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The Evolutionary Theory of Behavior Dynamics: Complexity, Darwinism, and the Emergence of High-Level Phenotypes

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M.A., Emory University, 2009
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An abstract of
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Abstract

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By Andrei Popa

McDowell (2004) instantiated low-level Darwinian processes in a computational theory of behavior dynamics. The theory causes a population of behaviors to evolve through time under the selection pressure of the environment. It has been tested under a variety of conditions and the emergent outcomes were repeatedly shown to be qualitatively and quantitatively indistinguishable from those displayed by live organisms (McDowell, in press). As empirical evidence accumulates and our understanding of the theory matures, the analogy between biological and behavioral evolution becomes more compelling. Expanding the exploration of this analogy becomes both necessary and fascinating. The main purpose of this project was to explore the effects of *mutation* and the environment's *value* and *conduciveness* on various dimensions of behavioral variability, in continuous choice environments. Secondly, qualitative predictions made by the Evolutionary Theory about the effects of changeover delays (COD) on behavior variability were verified against the behavior of college students in equivalent environments. The continuous choice behavior of college students was correctly predicted on eight out of eight behavioral dimensions. Thirdly, low-level characteristics of students' continuous choice behavior were compared with traditional measures of *impulsivity* and *sustained attention*, in an effort to investigate the potential equivalence between *mutation* and a property of the nervous system that produces *impulsivity*-like symptoms. The results were inconclusive, likely due to a lack of extreme *impulsivity* scores in the human sample. The findings presented in this paper provided significant additional evidence for the selectionist account as a valid mechanism of behavior change. In addition, the knowledge generated by the Evolutionary Theory provided important insights about clinically-relevant phenomena, such as *disordered variability* (or *impulsivity*) and raise the possibility of using the theory as a platform for simulating the emergence of specific high-level phenotypes. These implications appear even more fascinating considering that a connection with mental health was not explicitly sought, nor can it be traced to the inner-workings of the theory. This challenges our current understanding of mental illness and provides a new way of thinking about the evolution of behavioral repertoires and their emergent high-level characteristics.

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To Sir, With Love

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The Evolutionary Theory of Behavior Dynamics:

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Live organisms are in continuous interaction with the world that surrounds them. These interactions, in time, give rise to rich behavioral repertoires, dynamical constellations that affect and are affected by the outside world. The mechanisms that govern the continuous interaction between behavioral repertoires and their environmental consequences are not well understood (Dragoi & Staddon, 1999; McDowell, in press). Several types of explanations have been proposed, but, so far, none has met with overwhelming success. Although different in many respects, all existing theories share a common feature: behavioral repertoires are assumed to be governed by a central entity and subordinated to the fulfillment of *apriori* theoretical prescriptions (e.g. maximization). The Evolutionary Theory of Behavior Dynamics (McDowell, 2004), which constitutes the focus of this project, proposes a different type of explanation. It assumes that the order we observe in behavioral repertoires is not the product of a guiding process. Instead, the theory proposes, the structured high-level outcomes that we observe emerge naturally from the reiteration of low-level Darwinian processes of *selection*, *recombination*, and *mutation*. Therefore, behavioral repertoires are not, according to this framework, *pulled* towards goals, but rather *pushed* through time by selectionist forces, towards no specific end-state or goal. The high-level phenotypes are literally created moment by moment by the processes that govern the interaction between the organism and the world in which it is immersed (McDowell, 20110, in press).

The experiments discussed in this paper, although grouped under three specific aims, were motivated by an overarching question about the behavior of organisms: ***are behavioral repertoires, at a basic level, complex systems pushed through time by selectionist forces***? The three specific aims of this thesis were 1) to expand the knowledge about the Evolutionary Theory by learning about the functional role of various computational variables (e.g. *mutation*) on the emergent outcomes, 2) to explore the theory's potential of predicting the behavior of live organisms, and 3) to explore the relation between traditional measures of *impulsivity* and various low-level characteristics of continuous choice behavior in human participants. The rationale and significance of these three specific aimswill be discussedin detail at the end of the introductory section.Before doing so it is important to clarify the theoretical context of this research, which constitutes the focus of the next subsections.

Adaptive behavior

The object of study of behavior analysis is adaptive behavior, defined as *behavioral patterns* that, at least occasionally, result in positive outcomes. The outcomes can be separated into two categories: *resource acquisition* (e.g. food, access to water, social praise, attention from peers, etc.) or *threat escape or avoidance* (e.g. escape predators, avoid reprimands, avoidbeing grounded, lessen psychological tension, etc.). Behaviors that result in resource acquisition are called positively reinforced because something is added. Behaviors that result in avoidance or escape of threat are called negatively reinforced, because something is removed (escape) or prevented from occurring in the first place (avoidance). Whenever the environment permits it *escape* turns into *avoidance*. The overarching purpose of the discipline is to uncover the general principles that govern the relations between adaptive behavior and its consequences (Pierce & Cheney, 2004).

An example of a general relation between behaviors and positive outcomes is the mathematical statement known as the Matching Law. Discovered by Richard Herrnstein (Equation 1; 1961) and further developed by William Baum (1974; Equation 2 and its logarithmic form, Equation 3) and others, it expresses ratios of adaptive behaviors as a function of ratios of resource acquisition. It states that when free to choose between simultaneously available alternatives (continuous choice behavior) organisms tend to distribute their responses (or time) among alternatives in the same proportion in which resources are delivered by the alternatives.

$$\frac{\mathrm{B}_1}{\mathrm{B}_2} = \frac{\mathrm{r}_1}{\mathrm{r}_2} \text{Eq. 1}$$

$$\frac{\mathrm{B}_1}{\mathrm{B}_2} = b\left(\frac{\mathrm{r}_1}{\mathrm{r}_2}\right)^a \text{ Eq.2}$$

$$\log\left(\frac{\mathrm{B}_1}{\mathrm{B}_2}\right) = a\log\left(\frac{\mathrm{r}_1}{\mathrm{r}_2}\right) + \log(b)\text{Eq.3}$$

Equation 2, known as the power function matching equation, has two free parameters, *b* and *a*. The first parameter (*b*) captures the organism's *bias*(or preference) for one alternative or the other, preference due to other factors then the rates of resource acquisition. Usually, fluctuations in bias were caused by a difference in the *subjective values* of the alternatives (e.g. reward quality, etc.; Myers & Myers, 1977; Baum, 1979; Davison & McCarthy, 1988). In symmetrical-choice environments the bias parameter varies around unity ($b \approx 1$). The second parameter, the exponent of Equation 2, (*a*; the slope of the line described by Equation 3), is sometimes referred to as *sensitivity* to reinforcement (Baum, 1974). When the exponent equals unity ($a = 1$) the rates of responding perfectly match the rates of reinforcement. This outcome is called *perfect matching* and it means that the organism's behavioris perfectly controlled by its consequences. Note then when $b = a = 1$ Equation 2 is reduced to Equation 1. The outcome described by an exponent larger than unity ($a > 1$) is called *overmatching*. This deviation means that the organism tends to place more responses on the richer alternative, than otherwise predicted by perfect matching. When the exponent is smaller than unity ($a < 1$) the outcome is called *undermatching*. This means that the organismtends to place fewer responses on the richer alternative, than otherwise predicted by perfect matching. As the exponent decreases, the level of undermatching becomes more severe, up to the point of *complete indifference* ($a = 0$): the organism allocatesits behaviors at random, "oblivious" to environmental consequences (Davison & McCarthy, 1988;McDowell, 1988).

A plethora of research showed that Equation 2 is an excellent *descriptor* of steady-state choice-behavior (or behavior at equilibrium). It usually accounts for more than 90% of the variance and leaves random residuals. Moreover, the exponent (*a*) was usually found to vary around 0.8, which means that the organism's behavior is controlled by consequences, but not perfectly, the organism showing a slight tendency towards indifference (slight undermatching). Five decades of thorough experimentation showed that the power function matching equation accurately describes the relation between response and reinforcement ratios, across species and settings, from pigeons pressing levers to naturally occurring human behavior (Baum, 1974, 1979; Wearden & Burgess, 1982; Davison & McCarthy, 1988;McDowell, 1988; Dallery, Soto, & McDowell, 2005; McDowell, Caron, Kulubekova, & Berg, 2008; McDowell & Caron, 2010; see McDowell, 2012, for an in-depth discussion).

Behavior dynamics

The Power Function Matching Equation (Equation 2) is an excellent account of *behavior statics*, or behavior at equilibrium. Like any other descriptor, this mathematical statement provides valuable information about “how things are”, but remains silent about "how things came to be the way they are". Several accounts of behavior dynamics have been proposed over the years. Although different in form and underlying theory, they typically consist of a statement of a dynamic theory, from which a descriptive outcome is obtained. The melioration account(Vaughan, 1981; Herrnstein, 1982) and the maximization account (Baum, 1981; Rachlin et al., 1981) are two prominent examples of dynamic theories. A maximization account may assume that an organism tends to maximize the utility (*value*) of its behaviors; thus, a certain utility function may be proposed, namely, a function that expresses behavior’s *value* in terms of independent variables, like *benefit* and *cost*. Using this utility function a researcher may *predict* what the final outcome will be, assuming the organism’s tendency to maximize *value*. Most dynamic accounts assume an end-state (e.g. *maximum value*) and use analytical mathematical models to predict it. An in-depth discussion about various accounts and their present status goes beyond the purpose of this paper. A preliminary discussion about various categories and implementations, as well as the major obstacles in comparing their performance (e.g. lack of agreed-upon evaluative criteria), was recently provided by McDowell (in press). So far, no account has received wide acceptance and very few (if any) have been unequivocally falsified.

One theory that received considerable support in the past ten years is the Evolutionary Theory of Behavior Dynamics (McDowell, 2004), a theory that proposes a very different type of explanation for the dynamics of behavior.The next section will describe the theoretical framework to which this theory belongs, after which the theory will be described in detail.

Complexity, emergence, and evolution

The notion of "complexity" is usually encountered in twoidioms: complexity science and complex systems. Complexity science is the discipline that focuses on the study of complex systems. The crucial characteristic that differentiates complex systems from other systems is *emergence*(Holland, 1988). Emergence is understood as a process that, over time, gives rise to structures (e.g. behaviors, features) that are caused by the low-level processes that govern the system, but are not directly explained by these processes (Holland, 1988, 2000). A common example is the behavior of a school of fish. For an outside observer the group behaves as a coherent, ordered structure, as if it were guided by a central entity, in the same way in which the overall behavior of an army is guided by a general. An alternative explanation is that these (quite beautiful) high-level phenotypes emerge naturally from the individual behavior of each fish, who "follows" simple guidelines such as *swim in the same general direction*, *stay close* (to your fellow fish), *but not too close* (Neil deGrasse Tyson, in Liota & Fine, 2007[1]). The overall behavior of the group is thus *produced* by each fish following these simple rules, but cannot be directly explained by the individual behavior of its elements.

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[1] http://www.pbs.org/wgbh/nova/nature/emergence.html

Although it only recently started to regain attention in social sciences, the concept of *emergence*, or *spontaneous order*, is neither new nor peripheral. In 1767, Adam Ferguson, one of the champions of Scottish Enlightenment, wrote (bold added):

> "Mankind, following in the present sense of their minds, in striving to remove inconveniences, or to gain apparent and contiguous advantages, arrive at ends which even their imagination could not anticipate; and pass on, like other animals, in the track of their nature, without perceiving its end. He who first said, "I will appropriate this field; I will leave it to my heirs;" did not perceive, that he was laying the foundation of civil laws and political establishments.
>
> [...]
>
> Men, in general, are sufficiently disposed to occupy themselves in forming projects and schemes; but he who would scheme and project for others, will find an opponent in every person who is disposed to scheme for himself. Like the winds that come we know not whence, and blow whithersoever they list, the forms of society are derived from an obscure and distant origin; they arise, long before the date of philosophy, from the instincts, not from the speculations of men. The crowd of mankind, are directed in their establishments and measures, by the circumstances in which they are placed; and seldom are turned from their way, to follow the plan of any single projector.Every step and every movement of the multitude, even in what are termed enlightened ages, are made with equal blindness to the future; **and nations stumble upon establishments, which are indeed the result of human action, but not the execution of any human design.**"

(Adam Ferguson, *An Essay on the History of Civil Society*, 1819/1767, page 221-223)

If some of the first systematic discussions on the notion of emergence (or spontaneous order) date back 250 years or so, the first successful complexity theory, as in a theory that explained a real-world system that exhibits emergence,is not much younger. Although not as attention-grabbing as it was in the 19th century, Darwin's Theory of Evolution (Darwin, 1858) remains a formidable achievement. Not only it explained the emergent complexity of life,butprovided a new way of thinking about the relations between living organisms, the world that surrounds them, and time. The tremendous explanatory power of this theory was due to a fundamental shift in focus: *from the content* to be explained (e.g. human eye, the platypus, giraffes' necks, etc.) *to the low-level forces/mechanisms that produce the content*. By following, perhaps without explicit intent, in the footsteps of physics, a discipline that emphasizes forces and treats content as incidental, Darwin's Theory of Evolution not only set the foundations of modern biological sciences, but provided an entirely new way of thinking about the emergence and trajectory of living organisms (Mayr, 2001; Dawkins, 2009).

Two essential mechanisms of evolution are selection and mutation. *Natural selection*, the central tenet of evolutionary thought,is the only mechanism that causes the evolution of adaptations (Futuyma, 2009). It is often referred to as the self-evident mechanism, a direct consequence of fundamental characteristics of life itself: there are always more offspring than can survive, they differ in their ability to survive, and the features underlying these abilities are heritable (Hurst, 2009). In other words, natural selection is not a theory, a hypothesis about how life might work, but a consequence that follows from the fact that Organism X, reproducing before (or more) than Organism Y, passes its entire genetic material to the future generation, including any allele that may have provided some advantage for its reproductive success. If natural selection is the strongest mechanism, *mutation* is what allows evolution to occur in the first place, producing the raw material for genetic variation on which natural selection operates (Carlin, 2011; Loewe , 2008).In the words of Lewis Thomas, "*without this characteristic of DNA to blunder slightly we would still be anaerobic bacteria and there would be no music*" (*The Lives of a Cell : Notes of a Biology Watcher*, 1974).

Ironically, what makes emergence possible, also makes emergent properties very difficult to study. Because error, by definition, occurs at random, the existing predictive models cannot, in principle, be applied to emergent features. This unexpected difficulty is not posed only by slight differences in the system's initial conditions, as in the case of chaotic systems, which are deterministic (Strogatz, 1994). It stems from the probabilistic nature of the low-level processes that produce the emergent properties. This renders the evolution of complex systems computationally irreducible (Wolfram, 2002): steps (or computations) cannot be "skipped"; in order to observe an outcome one must wait for each computation to be performed, for the outcome to be created. Bypassing computational irreducibility is impossible in practice and, at least for now, seems impossible in principle. The only way to examine such systems is the brute-force computational approach: represent the problem abstractly, implement it in a computer program, perform all the computations, and analyze whatever outcome emerges.

Natural selection as general process, was proposed to govern not only the change in genetic makeup, but also the change that occurs in behavioral repertoires (Pringle, 1951;Catania, 1978, 1987; Donahoe et. al., 1993; Skinner, 1981; Staddon &Simmelhag, 1971) and in cultural practices (Glenn, 1988, 1989; Hayek, 1952a, 1952b, 1988; Lamal, 1997; Lamal&Greenspoon, 1991; Lloyd, 1985; Norton, 1997).

The Evolutionary Theory of Behavior Dynamics(McDowell, 2004) was developed to verify if the selectionist framework is a valid account for the dynamics of behavioral repertoires. It conceptualizes the behavioral repertoires of live organisms as complex systems pushed through time by low-level selectionist forces, towards no specific end-state or goal. The high-level phenotypes that we observe and analyze (e.g. *ADHD*-like symptoms, the Matching Law)are not stand-alone entities, but emergent properties, produced by the reiteration of the low-level processes that govern the system, but not directly reducible to them. It is an instance of complexity theory stated as a set of simple rules that cause *selection, reproduction*, and *mutation* to occur in a population of potential behaviors by means of a genetic algorithm (McDowell

&Popa, 2009). Behaviors in the theory are represented by integers, which constitute the behaviors' phenotypes; their corresponding binary representations constitute the behaviors' genotypes. Behaviors may be sorted into classes of adaptive (or operant) behavior, where similar behavioral phenotypes are represented by similar integer values. Therefore, integers are an abstract representation of real-world instrumental behaviors. For example, phenotype 101 (genotype 1100101), may becomputationally equivalent toa rat’s left-paw lever press, phenotype 105 (genotype 1101001) may becomputationally equivalent toa right-paw lever press, and a phenotype of 765 (genotype 1011111101) might represent rearing at the back of the cage (extraneous, non-target behavior).

Although the actual implementation required substantial effort, the logic of the theory is "simple enough to be written on a napkin" (McDowell 2012), as illustrated in Figure 1. At each generation, or time tick, a behavior is randomly selected and emitted from a population of behaviors, abstractly represented by numbers (integers and their corresponding binary representations). Emissions are followed by selection of parents for the next generations. If the emission did not result in positive outcomes, parents are selected at random. If the emitted behavior resulted in a positive outcome, parents are selected based on their fitness: behaviors that are closer to the previously reinforced behavior have a higher chance of becoming parents. Regardless of how parents selected (at random or based on their fitness) they recombine in the same way, each parent having equal chances of contributing to the child's genotype. The population of children is affected by mutation: a small number of children behaviors are selected at random and one of the bits in their genotypes, also selected at random, is "flipped" from zero to one or one to zero. From this new, mutated population, a behavior is emitted at random and another cycle begins.The continuous application of Darwinian rules of *selection*, *recombination*, and *mutation*, in time, gives rise to ordered behavioral patterns that can be analyzed and compared to live data.

Extensive experimentation has shown that the Evolutionary Theory produces behavior that is qualitatively andquantitatively indistinguishable from that observed in live organisms. Steady-state behavior is well described by Herrnstein's hyperbola (McDowell, 2004), the power function matching equation (McDowell & Caron, 2007; McDowell Caron, Kulubekova, & Berg, 2008; McDowell & Popa, 2010), and the bivariate matching equation (McDowell, Popa, & Calvin, 2012). Remarkable agreement with live data was also found when examining the pattern of switching between alternatives (McDowell & Popa, 2010; Popa & McDowell, 2010), the distribution of inter-response times (IRTs; Kulubekova& McDowell, 2008), and specific characteristics of preference in rapidly changing environments (Kulubekova& McDowell, in press). Most importantly, these outcomes are not goals embedded in the theory, they cannot be traced to any of the rules that push the population of behaviors though time. These findings suggested that both molar (e.g. undermatching) and molecular behavioral features (e.g. inter-response time distributions) are emergent properties of the reiteration of the low-level Darwinian processes (for a comprehensive review see McDowell, in press).

The present project: motivation and specific aims

The focus of the present project wasthe low-level Darwinian process of *mutation*. Mutation is an essential process for biological evolution, providing the genetic variation on which selection operates (Loewe, 2008; Carlin, 2011). When investigating the parallel between biological evolution and behavioral evolution it becomes obvious that mutation deserves special attention. In regard to behavior, mutation essentially refers to a process that generates behavioral variability, a phenomenon that received a lot of attention, for two main reasons. First, it is essential for the evolution/development of behavioral repertoires. This point is self-evident: without some random variability an organism would be incapable to adjust to novelty (Staddon &Simmelhag, 1971; Futuyma, 2009; Mayr, 2001). Interestingly, mutation was shown to be essential for the evolution of virtual behavioral repertoires, McDowell (2010) showing that without mutation, behavioralrepertoires become stuck in one of the target classes.Second, behavior variability was shown to be a behavioral characteristic with potential adaptive value. For example, extensive research has shown that behavioral variability increases when the environments' *value*decreases (Antonitis, 1951; Eckerman&Lanson, 1969; Neuringer, 2002, 2009; Neuringer & Jensen, 2012; Stokes, 1995). It is important to note that behavior variability is not adaptive in itself, but by its consequences: increasedvariability results in a higher frequency of spontaneous behaviors,which have exploratory potential. Many of these behaviors may be unsuccessful (much like most biological mutations do not trigger major consequences). However, the increased variability may at least occasionally result in the discovery of new resources or in the emergenceof novel behaviors that may acquire existing resources that were previously out of reach. Previous studies indicated that decreasing the rate or magnitude of the reinforcement had similar effects on the behavior of the virtual organism. For example, McDowell & Popa (2010) showed that lower reinforcement rates produced lower exponent values (or *sensitivity*, a), an indicator of low environmental control on behavior. The decrease in exponent's values were accompanied by increased rates of switching between alternatives, effects well documented in the live organisms literature (Davison & McCarthy, 1988; McDowell, 2012).

If high behavioral variability may be a natural, adaptive reaction to low-*value* environments, it was suggested that too much behavior variability may have detrimental effects (Neuringer, 2009). The ADHD literature abounds in studies that show that the behavior of ADHD children is characterized by higher levels of behavior variability than that of controls (Castellanos et al., 2005; Rubia et al., 2007). It is worth noting however that there areno criteria for how much variability is too much.

McDowell & Popa (2010) suggested that *mutation*, one of the processes that animates the virtual organism, may becomputationally equivalent toa fixed property of the nervous system that, under certain environmental circumstances, induces *impulsivity*-like symptoms in live organisms. They showed that a higher rate of mutation produced steady-state choice-behavior characterized by lower *sensitivity* to reinforcement (lower exponents, a) and high frequency of switching between alternatives. Theyalso showed that arranging stronger reinforcers improved the behavior of virtual organisms characterized by high mutation rates. Preliminary studies (Popa & McDowell, 2011) showed that arranging richer environments had similar effects, producing higher exponents and lower frequencies of switching between alternatives. These results were congruent with findings from the ADHD literature whichsuggest that (1) the choice-behavior of ADHD diagnosed children is characterized by lower sensitivity to reinforcement (Barkley, 1997;Kollins et. al., 1997; Taylor et. al., 2010) and (2) that ADHD symptoms can be ameliorated by increasing the rate and magnitude of the reinforcement (Barkely, 2013; Pfiffner et. al, 1985; Pfiffner, 1996).

Changeover Delay in live (COD) and virtual (HD_{COD}) organisms

In addition to reward rate and magnitude, Taylor et. al. (2010) showed that arranging a changeover delay (COD; Findley, 1958) may increase the *sensitivity* to reward of ADHD children in continuous-choice settings. A changeover delay (COD) is an environmental variable that was introduced in concurrent-schedule procedures in order to prevent rapid switching between alternatives. It can be implemented in a variety of ways; the most common is to implement a "blackout" period immediately after a switch (or changeover) occurs. During this period, called the changeover delay (COD), even if a reinforcer is available, it is withheld until the delay elapses. Ifthe organism switches back it initiates another delay, and so on. When a COD is in effect rapid switching is costly for the organism, therefore the presence of a COD reinforces responding in bouts and discourages sporadic, hit-and-run responses. Among its most common effects are increased *sensitivity* to reinforcement (a), longer bouts of responding, and decreased frequency of switching (Shull &Pliskoff, 1967; Baum, 1974, 1979; Davison & McCarthy, 1988; Temple et. al., 1995). The name Changeover Delay technically refers to the time delays (measured in seconds) arranged by the experimenter. However, the term is used more broadly to refer to any environmental manipulation that makes rapid switching costly. For example, similar effects were obtained when increasing the physical distance between two levers (Davison

&McCarthy, 1988). Increased travel distance between alternatives caused the organism to switch less often, thus spending more time engaged in continuous responding[2].

Popa & McDowell (2010)showed that a specific feature of the binary strings(that abstractly represent the behaviors' genotypes), called Hamming Distance (HD; Hamming, 1950) affected the behavior of the virtual organism in similar ways in which a changeover delay affects the behavior of live organisms. This feature will be referred throughout this manuscript as "Hamming Distance changeover delay" and will be denoted with HD_{COD}. The way it is computed will be explained in detail in the next section. The effects of changeover delays on behavior variability were not extensively studied in the live-organism literature. Considering its behavioral effects, if the rate and magnitude of reinforcement are measures of the environment's *value*, then the changeover delay could be conceptualized as a measure of the environment's *conduciveness*, with low values facilitating rapid switching and high values discouraging rapid switches.

Given the important status of mutation in biological evolution, and its effects on the behavior of the virtual organism animated by the evolutionary theory (e.g. extinction at low rates, erratic behavior at high rates), its systematic study becomes a necessity for a better understanding of the Evolutionary Theory and of the analogy between biological and behavioral evolution. Furthermore, understanding the dynamic interplay between organismic (*mutation*) and environmental factors (*value*, *conduciveness*) may provide important insights about the emergence of high-level level phenotypes. The systematic study of these relations constitutes the first specific aim and the core of this project. In addition to learning about the theory, the present project took the first steps in verifying predictions made by the theory in experiments with live organisms (specific aims 2 and 3). The three specific aims are discussed below; Figure 2 may be helpful in clarifying the connections between them.

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[2] The author used this principle to prevent impulsive *email checking* and *internet surfing* during *writing* periods by unplugging the modem. The time required to restart the modem served as a changeover delay and resulted in less switching between alternatives and longer bouts of *writing* behavior.

Specific Aim 1

The first specific aim was to learn about the effects of reward rate, reward magnitude, and computational changeover delay on the behavioral variability of virtual organisms characterized by different mutation rates.Previous studies (McDowell & Popa, 2010) indicated that 1) high mutation rates produced behavioral characteristics similar to somethat were traditionally reported in ADHD studies (e.g. low *sensitivity*) and 2) more frequent and stronger rewards tended to prevent the emergence of these undesirable outcomes, at least to a certain extent, a practice recommended by most behavior management guides of ADHD (Barkely, 1995, 2013; Pfiffner et. al, 1985; Pfiffner, 1996). In addition, recent findings suggested that a changeover delay (COD; Findley, 1958) may successfully improve the *sensitivity* to reinforcement of ADHD children in continuous choice procedures (Taylor et. al., 2010). This provided an interesting opportunity to further investigate the computational equivalence between Hamming Distances arrangements and real-world changeover delays (COD).The present project expanded the number of dependent variables investigated beyond the ones usually examined in studies of continuous-choice performance (e.g. exponent values, bias parameters, changeover frequency). In addition, the range of reward rates, magnitudes, and mutation rates was significantly increased to better sample the parameter space; various Hamming Distance arrangements (HD_{COD}; discussed in detail in the next section) were also added to the experimental design.

