McDowell, 2013c; McDowell & Popa, 2009), which means that it is stated in the form of simple, low-level rules, the joint operation of which generates high-level, emergent outcomes that can be compared to data. In the ETBD, a population of potential behaviors evolves under the selection pressure of consequences from the environment. The behaviors in the population are referred to as potential because they may or may not be emitted. Each behavior is identified by a decimal (i.e., base-10) integer, which is referred to as the behavior's phenotype, and by the binary representation of that integer, which is referred to as the behavior's genotype. The top panel of Figure 1 shows a population of potential behaviors as a frequency distribution of integer phenotypes drawn at random from the range, 0 through 1023. The theory consists of three low-level rules that implement the Darwinian processes of selection, reproduction, and mutation.

Selection

At each tick of time, a behavior chosen at random from the population is emitted. Following this emission, a new generation of potential behaviors is built by choosing pairs of parent behaviors from the current population and recombining their genotypes to create child behaviors. The method of choosing parents depends on whether the emitted behavior produced a benefit (e.g., a reinforcer) or not. If the just-emitted behavior did not produce a benefit, then parent behaviors are chosen at random from the population. However, if the just-emitted behavior did produce a benefit, then parents are chosen on the basis of their fitness. The fitness-based choice of parents constitutes the theory's selection rule.

The fitness of a behavior is defined as the absolute value of the arithmetic difference between the behavior's integer phenotype and the integer phenotype of the behavior that just produced a benefit. For example, if the integer phenotype of the behavior that produced a benefit is 500, then the fitness of a behavior in the population with a phenotype of 614 is $|500\text{-}614| = 114$, the fitness of a behavior in the population with a phenotype of 490 is $|500\text{-}490| = 10$, and so on. Evidently, the smaller the arithmetic difference, the more similar the behavior is to the just-emitted behavior, and hence the greater is its fitness. All behaviors in the population are assigned fitness values when the just-emitted behavior produces a benefit. A fitness density function (FDF) is then used to choose parents for mating. The FDF is a probability density function that is defined solely by its mean (McDowell, 2004). It expresses probability density as a function of fitness, such that larger probability densities are associated with fitter behaviors (McDowell, 2004). This means that random sampling from the FDF favors obtaining relatively fit parent behaviors for mating. A fitness value is drawn at random from the FDF and the population of potential behaviors is searched for a behavior with that fitness. If one is found, then it becomes a parent. If one is not found, then another fitness value is drawn, and so on, until all parents have been chosen.

The result of the selection rule is that fitter behaviors are more likely to become parents than are less-fit behaviors. Because fitter parent behaviors tend to create fitter child behaviors, selection causes the new population of potential behaviors to cluster near the phenotype that just produced a benefit. This makes that phenotype, and phenotypes similar to it,

Population
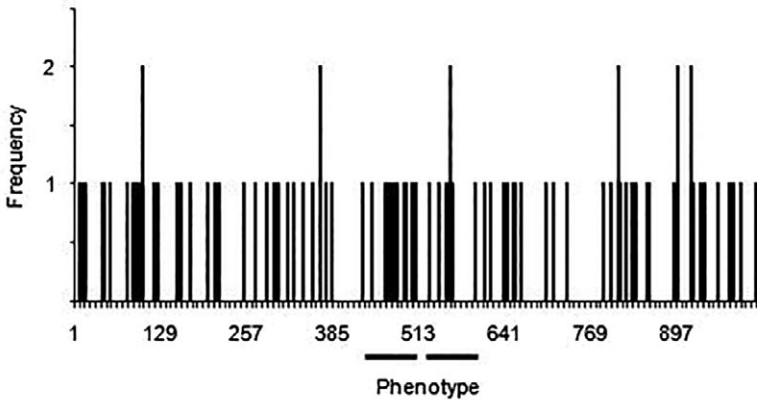
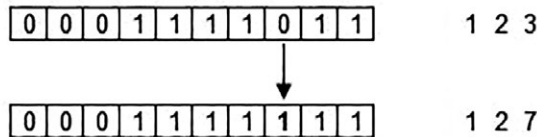## Bit string recombination
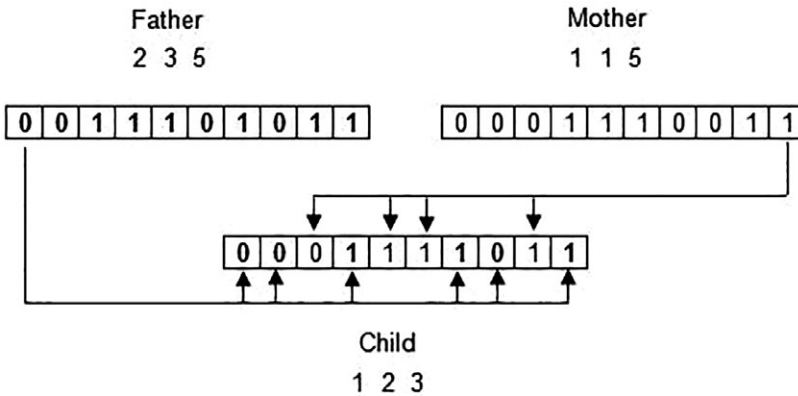
Mutation