Specific Aim 2

The second specific aim was to explore the theory's potential of predicting the performance of college students in continuous-choice settings.The concurrent-schedule procedure provided a suitable common ground for comparing the behavior of virtual and live organisms. This phase of the project constituted a necessary step in exploring the equivalence between *mutation* and *impulsivity*, as apparent from Figure 2. During this phase college students responded in continuous choice environments very similar to those arranged by the Evolutionary

Theory. Their behavioral characteristics were compared to those of virtual organisms. This phase was heavily exploratory and it wasintended to 1) provide initial information about the theory's potential of predicting human behavior and 2) to test the concurrent schedules procedure and assess its suitability for future research.

Specific Aim 3

The third specific aim was to explore the relation between *mutation* and *impulsivity*. The behavioral characteristics of students' continuous choice behavior were compared with traditional measures of *impulsivity* and *inattention*. The purpose was to verify whetherthe concurrent-schedule procedure itself canprovide information about potential low-level behavioral markers specific to highly *impulsive* participants. Such findings would allow comparisons between the continuous-choice characteristics of *highly impulsive* students to those of virtual organisms characterized by high mutation rates.

Taken together, these three phases provided a plethora of information about the inner-workings of the evolutionary theory, knowledge of special relevance to its intended, overarching purpose: ***to verify whetherbehavioral repertoires, at a basic level, are complex systems pushed through time by selectionist forces***. In addition, this project took the first steps in exploring the possibility of translating this knowledge into the real-world. One higher, long-term goal of successfully translating such knowledge is to eventually gain insight about clinically-relevant phenotypes (e.g. *pathologic impulsivity*). The experiments and analyses entailed by this project were divided into three phases, each focused on one specific aim. Due to the large volume of information, the three experimental phases (method, results, discussion) will be addressed separately, followed by a general discussion.

Phase 1: **Effects of environment's*value* and *conduciveness* on the continuous choice behaviorof virtual organisms characterized by various mutation rates.**

Method

Subjects. Subjectswere virtual organisms with repertoires of 100 behaviors. Their phenotypes ranged between 0 and 4,095. Their corresponding genotypes were padded with zeroes, where necessary, so that all genotypes had 12-character bit strings. The phenotype range was wrapped around itself in a circle, such that the absolute distance between 0 and 4,095 was equal to that between 0 and 1. At each generation (or time tick) one behavior was randomly emitted. Therefore, each behavior in the population, throughout an experimental session, had an equal chance of being emitted. For each pair of concurrent schedules the subjects began as naive, the initial population being selected at random from the 0 - 4,095 range.

Apparatus and materials.Experiments were run on commercially available, of-the-shelf desktops and notebooks. The program that instantiated the virtual organism and its virtual environment were developed in VB 2010, part of the Microsoft Visual Studio 2010 Integrated Development Environment, by McDowell and Calvin (McDowell, Popa, and Calvin, 2012). Data were stored in standard databases and analyzed using Microsoft Office Excel (except for the IRT and IBT measures).

Procedure.All organisms were allowed to evolve in symmetrical, continuous choice environments, with two target classes delivering reinforcement at random time intervals (concurrent RI RI schedules). Each target class encompassed 41 behaviors. The rest of 4,014 behaviors (4,096 - 82), representing almost 98% of all potentialphenotypes, were extraneous behaviors: they were never reinforced and can be conceptualized as "everything else" a live organism may do in an experimental chamber other than the target responses (e.g. pressing levers).

Figure 1provides an overview of the theory's functionality. At each moment in time, that is, for eachgeneration, a behavior was selected at random from the existing population. This constituted an emission. Although emissions are completely random, the structure of the population may be composed of very fit behaviors, which means that the probabilities of emitting a behavior from one of the target classes are not equal; furthermore, these probabilities change from generation to generation, depending on the consequences of previous emissions. Emissions, therefore, can be best described as random selections from a finite set of behaviors with an irregular, dynamic configuration. After an emission, the program selected parents for the new generation of behaviors. Parents were always selected with replacement from the existing population. The manner in which they were selected depended on the consequences of the last emission. If the previously emitted behavior was not successful (did not acquire a resource) parents were selected at random. If the behavior did acquire a resource, parents were selected based on their fitness. The fitness value of each behavior was calculated as the absolute distance between its own phenotype and the phenotype of the previously reinforced behavior. Behaviors that were closer, in absolute distance, to the previously reinforced behavior were considered fitter than behaviors that were further away(on the circular phenotype range). Therefore,fitter behaviors were characterized by smaller fitness values.For example, if the previously reinforced behavior was 500, behavior 550 (fitness value = $|550-500|$ = 50) is considered fitter than behavior 400 (fitness value = $|550-400|$ = 100).This method of calculating fitness values,based on the phenotype of the previously reinforced behavior (which becomes Fitness Zero) is called *individual fitness*.

An exponential function was then used to select parents based on their fitness. This function (Equation 4) expresses the probabilitydensity, p, associated with a parent beingchosen as a function of its fitness, x,

$$p(x) = ae^{-ax}, \qquad \text{Eq.4}$$

where, $0 < x < \infty$. The mean of this density function is

$$\mu = \frac{1}{a}. \qquad \text{Eq.5}$$

This equation is referred to as the parental selection function. It depends only on its mean (μ; Equation 5). The value of its mean influences the strength of the selection process. Smaller means characterize stronger selection processes (only very fit behaviors can become parents), and vice-versa: large means indicate weak selection events (low selection pressure),whichallow even behaviors with very low fitness (high *fitness value*, far away from the previously reinforced behavior) to become parents. The strength of the selection process was found to have similar effects on the performance of the virtual organisms as the magnitude of the reinforcement has on the performance of live organisms (McDowell, 2004; McDowell & Caron, 2007; McDowell et. al., 2008). Therefore, the mean of the parental selection function (μ) seems to be a computational equivalent of reinforcement magnitude, with smaller means (μ) being equivalent to larger magnitudes. Parents were selected bydrawing a fitness value at random from thedensity function using the procedure describedby McDowell (2004), and then searchingthe population of potential behaviors for abehavior with that fitness.

Once parents were selected, they recombined to give rise to a new, child behavior. The recombination method used is called bit-string recombination: every bit in the child's genotype had a 50% chance of coming from the corresponding slot in the father's genotype or from the corresponding slot in the mother's genotype.After a new population was obtained, it was affected by a small degree (rate) of mutation. The method used in this paper is called bit-flip by individual: a certain percentage of behaviors are randomly selected from the population and one bit in their genotype, at random, is flipped from 0 to 1 or 1 to 0. The percentage of behaviors affected by mutation is referred to as the mutation rate and its value is set by the experimenter in the beginning of the experiment; it is, therefore, a fixed property of the organism, unaffected by environmental factors. After the child population was affected by mutation a new behavior was randomly emitted and another cycle began. Selection of parents based on fitness tends to concentrate behaviors around the target classes. In contrast, random selection of parents and mutation are processes that introduce variation into the population.

All experiments arranged symmetrical-choice environments with11 pairsof independent, random-interval schedules (concurrent RI RI schedules). The average scheduled rate of reinforcement differed from component to component (e.g. RI 16 RI 84) but overall, the averages of the 11 schedules were equal for the two alternatives. Each RI RIpairwas in effect for 20,000 generations (or time ticks), hence an experiment lasted for 220,000 generations (20,000 x 11 RI RI pairs). Responses, obtained rewards, and changeovers between alternatives were summed over 500 generation blocks, yielding 40 data points for each RI RI pair. The 40 data points were averaged for each pair, yielding 11 data points per experimental session.

Independent variables

There were four independent variables: Hamming Distance changeover delay, reward rate (or density), reward magnitude, and mutation rate. They are described below. Because the Hamming Distancechangeover delay (HD_{COD}) requires some explanation, it will be discussed first.

The Hamming Distance Changeover Delay (HD_{COD})

Behaviors in the Evolutionary Theory are represented by integers (behaviors' phenotypes) and their corresponding binary strings (behaviors' genotypes). Obtaining one bit string from another is accomplished by "flipping" bits from 1 to 0 or 0 to 1. The number of bits that must be flipped in order to obtain another string of equal length is referred to as the Hamming Distance between the two strings (Hamming, 1950). For example, transforming 511 into 512 requires flipping 10 out of the 12 bits that make their genotypes (00**1111111111** → 00**1000000000**); therefore, the Hamming Distance between 511 and 512 is ten.

Popa & McDowell (2010) showed that the absolute difference between the Hamming Distance that separates thetarget classes ($HD_{BETWEEN}$) and the largest Hamming Distance found within a class (HD_{WITHIN}) affected the behavior of virtual organisms in similar ways as a COD affects the behavior of live organisms. When this difference ($HD_{BETWEEN}$ - HD_{WITHIN}) was larger or equal to three (3) the choice-behavior of the virtual organism was characterized by typical levels of undermatching (a ~0.8). When the difference decreased bellow three (3) *sensitivity* to rewarddecreased rapidly and approached very low values (a ~ 0.1), a trend accompanied by a large increase in the frequency of switching between alternatives.

Detailed mining of the same data revealed interesting underlying patterns that better explain the relation between Hamming Distances and the continuous-choice behavior of the virtual organism.In a continuous choice environment two collections of integers (phenotypes) are defined as target classes. In this example, the two target classes encompass behaviors 251-255 and 256-260 respectively (five behaviors in each target class). For each behavior in a target class one may calculate the Hamming Distance between that behavior and all other behaviors in the class (Figure 3). The average of these distances represents the average number of bits that must be flipped in that behavior's string in order to transform it into any other behavior from the same target class. By calculating this average Hamming Distance for all behaviors in a target class and averaging these averages, one obtains a measure of the average overall Hamming Distance between all behaviors in the same target class. In other words, an average number of bits that must be flipped in order to change any behavior in that target class into any other behavior *in the same class*. This average of averages will be referred to as the average Hamming Distance between behaviors in the same target class;it will be denoted HD_{SAME}.Following the same logic, one may compute the average overall Hamming Distance between all behaviors in one class and all behaviors in the *other class*. This overall average expresses the average number of bits that must be flipped in order to change any behavior from one target class into any behavior from the *other target class*. This average of averages will be referred as the average Hamming Distance between the behaviors fromone target class and the behaviors from the other target class;it will be denoted HD_{OTHER}.

When the difference between HD_{OTHER} and $HD_{SAME}$is small, it is "easy" for a behavior from one class to transition into the other class. The processes of mutation and recombination can easily give rise to a behavior that "falls" into the other class because only a few bits must be flipped. When the difference between HD_{OTHER} and $HD_{SAME}$is large, it is "difficult" for a behavior from one class to transition into the other class; mutation and recombination are less likely to produce behaviors that are several bits apart from their origin. Therefore, the absolute difference between HD_{OTHER} and HD_{SAME} can be conceptualized as a measure of the *overall average "difficulty" to switch* from one class to the other, referred to as environment's *conduciveness*. The difference between HD_{OTHER} and HD_{SAME} will be referred to asHamming Distance Changeover Delay and will be denoted with HD_{COD}.

Data reported by Popa & McDowell (2010) were re-analyzed in terms of the HD_{COD}; the results can be examined in Figure 4. For low HD_{COD} values,*sensitivity* (*a*) was very low (left panel) and the changeover frequency very high (right panel). As HD_{COD} increased, *sensitivity* increased slowly at first, and very sharply after HD_{COD} surpassed a certain interval (~[2, 3]); this phenomenon was accompanied by a large decrease in the frequency of switching between alternatives. Note that these results are almost identical, qualitatively and quantitatively, with those reported by Popa & McDowell (2010). The main advantage offered by this measure (HD_{COD}) is that it is a continuous variable. Also, it provides an explanatory mechanism for the phenomenon described initially.

As the figure illustrates, a certain minimum is necessary for obtaining typical levels of undermatching. Once above this minimum, further increases in the HD_{COD} hadvirtually no effect on behavior. However, Popa and McDowell (2011b) showed that when the mutation rate was increased, further increases in HD_{COD} do impact behavior, meliorating the detrimental effects of mutation. Therefore, increases in the HD_{COD} may not have a visible impact at typical mutation levels, but they may have important effects at high mutation rates.

Experimental design

Table 1 offers an overview of the experimental design. The rate of mutation was manipulated directly. The eight values chosen for this project were 5%, 10%, 20%, 30%, 40%, 50%, 75%, and 100%.The Hamming Distance changeover delay (HD_{COD}) cannot be manipulated directly, because the structure of the continuum of integers cannot be modified. Therefore, in order to modify the relation between the average Hamming Distances in the two classes, this variable was manipulated *indirectly*, by changing the location of the target classes.The six HD_{COD}

values chosen for this project were 1.4 (extremely low), 2.3, 3.4, 4.4 (high, historical standard), 5.4, and 6.4; they can be examined in Table 1, along with the locations that constituted the boundaries between classes.The overall reinforcement rate (or density) was manipulated directly. The smallest overall scheduled rate of reinforcement was ~3.4 rewards per 500 generations. The next four values were calculated so that they were 5 times, 10 times, 50 times, and 500 times higher than the smallest value. Therefore, the overall scheduled reinforcement rates (scheduled per 500 generations) were: ~3.4 (very scarce), ~17, ~34 (moderate), ~172, and ~1,723 (extremely rich). The middle value, 34, is very close to the one previously investigated (~28; McDowell & Popa, 2010); for the purpose of this project it is considered to be a standard, moderate reward rate. The magnitude of the reinforcement was manipulated directly by manipulating its computational equivalent, namely the strength of the selection process (McDowell, 2004; McDowell, Caron, Kulubekova, & Berg, 2008). The strength (or severity) of the selection process depends only on the mean of the parental selection function (μ, Equation 5), with smaller means indicating stronger selection events, therefore higher reinforcement magnitudes. The five values chosen for this project were 25 (strong selection), 50, 100 (moderate), 200, and 500 (weak selection, small reward magnitude).

Overall, the first phase entailed 8 x 6 + 8 x 4 + 8 x 5 = 112 experimental conditions. Five experiments were run for each condition. This yielded 560 experiments, with a total of ~120 million generations of responding, hence 120 million reiterations of the cycle Emission → Selection → Recombination → Mutation (and all the computations entailed by each step). Given these particular experimental settings, the average duration of an experiment (220,000 reiterations) was approximately 200 minutes. Therefore, the entire collection of experiments described here would require, under ideal conditions (no power outages, no down-times, etc.), approximately 1,200 hours (~50 days) of continuous running, at 100% processor usage. Given the high computational requirements, the exploratory nature of this study, and the vast amount of information, Rate x Magnitude x HD_{COD} interactions were not investigated. Their combined effects constitute a priority for future studies.

Results

Measures

Traditional descriptors of continuous-choice (behavior and reward rates, *sensitivity* bias, and proportion of variance accounted for). Behavior and reward rates on each alternative (B_1, B_2, r_1, r_2) were summed per 500 generation blocks. The 40 data points (20,000 generations / 500) were averaged, resulting in overall behavior and reward rates for each alternative, per RI RI component. Each experiment arranged 11 RI RI pairs (or components). For each RI RI pair, the ratios of behaviors (B_1/B_2) and obtained rewards (r_1/r_2) were transformed to logarithms, as required by Equation 3. The slope of the straight line formed by these 11data points gave the *sensitivity* value (a) for that particular organism, in that particular experiment. The intercept of the line, log(b), was used to calculate the bias parameter ($b = 10^{\text{INTERCEPT}}$). The correlation coefficient between logs of responses and rewards was squared (r^2), providing a measure of the proportion of variance accounted for (pVAF) by Equation 3. In addition, a total average frequency (per 500 generations) of target behaviors ($B_1 + B_2$) and obtained rewards ($r_1 + r_2$) was calculated for each organism.

The changeover (CO) profiles were examined by fitting a quadratic polynomial (Equation 6),

$$y = ax^2 + bx + c, \qquad \text{Eq.6}$$

to the average COs per RI RI component, pooled across the five repetitions (5 x 11 = 55 data points, averaged per 500 generations), where $y$is the average changeover (CO) frequency and x is the proportion of reinforcement obtained from the first alternative. As discussed by McDowell et. al (2008), the vertex of the fitted parabola is an estimate of the maximum CO rate for a set of concurrent schedules;it is given by Equation 7,

$$\mathrm{CO}_{\mathrm{MAX}} = c - \frac{b^2}{4a}. \qquad \text{Eq.7}$$

Topographic variability ($\Delta_{\mathrm{PHENOTYPE}}$). Behaviors' phenotypes are represented by integers. At each time tick a behavior is randomly selected from the population and it is emitted. This can be conceptualized as the moment-to-moment topographic variability of a live organism. A rat can press the lever, then go to the back of cage, then come back and press the other lever; or, it may "stay on task" and emit a bout of responses on one lever. Similarly, if we consider a class of operands between 512 - 552, the organism can "press the lever twice in a row" (e.g. 515, 535), then "wander in the back of the cage" (e.g. 985), then "explore the immediate proximity of the lever" (e.g. 557). The absolute difference between two consecutive phenotypes, or emissions(Δ) is a measure of how "abrupt", topographically different, two successive behaviors are. For example, the succession 512 - 980 can be conceptualized as "pressing this lever" - "run to the back of the cage" or "reading from a book" - "climbing the furniture". The average of all these consecutive differences ($\Delta_{\mathrm{PHENOTYPE}}$) provides a measure of the overall "smoothness" of continuous behavior.

Small $\Delta_{\mathrm{PHENOTYPE}}$ values indicate smooth transitions between activities. For example, the sequence 512, 514, 516, 556, 558, 556, which yields a $\Delta_{\mathrm{PHENOTYPE}}$ of 50/5 = 10, can be conceptualized as three consecutive lever presses followed by a pause spent in the close vicinity of the levers. On the other hand, the sequence 512, 912, 512, 102, 512, 102, which yields a $\Delta_{\mathrm{PHENOTYPE}}$ of 2,000/5 = 400, can be conceptualized as a lever press, immediately followed by going to the back of the cage, then immediately returning to the lever, and so on. Although both sequences contain the same number of target behaviors, the continuous behavior described by the two sequences is very different. The first sequence ($\Delta_{\mathrm{PHENOTYPE}}$ = 10) describes sustained on-task behavior followed by a pause spent close to the lever (analogous to a student that spends a chunk of time working on a paper and then checks his Facebook page for 10 minutes). The second sequence ($\Delta_{\mathrm{PHENOTYPE}}$ = 400) describes a behavioral pattern marked by rapid, abrupt changes:

sporadic target responding, followed by abandoning the task and rearing in a corner of the cage, followed by another target response, and so on (analogous to a student who writes a sentence, then goes to the kitchen, then writes another sentence, then watches TV for 5 minutes, and so on). The average, moment-to-moment topographic variability for one organism (or experiment) was calculated by averaging all the differences between two consecutive phenotypes (emissions), for an entire experiment (220,000 emissions → 219,999 differences). Averaging the five averages yielded a grand average (one data point) per experimental condition.

Inter Bout Time (IBT).The average time spent between bouts constitutes a low-level, basic measure of the time that elapses between the moment when the organism abandoned a sustained activity and the moment when it re-engaged in a sustained activity (on either alternative).A bout was considered to begin when a target behavior was emitted.All behaviors that followed were considered to be part of that bout. A bout was consider terminated when a switch occurred (changeover, a behavior occurred in the other target class) or when the organism emitted extraneous behaviors for more than ten consecutive time ticks. This condition was necessary because the organisms emitted a lot of extraneous responses that can be conceptualized as "doing something else", like rearing in the back of the cage. The decision to end a bout after ten time ticks was semi-arbitrary. Because of the large volume of data only thisduration was examined here but it would be interesting to investigate the effects of more or less relaxed definitions for what counts as a bout. It should be noted that the minimum bout length was three. Two consecutive responses were not counted as a bout;they were considered sporadic responses. The duration of an Inter Bout Intervalwas calculated as the difference between the end of one bout and the beginning of the next, regardless of the alternative in which the organism engaged (target class 1 or 2). The average inter bout time (IBT) for an experiment was obtained by averaging all the inter bout intervals, for the entire experiment (220,000 generations). Averaging the five averages yielded a grand IBT average (one data point) per experimental condition.

Bout frequency, bout length, and sustained (or in-bout) behavior. The average number of bouts was calculated for each experimental condition, averaged per 500 generations. Their average length (responses per bout) was obtained in a straightforward manner, by dividing the absolute frequency of bout behaviors by the absolute frequency of bouts. These variables were informative in themselves, but they also allowed to calculatethe average frequency of sustainedtarget behavior(or bout-behavior, averaged per 500 generations). Target behaviors can occur in sustained, ordered sequences, like a child spending one hour to *solve math problems*, another two hours *working on an assignment*, 40 minutes *playing video games*, and so on. They can also occur in sporadic instances, like working on a math problem for a few minutes, writing a few sentences for an assignment, going back to the math problem, and so on. All these are target responses, but there is a qualitative difference between the first, ordered pattern, which is highly desirable and more likely to produce high-quality work, and the second pattern, which denotes a sporadic, fractured behavior pattern. An overall analysis that would take into account only target behavior would ignore such differences, which may carry important information about the quality of behavioral patterns.Therefore, target behavior can be expressed as Sustained Behavior + Sporadic Behavior. From this relation, the proportion of sustained, or in-bout behavior can be calculated with the formula

$$\text{Sustained Behavior (\%)} = \frac{Bouts \cdot Average\ bout\ length}{All\ Target\ Behavior}, \qquad \text{Eq. 8}$$

which gives a quantity that varies between 1 (100% of target behavior occurred in bouts) and 0 (all target behavior was sporadic, disorganized behavior). To the author's knowledge, the proportion of sustained behavior and the moment-to-moment topographic variability ($\Delta_{\text{PHENOTYPE}}$) were not systematically investigated in the live-organism literature; they may constitute interesting and informative additions to the other behavioral measures investigated here.

General presentation format

In all the figures presented in this paper, the moderate environment, characterized by moderate reinforcing *value* (~34 reinforcers per 500 generations, μ = 100), was represented by a continuous black line with grey squares. In all figures, theleft panels depict effects of reinforcement density (or rate), the middle panels depict the effects of reinforcement magnitude (strength of the selection process), and the right panels depict effects of Hamming Distance changeover delay (HD_{COD}). In all figures the *x*-axis represents mutation rate (0 - 100%).

Sensitivity (*a*), changeovers (CO_{MAX}), and topographic variability ($\Delta_{PHENOTYPE}$)

Figure 5 shows the effects of various reinforcement densities (left), various strengths of the selection process (<=> reinforcement magnitude, middle), and various HD_{COD} values (right) on *sensitivity* values (*a*, panels 1, 2, 3), maximum changeover frequency (CO_{MAX}, panels 4, 5, 6), and topographic variability ($\Delta_{PHENOTYPE}$, panels 7, 8, 9), at different mutation rates. Overall, organisms characterized by higher mutation rates showed smaller *sensitivity* to reward, switched more often between alternatives, and displayed a larger moment-to-moment topographic variability. The effects of high mutation rates were mediated by the environment's *value*(left and center panels) and *conduciveness* (right panels), with one notable exception: varying the HD_{COD} values had almost no impact on $\Delta_{PHENOTYPE}$, regardless of the rate of mutation (Figure 5, panel 9).

***Sensitivity* (*a*): effects of reward rate (Figure5, panel 1)**.When the density of reinforcement was very low (~3.4reinf/ 500 gen) even organisms characterized by moderate mutation rates (~5-20%) displayed moderate *sensitivity* values,*a* never exceeding 0.75 and dropping rapidlyand to very low values as mutation rate increased above 30% ($a \rightarrow 0.1$). When the overall rate of reinforcement was increased to ~17reinf./500 gen, organisms characterized by low to moderate mutation rates showed typical *sensitivity* values (5 - 20%,*a*~0.8). As mutation rate increased, the exponent values decreased as well, but more slowly and towards larger absolute values. The largest impact was observed at mutation rates between 20% and 75%. In these conditions exponent values were noticeably larger (*a* ~ 0.5 - 0.25), but still described severe undermatching. When the reward density was increased to ~34 (moderate rate), mutation rates between ~5 - 15% produced typical *sensitivity* values (*a* ~ 0.8). *Sensitivity* decreased rapidly as the rate of mutation increased to 40-50% (*a* ~ 0.5). Organisms characterized by mutation rates higher than 50% showed severe levels of undermatching (*a* ~ 0.2). Increasing reinforcement density even further, to ~172 (per 500 generations) had virtually no effects on *sensitivity* values at low to moderate mutation rates (5-20%, *a* ~0.8). However, organisms characterized by high mutation rates (30-50%) performed remarkably well (*a* ~0.7).As the rate of mutation increased above 50% *sensitivity* decreased towards 0.5, far from the indifference to consequences exhibited in scarcer environments. When reinforcement density was increased to ~1,700, *sensitivity* varied around 0.8 for mutation rates between 5 and 20%, after which it decreased towards a minimum of 0.6 (100% mutation). When scheduling ~1,723 reinforcers per 500 generations, even though reinforcement was delivered at random intervals, the environment was so rich that most target behaviors acquired resources. The high exponent values produced by this environment at very high mutation rates may have been artifacts of the high rates of reinforcement and not the expression of behavior controlled by consequences.

***Sensitivity* (*a*): effects of reward magnitude (Figure 5, panel 2).** Overall, exponent values (*a*) increased with the strength of the selection process (Figure 5, panel 2), but the relation was mediated by mutation rate. As a reminder, the strength of the selection process was found to be computationally equivalent to the magnitude of the reinforcement (McDowell, 2004; McDowell et. al., 2008). The severity of the selection process depends on the mean (μ) of the parental selection function (Equation 5), with smaller means indicating stronger selection events (only very fit behaviors have real chances of becoming parents), hence higher reinforcer magnitudes. When the selection process was very weak (μ = 500) *sensitivity* was very low for all mutation rates, decreasing sharply from ~0.5 (5% mutation) towards 0.1 (mutation rates >20%). Increasing the strength of the selection process (μ = 200) produced noticeably higher *sensitivity* values at all mutation rates. For mutation rates of 5 and 10%,*sensitivity* varied around 0.8. It decreased to approximately 0.5 for mutation rates of 20%, after which it decreased towards 0.2.

Increasing the strength of the selection process even further (μ = 100, moderate magnitude) had little effect at low mutation rates (5-20%). However, stronger selection events had significant impact on the behavior of organisms characterized by mutation rates of 20-40%, with exponents varying between 0.5 and 0.8. As the rate of mutation increased above 50% s*ensitivity* decreased towards ~0.2, value that describes severe undermatching.When the severity of the selection process was increased even further (μ = 50), organisms characterized by mutation rates between 5 and 40% displayed typical *sensitivity* values (a ~ 0.8). With further increases in the rate of mutation, the exponents dropped towards 0.25 (at 100% mutation). Very strong selection processes (μ = 25) produced exponents that varied around typical values (a ~ 0.8) for mutation rates between 5 and 50%. As the rate of mutation increased towards 100% *sensitivity* decreased towards 0.4, a remarkably high value for this mutation rate.

***Sensitivity* (*a*): effects of the Hamming Distance changeover delay (HD_{COD}; Figure 5, panel 3).** When the rate of mutation was between 5% and 20% HD_{COD} values greater than ~3 produced exponents that varied around the typical values observed in live organisms (a ~0.8). When the HD_{COD} was 2.4 the exponents varied around 0.5, mathematically indicating a large degree of undermatching. When the HD_{COD} was 1.4 organisms characterized by mutation rates of 5-20% exhibited very severe undermatching (a ~0.2).When the rate of mutation increased above 20%, small HD_{COD}values (1.4 and 2.4) caused*sensitivity*to drop rapidlytoward small absolute values. Larger HD_{COD} values generally produced larger exponents, caused a less rapid decline in exponents' values, and produced larger absolute minimum values. As is apparent from the figure, it seems that HD_{COD} values can be grouped intothree categories, based on their effects on *sensitivity*: "low", "large", and "intermediate". HD_{COD} values of 1.4 and 2.4 can be labeled "low"values and 4.4, 5.4, and 6.4 can be labeled "large" (or "good") values (they produced "good" matching). The intermediate value, 3.4, seems to belong to a "grey" category, behaving as a "large" value at low-moderate mutation rates and as a "low" value at mutation rates greater than 30-40%.

Changeovers (CO_{MAX}): effects of reward rate (Figure 5, panel 4). Overall, as the rate of mutation increased,the frequency of changeovers between alternatives (CO_{MAX}) increased in a roughly hyperbolic pattern, at all reinforcement rates. Changes in the overall reinforcement density did not have a dramatic impact on CO_{MAX}, with one exception. When the overall scheduled reinforcement rate was extremely high (~1,723reinf/500 gen) organisms characterized by low-medium mutation rates (5-30%) switched noticeably less often than in all other conditions. In addition, as mutation rate increased, CO_{MAX} increased roughly logistically and not hyperbolically.

Changeovers (CO_{MAX}): effects of reward magnitude (Figure 5, panel 5). CO_{MAX} was noticeably affected by changes in the strength of the selection process (reinforcement magnitude). In this case, environments characterized by stronger selection events produced smaller CO_{MAX} values at all mutation rates (unlike changes in reinforcement density). Differences in CO_{MAX} increased as mutation rate increased, the most affected organisms being those characterized by medium mutation rates (20-30%). As the rate of mutation increased beyond these values the effects of various strengths of the selection process diminished considerably. The decrease in CO_{MAX} at higher reinforcement rates and magnitudes hasnot yet been investigated in the live organism literature, to the authors' knowledge. Therefore, it constitutes a direct, easy to test prediction made by the Evolutionary Theory.

Changeovers (CO_{MAX}) : effects of HD_{COD}(Figure 5, panel 6). The effects of various HD_{COD} values on CO_{MAX} were extremely interesting and somewhat puzzling. Overall, at all mutation rates, greater HD_{COD} values caused the organisms to switch less often between alternatives, which was expected. Also, for HD_{COD} values of 4.4, 5.4, and 6.4 ("large" values) , CO_{MAX} increased systematically with the rate of mutation, from ~1 changeover (5%) to ~5 changeovers (100% mutation) per 500 generations; these trends were also expected. What was surprising was the switching behavior produced by HD_{COD} values less than ~3.5. When the HD_{COD} was 1.4, organisms characterized by mutation rates of 5% switched most often between alternatives (almost 40 times more often than when HD_{COD} was 4.4). However, as the rate of *mutation increased*, CO_{MAX}*decreased*, reaching its minimum when mutation rate was 100%! Although its minimum, at 100% mutation, was still higher than all other CO_{MAX} values observed at 100% mutation, this pattern was not expected. A similar but less pronounced pattern was observed when HD_{COD} was increased to 2.4 (still "low" value): the maximum CO_{MAX} value was observed at 5% mutation (~16/500 gen) and the minimum, at 100% mutation (~5.5). When HD_{COD} was increased to 3.4, CO_{MAX}*increased* when the mutation rate increased from 5% to 20%, then*decreased* as the rate of mutation increased further. This pattern can be categorized as a "transition", or "hybrid" pattern, which is interesting considering that the 3.4. HD_{COD}value produced *sensitivity*values(*a*; Figure 5, panel 3) values that can be labeled as "intermediate" (*a* ~0.5), between mathematical indifference (*a* ~ 0.0) and typical undermatching (*a* ~0.8).

Topographic variability ($\Delta_{PHENOTYPE}$): overview.At each generation the organism emitted a behavior, abstractly represented by an integer. The absolute differences between two consecutive phenotypes, or emissions provided a measure of the topographical difference between two successive behaviors. It varies between 0 (same behavior is emitted twice in a row) and 2,047, half of the continuum's size (4,095). This is not too different from real world scenarios, where the behavior of a live organism is limited by a variety of factors (e.g. size of the accessible environment, biological constraints, etc). The average of all these consecutive differences ($\Delta_{PHENOTYPE}$) provided a measure of the overall "smoothness" of continuous behavior, with small $\Delta_{PHENOTYPE}$ values indicating smooth transitions between activities and large $\Delta_{PHENOTYPE}$ values indicating rapid, abrupt behavioral changes (e.g. sporadic target responding, followed by abandoning the task and rearing in a corner of the cage, followed by another target response, and so on). As illustrated in Figure 5 (panels 7, 8, 9), $\Delta_{PHENOTYPE}$ increased roughly hyperbolically with the rate of mutation. Overall, increasing the environment's *value* produced smaller $\Delta_{PHENOTYPE}$ values at all mutation rates. The effects were more pronounced at low-moderate mutation rates; they diminished as the rate of mutation increased. Different HD_{COD} values did not have a noticeable effect on $\Delta_{PHENOTYPE}$.

$\Delta_{PHENOTYPE}$: effects of reward rate (Figure 5, panel 7). As is apparent from Figure 5 (panel 7), increasing the overall reinforcement density from ~3.4 (very scarce environment) to ~34 (moderately rich environment) had asignificant impact at low mutation rates. For example, at 5% mutation, $\Delta_{PHENOTYPE}$ was reduced by approximately 30% (from ~900 to ~600). When increasing the rate of reinforcement to ~172, organisms characterized by low mutation rates exhibited much lower levels of topographic variability ($\Delta_{PHENOTYPE}$ reduced to ~250 at 5% mutation). When arranging extremely rich environments (~1,723reinf/500 gen) organisms characterized by mutation rates between 5% and 30% showed a large reduction in topographic variability ($\Delta_{PHENOTYPE}$ ~150 at mutation rates of 5 and 10%). Under all experimental conditions, the effects of higher reinforcement density decreased as mutation rate increased.

$\Delta_{PHENOTYPE}$: effects of reward magnitude (Figure 5, panel 8). Increasing the strength of the selection process (Figure 5, panel 8) produced smaller $\Delta_{PHENOTYPE}$values at all mutation rates. The effects were larger at small mutation rates, diminished as the rate of mutation increased, and were practically annulled at very large mutation rates.

$\Delta_{PHENOTYPE}$: effects of HD_{COD}(Figure 5, panel 9). As the rate of mutation increased, $\Delta_{PHENOTYPE}$ increased as well, in a roughly hyperbolical pattern. Different HD_{COD} values had little or no impact on $\Delta_{PHENOTYPE}$, regardless of the rate of mutation that characterized the virtual organisms.

Target behavior and obtained reinforcers

Figure 6 shows the effects of various reinforcement densities (left), various strengths of the selection process (middle), and various HD_{COD} values (right), on the overall frequency of target behavior (panels 1, 2, 3) and obtained rewards (panels 4, 5, 6), at various mutation rates. Behaviors and rewards were summed for both alternatives and averaged per 500 generations.

Overall, the frequency of target behavior and obtained rewards decreased systematically with the rate of mutation.

Target behavior and obtained reinforcers: effects of reward rate (Figure 6, panels 1 and 4).Increasing the reinforcement density while maintaining the strength of the selection process constant ($\mu = 100$; left panels) produced noticeable increases in the frequency of target behavior. These effects were very large at small mutation rates. In very scarce environments (~3.4 rewards) organisms characterized by mutation rates of 5% emitted, on average,approximately 25 target responses/500 generations. Increasing reinforcement density to ~17 caused the same organisms to emit almost three times more target responses (~75). Increasing reinforcement density to ~34 (moderate rate)increased the frequency of target behavior to approximately 110. Increasing reinforcement density to ~172 (very rich environment) produced approximately 200 target responses; increasing it to ~1,723 produced approximately 250 responses (per 500 generations). These effects diminished rapidly as the rate of mutation increased. For example, organisms characterized by 50% mutation emitted between 12 and 35 responses under the most extreme conditions (~3.4 reinforcers and ~1,723 reinforcers respectively). The pattern of obtained rewards (Figure 6, panel 4) closely followed the pattern of behavior frequency. At low mutation rates (5%) reinforcement densities between ~3.4 and ~34 produced between 2 and 17 reinforcers (per 500 generations). When reinforcement density was increased to ~172, same organisms acquired approximately 75 reinforcers. When the rate of reinforcement was ~1,723, the average number of acquired reinforcers increased to approximately 200. As the rate of mutation increased, the effects of reinforcement density decreased. Overall, in environments that arranged low to moderate reinforcement rates (~3.4 - 34 reinforcers / 500 generations) increases in mutation rate caused the frequency of target behavior (panel 1) and acquired rewards (panel 4) to drop quickly. Very rich environments (~172 and 1,723) maintainedrelatively high frequencies of target behaviors and obtained rewards even at mutation rates of 20 - 30%.

Target behavior and obtained reinforcers: effects of reward magnitude (Figure 6, panels 2 and 5).When reinforcement density was held constant (~34 reinforcers per 500 generations) systematic modifications in thestrength of the selection process (middle panels) had similar effects to those produced by increased reinforcement densities (left panels). The frequency of target behavior (Figure 6, panel 2) increased to very high values (frequency varied between 25 and 200) at 5% mutation. These effects decreased rapidly with the rate of mutation, becoming practically annulled at mutation rates larger than 50% (towards the operant, or baseline level of responding). Same effects were observed in the number of acquired rewards. Strong selection processes (high magnitudes) produced significant increases in the number of acquired rewards (from 8 to about 20, at 5% mutation). These effects decreased rapidly with the rate of mutation. Note that increasing either the rate or magnitude of the reinforcement had similar qualitative and quantitative effects on the frequency of target behavior (panels 1 and 2). Their effects on the number of acquired reinforces was qualitatively similar (panels 4 and 5). However, at mutation rates between 5 and 50%, arranging richer environments produced almost ten times more reinforcers (~200, at 5% mutation) than increasing reward's magnitude (stronger selection events; ~20, at 5% mutation). This result was not surprising. While both rate and magnitude tend to concentrate behaviors around the target classes, thus producing larger frequencies of target behaviors, increases in rate also cause more of these behaviors to be successful.

Target behavior and obtained reinforcers: effects of HD_{COD} (Figure 6, panels 3 and 6).As the rate of mutation increased, the frequency of target behavior decreased rapidly. The same pattern characterized the frequency of obtained rewards. Various HD_{COD} values had little effect on the frequency of target behavior, regardless of the rate of mutation. The only exception was observed when the HD_{COD} was very small (1.4). In this environment the average frequency of target behavior was approximately 30% higher than in all other conditions, but only at mutation rates of 5 - 20%. For higher mutation rates the differences were barely noticeable; the average frequency of target behavior was very similar at various HD_{COD} values.The pattern in the frequency of obtained rewards closely followed the pattern of target behavior. The average frequency of acquired rewards (per 500 generations) decreased rapidly as the rate of mutation increased. However, the effects of various HD_{COD} values were more pronounced than in the case of target behavior, especially at low-moderate mutation rates (5 - 30%). Small HD_{COD} values caused the virtual organisms to obtain more rewards, an effect that diminished as the rate of mutation increased.

Bout frequency and length

Figure 7 illustrates the effects of reinforcement density (left), reinforcement magnitude (middle),and HD_{COD} (right), on the average bout frequency (panels 1, 2, 3)and length (panels 4, 5, 6), at various mutation rates. Overall, organisms characterized by higher mutation rates emitted fewer bouts, of shorter length, a relation mediated by reward rate, reward magnitude, and HD_{COD}.

Bout frequency: effects of reward rate (Figure 7, panel 1). When the environment was rich (~172 and ~1,723 reinforcers per 500 generations) the average number of bouts increased with the rate of mutation, from ~2 (5% mutation) to ~ 5 (10-20% mutation), after which it decreased towards a minimum of ~ 1 bout/500 generations (100% mutation). For reinforcement ratesof ~34 and ~17, the average number of bouts decreased systematically with the rate of mutation, from ~4 (5-20% mutation) to approximately 0.75 (100% mutation). When the environment scheduled very few reinforcers (~3.4 rewards/500 generations) bout frequency decreased from a maximum of ~2.5 (5% mutation) to a very low absolute minimum (~0.25 at 100% mutation).

Bout frequency: effects of reward magnitude (Figure 7, panel 2). When reinforcement density was held constant (~34reinf / 500 generations), modifying reward magnitude had similar effects on bout frequency as modifying the reward density. As the rate of mutation increased, organisms placed in environments characterized by low reward magnitude (weak selection events,μ= 500 and 200) emitted fewer and fewer bouts. As the selection process became stronger (μ= 100, 50,and 25) the average bout frequency followed the same trend produced by high reinforcement densities: it increased as the rate of mutation increased from 5% to 10-20%, after which it decreased as the rate of mutation increased further (a trend probably caused by very large bout lengths, as will become apparent from the next paragraphs). It is important to note that bout frequency was heavily affected by both reinforcement rate and magnitude.Although the effects of rich environments and strong reinforcers diminished as the rate of mutation increased, they were still noticeable at high mutation rates (50-75%). Also, overall, stronger reinforcers tended to produce a slightly higher number of bouts than high reinforcement densities, effects more pronounced at mutation rates greater than 50%.

Bout frequency: effects of HD_{COD}.(Figure 7, panel 3). HD_{COD} values of 3.4, 4.4, 5.4, and 6.4 had little impact on bout frequency, regardless of the rate of mutation. When the HD_{COD} was 2.4 organisms characterized by mutation rates of 5% and 10% exhibited approximately 80% more bouts (~9/500 generation) than when the HD_{COD} was 3.4, 4.4, 5.4, or 6.4 (~5/500 generations). The same pattern, but more pronounced, was observed when the HD_{COD} was 1.4. Behavior characterized by mutation rates of 5% emitted approximately 17 bouts per 500 generations, almost four times more bouts than when the HD_{COD} was 3.4, 4.4, 5.4, or 6.4 (~5/500 generations). As the rate of mutation increased further, the effects of various HD_{COD} values became less pronounced, having very little impact once the rate of mutation increased above ~40%.

Bout length: effects of reward rate (Figure 7, panel 4). When reinforcement density was very large (~1,723 and ~172 per 500 generations)organisms characterized by mutation rates of 5% emitted remarkably long bouts. Their length varied between ~150 (~1,723 reinforcers, 5% mutation) and ~30 (~172 reinforcers, 10% mutation). The average bout length decreased as the rate of reinforcement decreased to ~34 reinforces (~25), ~17 reinforces (~17), and ~3.4 reinforces (~10). For all reinforcement densities, the average bout length decreased very rapidly as the rate of mutation increased. The detrimental effects of high mutation rates were more pronounced in environments that scheduled fewer reinforcers. In all environments, mutation rates higher than

~50% produced average bout lengths of ~3 responses/bout, the minimum number of responses that still constitutedа bout.

Bout length: effects of reward magnitude(Figure 7, panel 5). The effect of reward magnitude was very similar to that of reinforcement density. Weak to moderate selection events (μ= 500, 200, and 100) produced almost identical bout lengths as low to moderate reinforcement densities (~3.4, ~17, and ~34 reinforcers), at all mutation rates. When the selection events were very strong (μ= 50 and 25), organisms characterized by mutation rates of 5% emitted long bouts, with averages between ~45 and 70 responses per bout. As the rate of mutation increased, the average bout length decreased rapidly, reaching the theoretical minimum (3 responses/bout) when the rate of mutation increased above 50%. This trend was identical to that produced by very high reinforcement densities. However, at low mutation rates, high reinforcement densities produced bouts that were almost twice as long as those produced by strong selection processes. The overall large number of responses per bout produced by high reinforcement rates and strong selection events could explain why organismscharacterized by mutation rates of 5 and 10% emitted relatively few bouts (Figure 7, panels 1 and 2).

Bout length: effects of HD_{COD} (Figure 7, panel 6).HD_{COD} values of 3.4, 4.4, 5.4, and 6.4 had little impact on the average bout length, regardless of the rate of mutation. When the HD_{COD} was 2.4 organisms characterized by mutation rates of 5% and 10% exhibited bouts that were approximately 50% shorter than when the HD_{COD} was 3.4, 4.4, 5.4, or 6.4 (~12 responses per bout vs. ~20 responses per bout). The same pattern, but more pronounced, was observed when the HD_{COD} was 1.4. Organisms characterized by mutation rates of 5% emitted bouts with an average length of only ~6 responses per bout. As the rate of mutation increased further, the effects of various HD_{COD} values became less pronounced, having very little impact once the rate of mutation increased above ~30%.

Sustained (in-bout) behavior (%)and Inter-Bout Time (IBT). Figure 8 illustrates the effects of reinforcement density (left), reinforcement magnitude (strength of the selection process;

middle), and HD_{COD} (right), on the proportion of sustained (or in-bout) behavior (panels 1, 2, 3) and Inter-Bout Time (IBT; panels 4, 5, 6), at various mutation rates.Overall, organisms characterized by higher mutation rates exhibited smaller proportions of sustained behavior and took longer times, on average, to re-engage in sustained responding (starting another bout of responses) once a bout was terminated (longer IBT). Increasing the rate or the magnitude of the reinforcement improved the performance of organisms characterized by high mutation rates on both dimensions. Various HD_{COD} values had smaller impact, especially on IBT values.As a reminder, the proportion of sustained behavior (Equation 8) was calculated by dividing the frequency of target behavior that occurred in bouts (bouts x bout length) bythe frequency of target behaviors (averages per 500 generation blocks). Sustained behavior provided a measure of how structured, or organized, the target behavior is, by discarding the target sporadic responses.

Sustained behavior (%): effects of reward rate (Figure 8, panel 1).Overall, lower rates of reinforcement produced smaller proportions of sustained behavior. The effects of reinforcement rates increased at first, then decreased as the rate of mutation increased. Organisms characterized by mutation rates of 5% displayed a very high proportion of sustained behavior (> 95%), at all reinforcement densities. The only exception was observed when the rate of reinforcement was extremely small (~3.4reinf/500 generations): the average frequency of sustained behavior was approximately 80%. As the rate of mutation increased, the proportion of sustained behavior decreased as well. The effects of mutation were mediated by reinforcement density; high reinforcement densitiescaused organisms characterized by high mutation rates to emit fairly high proportion of sustained behavior. For example, when the overall reward density was ~172, the proportion of sustained behavior emitted by organisms characterized by mutation rates of 50% was approximately 54%. When the reward density was decreased to ~34 and ~17, the proportion of sustained behavior displayed by the same organisms (50% mutation) decreased to ~40% and ~32% respectively. Decreasing the overall reward rate even further (~3.4 rewards/500 generations) caused organisms characterized by moderate mutation rates (20%

mutation) to respond in a very disorganized manner. Less than 50% of their total target behavior was organized in bouts (sustained behavior), the majority consisting of sporadic responses. When the rate of mutation was 50% the proportion of sustained behavior was only ~17%.

Sustained behavior (%): effects of reward magnitude (Figure 8, panel 2). The effects of various reinforcer magnitudes were very similar to those produced by various reinforcement rates. However, weak selection events (μ= 500 and 200) produced slightly smaller proportions of sustained behavior than scarce environments (~3.4 and ~17/500 generations).

Sustained behavior (%): effects of $\mathbf{HD_{COD}}$ (Figure 8, panel 3). Overall, as the rate of mutation increased, the proportion of sustained behavior decreased. Large HD_{COD} values (4.4, 5.4, and 6.4) had very little impact on the proportion of sustained behavior, regardless of the rate of mutation. Organisms characterized by mutation rates of 5-10% responded almost exclusively in bouts, emitting very few sporadic target behaviors (proportion of sustained behavior > 95%). As the rate of mutation increased, the proportion of sustained behavior decreased towards very low minimum values (20% at 100% mutation). When the HD_{COD} was 2.4 and 1.4 ("low" values), the proportion of sustained behavior exhibited by organisms characterized by low mutation rates (5 and 10%) diminished from about 95% (large HD_{COD}= values) to approximately 80% and 70% respectively. At higher rates of mutation various HD_{COD} values had little or no effect on the proportion of sustained behavior.

Inter-Bout Time: effects of reward rate (Figure 8, panel 4). Increasing the reinforcement rate produced smaller IBTs; the effects were more pronounced as the rate of mutation increased. When the rate of reinforcement was very low (~3.4 rewards/500 generations) the average IBT increased sharply from approximately 180 time ticks (5% mutation) to approximately 2,000 time ticks (100% mutation). This trend was observed at all reinforcement densities, but was largely diminished in richer environments. For example, when the overall reward density was increased to ~17, the average IBT increased from approximately 80 time ticks (5% mutation) to approximately 1,100 time ticks (100% mutation). The increase was very large and rapid, but the absolute values, across all mutation rates, were practically reduced to half. Increasing the rate of reinforcement even further (~34, ~172, and ~1,723 reinforcers) diminished the effects of large mutation rates even further. The effects of reward density diminished as the density increased. For example, the overall differences between reward rates of ~34 and ~172 were overall larger than between reward rates of ~172 and ~1,723 (the change in IBT was rather small). Note that, overall, differences in IBT values at small-moderate mutation rates were rather large, in absolute values. For example, organisms characterized by mutation rates of 10% exhibited IBT values of ~230, ~100, ~75, ~35, and ~20, at reward densities of ~3.4, ~17, ~34, ~172, and ~1,723. These rather large differences were obscured in the figureby the huge differences observed at high mutation rates.

Inter-Bout Time: effects of reward magnitude(Figure 8, panel 5). The effects of various reinforcement magnitudes (various strengths of the selection process) on IBT were very similar to those produced by various reward densities. When the selection process was very weak (μ = 500) IBT increased sharply from approximately 160 time ticks (5% mutation) to approximately 2,700 time ticks (100% mutation). The same trend was observed for all reward magnitudes. The absolute values, however, were much smaller when the selection events were very strong (large magnitudes). For example, when the strength of the selection process was increased fromμ = 500 to μ = 200, the average IBT increased from approximately 80 time ticks (5% mutation) to approximately 1,500 time ticks (100% mutation). The increase was sharp, but the average IBT durations, across all mutation rates, were drastically reduced. Stronger selection events (μ=100, 50,and 25) counteracted the effects of large mutation rates even further, and were visible even at low mutation rates. For example, the average IBTs produced by organisms characterized by mutation ratesof 10% were~225, ~110, ~75, ~60, for means (μ) of 500, 200, 100, and 50. As the strength of the selection process increased, its effects on the average IBT decreased.

Inter-Bout Time: effects of HD_{COD} (Figure 8, panel 6).As apparent from, various HD_{COD} values had little impact on the average Inter-Bout Time (IBT). As the rate of mutation increased, the average IBT increased from approximately 50 time units (at 10% mutation) to approximately 1,000 time units (100% mutation). When the rate of mutation was small-moderate (5 - 20%) the effects of various HD_{COD} values were barely noticeable, varying between ~20 (HD_{COD} = 1.4) and ~60 (HD_{COD} = 6.4), at 5% mutation. As the mutation rate increased, the effects of various HD_{COD} values became more pronounced, with larger HD_{COD} producing greater IBTs, but still much smaller in absolute values than those produced by low reward rates or magnitudes.

Discussion

The purpose of the first phase was to learn about the effects of mutation on various behavioral features of continuous choice, and about the mediating effects of different reward rates, reward magnitudes, and Hamming Distance Changeover Delays (HD_{COD}). The dependent variables included the traditional measures examined in the live organisms literature (*sensitivity*, response and reward rates, etc.), but also low-level characteristics pertaining to behavior variability, some of which have not been investigated in the live organisms literature (e.g. $\Delta_{PHENOTYPE}$).

General effects of mutation

In environments characterized by a large HD_{COD} (4.4; low *conduciveness*),that scheduled a moderate number of reinforcers (e.g. ~34 reinforcers per 500 generations), of moderate magnitude (μ = 100), organisms characterized by higher mutation rates performed much worse than those characterized by smaller mutation rates. As the rate of mutation increased, *sensitivity* to reinforcement(*a*) decreased from typical values at moderate mutation rates (*a* ~0.8 at 5-20% mutation) toextreme undermatching (*a*~0.2for mutation rates higher than 50%). The decrease in *sensitivity* was accompanied by a largeincrease in the frequency of switchingbetween alternatives (high CO_{MAX}).These results reliably paralleled previous findings (McDowell & Popa, 2010). Moreover, the outcomes generated by the computational theory were robust with respect to the size of the continuum of integers (4,096 instead of 1,024) and to the form of the parental selection function (exponential instead of linear; McDowell & Popa, 2010).In addition to low *sensitivity*and high changeover frequency, organisms characterized by higher mutation rates emitted much lower rates of target behavior and obtained significantly fewer rewards. They emitted fewer bouts, of shorter length, and took much longer to re-engage in sustained behavior once a bout was terminated (larger IBT). They exhibited much smaller proportions of sustained behavior, their target behavior being sporadic and disorganized. The temporal disorganization was accompanied by abrupt topographical changes (large $\Delta_{\text{PHENOTYPE}}$).