Fig. 1. (Top). A frequency distribution of 100 potential behaviors chosen at random from the integer phenotype range, 0 through 1023. The horizontal bars beneath the *x*-axis identify phenotype ranges that might represent two response classes, for example, left and right lever presses. (Center). Father and mother genotypes recombine to produce a child genotype by contributing some of their bits to the child's bit string. (Bottom). A behavior is subjected to mutation by flipping a random bit in its bit string from 1 to 0 or 0 to 1. Reprinted from "Toward a Mechanics of Adaptive Behavior: Evolutionary Dynamics and Matching Theory Statics," by J. J McDowell and A. Popa, 2010, *Journal of the Experimental Analysis of Behavior*, *94*, p. 259. Copyright 2010 by Wiley.

more likely to be emitted in the next tick of time. The degree of clustering depends on the mean of the FDF. Small FDF means, which

permit only very fit behaviors to be chosen as parents, cause a greater degree of clustering than do large FDF means, which permit a

greater number of less fit behaviors to be chosen as parents. The FDF mean has been interpreted as a cost/benefit parameter that can be understood as representing the magnitude of the reinforcer and/or the cost of the target responding (McDowell, 2004; McDowell, Caron, Kulubekova, & Berg, 2008).

Reproduction

Regardless of how parent behaviors are chosen, they reproduce by contributing bits from their genotypes to build a child genotype, as illustrated in the center panel of Figure 1. In this example, each bit in the child's bit string comes from the same location in either the father's bit string or the mother's bit string. The decimal-integer phenotypes that correspond to the binary strings are also shown in the panel. As a refresher, note that the father's integer phenotype may be obtained from its genotype by calculating the sum, $0(2^9) + 0(2^8) + 1$ $(2^7) + 1(2^6) + 1(2^5) + 0(2^4) + 1(2^3) + 0(2^2) + 1$ $(2^1) + 1(2^0)$, where the factor multiplying each power of 2 is the 0 or 1 in the father's bit string. The sum of this expression is 235.

Mutation

Once a new population of potential behaviors is built, it is subjected to a small amount of mutation. This is accomplished by drawing a percentage of behaviors from the population and subjecting them to mutation. This percentage is referred to as the mutation rate. Mutation is applied to a behavior's bit string by flipping a randomly chosen bit in the string from 0 to 1 or 1 to 0, as illustrated in the bottom panel of Figure 1.

Discussion of the Theory

The material presented above describes the theory in its entirety. It is simple enough to be explained using illustrations drawn on the back of an envelope, or on a napkin at the local coffee shop (cf. Cox & Forshaw's, 2012, discussion of quantum theory). The algorithmic operation of the theory generates Darwinian variation and selection of behavior. Variation is caused by the recombination of randomly chosen parents, and by mutation. Selection is caused by the recombination of parents chosen on the basis of their fitness.

The flowchart in Figure 2 illustrates the overall operation of the theory. A random behavior is emitted from the initial population (top); if it produces a benefit, then the left path is followed, otherwise the right path is followed. The shaded rectangles represent the three rules of the ETBD. After a new population is built (bottom), a random behavior is emitted from that population, and the cycle repeats. This produces a continuous stream of behavior that may be recorded and studied just as if it were the behavior of a live organism.

Evidently, the ETBD is conceptually simple. Remarkably, it is also parametrically simple. Only two parameters materially affect the outcome of the operation of the theory's rules. These are the mean of the fitness density function, and the mutation rate (McDowell, 2013b, pp. 738ff). The former regulates the strength of selection, and the latter regulates the degree of variation.

As is the case for all complexity theories, emergent outcomes cannot be deduced by inspecting or mathematically manipulating the theory's rules. Instead, the rules must be made to operate repeatedly, usually by means of a computer program, to generate emergent outcomes that can be compared to data. In the case of the evolutionary theory, the rules are used to animate an artificial organism (AO) that can be placed in any desired experimental environment.

Evidence Supporting the Evolutionary Theory

Emergent equilibria and dynamic phenomena generated by the evolutionary theory that are consistent with the behavior of live organisms are summarized in this section. These results were obtained using implementations of the theory as they were originally stated for single (McDowell, 2004) and concurrent schedules (McDowell et al., 2008), and as they were described in the previous section. No special parameter values or tunings were used, and no material modifications were made to the theory to obtain any of these results.

Emergent Equilibria

Quantitative and molar phenomena.
Single interval schedules. AOs animated by the ETBD exhibit behavior on single random
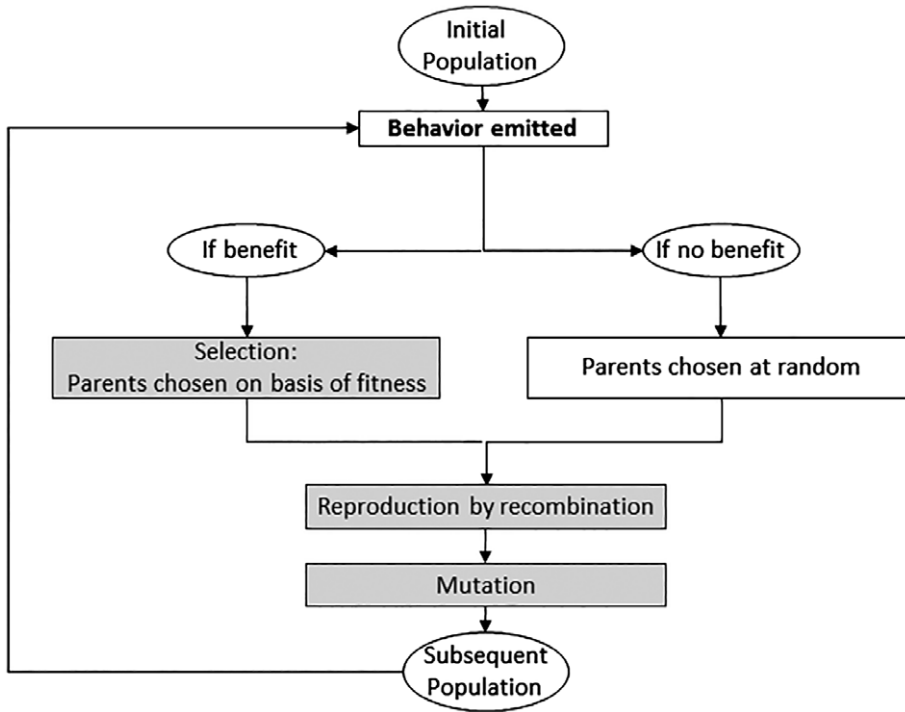
Fig. 2.   Flowchart illustrating the operation of the evolutionary theory. If an emitted behavior produces a benefit, then the left pathway is followed, otherwise the right pathway is followed. The shaded rectangles represent the three rules of the evolutionary theory. Reprinted from "A Quantitative Evolutionary Theory of Adaptive Behavior Dynamics," by J. J McDowell, 2013, *Psychological Review, 120,* p. 735. Copyright 2013 by the American Psychological Association.

interval (RI) schedules of reinforcement that conforms at equilibrium to the generalized hyperbola (McDowell, 1986),

$$B = \frac{br^a}{r^a + c}, \qquad (1)$$

where *B* represents response rate, *r* represents reinforcement rate, and *a, b,* and *c* are parameters of the equation (McDowell, 2004; McDowell & Calvin, 2015; McDowell & Caron, 2007). It is well known that the behavior of live organisms working on single variable-interval (VI) schedules conforms at equilibrium to this equation (de Villiers, 1977; evidence when $a \neq 1$ is reviewed by McDowell, 2013a, pp. 1010ff, and includes Dallery, McDowell, & Lancaster, 2000; data from McDowell & Dallery, 1999, reanalyzed by McDowell, 2005; and Soto, McDowell, & Dallery, 2005).

Concurrent interval schedules. AOs animated by the theory exhibit behavior on concurrent RI RI schedules that conforms at equilibrium to the power-function matching equation (Baum, 1979; Wearden & Burgess, 1982),

$$\frac{B_1}{B_2} = b\left(\frac{r_1}{r_2}\right)^a, \qquad (2)$$

where the numerical subscripts refer to the two response alternatives, and *a* and *b* are parameters of the equation (McDowell et al., 2008). The conformance of human and animal behavior to this equation is also well known (Baum, 1979; McDowell, 2013a; Wearden & Burgess, 1982). At moderate mutation rates, the exponent, *a*, for the AOs varies around 0.8 (McDowell et al., 2008; McDowell and Popa, 2010; Popa and McDowell, 2016). Again, it is well-known that the exponent for live organisms varies around this value (Baum, 1979; McDowell, 2013a; Wearden & Burgess, 1982).

AOs animated by the theory exhibit absolute response rates in each component of a

concurrent RI RI schedule that at equilibrium conform to

$$B_1 = \frac{b_1 r_1^a}{r_1^a + \frac{c_1}{c_2} r_2^a + c_1}, \qquad (3)$$

and

$$B_2 = \frac{b_2 r_2^a}{\frac{c_2}{c_1} r_1^a + r_2^a + c_2}, \qquad (4)$$

where the numerical subscripts refer to the two alternatives of the schedule, and a, the bs, and the cs are parameters of the equations (McDowell, 2013b; McDowell & Calvin, 2015; McDowell & Popa, 2010). Note that Equations 3 and 4 are functions of two variables, r_1 and r_2, which means that they describe surfaces in three-dimensional coordinate systems. The quotient of Equations 3 and 4 is Equation 2, where b in that equation equals $(b_1 c_2)/(b_2 c_1)$. Equations 3 and 4 are versions of McDowell's (2013a) Equations $7'$ and $8'$; he reviewed in detail the empirical evidence bearing on those equations (pp. 1013ff, including data from Dallery, McDowell, & Soto, 2004, reanalyzed by McDowell, 2005; Dallery, Soto, & McDowell, 2005; McDowell & Caron, 2010a, 2010b) and concluded that they accurately described the behavior of live organisms working on concurrent interval schedules.

AOs animated by the theory exhibit behavior on concurrent RI RI schedules, where both rate and magnitude of reinforcement are varied, that conforms at equilibrium to the bivariate, or concatenated, matching equation (Baum & Rachlin, 1969; Davison & McCarthy, 1988; Killeen, 1972; Rachlin, 1971),

$$\frac{B_1}{B_2} = b \left(\frac{r_1}{r_2} \right)^{a_r} \left(\frac{m_1}{m_2} \right)^{a_m}, \qquad (5)$$

where m represents magnitude, and b, a_r, and a_m are parameters of the equation (McDowell, Popa, & Calvin, 2012). Cording, McLean, and Grace (2011) reviewed in detail the evidence bearing on this equation and concluded that it accurately describes behavior in experiments with live organisms. At moderate mutation rates, the exponent on the reinforcement rate ratio, a_r, for the AOs varies around 0.8 and the exponent on the magnitude ratio, a_m, varies around 0.6 (McDowell, Popa, & Calvin, 2012).