Mutation and ADHD

The behavioral constellation described above is strikingly similar to behavioral characteristics observed in ADHD-diagnosed children. When compared to their non-diagnosed counterparts, the continuous-choice behavior of children who received an ADHD diagnostic was characterized by diminished *sensitivity* to reward (a~ 0.3) and a high frequency of switching between alternatives (Kollins et. al., 1997; Taylor et., al., 2010). In addition, core features of hyperactive-impulsive children include short amounts of time spent on task and decreased productivity, rapid task abandonment, and difficulties re-engaging in task behavior once the activity was abandoned (Mash &Barkley, 2003). The topography of their behavior is also an issue of concern, hyperactive-impulsive children being described as displaying abnormally high levels of motor activity (Abikoff&Gittelman, 1985), "always on the go", "moving as being driven by a motor", "unable to sit still", "moving about", "rapidly distracted by interfering stimuli/activities" etc. (Mash & Barkley, 2003; Waslick& Greenhill, 2004).

Interestingly, a single organismic feature, namely mutation rate, produced the entire constellation of behavior characteristics described above. In ADHD children similar behavioral features are apparently produced by one property of the nervous system that directly affects behavioral inhibition (Barkley, 1997; Martinnussen et. al, 2005; Tamm et. al., 2004).The resemblance between the behavioral constellations of children that received an ADHD diagnostic and those of virtual organisms characterized by high mutation rates is striking. The fact that this entire constellation emerged freely, unguided, from the reiteration of Darwinian processes was even more remarkable.

High environmental *value* (reward rate and magnitude) and low *conduciveness* (high $\mathbf{HD_{COD}}$).Increasing the rate or magnitude of the reinforcement had positive effects on the behavior of virtual organisms characterized by high mutation rates, on almost all dimensions investigated. When placed in more *valuable* environments (increased reinforcement rate or magnitude) they showed increased*sensitivity* to reward (a ~0.5-0.8), switched less often between alternatives (decreased CO_{MAX}), exhibited increased frequency and quality oftarget behavior (increased number of bouts, increased bout length, and increased proportion of sustained behavior), took less time to re-engage in sustained responding (shorter IBTs), showed largereductions in their moment-to-moment topographic variability ($\Delta_{PHENOTYPE}$), and acquired more rewards. These results were in agreement with generally accepted knowledge about the behavioral management of ADHD symptoms in humans. The beneficial effects of high reinforcement rates on ADHD symptoms in children is widely recognized in the ADHD literature (Freibergs& Douglas, 1969, referred in Douglas, 1985; Douglas & Parry, 1994; Konrad et. al., 2000; Parry& Douglas, 1983; Worland et. al., 1973; Barkley, 1995, 2002, 2013). In addition, the necessity of increased reward rate and magnitude in managing the behavior of ADHD children is widely acknowledged by researchers and practitioners alike, being a core component of most training guides for parents and teachers (Barkley, 1997, 2013; Pfiffner et. al., 1985; Pfiffner, 1996).

Overall, increasing the HD_{COD} values, thus decreasing the environment's *conduciveness*, had much lower impact on behavioral variability than increased reward rate or magnitude, with a few exceptions. Organisms characterized by high mutation rates switched less between alternatives (lower CO_{MAX} values), effects comparable to those produced by higher reward rates and magnitudes; also, they showed small increases in *sensitivity* to reward (a), but the effects were much less pronounced. Higher HD_{COD} values did not seem to affect the other six behavioral dimensions in noticeable ways. Note that the HD_{COD} value used as "standard" in this study (4.4, between 511 and 512) was already "large", previously shown to produce typical undermatching. Therefore these outcomes were not surprising, being perfectly aligned with previous findings (McDowell & Caron, 2007; McDowell et. al., 2008, McDowell & Popa, 2010; Popa & McDowell, 2010) and the live-organism literature (Davison & McCarthy, 1988) which indicated that after a certain threshold further increases in COD did not have noticeable effects on continuous choice.

Low environmental *value* (low rate and magnitude) and high *conduciveness* (low $\mathbf{HD_{COD}}$).Increasing the rate or magnitude of reinforcement improved the behavioral symptoms of organisms characterized by high mutation rates. Low-*value* environments acted in the opposite direction, aggravating their already disorganized behavior. These effects were not surprising, and werecongruent with similar findings reported in the ADHD literature (Sonuga-Barke et. al., 1992; Schweitzer &Sulzer-Azaroff, 1995). Interestingly, low-*value* environments had detrimental effects on the behavior of organisms characterized by low mutation rates as well. In fact, very low reinforcement ratesand magnitudes caused organisms characterized by low mutation rates to behave more erratically than organisms characterized by high mutation rates, in high-*value* environments, an interesting phenomenon that will be revisited shortly.

Human studies are relatively scarce, but the general effects of low reinforcement rates and magnitudes are well known in the non-human literature. In continuous-choice settings one ofthe most common effects was a decrease in *sensitivity* to reinforcement (Baum, 1974, 1979; Davison & McCarthy, 1988; see also McDowell, 2012 for a general review).In addition, numerous studies indicated that behavior variability (a low-level descriptor of ADHD behavior; Castellanos et al., 2005; Rubia et al., 2007), varied systematically with reward density, with high densities reducing variability levels and low densities and extinction increasing variability levels (Lee et. al., 2007). This phenomenon was observed on a variety of dimensions thatcharacterize responses, such as response location (see Antonitis, 1951; Eckerman&Lanson, 1969), intensity (Notterman&Mintz, 1965), topography (overt form; Stokes, 1995), and frequency (Mechner, 1958). Relatively recent findings from experiments with less complex organisms complement data obtained with various vertebrates. Queitsch, Sangster, & Lindquist (2002) (in Roberts &Gharib, 2006) showed that under high levels of environmentally induced *stress* (e.g. increased heat) fruit flies (Drosophila Melanogaster) show increased phenotypic variation, caused by outbursts in mutation rates. Taken together, these results suggest that increased behavior variability may not always be an expression of pathology, but quite the opposite, a natural response of life forms in general to low-resource environments (stressful environments; Neuringer, 2009), thus bringing into question the general interpretation of low-*sensitivity* values (*a*) as indicators of pathology.

The choice-behavior of virtual organisms characterized by high mutation rates was not affected by low HD_{COD} values in significant ways. In contrast, the effects of low HD_{COD} values on the behavior of organisms characterized by *low-moderatemutation* rateswere extremely interesting: they had little or no effect on some behavioral features, while profoundly debilitating others. These organisms showed almost complete indifference to reinforcement ($a \sim 0.2$), exhibited almost five times more bouts, but almost five times shorter, and the highest proportion of sustained (in-bout) behavior did not exceed~70%. The frequency of target behavior and obtained rewards were noticeably higher as compared to those produced by high HD_{COD} values, while their moment-to-moment behavior variability ($\Delta_{PHENOTYPE}$) and Inter-Bout Times (IBTs) were practically unaffected.

Different environmental features,different low-level mechanics, similarhigh-level outcomes.Upon a close examination of the low-level mechanics of behavior, the coherence of these results becomes evident. The HD_{COD}either facilitates or impedes the transition between one target class to the other, which is why it was conceptualized here as a measure of environment's*conduciveness*. Modifications in HD_{COD}values do not affect behavior directly.

Unlike rate and magnitude, higher HD_{COD} values do not concentrate more behavior around the target classes. It simply impedes rapid switching, much like in the real world, where it makes switching less appealing (Davison & McCarthy, 1988).

Conversely, *low rates*of reinforcement translate intofewerselection events. In conjunction with a moderate strength of the selection process, low rates result in *low frequencies of moderately fit child-populations*. Behavioral repertoires are concentrated around the target classes *less often*, hence less target behavior, fewer rewards, fewer bouts of shorter lengths, greater phenotypic variability (more extraneous behavior means more random selections of parents), etc. *Low magnitudes* of reinforcement (weaker selection events), on the other hand, result in *moderate frequencies of unfit child-populations*. *Ceteris paribus*, weak selection means that *less fit*behavior is concentrated around the target classes.Behavioral outcomes look the same as those produced by low rates (less target behavior, less rewards, etc.), but through slightly different mechanisms: not because behavior is concentrated *less often*, but because selection eventsresult in *less fit*populations.

In contrast, low HD_{COD} values do not act directly on the quantity of target behavior, but rather on its structure. When a behavior from one target class is reinforced, the selection event that follows concentrates the subsequent population of children around the target classes. However, when the genotypes of two (fit) parents recombine, each bit in a child's string has a 50-50 chance of coming from one parent or the other.A low HD_{COD} means that the necessary number of bits (on average), required to "move" a behavior from one target class to the other is small. Therefore, when the HD_{COD} is low, selection events triggered by behaviors in one class have high chances of producing child-behaviors that belong to the other class. This effect is further enhanced by mutation, which operates by randomly selecting a small percentage of behaviors (e.g. 10%) and randomly flipping one of the bits in their genotype. When the number of bits necessary to "move" a behavior in the other target class is high (high HD_{COD}) the chances that mutation will result in behaviors from the other class are small. When the HD_{COD} is low, it's easy for mutants to become behaviors in *the other* class.

Given the way these processes work (recombination and mutation), it follows that low HD_{COD} values produce erratic behavior through very different mechanisms than low rates or magnitudes. For example, low rates and magnitudes result in low *sensitivity* because the overall amount of target behavior decreases so low that many selection events are followed by long strings of extraneous behavior, and the next target behavior falls in one target or another due to chance rather than to the consequences triggered by the previously reinforced behavior (which dissipate quickly). In contrast, low HD_{COD} values result in low *sensitivity* because they allow selection events triggered by one target class to result in target behaviors from the other class, thus causing a large increase in the number of changeovers. They provoke ruptures in the behavior structure, not its quantity, by severely altering the ratios of behaviors and rewards. This would explain why low HD_{COD} values were more debilitating than low rates or magnitudes, causing almost complete indifference (a ~0.2) even in organisms characterized by low mutation rates (5%). It would also explain the seemingly aberrant patterns of changeovers produced by low HD_{COD} values at various mutation rates (Figure 5, panel 6). Although low HD_{COD} values produced more switches at all mutation rates (which was expected), the highest rate of switching was observed at the lowest mutation rates, CO_{MAX} *decreasing* with the rate of mutation. At low mutation rates, many selection events resulted in changeovers, through the mechanism described above. As the rate of mutation increased, the populations of children became more spread out across the continuum, resulting in fewer target behaviors altogether, thus decreasing the number of opportunities for switches to occur.In addition, it explains why low HD_{COD} values had virtually no effect on topographic variability ($\Delta_{PHENOTYPE}$). If a selection event triggered by one target class produces a behavior from the other class, theirphenotypes are still very close.

Summary

Overall, the effects of high mutation rates on the behavior of virtual organisms animatedby the Evolutionary Theory were remarkably congruent with existing knowledge about the behavior of ADHD-diagnosed children. Organisms characterized by higher mutation rates showed decreased *sensitivity* to reward (*a* ↓), switched more often between simultaneously-available activities (CO_{MAX} ↑), engaged less often in continuous-responding (bouts ↓), abandoned the task faster (bout length ↓), and took longer to re-engage in sustained responding (IBT ↑). Overall, their highly variable ($\Delta_{PHENOTYPE}$ ↑) and disorganized behavior (sustained behavior ↓) caused them to acquire significantly fewerresources than organisms characterized by lower mutation rates.Furthermore, arranging richer environments or delivering stronger rewards counteracted (at least to some extent) the detrimental effects of high mutation rates, results in agreement with widely accepted knowledge and findings about the behavior of ADHD children. What makes these similarities even more remarkable is that the collection of behavioral symptoms described above and the phenomena that surrounded them(e.g. effects of reward rate) were not goals embedded in the theory. This remarkably coherent constellation emerged freely during the dynamic interaction between organisms and the environments in which they were immersed, interactions governed by low-level Darwinian processes of selection, recombination, and mutation. These results add to the already large body of data (McDowell, in press) that support the validity of Darwinian processes as a causal account for the dynamics of adaptive behavior.

Implications

The reiteration of Darwinian processes gave rise to similar high-level outcomes, despite different configurations of the initial conditions (various mutation rates, various reward densities, etc). As noted earlier, organisms characterized by low mutation rates that evolved in low-*value* environmentsdisplayed behavioral characteristics that in many cases were indistinguishable from those displayed by organisms characterized by high mutation rates in high-*value* environments. Figure 9 may help illustrate this phenomenon and its far-reaching implications. The figure depictsthe behavioral characteristics of five virtual organisms. Each of the nine axes depicts one of the nine dependent variables, with zero in the center of the radar-type graph. The order of the nine variables was changed so that variables for which "low" values mean "desirable", "good" outcomes were close together (CO_{MAX}, $\Delta_{PHENOTYPE}$, and IBT; first three black axes). Uniting the nine points resulted in an irregular surface that provides an overall visual description of an organism's behavioral characteristics. The raw values were transformed, where necessary, by dividing them by a multiple of 10 (specified below, next to each variable). The purpose was to bring all variables to a comparable scale that would allow a visual depiction. From the first, perpendicular axis, going clockwise, the nine variables are: CO_{MAX} (/10), $\Delta_{PHENOTYPE}$ (/10,000), IBT (/10,000), *Sensitivity* (*a*), Responses (/100), Rewards (/100), Bouts (/10), Bout Length (/100), and Sustained behavior (%).

An organism that displayed low behavior variability (desired outcome) is characterized by a small black area and a large grey area (panel 1). Panels 2, 3, 4, and 5 depict organisms that displayed high variability. Thesefour constellations of behavioral characteristics can be described as highly variable, very similar to each other, and very different from the constellation depicted in panel 1. Despite their apparent similarities, they were all caused by different combinations of organismic and environmental features, specified in the upper-left corner of the figure. Similar, apparently maladaptive, behavioral characteristics were produced primarily by environmental features (e.g. panel 2, very low reward magnitude), by an organismic characteristic (e.g. panel 5, 100% mutation rate), or by various combinations of environmental-organismic features (panels 3 and 4).

The similarities between the behavioral characteristics depicted in panels 2 and 4 become more interesting when considering the vast body of data that repeatedly showed that increased variability may be a natural response of live organisms triggered by low-*value* environments (see Neuringer, 2009, for an overview), thus bringing into question the general interpretation of low-*sensitivity* values (*a*) as indicators of pathology. However, the similarity between the surface behavioral characteristics depicted in panel 2 and those depicted in panel 5 may have even deeper implications. On the surface, these two behavioral constellations are not simply similar, they are similar in a pathologic way. If these behavioral characteristics would have been observed in two young children, it would have been extremely difficult to resist the temptation of diagnosing both with the same psychological disorder (most likely ADHD), when in fact the outcome depicted in panel 2 was produced by an organism characterized by a low mutation rate (10%) immersed in a environment with very low-rewarding *value* (very low reward magnitude). These results suggests that assigning diagnostics based only on observed behavioral characteristics may result in grouping together highly "impaired" individuals (panel 5, 100% mutation) and quite "healthy" individuals (panel 2, 10% mutation).This hypothesis and its implications will be revisited in the general discussion section.

Phase 2: Effects of Changeover Delays on the continuous-choice behavior of virtual organisms and college students.

The purpose of the first phase of this project was to learn about the effects of various reward rates, reward magnitudes, and Hamming Distancechangeover delays (HD_{COD}), on the continuous choice-behavior of virtual organisms characterized by various mutation rates. The purpose of the second phase was to explore the Theory's potential for predicting the behavior of college students in continuous choice environments, as a function of changeover delay (COD), along the same behavioral characteristics investigated in the first phase.

Method

Participants

The human participants were 38 Emory undergraduate students, males and females, ages between 18 and 21. Their low-level behavioral characteristics in continuous-choice environments were contrasted against those displayed by virtual organisms characterized by mutation rates of 10%, placed in environments characterized bydifferent HD_{COD} values.

Apparatus and materials

Experiments were run on an off-the-shelf desktop computer hardware. The computer program that arranged the continuous-choice procedure (concurrent RI RI schedules) was written by author in VB 2010, part of the Microsoft Visual Studio 2010 Integrated Development Environment (IDE).

Procedure

The 38 participants responded in a continuous-choice procedure that arranged sevenconcurrent, independent Random Interval schedules. The exact details are provided in Table 2.The testing environment was kept as simple as possible; Figure 10 provides an illustration of thestudents' visual experience during testing. During the procedure, the screen displayedthree elements: two buttons and a text box that displayed the total number of acquired rewards (1 point = 1 reward). The buttons were mouse-operated (mouse left click = response). All participants received the following instructions:

> *"Thank you for choosing to participate in this study. This task investigates the basic mechanisms that allow us to adapt to dynamic environments. When the session will begin the screen will display a number of buttons. You may obtain points by operating the buttons displayed on the screen. Use the mouse to click (operate) the buttons. Your objective is to figure out how the environment works. The acoustic cues will help, so make sure you put on the headset. Once you begin a session it is very important that you focus on task. The time component is crucial, so please refrain from using the phone, etc. The end of the session is signaled by a message box that asks you to notify the experimenter. Press the red button to begin the session. Thank you."*

All experimental sessions started with a very rich pair of identical schedules, which scheduled reinforcements, on average, every 700 milliseconds, or 0.7 seconds (RI 0.7 RI 0.7). This wascalled the Acquisition component, which was included to allow the participants to become acquainted with the task.The next five RI RI pairs were presented in random order for each participant. The last (7th) component of the experimental session was an extinction phase during which no reinforcers were scheduled. Once the extinction phase was over a message box announcedthe end of the experimental session thanked students for their participation. An experimental session lasted for approximately 18 minutes.The first and last components were in effectfor 50 seconds each. The five intermediary components were in effect for 200 seconds each. The transition from one component to another was signaled by a short sound. This stimulus was always the same. Its purpose was to signal participants that something changed in the environment, without providing additional cues. The delivery of a reward was signaled by a very short sound and by incrementing the total number of points by 1. This sound was different from the sound that signaled the transition from one component to another.

Participants were randomly assigned to one of the two experimental groups: "No_COD" or "COD_2s". In the "No_COD" condition (N = 20) the two concurrent Random Interval schedules ran on two physically distinct alternatives (on two buttons, Figure 10, left panel) and no changeover delay (COD) was in effect. This means that whenever the participant switched from one alternative (button) to the other, if a reward was available on that alternative it was delivered immediately, without delay, contingent on the switch-response. In the "COD_2s" condition (N = 18), both schedules ran on the same physical alternative (the right button, Figure 10, middle and right panels). The left, grey button acted as a Findley-Key, or a changeover key (Findley, 1958). The function of this button was to switch between the available alternatives (schedules), signaled by two different colors. In the No_COD condition, the two schedules were arranged on different buttons, left and right. In the COD_2s condition, the concurrent schedules were run on the same button, one during the green color and one during the red color. The participant could switch between the schedules (alternatives) at any point, by pressing the Findley-button, but only one alternative was visible at a time (the right button was either red or green, not both). In this condition, a changeover delay of 2 seconds (COD 2s) was implemented on each key. This means that whenever the participant pressed the Findley-button (thus changing the color of the right button, or switching between alternatives),s/he triggered the changeover delay interval which in this study was set at two seconds. During this period, target responses had no effect; even if a reward was already available (the timer for the non-visible alternative ran in the background), it was only delivered contingent on the first response that occurred after the delay elapsed. If the participant switched back, another 2-second delay started, and so on. In theory, a participant could go through the entire testing time without acquiring any rewards.

The raw data from concurrent schedules was recorded in text files. Whenever an eventoccurred (the only possible events were responses on one of the two alternatives), the program recorded the time signature, the type of event (click on the first or second button), and its consequence, if any (reinforced or not). The raw data were imported into Microsoft Excel for analysis.

Results

Measures

The data sets produced by college students were analyzed in a manner similar to the data sets produced by the virtual organisms animated by the Evolutionary Theory (Phase 1). The behavioral measures were also calculated in the same manner (detailed bellow), with two exceptions. First, the moment-to-moment phenotypic variability ($\Delta_{PHENOTYPE}$) could not be computed. The traditional method of recording human input (buttons, clicks) does not allow for the calculation of this behavioral dimension. In the search for a procedure that would allow more direct comparisons between virtual and human organisms, a completely different method of recording human input has been developed, which would address the $\Delta_{PHENOTYPE}$ issue. It constitutes the focus of an extensive research project that will be discussed in the Future Directions subsection. Second, the frequencies of responses, rewards, etc. were reported per minute; in the case of virtual organisms they were reported per 500-generation blocks.Response and reward rates were summed for each RI RIschedule, for each alternative. The behavior and reward ratios (B_1/B_2 and r_1/r_2) were converted to logarithms; the slope of these six data points (the Extinction component was not included because the reward rates were always zero) gave the *sensitivity* to reward (*a*, the exponent of Equation 2, slope in Equation 3) of that participant, in that particular environment. The intercept of the line was used to calculate the bias parameter ($b = 10^{\text{INTERCEPT}}$), and the squared correlation coefficient (r^2) provided the proportion of variance accounted for (pVAF) by Equation 3.

The total number of responses, rewards, bouts, and changeovers were calculated for each participant and divided by the total number of minutes spent in the six schedules. The average bout length was obtained by counting all the responses that occurred in bouts and dividing by the total number of bouts. The proportion of sustained (in-bout) behavior was calculated in the same manner described in Phase 1 (Equation 8). The overall absolute frequency of sustained behavior was divided by the overall absolute frequency of target behavior (thus eliminating the target sporadic responses).A bout was considered any sequence of three or more consecutive responses on one alternative. A bout was considered terminated when the participant switched to the other alternative.In the case of virtual or non-human organisms, it is many times necessary to establish additional criteria for what terminates a bout, due to the presence of extraneous responses (e.g. phenotypes outside the target class, rearing at the back of the cage). No additional criteria were necessary here: the rates of behavior were extremely high (~2.5 per second), without noticeable pauses.

Behavioral characteristics of students' continuous-choice behavior: overview

The traditional characteristics of continuous-choice are illustrated in Table 3. Overall, the data sets were well described by Equation 3, which explained approximately 70% of the variance (r^2:*M* = 0.68, *Mdn* = 0.78, *SEM* = 0.04). The residuals left by Equation 3 were standardized and plotted against the predicted log (B_1/B_2) values. Visual inspection of the plots did not reveal the presence of systematic trends, conclusion supported by the very weak Pearson (r) correlations (*M* = 0.13, *Mdn* = 0.05, *SEM* = 0.03). The bias parameter ($b = 10^{\text{INTERCEPT}}$) varied around unity (*M* = 0.97, *Mdn* = 0.97, *SEM* = 0.01), an expected outcome in symmetrical-choice environments (the overall scheduled rates of reinforcement were, overall, identical on the two alternatives).

The average slope values obtained from Equation 3(*sensitivity*, *a*) were 0.47 in the No_COD condition (*Mdn* = 0.47, *SEM* = 0.06) and 0.66 in the COD_2s condition (*Mdn* = 0.7, *SEM* = 0.06), with an overall average of 0.56 pooled across conditions (*N* = 38; *Mdn* = 0.59, *SEM* = 0.04). These values are comparable with those previously reported in studies with human participants. For example, Kollins, Newland, &Critchfield (1997) examined data from 13 studies with human participants and found a median slope (*a*) of 0.7, almost identical to the one observed in the COD_2s groupand a little lower than the one observed in a review ofstudies with non-human subjects (*a* ~0.85; Baum, 1979).The No_COD group was characterized by smaller *sensitivity* values, thus bringing down the overall average. This was an expected outcome, produced by the experimental manipulation, and will be discussed in the next section. However, when comparing the COD_2s data with those reported by Kollins, Newland, &Critchfield (1997), despite the virtually identical median values (~0.7), the data sets described here were characterized by a slightly more accentuated tendency towards undermatching.

This slight general tendency was most likely due to two factors. First, participants were exposed only once to each RI RI component, and for a very short period of time (e.g. 200 seconds). Second, no "transition data" were discarded from the analysis. The matching equations (including Equations 2 and 3) are mathematical descriptorsof steady-state behavior, or behavior at equilibrium. The common procedure in the field is to discard the periods of transition between RI RI components (the transition) and keep only steady-state data (the last period of an RI RI component). The analyses discussed here were conducted on all data, including the transition periods, which, by definition, add a certain level of noise to the data sets. This decision was motivated by the short period of time spent in each RI RI component (e.g. 200s) which made it difficult to identify a common criterion regarding the period to be discarded.

Overall, the results described above were well described by Equation 3, despite keeping the "transition" data, the short duration spent in each RI RI component, the very high rates of reinforcement (~ one reward / second, on average), and the participants' complete lack of experience with the environment or the procedure. This suggested that long testing periods, a major obstacle in experimenting with human participants, may notbe necessaryfor obtaining robust results. It is possible that designing a more familiar environment, richer in rewards, may have contributed substantially to the robustness of the results reported here. Traditionally, such environments involved levers or large buttons, which are outside of the day-to-day experience of most college students. Also, the scheduled rates of reinforcement were similar to those arranged in experiments with non-human subjects (e.g. RI 60 RI 120 → ~1.5 rewards/minute), probably too low to keep students engaged for long periods of time. In contrast, the procedure described here implemented a testing environment much closer in design to the everyday experience of college students (e.g. using a regular computer and a mouse to operate two buttons on the screen). Also, the high pace of the experimental task may have contributed to keeping the students engaged, which in turn may have been reflected in the robust parameter values that described their choice-behavior. These hypotheses need further verification. The results described here suggest that this implementation is promising for investigating the continuous-choice behavior of human participants.