These values are also observed in experiments with live organisms (Baum, 1979; Cording et al., 2011; Wearden & Burgess, 1982).

Discussion of interval schedules. Fits of Equations 1-5 to data generated by the AOs consistently leave little residual variance, and no residual error when all parameters in the equations are allowed to vary freely (McDowell, 2013b). It may be worth emphasizing that the quantitative relations asserted by Equations 1 were not, nor could they have been, built into the low-level rules of the theory. They also cannot be deduced analytically from those rules. Instead, the quantitative relations are emergent outcomes caused by the algorithmic operation of the theory's rules. In other words, they are steady states generated by the theory's evolutionary dynamics.

Concurrent ratio schedules. AOs animated by the theory exhibit behavior on concurrent random ratio random ratio (RR) schedules with unequal ratios in the components that shows exclusive preference for the smaller ratio. On concurrent RR RR schedules with equal ratios in the components, AOs animated by the theory show exclusive preference for one or the other alternative, provided the equal ratios are not too large (McDowell & Klapes, 2018). These outcomes are also observed in experiments with live organisms (evidence reviewed by McDowell & Klapes, 2018, including Green, Rachlin, & Hanson, 1983; Herrnstein, 1958, 1970; Herrnstein & Loveland, 1975; Horner & Staddon, 1987; MacDonall, 1988; Shah, Bradshaw, & Szabadi, 1989).

Discussion of quantitative and molar phenomena Note that the dynamics of the evolutionary theory produce all of the equilibrium outcomes that have been observed in experiments with live organisms working on concurrent interval schedules and concurrent ratio schedules with unequal or equal ratios in the components. Researchers have typically offered different explanations for the different equilibrium outcomes on these schedules, often referring to them as matching, maximizing, and reward-following (Horner & Staddon, 1987; Staddon, 2016, pp. 247ff). Different explanations appear to be required because, for example, matching cannot explain either outcome on concurrent ratio schedules, and maximizing cannot explain the outcome on concurrent ratio schedules with equal ratios in the components (McDowell & Klapes, 2018).

As the evidence summarized here indicates, however, different explanations of the three outcomes are not required, for one will suffice. All are produced by the dynamics of the evolutionary theory (McDowell & Klapes, 2018).

Additional equilibrium phenomena.

Single interval schedules. In fits of Equation 1 to the steady-state behavior of AOs working on single RI schedules, the asymptote, b, of the equation varies directly with reinforcer magnitude, as represented by the FDF mean (McDowell, 2004; McDowell & Caron, 2007). This relationship between the asymptote of the equation and reinforcer magnitude is also observed in experiments with live organisms (Dallery & Soto, 2004; Dallery et al., 2004; McDowell, 2013a).

Concurrent interval schedules. AOs working on concurrent RI RI schedules show orderly biased responding when reinforcer magnitude is varied in one component (McDowell et al., 2008). They also show changeover rates that are lowest when the reinforcement rates in the two alternatives differ substantially, that are highest when the reinforcement rates in the two components are equal, and that vary approximately as a quadratic when plotted against reinforcement proportions obtained in one of the components (McDowell et al., 2008). In addition, changeover rates vary inversely with reinforcer magnitude (Popa & McDowell, 2016). The behavior of AOs on these schedules is also less variable when reinforcer magnitude and/or reinforcement rate is large, than when one or both of these quantities is/are small (Popa & McDowell, 2016). All of these phenomena have been observed in experiments with live organisms. The literature on biased responding was reviewed by McDowell et al. (2008), and includes Baum (1974b, 1979), McDowell (1989), and Wearden and Burgess (1982). The literature on CO phenomena was reviewed by McDowell et al. (2008) and by Popa and McDowell (2016), and includes Alsop and Elliffe (1988), Baum (1974a), Brownstein and Pliskoff (1968), and Herrnstein (1961). The literature on behavioral variability was reviewed by Popa and McDowell (2016), and includes Doughty, Giorno, and Miller (2013); Lee, Sturmey, and Fields (2007); Neuringer, Kornell, and Olufs (2001); and Stahlman and Blaisdell, (2011).

Concurrent ratio schedules. AOs working on concurrent RR RR schedules with equal ratios in the components show steady-state preference that changes from exclusive to partial as a continuous function of the equal ratio value (McDowell & Klapes, 2018). This continuity is also observed in experiments with live organisms (evidence reviewed by McDowell & Klapes, 2018, including Horner & Staddon, 1987; Staddon, 2016).