Effects of changeover delay on the behavior variability of virtual organisms (HD_{COD}) and college students (COD)

Data produced by college students in the No_COD (*N* = 20)and COD_2s (*N* = 18) conditions were compared to those produced by virtual organisms animated by the Evolutionary Theory in environments characterized by various HD_{COD} values. In the figures described below the data produced by virtual organisms is always presented in the left panels (HD_{COD} = 1.4, 2.4, 3.4, 4.4, 5.4, 6.4). The data produced by college students under the "No_COD" and "COD_2s" experimental conditions is always presented in the right panels (averaged per experimental condition, with the error bars indicating standard errors of the mean, *SEM*).

The Evolutionary Theory correctly predicted the direction of the differences between groups on eight out of eight behavioral measures. When compared to the No_COD group, the participants in the COD_2s condition, on average, showed greater *sensitivity* to reward (*a*), switched less often between alternatives, emitted *fewer*responses, obtained *fewer*rewards, emitted fewer, but longer bouts, displayed a greater proportion of sustained behavior (%), and exhibited greater inter-bout times (IBT). On four out of eight behavioral dimensions the differences were statistically significant (a summary is provided in Table 4).

***Sensitivity* and Changeovers**

Figure 11 depicts*sensitivity* values (the exponent, *a*; top panels) and changeover frequencies (bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. When the Hamming changeover delay was low (HD_{COD} = 1.4), the continuous choice behavior of the virtual organism was characterized by severe undermatching (*a* ~0.25). It's maximum changeover frequency (CO_{MAX}) varied around 28 / 500 generations. Increasing the HD_{COD} caused systematic increases in *sensitivity* (*a*), accompanied by a noticeable reduction in the frequency of switching between alternatives. The differences produced by various HD_{COD} values were larger at first, but tended to disappear once the HD_{COD} was increased beyond ~3.0. Similar patterns were observed when examining the data produced by college students. In the No_COD condition the average *sensitivity* values (*a*) varied around 0.47 (pronouncedundermatching; panel 2) and the average frequency of changeovers (COs/minute) varied around 50 (panel 4). The averaged *sensitivity* (*a*) values in the COD_2s group was 0.66, significantly larger than the No_COD group, $t(18) = 2.19$, $p < 0.05$ (one-tailed). Also, the COD_2s group switched, on average, significantly less than the No_COD group, $t(18) = -1.99$, $p < 0.05$ (one-tailed).

Target behavior and obtained rewards

Figure 12 depictsaverage frequencies of target behavior (top panels) and obtained rewards (bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values, averaged per 500 generations. As the HD_{COD} increased from 1.4 towards 6.4, the average frequency of target behavior (top left) decreased from ~100 towards ~70 (per 500 generations). The same pattern was observed when examining the frequency of obtained rewards (bottom left): a decrease from ~20 towards ~14 (per 500 generations). The differences produced by various HD_{COD} values were larger at first, but tended to disappear once the HD_{COD} was increased beyond ~3.0. Similar changeover delay effects were observed in the results produced by college students (right panels). Students in the "COD_2s" condition, on average, emitted fewer behaviors (~87 vs. ~110; top right) and obtained fewer rewards (~33 vs. ~42; bottom right) than students in the No_COD condition. The average decrease in the number of obtained rewards caused by a 2-seconds COD was statistically significant, $t(18) = -3.44$, $p < 0.01$ (one-tailed).

Bout frequency and bout length

Figure 13 depictsaverage frequencies of bouts (top panels) and the average bout length (responses/ bout; bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. As the HD_{COD} increased from 1.4 towards 6.4, the average frequency of bouts decreased from ~12.5 to ~5 (per 500 generations). The decrease in bout frequency was accompanied by an increase in bout length (the average number of responses within a bout), which increased from ~5.5 to ~14. The differences produced by various HD_{COD} values were larger at first and diminished fast once the HD_{COD} was increased beyond ~3.0. Similar effects were observed when examining the results produced by college students. The average bout frequency emitted by students in the No_COD condition was approximately 8.0/minute, larger than the bout frequency observed in the COD_2s group ($M = 6.4$). In addition, students in the COD_2s group emitted longer bouts ($M = 13.5$) than students in the No_COD group ($M = 7.2$). Although both differences were in the direction predicted by the theory, they did not reach statistical significance.

Sustained behavior (%) and Inter-Bout Time (IBT)

Figure 14 depictsthe percent of sustained behavior (top panels) and the average inter-bout time (IBT; bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. As the HD_{COD} increased from 1.4 towards 6.4, the average proportion of sustained behavior (%) increased from ~65% to ~95%. The average duration of the inter-bout times (IBT) increased as well, from ~ 30 to ~75 time units. In both cases, the differences produced by various HD_{COD} values diminished once the HD_{COD} was increased beyond ~3.0. Similar effects were observed when examining the results produced by college students. Students in the "COD_2s" condition, on average, exhibited a significantly higher proportion of sustained behavior (M = 67%) than the students in the No_COD group (M = 51%), $t(18) = 1.96$, $p < 0.05$ (one-tailed). They also exhibited larger IBT values (*M* = 115) than students in the No_COD group (*M* = 69). Although in the predicted direction, this difference did not reach statistical significance.

Discussion

Overall, the Evolutionary Theory performed remarkably well in predicting the low-level characteristics of students' continuous-choice.When compared to students in the No_COD condition, the students in the COD_2s group, on average, showed significantly higher *sensitivity* to reward (*a*), switched significantly less often between alternatives, obtained significantly *fewer*rewards, and displayed a significantly higher proportion of sustained behavior;they emitted *fewer*responses, fewer but longer bouts, and took longer to re-engage in sustained behavior upon the termination of a response sequence (longer IBT).

Increases in *sensitivity* (*a*) and decreases in CO frequencies are not at all surprising (Baum, 1982; Davison & McCarthy, 1988). However, no systematic study with live organisms, humans or non-humans, has ever investigated this collection of behavioral features in a systematic way (to the author's knowledge). The fact that the theory made accurate predictions on all eight behavioral dimensions, and that four of the predicted differences reached statistical significance despite the relatively small sample sizeswas remarkable. A post hoc power analysis (G*Power 3.1; Erdfelder et. al, 1996; Faul et. al., 2007) revealed that, considering the existing sample sizes and the observed effect size (Cohen’s d’ ~ 0.6; Cohen, 1977), the achieved power was approximately 0.53, value which can be interpreted as modest. An a priori analysis indicated that achieving reasonable power (0.8) to detect a medium effect size (Cohen's d' ~ 0.5) would require approximately 50 participants per experimental group.

These findings provide strong support for the computational equivalence between the Hamming Distance changeover delay (HD_{COD}) and the changeover delay (COD) used in experiments with live organisms (Baum, 1982; Davison & McCarthy, 1988; Davison, 1991; Jimenez &Aparicio, 2009).This finding adds to increasing knowledge about the functional equivalence between computational variables and real-world parameters (e.g. the strength of the selection process <=> reinforcement magnitude; McDowell, 2004; McDowell et. al., 2008). Most importantly, the results described above constituted an important step in the verification of the theory, that of creating new knowledge about the behavior of live organisms. The ability to formulate accurate and testable predictions about unknown phenomena is arguably the ultimate test of a theory's robustness. The data presented above constitute a first, promising step in this direction. Corroborated with ten years of robust empirical findings (McDowell, in press) they suggest that the Theory's translational potential is definitely worth pursuing.

Phase 3: Continuous-choice behavior and traditional measures of ***impulsivity/inattention*****.**

The purpose of the first phase of this project was to learn about the effects of various reward rates, reward magnitudes, and Hamming Distance changeover delay (HD_{COD}), on the continuous choice-behavior of virtual organisms characterized by various mutation rates. The purpose of the second phase was to explore the Theory's potential forpredicting the effects of a changeover delay on the low-level behavior characteristics of students' continuous-choice behavior. The purpose of the third phase was to explore the relation between thelow-level behavior characteristics of students' continuous-choice behaviorand traditional measures of *impulsivity*and *inattention*. The rationaleof this phase, outlined in Figure 2,was to explore the computational equivalence between the Darwinian process of *mutation* and a property of the nervous system that causes *impulsivity*-like symptoms in live organisms, via the concurrent-schedule procedure.

Method

Participants.

Participants were the same 38 Emory undergraduate students who participated in Phase 2.

Apparatus and materials.

The Continuous Performance Test was administered on the off-the-shelf computer used for the concurrent-schedule procedure (Phase 2). The self-reported measures of impulsivitywere administered in pen-and-paper format.

Procedure.

Table 5 depicts the succession and duration of the tasks. The concurrent-schedule task (Phase 2) was followed by a short break, after which the participant was administered the Continuous Performance Test - Identical Pairs (CPT-IP; Cornblatt et. al., 1988, 1989). The task took 10 minutes to complete. It consisted of numbers flashing on the screen in rapid succession. The numbers were composed of 2, 3, and 4 digits respectively (2 digits first, 4 digits last). The participants' task was to respond (by pressing the left mouse button) whenever two successive numbers were identical. The CPT was followed by a short break, after which the participant was administered the self-report measures (pen-and-paper format).

Instruments

In total, there were 13 different self-report measures of *impulsivity* and one for *inattention*. They are described below. An additional instrument, the Social Desirability Scale (SDS), was used to investigate the participants' tendency to manage their social image, providing answers they thought were expected by a potential reader or that would portray them in what someone might interpret as a "better light".

The Adult Attention Deficit Disorders Evaluation Scale (A-ADDES) is a 58-item self-report inventory of *impulsivity* and *inattention*, shown to have excellent psychometric properties, based onestablished national norms (McCarney& Anderson 1996). It consists of a series of statements that describe specific behaviors. Participants rate the frequency withwhich they engage in each behavior on a 5-point scale, ranging from 0 (“*do not engage in behavior*”) to 4 (“o*ne to several times per hour*”). It provides two separate subscores, one for *Inattention* and one for *Hyperactivity*/*Impulsivity*. Its internal consistency was shown to be very high (0.99 overall), with test-retest reliability varying around 0.90 for the two subscales (Anastopoulos& Shelton, 2001). The adult version is considered appropriate for ages between 18 and 65, and therefore was suitable for the present project.

The UPPS-P behavior impulsivity scale is a 59-item inventory intended to describe five features of impulsive behavior. Negative Urgency addresses outcomes that may stem from a tendency to act on strong, usually negative impulses (e.g. anxiety, anger, etc.). Lack of Perseverance refers to an individual’s ability to complete tasks despite boredom. Lack of Premeditation assesses the ability to “think before acting”, to analyze the potential consequences of an action and use that information to guide behavior. Sensation Seeking intends to describe behavioral outcomes that stem from a need for intense stimulation. These four subscales constitute the core of the original UPPS scale (Whiteside &Lynam, 2001). The fifth component, Positive Urgency, was added later in an attempt to describe impulsive behaviors resulting from high positive moods (Cyders et. al., 2007). The UPPS-P inventory was shown to have good internal consistency (Whiteside &Lynam (2001) and its subscales seem able to capture unique facets of impulsivity (Whiteside et al., 2005). It was successfully used in characterizing impulsivity-related disorders, such as substance abuse, pathological gambling, and ADHD subtypes (Miller et al., 2003; Cyders et al., 2007; Verdejo-Garcia et al., 2007; Miller et al., 2010).

The Sensation Seeking Scale V (SSS-V, Zuckerman, 1971, 1996) is a forced-choice, 40-item self-reported inventory that measures various dimensions of sensation seeking. Aside from the general score, the scale provides four specific subscores (each based on 10 items): Thrill and Adventure Seeking, Experience Seeking, Disinhibition, and Boredom Susceptibility. The scale has been extensively tested and was shown to have excellent psychometric properties

(Zuckerman, 2007a, b). Its extensive use and validity recommend it as an instrument of choice for assessing *impulsivity*-related behaviors in adolescents (Zuckerman, 1983).

Results

Coding Surveys

The raw scores were coded as follows. For A-ADDES the raw scores were coded according to the Hawthorne manual (McCarney& Anderson, 1996), coding that takes into account the national averages, gender, and age. The standard scores vary between 0 and 15. The standard scale is reversed, so that high raw scores become low standard scores. For example, an *extremely impulsive* participant would obtain a raw score of 105 (on a scale from 0 to 108) and a standard score of 0 (zero), on a scale from 0 to 15. Because none of the other scales are reversed, after the raw scores were standardized, the scale was re-reversed, solely for consistency reasons: if "more" is always "more" it makes the results easier to read. For the UPPS-P, SSS, and SDS the raw scores were converted to *z*-scores.

CPT-IP measures

CPT tasks in general are widely used in the ADHD literature and have beenshown to be successful in differentiating between ADHD and non-ADHD participants (Losier et. al., 1996). This particular version (CPT-IP; Cornblatt et. al., 1997)was shown to have very good psychometric properties and is used nation-wide to assess the quality and quantity of sustained attention (Nestor et. al., 1991). In addition, it was shown to be a little harder than other CPTs (Cornblatt et. al., 1988; Adler et. al., 2001), thus allowing for a finer differentiation in the students' performance. The CPT-IP task offered information about the number of correct responses, or hits (correct identification of identical pairs) and number of false alarms (incorrect identification of catch trials as correct answers). Based on the overall proportions of hits and false alarms the program calculates two indices, d-prime (d') and beta (β). The first index, d', called a discriminative index, is the most commonly reported measure. It provides a measure of the participant's ability to discriminate signal from noise and is considered to be a measure of attentional capacity, with lower values indicating worse (lower) ability to discriminate between signal and noise. The second index, beta (β), is interpreted as an index of motivation, and apparently captures a participant's tendency to over-respond ("risk-taking attitude") or under-respond ("conservative attitude"), with higher values indicating a more conservative tendency (Cosway et. al., 2002; Cornblatt, 1988, 1989). Both measures are calculated automatically at the end of the task.

Continuous-choice measures

The continuous-choice measures were the measures obtained in Phase 2: *sensitivity* to reward (*a*) the exponent of Equation 2), frequencies (per minute) of changeovers (CO/min), target behavior (B/min), obtained reinforcers (Reinf/min), and bouts (Bouts/min), average bout length (Bout Length), Sustained Behavior (%), and Inter-Bout Time (IBT).

The correlational analyses were conducted using the R statistical package (R Development Core Team, 2013). This phase required a two-step analysis. The first step was to analyze the relation between behavioral characteristics of continuous-choice, on one hand and the survey and CPT-IP scores, on the other hand. Because the first were, as expected, influenced in systematic ways by the presence or absence of a changeover delay (COD), these analysis were conducted separately for the two groups: No_COD (*N* = 20) and COD_2s (*N* = 18).The second step, included for verification purposes, was to examine the relation between the traditional measures of *impulsivity* and *inattention*. This analysis was conducted on all 38 scores, combined, because these scores were not subject to experimental manipulations.

Continuous-choice and measures of***impulsivity*****/*****inattention***

Overall, the results were inconclusive. Figure 15 depicts the correlation coefficients (*r*) that described the relations between continuous-choice characteristics (vertical) and survey and CPT-IP measures (horizontal). The figure only retained the relations that were statistically significant. Due to the very large volume of data, the relations that were not significant were excluded from description and discussion, with a few exceptions that appeared informative. The shaded values emphasize negative relations. Very few correlations were significant, many at the 0.05 level, all modest in strength; their average size was ~0.5 for the No_COD group (average r^2= 0.25,SD = 0.09) and ~0.49 for the COD_2s group (average r^2= 0.24, SD = 0.04).

No_CODgroup

SSS-V. The proportion of sustainedbehavior (%) correlated significantly with the Experience Seeking score of SSS-V ($r = 0.41$, $p < 0.05$). The correlation was positive, indicating that as the Sensation Seeking score increased, the proportion of sustained behavior increased as well.

UPPS-P. There were no significant correlations between the UPPS-P scores and continuous-choice characteristics.

A-ADDES. As the overall A-ADDES score increased, the average bout length increased as well ($r = 0.42$, $p < 0.05$). The *Hyperactivity*/*Impulsivity* score correlated significantly with four continuous-choice characteristics. As the *Hyperactivity*/*Impulsivity* score increased, the exponent, *a*, increased ($r = 0.44$, $p < 0.05$), the average bout-length increased ($r = 0.55$, $p < 0.05$), the proportion of sustained behavior increased ($r = 0.46$, $p < 0.05$), and the Inter-Bout Time, IBT, decreased ($r = -0.43$, $p < 0.05$).

CPT-IP. The discrimination indices, d', did not correlate significantly with any continuous-choice characteristic. The second CPT measure, beta (β; tendency to over- or under-respond), correlated significantly with the average bout length ($r = -0.44$, $p < 0.05$): the tendency tounder-respond increased as the average bout length decreased.

COD_2s group

SSS. There were no significant correlations between the SSS scores and the continuous-choice characteristics.

UPPS-P.In the COD-2s group, UPPS-P_{TOTAL} correlated significantly with three continuous-choice characteristics. As the total UPPS-P score increased, the bout frequency (bouts/min) increased ($r = 0.48$, $p < 0.05$), the proportion of sustained behavior increased ($r =$

0.47, $p < 0.05$), and the Inter-Bout Time (IBT)decreased($r = -0.45$, $p < 0.05$).Positive Urgency correlated significantly with the proportion ofsustained behavior ($r = 0.45$, $p < 0.48$). Lack of Premeditation correlated significantly with bout frequency (bouts/min: $r = 0.5$, $p < 0.48$). Negative Urgency correlated significantly with the exponent, a ($r = 0.5$, $p < 0.05$), with bout frequency ($r = 0.51$, $p < 0.05$), and with Inter-Bout Time, IBT ($r = -52$, $p < 0.05$).

A-ADDES. As the overall A-ADDES scores increased, the proportion of sustained behavior decreased ($r = -0.45$, $p < 0.05$). Unlike in the No_COD group, the *Hyperactivity*/*Impulsivity* subscale did not correlate significantly with any continuous-choice characteristic. The *Inattention* score correlated significantly with the proportion of sustained behavior ($r = -0.51$, $p < 0.05$).

CPT-IP.The discrimination indices, d', correlated significantly with the exponent, a: as d' increased (better discrimination, or less *impulsivity*), the exponent increased as well ($r = 0.45$, $p < 0.05$). The CPT-IP*sensitivity* parameter (β) correlated significantlywith the average behavior frequency (B/min): as β (the tendency to be more conservative) increased, behavior frequency decreased ($r = -0.5$, $p < 0.05$).

For several reasons, the correlations described above seem to be more likely due to chance (Type I errors) than to actual meaningful trends. First, only 27 correlations were significant, out of 270. Out of them, only two were significant at 0.01 level. In addition, the average effect sizes were modest, with an average r^2 of 0.24 (SD = 0.07). The significant correlations were inconsistent from group to group and variable to variable. For example, in the No_COD group some of the few significant correlations were between concurrent-schedules variables and some of theA-ADDES scores, but none with UPPS-P scores. In the COD_2s group the situation was reversed:many (of the few) significant correlations involved UPPS-P scores, but only two involved A-ADDES scores.

Relations between various measures of*impulsivity*/*inattention*

The outcomes generated by the Evolutionary Theory (Phase 1) werevery robust and in agreement with the live-organisms literature.The predictions about the low-level behavioral characteristics of students' continuous-choice (Phase 2) were correct on all eight behavioral dimensions (with fourreaching statisticalsignificance). The unsatisfactory results described above (Phase3) were unexpected and in disagreement with both the theory's predictions and with the results previously reported in the live-organism literature.

A close examination of the traditional measures of *impulsivity* and *inattention*revealed that the *impulsivity* scores of the 38 participants 1) were not very variable, clustered around (and even below) the theoretical average and 2) includedextremely few very high scores. In addition, the correlations between the scores obtained with different instruments were rarely significant and only modest in size, probably due to the small variability and lack of extreme scores. Figure 16 depicts the correlation coefficients between the various measures of *impulsivity*/*inattention* (self-reported and CPT-IP). Due to the large volume of data, only the statistically significant relations were reported (* $p< 0.01$, ** $p< 0.05$).

Within instruments.

The correlation between the two CPT-IP measures, d-prime (d') and sensitivity (β), wasnot significant.The two subscales of A-ADDES were highly correlated with the A-ADDES total score (*Hyperactivity*/*Impulsivity*: $r = 0.9$, $p < 0.01$; *Inattention*: $r = 0.87$, $p<0.01$). The relation between the two subscales was noticeably weaker ($r = 0.57$, $p< 0.01$).

All UPPS-P subscales correlated significantly with the total score ($p< 0.01$), with correlation coefficients varying between 0.44 (lack of perseverance) and 0.84 (positive urgency). The relations between subscales varied in strength. Negative Urgency correlated significantly with the total score ($r = 0.78$, $p< 0.01$), Positive Urgency ($r = 0.57$, $p<0.01$), Sensation Seeking ($r = 0.28$, $p <0.05$), lack of Perseverance ($r = 0.34$, $p<0.05$), and lack of Premeditation ($r = 0.44$, $p< 0.01$). Lack of Premeditation correlated significantly with the total score ($r = 0.67$, $p< 0.01$) and Positive Urgency ($r = 0.52$, $p< 0.01$), but not with Sensation Seeking and lack of Perseverance.

Lack of Perseverance correlated significantly with Positive Urgency ($r = 0.29$, $p < 0.05$), but not with Sensation Seeking. Overall, 11 out of 15 relations were significant and the coefficients of determination (r^2) were small ($M = 0.27$).

The relation between the total SSS-V score and its subscales was good. SSS-Totalcorrelated significantly with Boredom Susceptibility ($r = 0.54$, $p < 0.01$), Disinhibition($r = 0.72$, $p < 0.01$), Experience Seeking($r = 0.76$, $p < 0.01$), and Thrill and Adventure Seeking($r = 0.76$, $p < 0.01$).At a subscale level, Boredom Susceptibility correlated significantly with Disinhibition($r = 0.32$, $p < 0.05$) but not with Experience Seeking and Thrill and Adventure Seeking.Disinhibition correlated significantly with Thrill Seeking ($r = 0.35$, $p < 0.05$) and Experience Seeking ($r = 0.31$, $p < 0.05$). Experience Seeking and Thrill and Adventure Seeking correlated among each other ($r = 0.59$, $p < 0.01$). Overall, out of 10 relations eight were significantand the coefficients of determination (r^2) were small ($M = 0.3$).

Betweeninstruments

CPT-IP and inventories

D-prime (d') correlated significantly with four self-report measures (out of 13), A-ADDES *Inattention* ($r = -0.45$,$p < 0.01$), A-ADDES *Hyperactivity*/*Impulsivity* ($r = -0.42$, $p < 0.01$), A-ADDES total ($r = -0.49$, $p < 0.01$), and the lack of Perseverance subscale of the UPPS-P inventory ($r = -0.28$, $p < 0.05$). All relations were inverse-proportional, with d' decreasing with increased self-reported scores of *Inattention*, *Hyperactivity*/*Impulsivity*, and Lack of Perseverance. Note that overall d' correlated significantly with the A-ADDES total score and its subscales (modest effect sizes, average r ~0.40), with only one UPPS-P subscale, and none of the SSS-V scores. Sensitivity (β) correlated significantly with two self-reported measures (out of 13); bothwere subscales of the UPPS-P inventory and both relations were very modest: Negative Urgency ($r = -0.29$, $p < 0.05$) and Positive Urgency ($r = -0.35$, $p < 0.05$). Both relations were inverse-proportional, with β decreasing (increased tendency of answering "*yes, the stimuli are* *identical*") as either negative or positive urgency increased. It did not correlate significantly with any of the A-ADDES or SSS-V scores.

A-ADDES and UPPS-P

Overall, out of 18 relations, only eight were significant, one in the counter-intuitive direction. A-ADDES-*Inattention* correlated significantly with Sensation Seeking (r = -0.34, p< 0.05) and lack of Perseverance (r = 0.61, p< 0.01), but not with UPPS-P total score, Positive Urgency, lack of Premeditation, and Negative Urgency. A-ADDES-*Hyperactivity/Impulsivity* correlated significantly with UPPS-P total score (r = 0.38, p< 0.05), Positive Urgency (r = 0.34, p< 0.05), lack of Perseverance (r = 0.44, p< 0.01), and lack of Premeditation (r = 0.38, p < 0.01), but not with Sensation Seeking and Negative Urgency. A-ADDES total score correlated significantly with Positive Urgency(r = 0.34, p< 0.05) and lack of Perseverance (r = 0.6, p< 0.01), but not with UPPS-P total score, Sensation Seeking, lack of Premeditation, and Negative Urgency. Overall, the relations were modest (average r = 0.42, r^2 ~0.17) .

UPPS-P and SSS-V

Overall, out of 30 relations, only 11 were significant. Negative Urgency correlated significantly only with Disinhibition (r = 0.34, p< 0.05). Lack of Premeditation did not correlate significantly with any of the SSS scores. Lack of Perseverance correlated significantly only with Disinhibition (r = 0.39, p< 0.01). UPPS-P Sensation Seeking correlated significantly with SSS-Total (r = 0.71, p< 0.01), Thrill and Adventure Seeking (r = 0.82, p< 0.01), Experience Seeking (r = 0.6, p< 0.01), and Disinhibition (r = 0.49, p< 0.01), but not with Boredom Susceptibility. Positive Urgency correlated significantly only with Disinhibition (r = 0.37, p< 0.05). UPPS-P total score correlated significantly with SSS-Total (r = 0.51, p< 0.01), Thrill and Adventure Seeking (r = 0.37, p< 0.05), Experience Seeking (r = 0.4, p< 0.05), and Disinhibition(r = 0.56, p< 0.01), but not with Boredom Susceptibility. Overall, the relations were modest (average r = 0.50, r^2 ~0.25) .

A-ADDES and SSS-V.Overall, out of 15 relations, none was statistically significant.

Discussion

Overall, the correlations between various measures of *inattention* and *impulsivity*were either non-significant (44 out of 90) or modest in size(average r = 0.50, *SD* = 0.17, *Mdn* = 0.45). A closer examination of the raw scores revealed that the level of variability in the present sample was small on all measures, with most scores clustered around the theoretical averages, and almost no extremely high scores).