Emergent Dynamic Phenomena

Behavior in rapidly changing environments. In concurrent RI RI schedules that arrange rapidly changing reinforcement rate ratios in single sessions (e.g., Davison & Baum, 2000), AOs animated by the theory show orderly cumulative changes in preference at small time scales, and orderly increases in the exponent of power function matching (Eq. 2) as reinforcers are obtained. The exponent increases from near zero (indicating no preference) at the start of a new within-session schedule to its equilibrium value after just a few reinforcers, and it reaches a higher value for larger overall reinforcement rates (Kulubekova & McDowell, 2013). Davison and Baum (2000) observed all of these phenomena in the behavior of their pigeons. The AOs also show detailed, reinforcer-by-reinforcer development of, and reversals in, preference that are indistinguishable from those Davison and Baum reported for their pigeons (Kulubekova & McDowell, 2013). Finally, these dynamic phenomena are more pronounced at higher reinforcement rates for both the AOs and the pigeons. The figures in Kulubekova and McDowell's (2013) article, which compare the behavior of AOs to the behavior of Davison and Baum's pigeons, provide striking evidence for the agreement between theory and data with respect to these detailed, small time scale, dynamic phenomena.

Concurrent ratio schedule changes. McDowell and Klapes (2018) showed that when the ratio value of a concurrent RR RR schedule with equal ratios in the components is changed, the behavior of AOs animated by the theory adjusts rapidly to the new schedule value, even if the change in the ratio value is large. Horner and Staddon (1987) observed this rapid adjustment of preference in experiments with pigeons.

Additional dynamic phenomena. The acquisition of instrumental responding by AOs animated by the theory is rapid; after just a few reinforcers (sometimes only one) instrumental responding increases quickly to a relatively high rate (McDowell, 2013b). McDowell (2013b) cited findings reported by Skinner (1938) that document this feature of acquisition in the behavior of live organisms.

The extinction of an AO's instrumental responding is more gradual, and is usually irregular. In addition, it sometimes shows ringing, which refers to repeated bursts of responding followed by periods of relatively low response rate, as if the AO were periodically testing the operandum to determine whether it might be working again (McDowell, 2013b). McDowell (2013b) cited findings reported by Skinner (1938) that document these properties and features of extinction in the behavior of live organisms.

Cumulative records of AOs' responding on single RI schedules show roughly constant instantaneous slopes with occasional irregularities, such as brief periods of pausing, response acceleration, and response deceleration (McDowell, 2013b). These are well-known features of the behavior of live organisms working on VI schedules (McDowell, 2013b; Skinner, 1938). In addition, interresponse time distributions for AOs working on RI schedules are comparable to those obtained from live organisms when the cost of responding is low (evidence reviewed by McDowell, 2013b, and by Kulubekova & McDowell, 2008, including Bennett, Hughes, & Pitts, 2007; Shull & Grimes, 2003).

Fitting the theory to data. Li, Hautus, and Elliffe (2018) described a novel method of fitting computational theories to data from individual organisms. Li, Elliffe, and Hautus (in press) used a version of this method to fit the ETBD to data from Davison and Baum's (2000) experiment (just described), in which rapidly changing within-session reinforcer ratios were arranged. They concluded that the theory accounted relatively well for the distribution of responding between operanda in individual birds. Important questions have been raised about this method and the interpretation of its results (e.g., Li, Elliffe, and Hautus, in press; McDowell & Klapes, 2018), but if these questions can be answered satisfactorily, then Li et al.'s method will be a useful addition to the tools used to evaluate computational theories.

Second-Stage Predictions of the Evolutionary Theory

The outcomes and phenomena summarized in the previous section are, in a sense, predictions of the evolutionary theory. But they are predictions of empirical results that in many cases are already well known. A second-stage prediction refers to a prediction for which adequate data to test the prediction do not exist or, in a few cases, where such data do exist but have not been analyzed in a way that permits an effective test of the prediction (McDowell & Calvin, 2015; von Neumann & Morgenstern, 1944/2007, pp. 7-8).

Single-Alternative Interval Schedules

When Equation 1 is fitted to data from AOs animated by the theory, the parameters b and c covary positively, and approximately linearly. Both parameters increase as the cost/benefit of responding becomes more favorable (McDowell, 2004, p. 312). McDowell (2004, pp. 312ff) reported evidence consistent with this prediction by reanalyzing data from Dallery et al.'s (2000) experiment with rats that pressed levers for a range of concentrations of sucrose in water. However, no new experiments have been conducted to test this prediction.

Bivariate Matching

In experiments that vary both reinforcement rate and reinforcer magnitude in concurrent schedules, AOs' rate of changeovers as a function of the reinforcement rate ratio and reinforcer magnitude ratio is evidently described by an elliptic paraboloid,

$$CO\ rate = Ax^2 + By^2, \qquad (6)$$

where CO = changeover, x and y are the logs of the reinforcement rate and reinforcer magnitude ratios, and A and B are parameters of the equation (McDowell et al., 2012). An elliptic paraboloid is a quadric surface with elliptic horizontal cross sections and parabolic vertical cross sections. This equation was not built into the rules of the theory, nor could it have been,

and it is not a mathematical consequence of any rule or combination of rules. In other words, the equation cannot be obtained by examining and mathematically manipulating the rules of the theory. Instead, Equation 6 is an emergent property of the theory's dynamics. It was obtained by inspecting the CO rates from the AOs and selecting a likely candidate surface to describe them.