A-ADDES.The A-ADDES scores were standardized according to the manual (McCarney& Anderson, 1996), on a scale from 0 to 15. The authors found that the average standard scores (for both *inattention* and *impulsivity*) were approximately 6 for the general population and approximately 13 for participants who had an ADHD diagnostic. In the present sample the average standard scores were 7.2 for *inattention* (*Mdn* = 7, *SD* = 2.8) and 9.6 for *impulsivity* (*Mdn* = 10, *SD* = 2.5). Although the *impulsivity*scores seem high, they are still well below the values identified by the authors as "problematic" (13). In addition, the A-ADDES *Hyperactivity* / *Impulsivity* scores correlated only modestly with the UPPS-P inventory subscales and not at all with any of the SSS-V scales. *Impulsivity* is considered a multi-dimensional construct (Evenden, 1999) and it is possible that the UPPS-P and SSS-V inventories tap into different domains than the A-ADDES subscale. However, it seems unlikely that none of the 11 subscales of UPPS-P and SSS-V taps into a similar *impulsivity* domain. Moreover, the relation with the CPT-IP measure generally interpreted as a measure of *impulsivity* (d') was also modest (r^2 = 0.17).The A-ADDES *impulsivity* scores were the highest *impulsivity* scores in the sample and this subscale was the only one that correlated (although modestly) with the laboratory measure d'. The scores obtained with the UPPS-P and SSS-V inventories showed even less variability and were closer to their theoretical average.

UPPS-P. Table 6 depicts the theoretical scores for the UPPS-P inventory (all subscales), the values observed in the present sample, and the values observed in the control group in a recent ADHD study (Miller et. al., 2010). The scores observed in the present sample are very similar to (and sometimes smaller than) their theoretical average and the ones reported by Miller et. al. (2010) on all subscales, which suggests that the scores observed in the present sample are quite low, far from values that could be interpreted as "problematic". To add to the confusion, the highest scores observed in the present sample were the Sensation Seeking subscale scores, which correlated significantly with the subscales of UPPS-P, but not with the *Impulsivity* subscale of A-ADDES. Instead, it correlated significantly with the *Inattention* subscale of A-ADDES, and the relation was inverse-proportional: higher sensation seeking tendencies were correlated with lower inattention scores.

SSS-V. The same was true for the SSS-V scale (Zuckerman, 1971, 2007), as illustrated in Table 7. The average total score was 18.5 (*Mdn* = 19, *SD* = 6.1), smaller than both their theoretical averages and the values previously reported to describe control groups (*M* = 19.5, *SD* = 5.5, Ridgeway&Russel, 1980;*M* = 20.6, *SD* = 6.5, McDaniel & Mahan, 2008). Furthermore, McDaniel & Mahan (2008) observed correlation coefficients between the SSS-V subscales and the total score that varied around 0.6, comparable with the values observed in the present sample (*r* ~ 0.65).

CPT-IP.In the case of the main CPT-IP measure, d-prime (d'), things are quite unclear. Table 8 depicts the results observed in the present sample and results previously reported in groups with various diagnostics and control groups. As a reminder, lower d' values indicate low discrimination ("undesirable" outcome) and high values indicatehigh discrimination("good" outcome). The present sample was characterized by an average d' of 2.12 (*SD* = 0.78). Barr et al. (2008), in a study on schizophrenia, reported d' values around 2.1 in the *schizophrenia* group (almost identical with this sample!) and values around 3.3 (better discrimination) in the control group.Almost identical values were observed by Dyer et. al. (2008), who reported d' values of approximately 2.0 in the schizophrenia group. Their manipulation did not involve a non-diagnosed group because they used d' to measure before-after treatment effects. After treatment both the placebo group and the experimental group were characterized by higherd' values (better discrimination): 2.5 in the placebo group and 2.7 in the experimental group. Very interesting results were reported by Rutschmann et al. (1977), in a study on children classified as being at "ultra-high risk" of developing schizophrenia. The d' statistic was identical for controls and ultra-high-risk at age 7-8y, (d' ~1.0, poor discrimination), was ~2.0 for controls (similar to the present sample)and 1.5 for ultra-high-risk at age 9-10y, and ~2.3 for controls and ~2.0 for ultra-high-risk at age 11-12y (both similar to the 2.12 observed in the present sample). Cornblattet. al. (1988), in a study involving controls, non-diagnosed participants, observed d' values that varied around 1.6 at test and 2.0 at re-test. Cornblatt et. al. (1989), observed d' values that varied around ~1.9 in a control group, ~1.85 in a depression group, and 0.75 (very low value, very poor discrimination) in a schizophrenia group.

The data described above suggests that the d' statistic needs to be interpretedwith caution, since the d' values observed in some studies in the control groups were lower(worse outcome) than d' values that, in other studies, characterized depressed, ADHD, or schizophrenia groups. The potential of the d' statistic to provide knowledge about pathologic behavior is unclear, especially considering that differences in age (Rutschmann et. al., 1977) or one previous exposure to the task were enough to produce noticeable improvement in d' values, both in control (Cornblatt et. al., 1988) and schizophrenia groups (Dyer et. al., 2008).

In summary, the results of the third experimental phase were inconclusive. Thescores obtained on self-reported measures of *impulsivity*/*inattention*and on the CPT-IP task could not be corroborated with low-level characteristics of continuous-choice behavior. The *impulsivity*/ *inattention* scores were low. They varied around or below their theoretical averages and, overall, fell below values previously reported in the literature to describe control groups. This made it difficult to verify their relation with behavioral characteristics of continuous-choice. In addition, the sample examined here was composed of young adults, and the severity of ADHD symptoms is known to decline with age (Rutschmann et. al., 1977).

A power analysis was conducted using G*Power 3.1 (Erdfelder et. al, 1996; Faul et. al., 2007). The results indicated that the achieved power for detecting an average effect size (Cohen's d' ~ 0.5; Cohen, 1977) was fairly high (~0.73) for the *within* group analyses (N_1 = 17, N_2 = 20) and very high overall (0.96 for N = 37). These results are congruent with the hypothesis formulated earlier: the variability in *impulsivity* scores was not large enough to allow for sensible differentiations among participants.

A close examination of gender differences (Table 9) strengthened this conclusion. The average scores were small, varying closely around average (zero, for *z*-scores). Differences between the average scores of males and females were very small and in the expected direction. Males scored slightly higher on *impulsivity* dimensions, females scored lightly higher on the *inattention* subscale of A-ADDES, in accordance to previous findings (McCarney& Anderson, 1996; Barkley, 2005, 2013).

The potential of the concurrent-choice procedure of discriminating between non-diagnosed and ADHD-diagnosed participants was verified in previous studies along general dimensions such as *sensitivity* to reward (*a*) and frequency of changeovers (Kollins et. al., 1997; Taylor et. al., 2010). Behavioral measures like those examined here (e.g. sustained behavior, IBT, etc.) have not yet been investigated, to the author's knowledge, in continuous-choice settings with human participants. Verifying their potential of informing about pathologic (or even just problematic) *impulsivity*/*inattention* features will require experimental groups characterized by greater levels of *inattention*/*impulsivity*, preferably non-medicated participants that received ADHD diagnoses. When this project was initiated the involvement of special populations was considered premature, mainly on ethical grounds. The validity of the concurrent-schedule procedure, built specifically for this project, was not verified at that time. Neither was the potential of the Evolutionary Theory to make predictions about the continuous-choice behavior of live organisms. The results generated by this project indicated that these two issues are no longer problematic. The concurrent-schedule implementation described here produced robust results, congruent with the vast literature on this topic. The fact that a remarkably short testing-time was enough to generate good results is the real gain: this will allow the testing of human participants without losing accuracy and, most importantly, without inducing high stress levels. In addition, the fact that the Evolutionary Theory made specific predictions about the continuous-choice behavior of live organisms, corroborated the vast amount of knowledge gained about the theory itself, provides the necessary support and incentive to begin expanding this research enterprise to clinically-relevant human behavior.

General Discussion

The overarching purpose of this thesis was to expand the knowledge about the Evolutionary Theory of Behavior Dynamics and to begin exploring its translational potential. The first specific aim was to explore the effects of the Darwinian process of mutation on the behavior variability of virtual organisms, and the mediating role of three environmental characteristics: reward rate, reward magnitude, and changeover delay (HD_{COD}). The second specific aim was to test predictions made by the Evolutionary Theory about the effects of a changeover delay (COD) on the continuous choice behavior of college students. The third specific aim was to explore the potential equivalence between *mutation* and a biological variablethat induces *impulsivity*-like symptoms in live organisms.

Because the Evolutionary Theory cannot cast predictions in the same way as traditional theories do, learning about the effects of various variables and processes requires running the theory, performing all the necessary computations, and then examining the emergent outcome. The present projectproduced important knowledge about the effects of *mutation* on the behavior variability of virtual organisms, and about the mediating role of the environment's*value* and *conduciveness*. This knowledge added to ten years of fruitful efforts (McDowell, in press) and provided important insight about the emergence of high-level phenotypes from the reiteration of Darwinian processes. In addition, the behavior characteristics produced by high mutation rates were remarkably similar to behavioral descriptions of ADHD. This parallel was strengthened by the mediating effects of environmentalcharacteristics, functionally similar to those reported in the ADHD literature. In addition to expanding the theoretical knowledge about the EvolutionaryTheory and the potential equivalence between specific high-level phenotypes of virtual organisms and clinically-relevant phenotypes (Phase 1), this project provided the first laboratory evidence supporting the theory's potential for predicting human behavior (Phase 2).Taken together, these findings provide further support for the selectionist paradigm as a valid account of behavior dynamics, and for the Evolutionary Theory, as a valid instantiation, with translational potential that is worth pursuing. In addition, they may have important implications for the way we conceptualize and study mental disorders, implications that will be discussed in the next subsection.Unfortunately, the computational equivalence between *mutation* and a hypothesized biological variable that produces *impulsivity*-like symptoms in live organisms remains uncertain (Phase 3). The practical and theoretical obstacles in establishing this equivalence will constitute the focus of the last subsection of this manuscript.

Theoretical implications

The results described in the first phase of this project may have important implications for the field of mental health. They suggest that an organism's behavior cannot be studied meaningfully outside the environment in which it emerged, for two main reasons. First, similar high-level phenotypes may be generated by various combinations of different factors (Figure 9), impossible to identify from the outcome itself. Second, similar high-level phenotypes may impact the organisms that exhibit them in different ways: what may resemble a maladaptive constellation of traits may actually be *adaptive* responses, triggered by the environments' scarcity.

The traditional approach to clinically-relevant phenotypes such as ADHD relies heavily on high-level descriptions (how behaviors look like), which, in turn, are used to assign individuals to research groups (e.g. the ADHD group). If extremely similar behavioral constellations can be produced by numerous combinations of factors, as suggested by the Evolutionary Theory, individuals in different research samples may differ greatly in how their behavioral characteristics came about. In some individuals they may have been generated almost entirely by organismic (biological) variables, in others by environmental characteristics, and in most individuals, by combinations of factors from both categories. This would lead to highly heterogeneous groups of individuals, whose behavioral characteristics would be assessed and approached in the same way (due to surface similarities), in turn causing different studies to reach different (or even contradictory) conclusions. This would explain, for example, why the number of studies that found connections between ADHD diagnostics and candidate genes was not much greater than the number of failed replication attempts (Waldman &Gizer, 2006) or why behavioral treatments are sometimes just as effective as medication in managing ADHD symptoms, as suggested by a recent examination of ~170 studies (Fabiano et. al., 2008).If this hypothesis is correct, it follows that the study of psychological disorders must include, in addition to high-level descriptions, low-level functional analyses of the behavioral patterns that appear problematic. Attributing them by default to biological factors may be inaccurate, since they emerged from the dynamic interaction between a particular organism and a particular environment.An emergent property cannot be understood outside the *system* that created it: a *uniqueorganism-environmentstructure*, continuously pushed through time by Darwinian forces.

Limitationsand Future Directions

The results obtained in the first phase of this project provided important information about the effects of various mutation rates on various characteristics of continuous choice-behavior. However, this project was focused on mutation rates that varied between 5% and 100%. The next step will be to examine the effects of very small mutation rates on the same behavioral characteristics. McDowell & Popa (2010) showed that at mutation rates less than 5% the choice behavior of virtual organisms tended to become less sensitive to environmental consequences, as reflected by accentuated tendencies towards undermatching (a ~0.6). A thorough examination of the effects of very small mutation rates (0% - 5%)will provide a more complete picture of the effects of mutation on choice-behavior.

The present study investigated the separate effects of three environmental variables on choice-behavior, at various mutation rates. The next step will be to examine the combined effects of these variables. In addition, the present study investigated organisms that differed only in the rate of mutation that characterized them; all other characteristics were kept constant and identical with previous studies. For example, all organisms had behavioral repertoires of 100 behaviors (the population size), selected from the 0 - 4,095 range. Recent pilot studies (Frankel, A.& Kelley, S.,personal communication, July 2013) suggested that the size of the behavioral repertoires has important effects on behavior. This organismic feature may be equivalent to the behavioral diversity/richness of a live organism, indicating the number of behavioral options an organism has at a particular time (e.g. a wide vocabulary, narrow emotional repertoire, etc). This variable is different than the size of the target classes (environmental feature), which indicates how many behaviors with different phenotypes can trigger similar consequences (the size of the operant class). The importance of these variables becomes easier to grasp if one thinks about the very rigid behavioral repertoires of autistic children (Neuringer, 2009) or the important focus on building social skills in the repertoires of depressed clients (Pierce & Cheney, 2004).The combined effects of various population and class sizes are bound to influence choice behavior in important ways. When added to the already suggested pathways (small mutation rates, various combinations of reward rates and magnitudes, etc.) it becomes evident that, although the Evolutionary Theory is "simple enough to be written on a napkin" (McDowell, 2012), the outcomes it generates are not.

In addition to producing behavioral outcomes consistent with those observed in live organisms (phase 1), the Evolutionary Theory made accurate qualitative predictions about the behavior of college students on all eight behavioral dimensions (with four reaching statistical significance). These results were quite remarkable, indicating that the theory's translational potential is definitely worth exploring. In doing so, it would be useful to adapt the concurrent-schedule procedure in ways that would permit more direct comparisons between the behavior of virtual and human organisms. One option is to conceptualize the testing environment as a two-dimensional space and to represent the target classes as regions within this space (through Cartesian coordinates). Instead of "pressing buttons" the participant will "click within a certain region". The Cartesian coordinates of each response (click) can be recorded, allowing the precise calculation (in pixels) of $\Delta_{\text{PHENOTYPE}}$ (the moment-to-moment behavior variability). In addition, this procedure will allow for the precise manipulation of the size of target classes (the target regions) and the number of extraneous options (the total size of region). In general, it will allow for more direct comparisons between the behavior of virtual organisms and human participants, an important step for exploring the Theory's ability to predict human behavior in laboratory settings.

The third aim of this project was to verify the potential equivalence between mutation and a property of live organisms that produces *impulsivity*-like symptoms in live organisms. The results were inconclusive, mainly due to a lack of high scores on traditional measures of *impulsivity* in the present sample (non-diagnosed college students). These results suggest that in order to verify this connection, future experiments should include participants characterized by high levels of *impulsivity*, preferably ADHD-diagnosed participants. Nevertheless, the other extreme also needs to be considered. The manner in which the construct *impulsivity*is discussed in literature tends to convey, most likely unintentionally, the attitude that it is a fundamentally negative characteristic, like myopia:in an ideal, healthy organism, it would not exist at all. The potentially maladaptive effects of extremely low *impulsivity* scores were rarely discussed, with a few notable exceptions. For example, Neuringer (2009) discussed the maladaptive role of high behavior variability levels, but also those of extremely low variability levels, as observed in the stereotypical behavior of children diagnosed with autism. The connection between *variability* and *impulsivity*however, was not explored systematically; at this point the conceptual and empirical relation between the two constructs remains unclear. An examination of the relation between very low impulsivity scores, continuous choice behavior, and low mutation rates (in the Theory), could provide valuable insight about the potential adaptive role of *impulsivity*, its maladaptive extremes, and the *context* in which they need to be understood.

Concluding remarks

The more we learn about the Evolutionary Theory, the story it reveals about the evolution of behavioral repertoires becomes more complicated, more interesting, and more coherent. Emerging freely from the reiteration of low-level Darwinian processes, the high-level outcomes produced by the theory showed a remarkable inner-coherence, in qualitative and quantitative agreement with the behavior of live organisms (see McDowell, in press, for a review). The possibility that human behavioral repertoires are complex systems pushed through time by low-level Darwinian processes becomes harder and harder to ignore.

The structures and phenomena that make our world, from tadpoles to rainbows, and from cave paintings to philosophy and the stock market, are diverse and, *prima facie*, overwhelmingly complicated. Historically, the more we learned about them, the more complicated they appeared to be. That is until a new way of looking at them reveals a fundamental simplicity that runs deep underneath the observable (Feynman, 1981[3]). The diversity of life was explained by a few low-level mechanisms that, over billions of years, created what we see today (Darwin, 1858; Mayr, 2001; Dawkins, 2009). The universe itself was traced back to twelve fundamental particles and four forces (CERN, 2012[4]). At this point, the field of psychology seems to be in a "complicated" phase, with numerous competing theories, vast collections of sound, yet disconnected findings, and still in search ofmechanisms and rules. The complexity paradigm (Ferguson, 1776, Hayek, 1952, 1980; Holland, 1988, 2000; Wolfram, 2002) suggests that all phenomena that interest us, from ADHD tomoral behavior andtraffic laws, are emergent properties, produced (but not directly

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[3] https://www.youtube.com/watch?v=FXiOg5-l3fk

[4] http://home.web.cern.ch/about/physics/standard-model

explained) by simple rules reiterated over time. In order to understand such systems and their emergent properties one must identify the rule that create them.

It has been proposed that the rules that create these outcomes are low-level selectionist processes, hypothesized to unify biology, behavior, and culture (Pierce&Cheney,2008), to produce the phenomenon referred to as consciousness (Edelman, 2006), and to bridge the quantum and classical realities (Zurek, 2009). The Evolutionary Theory of Behavior Dynamics (McDowell 2004, 2013) is a computational theory that implemented the selectionist hypothesis in an attempt to explain the evolution of behavioral repertoires of live organisms. It is also the first step psychology takes towards a science of complexity, and, as shown by ten years of failed falsification attempts, it is a promising one.

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Table 1

The table provides an overview of the experimental conditions examined in the first phase of this project. The environments referred to as "moderate" (or "standard" in the case of the HD_{COD} manipulation), on grey background, arranged a moderate overall reward rate (~34/500 generations), a moderate strength of the selection process (parental selection function mean, μ = 100), and a computational changeover delay (HD_{COD}) that can be described as "high", and that coincides with the traditional location of the target classes, between 511 and 512 (Hamming Distance = 10). When one variable was allowed to vary the other two were kept constant. For example, when investigating the effects of various reinforcement densities (top third of the table), the strength of the selection process and the HD_{COD} were kept constant (μ = 100, HD_{COD} = 4.4, when the target classes were defined separated by a HD of 10, between 511│512).

Description	**Overall reward density** (per 500 generations)	**Parental Selection Function mean (μ)** (lower means = stronger selection ~ higher reinforcement magnitude)	**Hamming Changeover Delay (HD_{COD})** ($HD_{COD} = HD_{OTHER} - HD_{SAME}$; the table also depicts the value of the Hamming Distance between the target classes and its location on the continuum)
Extremely high rate	1,723	100	4.4 (HD 10, 511 | 512)
High rate	172	100	4.4 (HD 10, 511 | 512)
Moderate rate and magnitude	34	100	4.4 (HD 10, 511 | 512)
Low rate	17	100	4.4 (HD 10, 511 | 512)
Very low rate	3	100	4.4 (HD 10, 511 | 512)
Very strong selection	34	25	4.4 (HD 10, 511 | 512)
Strong selection	34	50	4.4 (HD 10, 511 | 512)
Moderate rate and magnitude	34	100	4.4 (HD 10, 511 | 512)
Weak selection	34	200	4.4 (HD 10, 511 | 512)
Very weak selection	34	500	4.4 (HD 10, 511 | 512)
High HD_{COD}	34	100	6.4 (HD 12, 2,047 | 2,048)
High HD_{COD}	34	100	5.4 (HD 11, 1,023 | 1,024)
High, Standard HD_{COD}	34	100	4.4 (HD 10, 511 | 512)
Moderate-High HD_{COD}	34	100	3.4 (HD 9, 255 | 256)
Moderate HD_{COD}	34	100	2.4 (HD 8, 383 | 384)
Low HD_{COD}	34	100	1.4 (HD 7, 447 | 448)

Table 2

Brief description of the difference between the two experimental conditions (first two columns, No_COD and COD_2s), the means of the Random Interval schedules for the two alternatives (column 3), the ratio of scheduled reinforcement for each RI RI component (column 4), the period of time for which each component was in effect (in seconds), and the order in which the components were presented. Note that except the difference described in the first two columns, the procedure was identical for the two groups.

Experimental condition (# of participants)		**Means of the Random Intervals (seconds)**		**Mean ratios**	**Time in effect**	**Order**
Group No_COD (*N* = 20)	**Group COD_2s** (*N* = 18)					
The two schedules were arranged on two different physical alternatives (two buttons). No COD was in effect.	The two schedules were arranged on one physical alternative (the right button). Switching between the two schedules was done by pressing the left button, called the Findley-button. Every press of the Findley-button started a 2-second COD.	RI 0.7	RI 0.7	1	50s	Always first
		RI 2.4	RI 1.2	2	200s	Random order
		RI 2.1	RI 1.5	1.4	200s	
		RI 1.8	RI 1.8	1	200s	
		RI 1.5	RI 2.1	0.7	200s	
		RI 1.2	RI 2.4	0.5	200s	
		Extinction	Extinction	n/a	50s	Always last

Table 3

Macro-level descriptors of the continuous-choice behavior of college students: sensitivity (a, the slope described by Equation 3), bias (b = $10^{INTERCEPT}$), the proportion of variance accounted for by Equation 3 (pVAF), and the correlation coefficient between the standardized residuals left by Equation 3 and the predicted values. For each of the four variables the table provides averages, medians, and standard errors of the mean, for all participants (N = 38, white background), the No_COD group (N = 20, pink background), and the COD_2s group (N = 18, blue background).

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	Sensitivity (*a*)			**Bias (*b*)**			**pVAF (Eq. 3)**			**Pearson residuals**		
	All	**No COD**	**COD 2s**	**All**	**No COD**	**COD 2s**	**All**	**No COD**	**COD 2s**	**All**	**No COD**	**COD 2s**
Avg.	0.56	0.47	0.66	0.97	0.99	0.94	0.68	0.66	0.71	0.13	0.09	0.18
Median	0.59	0.47	0.70	0.97	0.98	0.96	0.78	0.79	0.76	0.05	0.03	0.18
SEM	0.04	0.06	0.06	0.01	0.02	0.02	0.04	0.07	0.06	0.03	0.04	0.05

Table 4

The eight behavioral measures (column 1), the averages for each experimental group (with standard errors of the mean in parenthesis; columns two and three), the conclusion of the F-test for equality of variance, and the conclusion of 1-tailed t-tests. The values in bold, on grey background, indicate the four differences that reached statistical significance.

Behavioral measure	**No_COD** *M* (*SEM*)	**COD_2s** *M* (*SEM*)	**Variances (results of F-Tests)**	**1-tailed *t*-test**	
				t	***p***
***a* (*sensitivity*)**	0.47 (0.05)	0.66 (0.06)	**Equal**	**2.19**	**0.018**
CO/min	51 (8.5)	29 (6.0)	**Equal**	**-1.99**	**0.028**
B/min	112 (13.5)	87 (9.9)	Unequal	-1.44	0.091
r/min	42 (2.1)	33 (1.7)	**Unequal**	**-3.44**	**0.001**
Bouts/min	8.2 (0.8)	6.4 (1.0)	Equal	-1.34	0.106
Bout Length	7.2 (1.0)	13.5 (3.8)	Unequal	1.59	0.064
Sustained behavior (%)	0.51 (0.05)	0.67 (0.07)	**Equal**	**1.96**	**0.029**
IBT	40 (17)	55 (49)	Unequal	0.90	0.053

N.B. The mean comparison was "COD_2s" - "No_COD".

Table 5

The concurrent-schedule procedure (described in Phase 2) was followed by a short break, after which the participants were administered the CPT-IP computer task (10 minutes), and four personality inventories (last columns).

Task	**Duration**	**Notes**		
Concurrent Schedules procedure (~17 minutes)				
Break	5-10 min			
Continuous Performance Test (CPT-Identical Pairs)	10 min	*Sustained attention, behavior inhibition*		
Break	5-10 min			
Questionnaires	~30 min	**Questionnaire, purpose, #items**		
		A-ADDES (Adult Attention Deficit Disorders Evaluation Scale)	*Inattention, Impulsivity*	58 (2 subscales)
		UPPS-P	*Impulsivity*	59 (5 subscales)
		Sensation Seeking Scale V (SSS-V)	*Impulsivity*	40 (4 subscales)
		Social Desirability Scale (labeled as Personal Reaction Inventory - PRI)	*self-management tendencies*	33

Table 6

Comparisons between the UPPS-P theoretical scores (Minim, Maxim, Average), the scores observed in the present sample (Minim, Maxim, Average, Median, SD), and the scores reported by Miller et.al. (2010) for a control group with comparable demographic characteristics.

	Theoretical			**Observed**					**Miller et al. (2010 - control group)**	
	Min	**Max**	**Avg.**	**Min**	**Max**	**Avg.**	**Med**	**SD**	**Avg.**	**SD**
Neg. Urg.	12	48	30	16	38	27.9	28	5.7	21.9	6.8
(lack of) Prem.	11	44	27.5	12	32	21.9	23	5.5	22.1	5.0
(lack of) Persev.	10	40	25	12	31	19.8	19	4.9	19.1	4.8
Sens. Seek	12	48	30	18	45	32.6	33	7.6	30.1	9.0
Poz. Urg.	14	56	35	14	50	26.6	26	8.6	n/a	n/a
UPPS-P	59	236	147.5	84	177	129	131	21.6		
UPPS-P (minus Positive Urgency)			**129.0**			**129.0**				

Table 7

Comparisons between the SSS-V theoretical scores (Minim, Maxim, M = 5, not included), the scores observed in the present sample (Minim, Maxim, Average, Median, SD), and the total scores (Mean and SD) reported for control groups in two studies with comparable demographics (Ridgeway &Russel, 1980; McDaniel & Mahan, 2008).

SSS-V subscale	**Theoretical**		**Observed**					**Ridgeway&Russel (1980)**		**McDaniel & Mahan (2008)**	
	Min	Max	Min	Max	*M*	*Mdn*	*SD*	*M*	*SD*	*M*	*SD*
Boredom Susceptibility	0	10	0	8	3.2	3	1.9	n/a	n/a	n/a	n/a
Disinhibition	0	10	0	9	4.1	4	2.3	n/a	n/a	n/a	n/a
Experience Seeking	0	10	2	9	4.8	5	1.8	n/a	n/a	n/a	n/a
Thrill and Adventure Seeking	0	10	0	10	6.3	7	2.7	n/a	n/a	n/a	n/a
SSS total	0	40	3	29	18.5	19	6.1	19.5	5.5	**20.6**	**6.5**

Table 8

Comparisons between the CPT-IP d-prime values (d'; discrimination index) observed in the present sample (grey background) and those reported in various studies (first column), in diagnosed and non-diagnosed groups (second column).

Study	**Group diagnostic**	**d' values**	
		M	***SD***
Present sample	none <=>"Control"	2.1	0.78
Barr et. al.(2008)	Schizophrenia	2.1	0.8
	Control	3.3	0.62
Dyer et. al. (2008)	Schizophrenia - Treatment: Pre-Test	2.1	0.8
	Schizophrenia - Treatment: Post Test	1.9	0.7
	Schizophrenia - Placebo: Pre-Test	2.5	0.8
	Schizophrenia - Placebo: Post Test	2.7	0.8
Rutschmann et. al. (1977)	Control - 7-8y	≈ 1.0	n/a
	Control - 9-10y	≈ 2.0	n/a
	Control - 11-12 y	≈ 2.3	n/a
	High-Risk - 7-8y	≈ 1.0	n/a
	High-Risk - 9-10y	≈ 1.5	n/a
	High-Risk - 11-12 y	≈ 2.0	n/a
Cornblatt et. al. (1988)	Control - Test	1.6	0.7
	Control - Retest	2.0	0.5
Cornblatt et. al.(1989)	Control	≈ 1.9	1.05*
	Depressed	≈ 1.85	1.84*
	Schizophrenia	≈ 0.75	1.67*
	*= recalculated based on *SEM* ~0.2 (*N* = 28, 17, and 14)		

Table 9.

Gender differences on various dimensions of impulsivity and inattention. The scores for UPPS-P, SSS-V, and PRI are expressed in z-scores. The scores on A-ADDES and CPT (d') were not converted into z-scores, being already expressed in standard units, as discussed in the Methods section. The average scores were small, varying closely around average. Differences between the average scores of males and females were very small and in the expected direction. Males scored *slightly higher on impulsivity dimensions, females scored lightly higher on the inattention subscale of A-ADDES, and the averages of the two groups were almost identical and equal to zero on the Social Desirability Scale (noted here with PRI, Personal reaction Inventory).*

Measure		**Females (*N* = 29)**			**Males (*N* = 9)**		
		Average	**Median**	**SEM**	**Average**	**Median**	**SEM**
A-ADDES	**Inaten.**	**8.04**	8.50	0.49	**7.11**	8.00	1.12
	Hyp/Imp.	**5.18**	5.00	0.50	**6.22**	6.00	0.55
	A-ADDES	**13.21**	13.00	0.88	**13.33**	15.00	1.59
UPPS-P	**Neg. Urg.**	**-0.07**	-0.08	0.20	**0.20**	0.36	0.24
	(lack of) Prem.	**-0.13**	0.01	0.20	**0.40**	0.19	0.27
	(lack of) Persev.	**-0.04**	-0.38	0.19	**0.12**	0.03	0.35
	Sens. Seek	**-0.07**	-0.02	0.19	**0.21**	0.31	0.33
	Poz. Urg.	**-0.04**	-0.19	0.19	**0.12**	-0.08	0.36
	UPPS-P	**-0.10**	0.00	0.20	**0.30**	0.09	0.27
SSS-V	**Boredom Susceptibility**	**-0.07**	-0.11	0.18	**0.23**	-0.11	0.40
	Disinhibition	**0.03**	-0.06	0.21	**-0.11**	-0.06	0.20
	Experience Seeking	**0.03**	0.09	0.19	**-0.09**	0.09	0.34
	Thrill and Adventure Seeking	**-0.07**	0.27	0.19	**0.23**	0.27	0.34
	SSS	**-0.03**	0.09	0.20	**0.11**	-0.08	0.29
PRI	**Soc. Dez.**	**0.00**	0.07	0.20	**0.01**	-0.04	0.32
CPT	**d'**	**2.16**	2.10	0.16	**2.00**	1.93	0.21

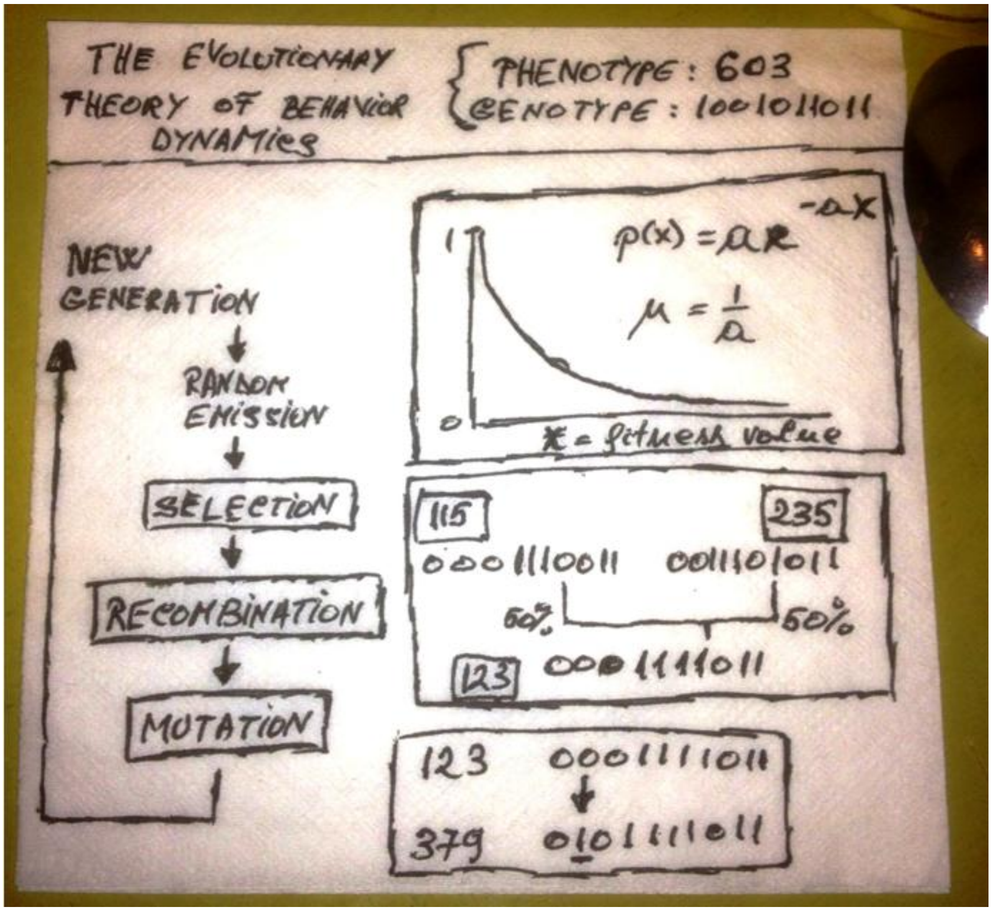


Figure 1.The figure provides an overview of the theory's functionality. At each generation, or time tick, a behavior is randomly selected and emitted from a population of behaviors, abstractly represented by numbers (integers and their corresponding binary representations). Emissions are followed by selection of parents for the next generations. If the emission did not result in positive outcomes, parents are selected at random. If the emitted behavior resulted in a positive outcome, parents are selected based on their fitness: behaviors that are closer to the previously reinforced behavior have a higher chance of becoming parents. Regardless of how parents selected (at random or based on their fitness) they recombine in the same way, each parent having equal chances of contributing to the child's genotype. The population of children is affected by mutation: a small number of child-behaviors are selected at random and one of the bits in their genotypes, also selected at random, is "flipped" from zero to one or one to zero. From this new, mutated population, a behavior is emitted at random and another cycle begins.The continuous application of Darwinian rules of selection, recombination, and mutation, in time, gives rise to ordered behavioral patterns that can be analyzed and compared to live data.

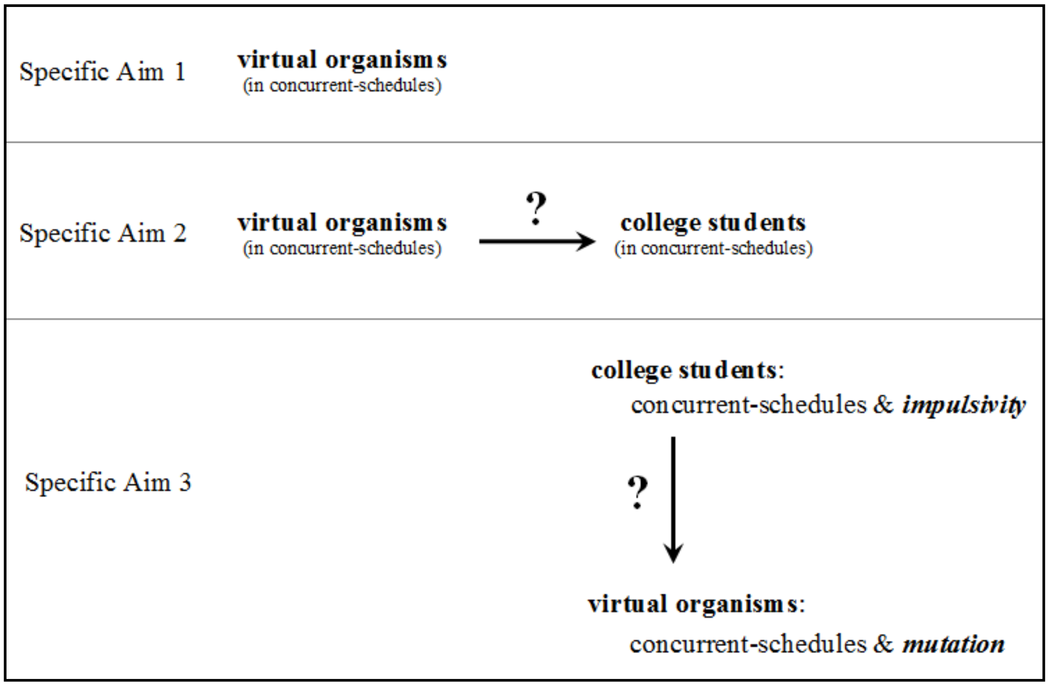


Figure 2.The figure illustrates the connection between the three specific aims of this project. The first specific aim was to learn about the effects of reward rate, reward magnitude, and Hamming Distance changeover delay (HD_{COD}) on the behavioral variability of virtual organisms characterized by different mutation rates. The second aim was to verify the theory's potential of predicting the performance of college students in continuous-choice settings. The third aim was to use the information obtained in the first two phases (specific aims 1 and 2) to explore the relation between *mutation* and *impulsivity*.

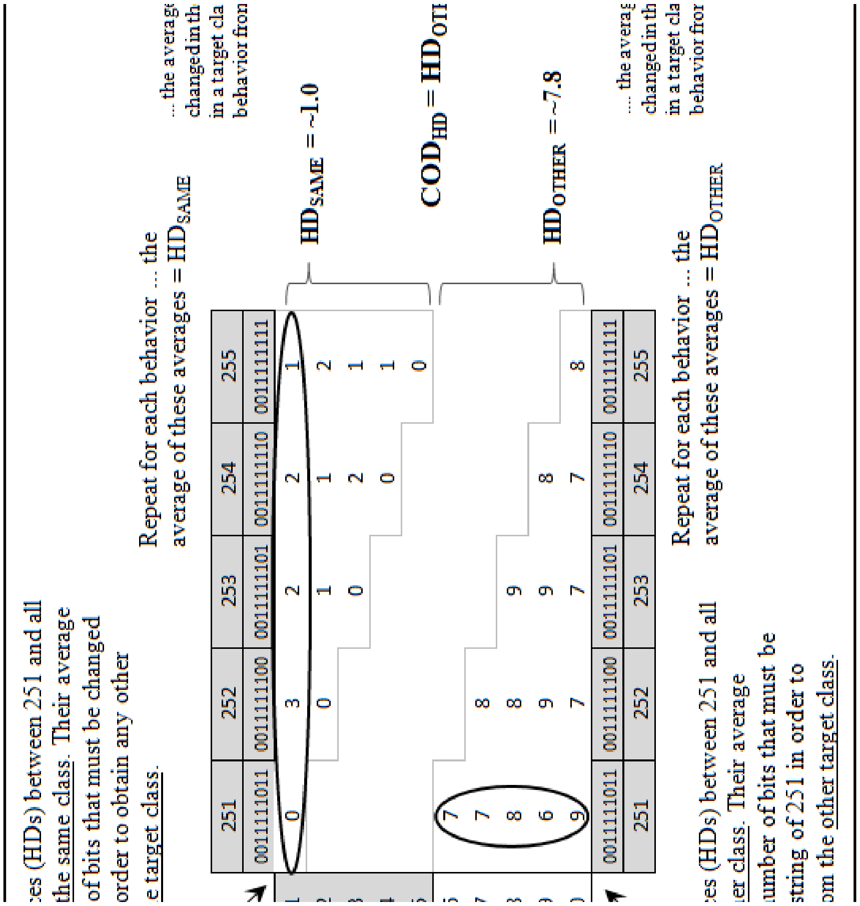


Figure 3.The figure outlines the calculation of the Hamming Distance changeover delay (HD_{COD}) as a function of HD_{OTHER} - HD_{SAME}. HD_{OTHER} (top of the figure) is obtained by averaging all the Hamming Distances between all behaviors in a target class and all behaviors in the *other* class. HD_{SAME} (lower part of the figure) is obtained by averaging all the Hamming Distances between all behaviors in a target class and all behaviors in the *same* class. The difference between the two averages can be conceptualized as a measure of the *overall average "difficulty" to switch* from one class to the other. This difference was referred to as environment's *conduciveness*, where high *conduciveness* is described by low HD_{COD} values, which is characteristic of environments that facilitate rapid switching between alternatives.

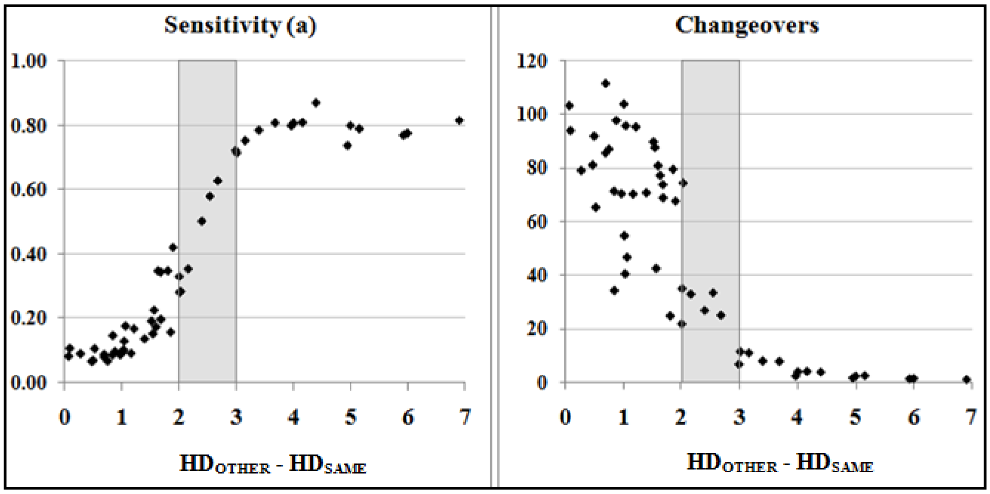


Figure 4.Sensitivity (*a*; left panel) and frequency of switching (changeovers, right panel), asa function of $HD_{COD} = HD_{OTHER} - HD_{SAME}$ (reanalysis of data reported by Popa& McDowell, 2010).*Sensitivity*(*a*) increased as HD_{COD} increased, in a roughly logistical pattern, which indicated the presence of a certain threshold-area: bellow certain HD_{COD} values *sensitivity* was always very low; above this threshold,further increases in HD_{COD} did not have noticeable impact on *sensitivity*. The frequency of switching correlated negatively with *sensitivity*: very high frequencies of switching were associated with severe undermatching (low HD_{COD}) and vice versa.

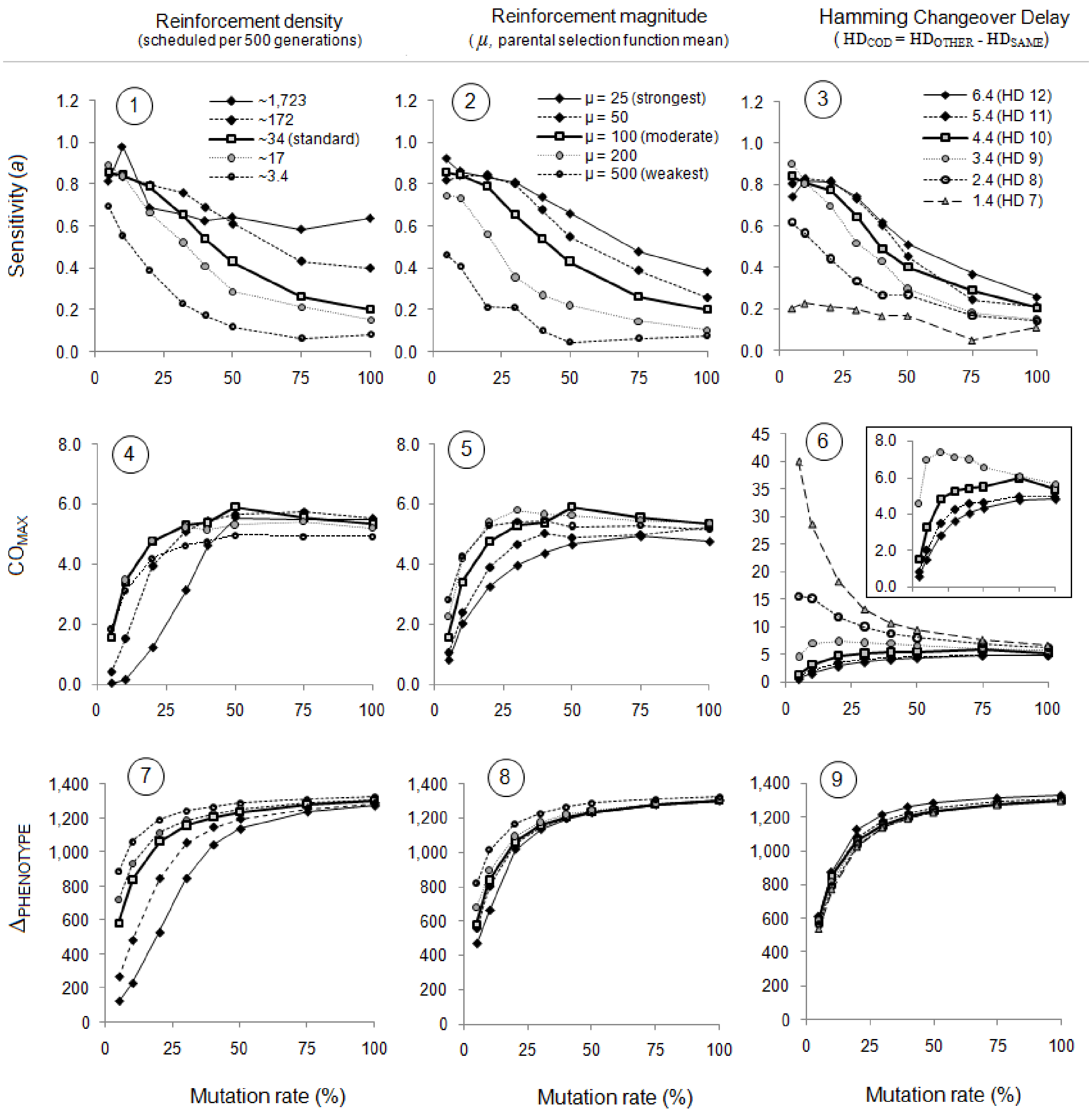


Figure 5.Figure 5 shows the effects of various reinforcement densities (left), various strengths of the selection process (<=> reinforcement magnitude, middle), and various HD_{COD} values (right) on *sensitivity* values (*a*, panels 1, 2, 3), maximum changeover frequency (CO_{MAX}, panels 4, 5, 6), and topographic variability ($\Delta_{PHENOTYPE}$, panels 7, 8, 9), at different mutation rates.

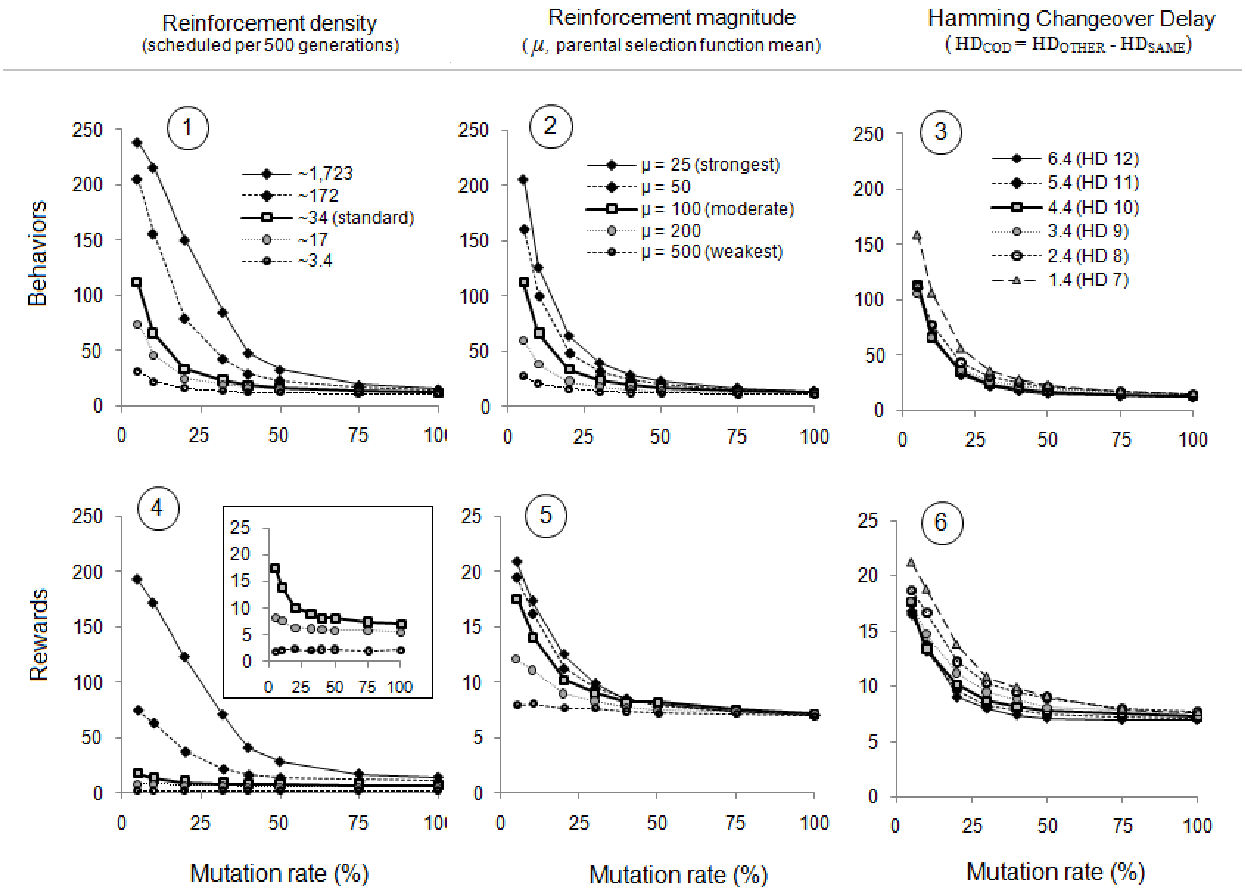


Figure 6.Figure 6 shows the effects of various reinforcement densities (left), various strengths of the selection process (middle), and various HD_{COD} values (right), on the overall frequency of target behavior (panels 1, 2, 3) and obtained rewards (panels 4, 5, 6), at various mutation rates. Behaviors and rewards were summed for both alternatives and averaged per 500 generations.