McDowell et al. (2012) found that fits of Equation 6 to data from their AOs showed that COs become more frequent as the reinforcement rates in the two components become more similar, and/or as the reinforcer magnitudes become more similar. In addition, the CO rate increases more rapidly when reinforcement rates become more similar than when reinforcer magnitudes became more similar. In other words, just as response allocation is less sensitive to the reinforcer magnitude ratio than to the reinforcement rate ratio, CO rate is less sensitive to differences in reinforcer magnitude than to differences in reinforcement rate. McDowell et al. also found that the decreased sensitivity of CO rates to differences in reinforcer magnitude relative to differences in reinforcement rate is more pronounced when large ranges of RI values and large ranges of reinforcer magnitudes are arranged. These predictions regarding the CO rate in bivariate matching experiments have not been tested.

A Critical Experiment Comparing Matching Theory and the ETBD

Consider an experiment that arranges a set of five concurrent schedules, where reinforcer magnitude varies in one component, but remains unchanged in the other. In fits of Equations 3 to the behavior of AOs animated by the theory, where the bs are constrained to remain constant across all five schedules, or where they are constrained to be equal in the two components of each schedule (which are requirements of two versions of matching theory, McDowell, 2013a), large percentages of variance are accounted for, but statistically significant trends with moderate effect sizes are observed in the residuals (McDowell & Calvin, 2015). In other words, according to the ETBD, the matching theory versions of these equations are false. In a reanalysis of data from Dallery et al. (2005), who conducted this

experiment with human participants, McDowell, Calvin, Hackett, and Klapes (2017) found exactly this result, namely that fits of Equations 3 accounted for large percentages of variance, but left systematic trends with moderate effect sizes in the residuals.

In the concurrent-schedule experiment just described, the evolutionary theory also predicts how the parameters of Equations 3 vary as a function of reinforcer magnitude (McDowell & Calvin, 2015, Fig. 5). This prediction has not been tested, and existing data do not permit reliable estimates of the parameters to be obtained because the absolute response rate domains of the equations were not adequately sampled. McDowell and Calvin (2015) described several properties of experimental designs that must be in place in order to test this prediction effectively.

Concurrent Ratio Schedules with Unequal Ratios in the Components

According to the evolutionary theory, on concurrent ratio schedules with unequal ratios in the components, partial rather than exclusive preference will be observed for ratio pairs under two conditions (McDowell & Klapes, 2018). One condition is when both ratios are relatively large, while the difference between the ratios also remains large. In other words, even though there is a large difference between the ratios, preference will be partial. The second condition is when both ratios are relatively small, even though the smaller ratio would otherwise produce exclusive preference, for example, if it were paired with a larger ratio. McDowell and Klapes (2018) noted that there is scattered evidence consistent with these predictions in the literature, but the predictions have not been tested systematically.

Material Interpretations of the Evolutionary Theory

The algorithmic operation of the ETBD may appear to be disconnected from material reality (e.g., Shahan, 2017). Behaviors are not integers with corresponding binary bit strings that recombine, undergo mutation, and so on. Given that the theory can account for a range of adaptive behavior in the real world, it seems that the workings of the theory must be

connected to material reality in some way. This has been discussed in many of the papers published on the theory, but it was most thoroughly treated by McDowell (2013d), and most recently discussed by McDowell (2017, pp. 136ff) and McDowell and Klapes (2018). McDowell's (2017) treatment deals with functional theories in general, of which the ETBD is an instance.

Most of the discussion about material interpretations of the theory centers around two possibilities. The first is that actual neural mechanisms may be found that correspond to the elements of the theory. According to this interpretation, the algorithmic operation of the theory is materially equivalent to the operation of the brain. The second interpretation is philosophically more complicated. It asserts that there is no direct correspondence between the algorithmic operation of the theory and the physical operation of the brain. Instead, this second interpretation asserts that the two sets of operations, both of which are themselves material, are different ways of producing the same result. In this case the operation of the theory may be said to be computationally, or functionally, equivalent to the operation of the brain.

Material Equivalence

Evidently, the most direct way to interpret the connection between the ETBD and the material world is to suppose that there are actual brain mechanisms that correspond to the elements and operations of the theory. According to Staddon and Bueno (1991), "…if our…theory really works well as an explanation for behavioral data, it must reflect something true about the neural processes that underlie those data" (p. 6).

The idea that the brain might operate as a selectionist, or evolutionary, system has been discussed since at least the 1950s, and several authors have presented extensive theories of selectionist brain functioning (Edelman, 1978, 1987; Hayek, 1952a, 1952b; Pringle, 1951). McDowell (2010) discussed Edelman's (1987) theory of neural Darwinism in detail, and considered how it might constitute a material implementation of the ETBD in brain functioning. Other authors have discussed how certain elements of the evolutionary theory might be instantiated in the brain. For example,

Popa and McDowell (2016) suggested that mutation might correspond to spontaneous fluctuations in the brain's default mode network. Fernando, Karishma, and Szathmáry (2008) described how elements of neural-circuit replication and recombination might occur in three-dimensional volumes of brain tissue.

Needless to say, it is not possible at the present time to conclude that the brain operates according to evolutionary principles. But this is an appealing idea, for organic evolution may have engineered a copy of itself in the nervous systems of living organisms to regulate their behavior during their individual lifetimes.

Functional Equivalence

According to a functional equivalence interpretation of the theory, it is taken as a given that there are no direct mappings between the algorithmic operations of the ETBD and the physical operations of the brain. However, to the extent that the two sets of operations produce the same outcomes, we may say that they are functionally equivalent. Put another way, the two sets of operations are different ways of doing the same thing.

Richard Feynman (1985/2006) provided an interesting example of functional equivalence in his discussion of calculating the product of 3 and 15. One way to do this is by using the multiplication tables and the rules of arithmetic taught in elementary school. Specifically, line up the two numbers on a sheet of paper (15 on top), multiply 3 times 5 to get 15, but carry the 1; multiply 3 times 1 to get 3 and add the carried 1, giving 4, which leads to the answer, 45. But this product can also be obtained just by counting. Specifically, get 3 jars, count 15 beans into each, pour the beans from the three jars onto a table and count them, which gives a total of 45. These are two different sets of operations; one uses the multiplication tables and the rules of arithmetic; the other uses beans, jars, and counting. But the two sets of operations can be said to be functionally equivalent because they give the same answer.

Functional equivalence is well known in science. In particle physics, for example, Heisenberg's matrix mechanics, Schrödinger's wave mechanics, and the Dirac-Feynman path

integral formalism are functionally equivalent theories of quantum phenomena (Cox & Forshaw, 2012). Although the three theories are implemented in very different ways, they give the same answers, all of which agree in detail with experimental measurements. Note that the experimental measurements themselves are determined by the operations of the physical world. Note also that the physical world is not likely to work in three different ways, corresponding to the three theories. In fact, the physical world is not likely to work according to any one of the theories (Cox & Forshaw, 2012; Lewis, 2016; McDowell, 2013d). Hence, as McDowell (2013d) pointed out, the operations of the three theories, plus the operations of the physical world (whatever they may be), are all functionally equivalent.

According to a functional equivalence interpretation of the evolutionary theory, its operations are as detached from the brain as are the operations of quantum theories from the physical world. Most physicists have learned to accept this detachment, given the extraordinary success of the quantum theories, although achieving this acceptance entailed a long and sometimes contentious struggle (Cox & Forshaw, 2012; McDowell, 2013d). Consider Feynman's (1985/2006) trenchant comments about theories in general, and about his path integral formalism in particular:

> [physicists have] learned to realize that whether they like a theory or they don't like a theory is *not* the essential question. Rather, it is whether or not the theory gives predictions that agree with experiment. It is not a question of whether a theory is philosophically delightful … or perfectly reasonable from the point of view of common sense. The [path integral formalism is] absurd from the point of view of common sense. And it agrees fully with experiment. (p. 10).

According to a functional equivalence interpretation of the ETBD, the operations of the theory and the operations of the brain are different ways of doing the same thing. Put another way, neurophysiological functioning, whatever its details might be, is the brain's way of generating evolutionary dynamics.

General Discussion

The evidence summarized in this article constitutes substantial empirical support for the evolutionary theory. Of particular note is the theory's ability to provide a single account of steady-state behavior on concurrent interval schedules and concurrent ratio schedules with unequal and equal ratios in the components, such that different explanations of behavior in these three environments are not necessary. Another noteworthy outcome is the theory's correct prediction of the numerical values of the exponents typically observed in matching and bivariate matching experiments with live organisms (Eqs. 2). According to the theory, these specific numerical values are the result of evolutionary dynamics.

Other prior-principle theories of instrumental behavior have appeared in the literature over the past 25 or so years. These include the reflex reserve theory mentioned earlier (Catania, 2005; Killeen, 1988), various neural network theories (e.g., Donahoe, Burgos, & Palmer, 1993), a theory of arousal coupled to responses in memory (Killeen, 1994; Killeen & Bizo, 1998), a theory of cognitive processing (Shimp, Childers, & Hightower, 1990), and a cognitive expectancy theory (Dragoi & Staddon, 1999). To date, none of these theories has garnered empirical support as extensive as that summarized here for the ETBD. In addition, counterevidence for and criticism of reflex reserve theory (Berg & McDowell, 2011) and neural network theories (Calvin, 2012; Calvin & McDowell, 2015, 2016; Kehoe, 1989; Marr, 1997, 2000; McDowell 2013d) have appeared in the literature.

Two additional developments in the ETBD are worth mentioning. The first is an implementation of stimulus control. McDowell, Soto, Dallery, and Kulubekova (2006) proposed an addition to the evolutionary theory that permits behavior to come under the control of discriminative stimuli, including temporal stimuli such as those associated with fixed-interval and differential-reinforcement-of-low-rate schedules. The implementation is based on Mazur's (1997) hyperbolic delay theory of conditioned reinforcement and the Rescorla-Wagner theory

of associative learning (Danks, 2003; Sutton & Barto, 1998). It allows, among other things, different patterns of behavior to develop and to be maintained under different stimulus conditions. It also allows AOs to work to change from less favorable reinforcement contexts to more favorable ones. Importantly, McDowell et al.'s implementation does not alter any of the existing rules of the evolutionary theory; instead, it adds new rules that permit stimulus control to develop. Berg (2011) studied a version of McDowell et al.'s implementation and found good discriminative responding in AOs animated by the theory. He also found that the AOs worked to change reinforcement contexts just as live organisms do. Unfortunately, Berg's implementation uses two different parameters to represent reinforcer magnitude. This is theoretically problematic, and introduces practical uncertainties when using his implementation in computational experiments. Nevertheless, Berg's results suggest that some form of McDowell et al.'s implementation of stimulus control in the ETBD is likely to be successful.

The second additional development in the ETBD is an implementation of punishment superimposed on concurrent schedules of reinforcement (work done in collaboration with Bryan Klapes). Without changing the existing rules of the theory, this implementation allows behavior to be affected by punishment frequency, punisher magnitude, and reinforcement context. Reinforcement context modulates the effect of punishment such that a punisher with a given frequency and magnitude suppresses behavior less in the presence of a high rate of reinforcement than in the presence of a low rate of reinforcement. This may be viewed as a kind of aversion to reinforcement loss. In other words, punishment not only delivers an aversive punishing stimulus, but also an aversive loss of reinforcement due to response suppression. These two effects compete to determine the degree of the response suppression; the aversive punishing stimulus acts to suppress responding while the aversive loss of reinforcement acts to maintain it. The relevant computational studies for this project have been completed, and the results are consistent with findings from experiments with live organisms, including a preference shift toward overmatching when equal schedules of punishment are superimposed on the two alternatives (Farley, 1980; Reed & Yoshino,

2005). This work has not yet been published, but a preprint is available upon request.

Additional research on the ETBD is currently underway, including studies of stimulus control in chained schedules, the tracking of unsignaled changes in reinforcement rate ratios on concurrent interval schedules (as reported for rhesus monkeys by Corrado et al., 2005, and Sugrue, Corrado, & Newsome, 2004), and delay discounting. The navigation of grid worlds by AOs is also being investigated (McDowell et al., 2006). Grid worlds are often a focus of research in artificial life and artificial intelligence because they entail learning about the location of resources on a two-dimensional surface (Mitchell, 2009; Russell & Norvig, 2003). The study of AOs navigating grid worlds is a first step toward animating mechanical agents with the ETBD.

In addition to basic science research, clinical translational research using the ETBD is underway as well. This includes studying the behavior of AOs with attention-deficit/hyperactivity disorder (ADHD), which is produced by arranging high mutation rates. When the rate of mutation is high, behavior is more likely to shift out of a target (i.e., a reinforced) class of phenotypes than when the rate of mutation is moderate. An observer might report this as inattention to the target, or as impulsive switching to other behaviors, or as some combination of the two. The symptom dimension that is reported might depend on how different the switched-to phenotypes are from the target phenotypes. If they are very different, then the shift out of the target class may be seen as impulsive behavior; if they are not very different, then the shift out of the target class may be seen as inattentive behavior.

Interestingly, some evidence suggests that children with ADHD show lower sensitivity to reinforcement in concurrent schedules than controls, that is, the *a* parameter in Equation 2 is lower for these children (Kollins, Lane, & Shapiro, 1997; Taylor, Lincoln, & Foster, 2010). This is precisely what is observed in AOs when the rate of mutation in the evolutionary theory is relatively high (McDowell et al., 2008). Furthermore, arranging higher rates of reinforcement for children with ADHD has been reported to normalize their symptoms (American Psychiatric Association, 2013; Barkley, 2002; Stattin, Enebrink, Özdemir, & Giannotta, 2015). Similarly, in a study

of AOs animated by the evolutionary theory, Popa and McDowell (2016) found that, in the presence of a high mutation rate, increasing the rates of reinforcement for the target behaviors increased the exponent of Equation 2 to a more normal level. In view of these two correspondences between the evolutionary theory and the clinical literature, it appears reasonable to model ADHD by increasing the rate of mutation in the evolutionary theory. Given a plausible computational model, it may be possible to study additional features of ADHD, and to test interventions for the disorder, using AOs animated by the theory (McDowell, 2013b).

In addition to modeling ADHD, methods of modeling depression and bipolar disorder are also being explored. An initial foray into this modeling has focused on the mean of the fitness density function. Recall that this parameter determines selection strength. In depression, or in the depressed phase of bipolar disorder, selection strength may be weaker than normal, reflecting anhedonia. In the manic or hypomanic phase of bipolar disorder, selection strength may be stronger than normal, resulting in excessive behavior. Recall that selection strength in the ETBD affects the asymptote, b, of Equation 1, which describes behavior on single RI schedules. Specifically, the b parameter varies directly with selection strength. Bradshaw and Szabadi (1978), and Szabadi, Bradshaw, and Ruddle (1981) studied the behavior of two individuals with bipolar disorder working on variable-interval schedules of monetary reinforcement during several manic, euthymic (normal), and depressive phases of their illness. They fitted a form of Equation 1 to data from these individuals and found that b varied with the phase of their illness in the manner predicted by the preliminary ETBD model of bipolar disorder presented here. Specifically, b was larger during manic phases and smaller during depressed phases when compared to its value during euthymic phases of the illness. Again, this correspondence between the theory and clinical findings suggests that the ETBD might prove useful as a model for studying, and perhaps developing interventions for, depression and bipolar disorder.

In conclusion, the extensive support for the ETBD summarized in this article suggests that the theory is a strong candidate for a comprehensive prior-principle theory of adaptive behavior. The theory is conceptually and parametrically simple, and it tells an appealing story about behavior, namely, that it evolves in ontogenetic time under the selection pressure of consequences from the environment.

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