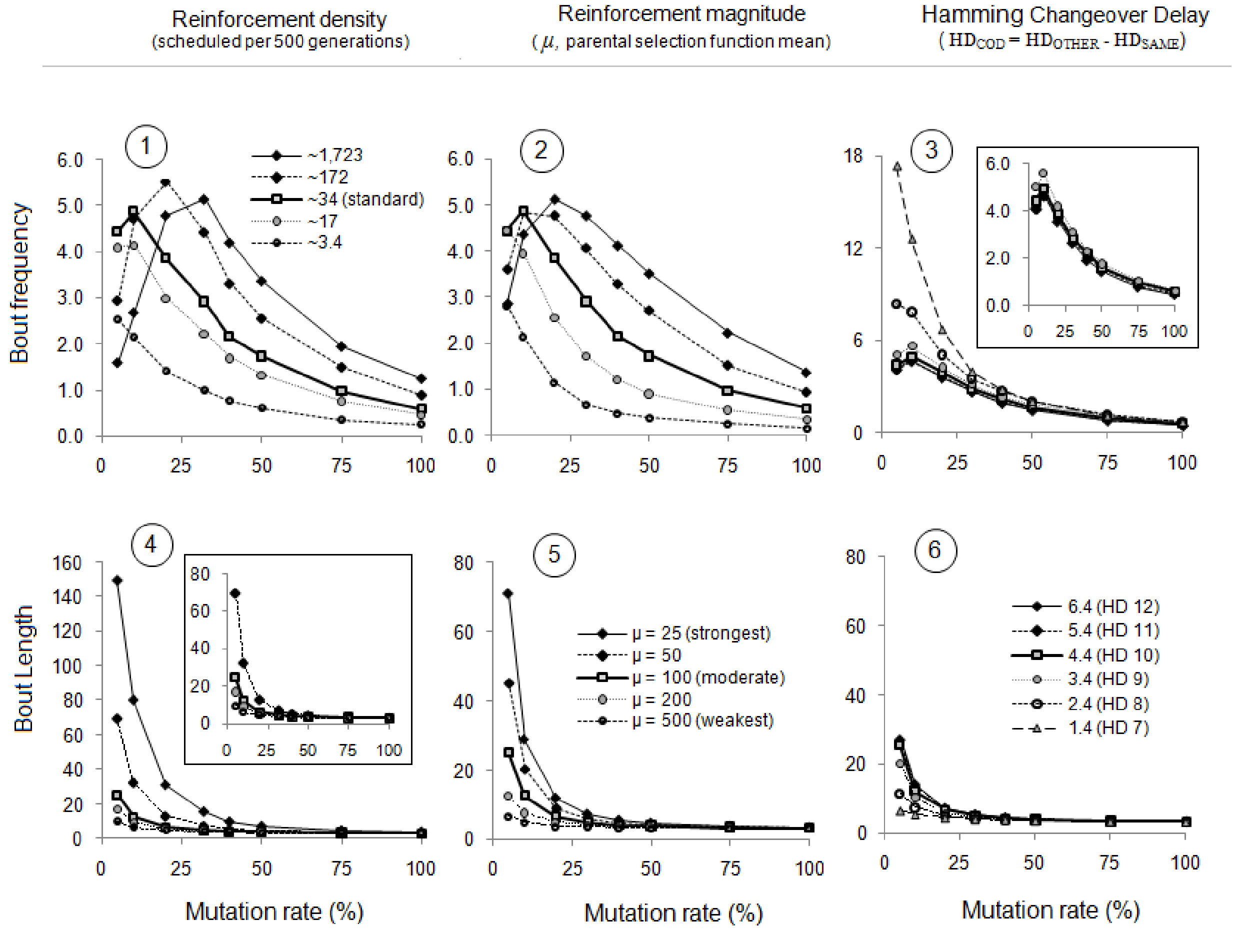


Figure 7.Figure 7 illustrates the effects of reinforcement density (left), reinforcement magnitude (middle),and HD_{COD} (right), on the average bout frequency (panels 1, 2, 3)and length (panels 4, 5, 6), at various mutation rates. Overall, organisms characterized by higher mutation rates emitted fewer bouts, of shorter length, a relation mediated by reward rate, reward magnitude, and HD_{COD}.

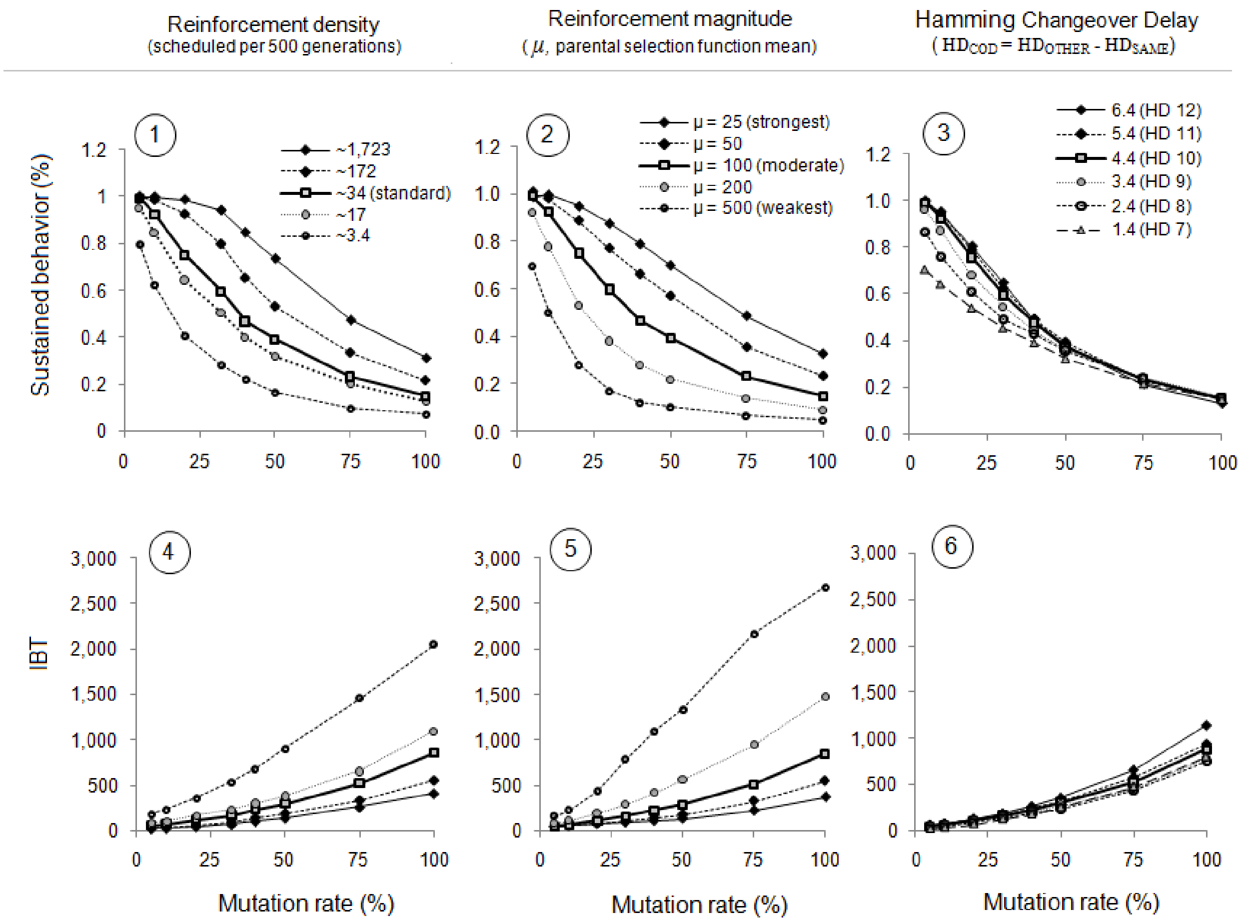


Figure 8.Figure 8 illustrates the effects of reinforcement density (left), reinforcement magnitude (strength of the selection process; middle), and HD_{COD}values (right), on the proportion of sustained (or in-bout) behavior (panels 1, 2, 3) and Inter-Bout Time (IBT; panels 4, 5, 6), at various mutation rates.

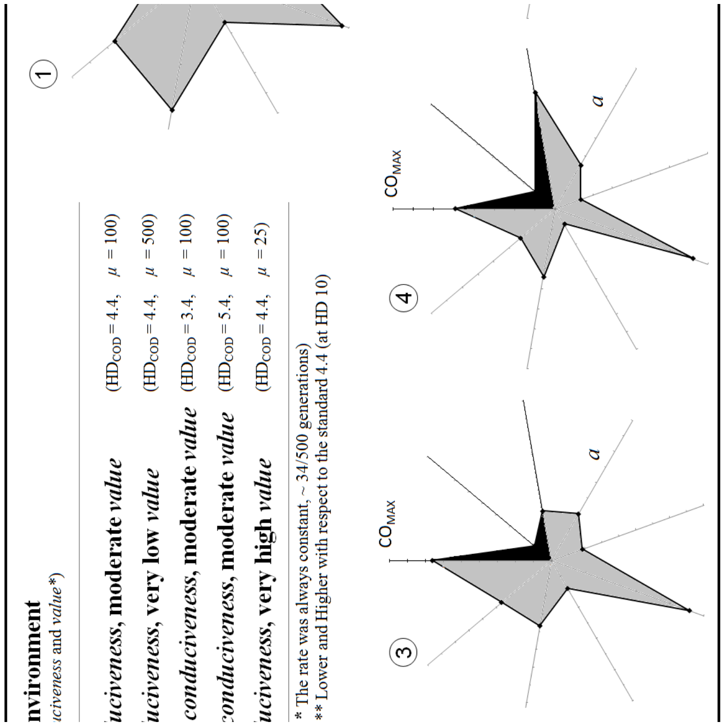


*Figure 9.*Figure 9 depicts the behavioral characteristics of five virtual organisms. Each of the nine axes depicts one of the nine dependent variables, with zero in the center of the radar-type graph. The order of the nine variables was changed so that variables for which "low" values mean "desirable", "good" outcomes were close together (CO$_{MAX}$, $\Delta_{PHENOTYPE}$, and IBT; first three black axes). Uniting the nine points resulted in an irregular surface that provides an overall visual description of the organism's behavioral characteristics. The raw values were transformed, where necessary, by dividing them by a multiple of 10 (in parenthesis, next to each variable). The purpose was to bring all variables to a comparable scale that would allow a visual depiction. From the first, perpendicular axis, going clockwise, the nine variables are: CO$_{MAX}$ (/10), $\Delta_{PHENOTYPE}$ (/ 10,000), IBT (/10,000), *Sensitivity* (*a*), Responses (/100), Rewards (/100), Bouts (/10), Bout Length (/100), Sustained behavior (%).An organism that displayed low behavior variability (desired outcome) is characterized by a small black area and a large grey area (panel 1). Panels 2, 3, 4, and 5 depict organisms that displayed high variability. The constellations of behavioral characteristics depicted in panels 1, 2, 3, and 4 can be described as highly variable, are very similar to each other, and very different from the constellation depicted in panel 1. Despite their apparent similarities, they were all caused by different combinations of organismic and environmental features.

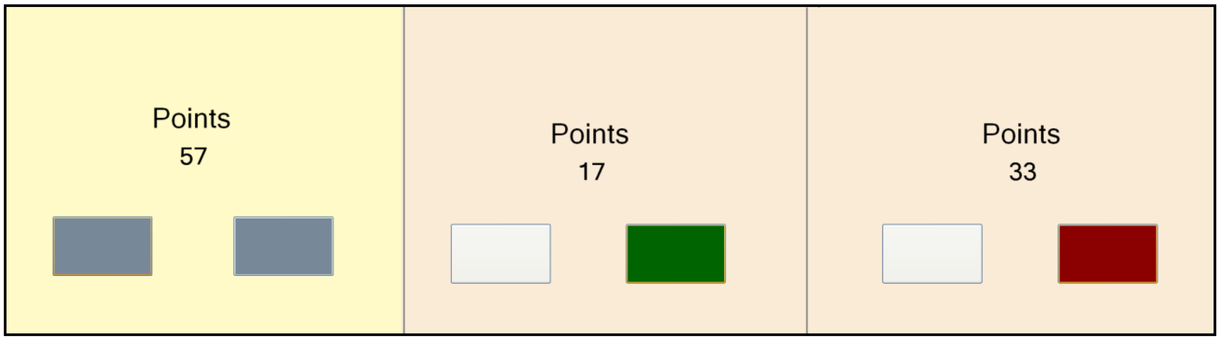


*Figure 10.*The figure provides an illustration of the students' visual experience during the concurrent-schedule procedure. In the No_COD condition (left panel) the two concurrent schedules ran on different physical alternatives, two grey buttons. In the COD_2s condition (middle and right panels) the two concurrent schedules ran on the same physical alternative (the right button); the color of the key (red or green) signaled the participant that a different schedule was in effect. The participant could switch between alternatives by pressing the changeover button(left grey button).

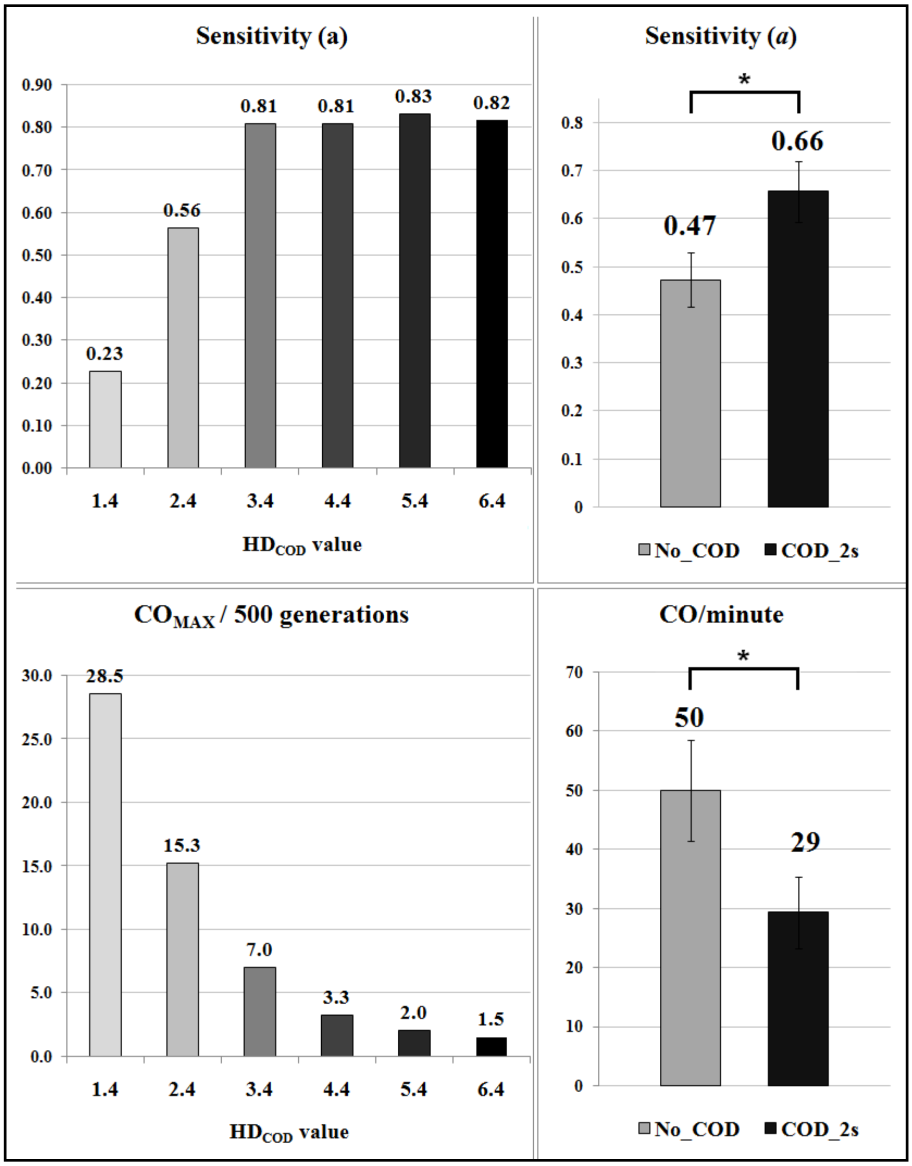


Figure 11.The figure depicts *sensitivity* values (the slope of Equation 3, *a*; top panels) and changeover frequencies (bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. The right panels depict results produced by college students when the duration of the changeover delay was zero seconds ("No_COD" condition) and two seconds ("COD_2s" condition). The error bars represent standard errors of the mean (*SEM*). Asterisks indicate significant differences between conditions (* $p < 0.05$).

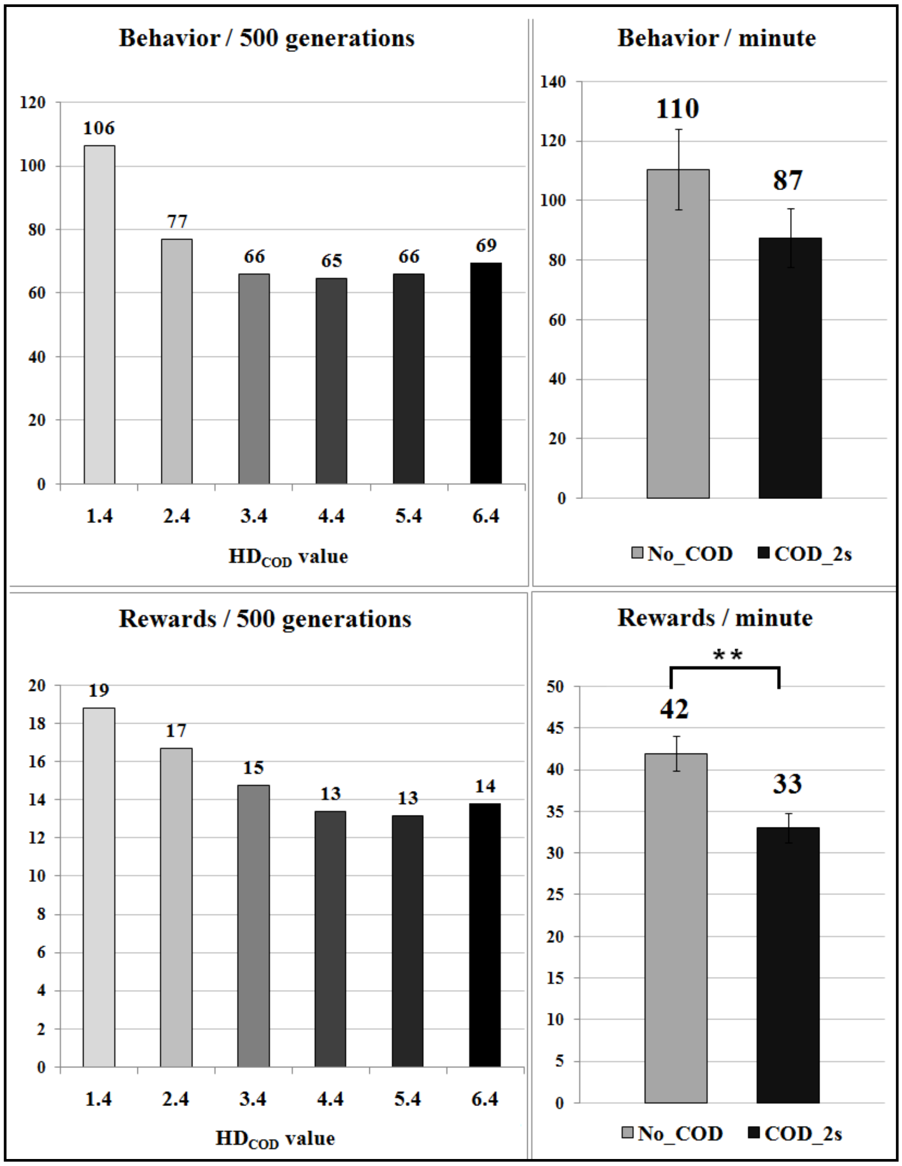


*Figure 12.*The figure depicts average frequencies of target behavior (top panels) and obtained rewards (bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD$_{COD}$ values, averaged per 500 generations. The right panels depict results produced by college students when the duration of the changeover delay was zero seconds ("No_COD") and two seconds ("COD_2s"), averaged per minute. The error bars represent standard errors of the mean (*SEM*). Asterisks indicate significant differences between conditions (** $p< 0.01$).

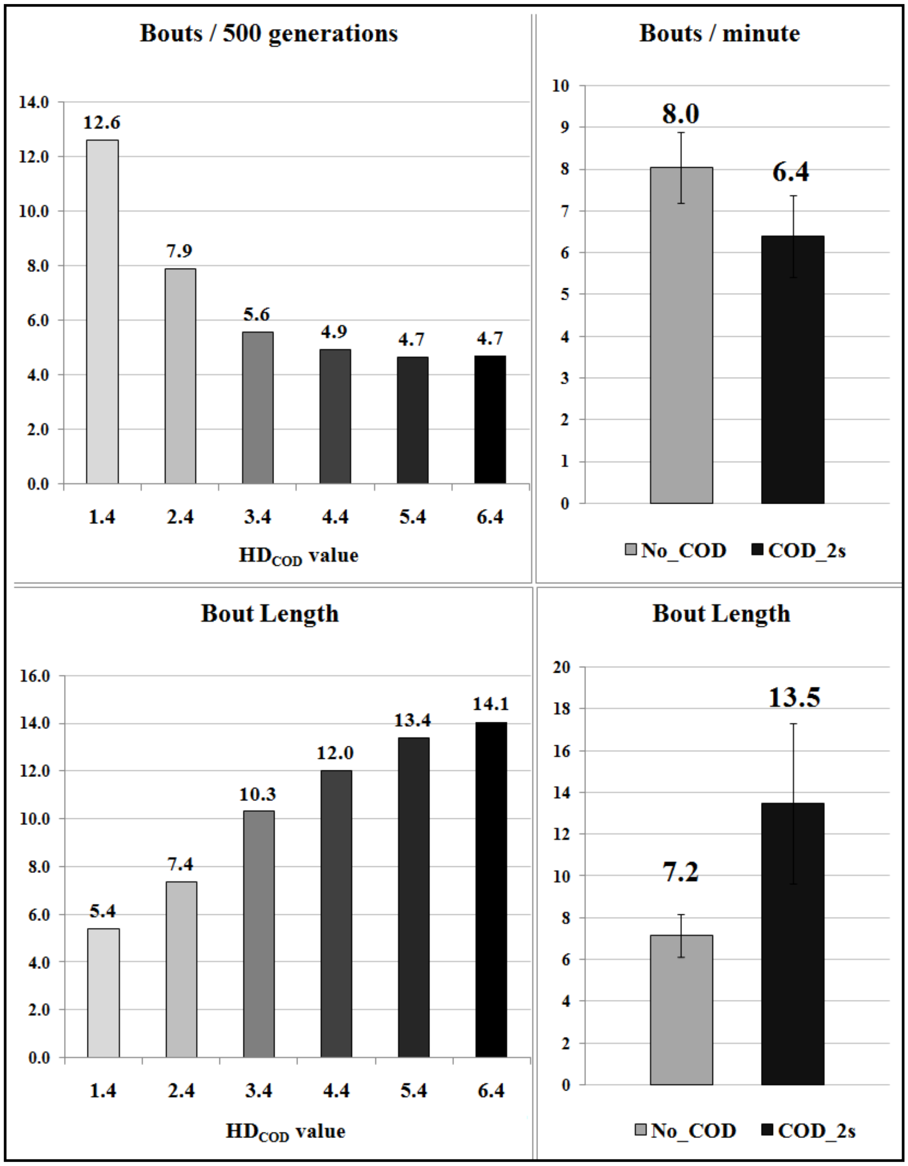


Figure 13.The figure depicts average frequencies of bouts (top panels) and the average bout length (responses/ bout; bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. The right panels depict results produced by college students when the duration of the changeover delay was zero seconds ("No_COD") and two seconds ("COD_2s"). For bout frequency (top panels) the figure depicts averages per 500 generations; for college students, it depicts averages per minute. The error bars represent standard errors of the mean (*SEM*).

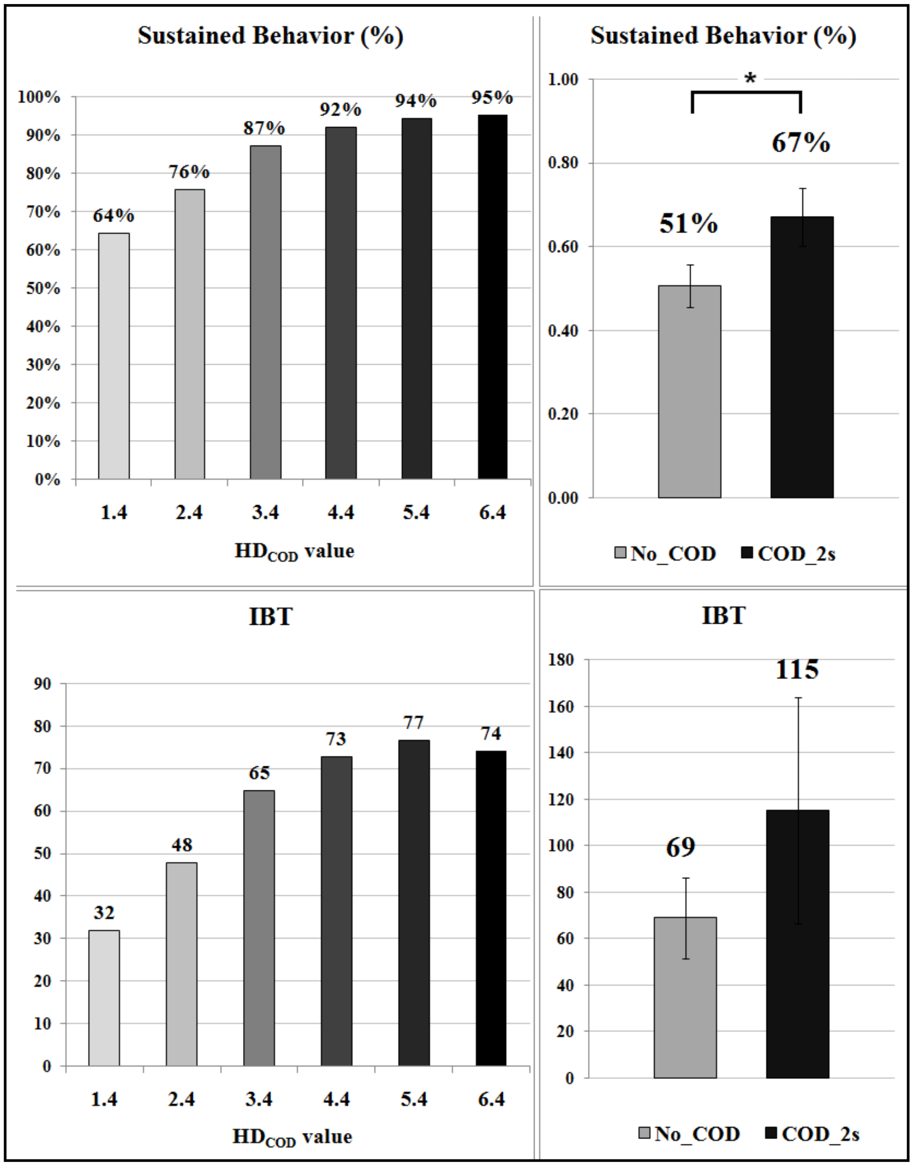
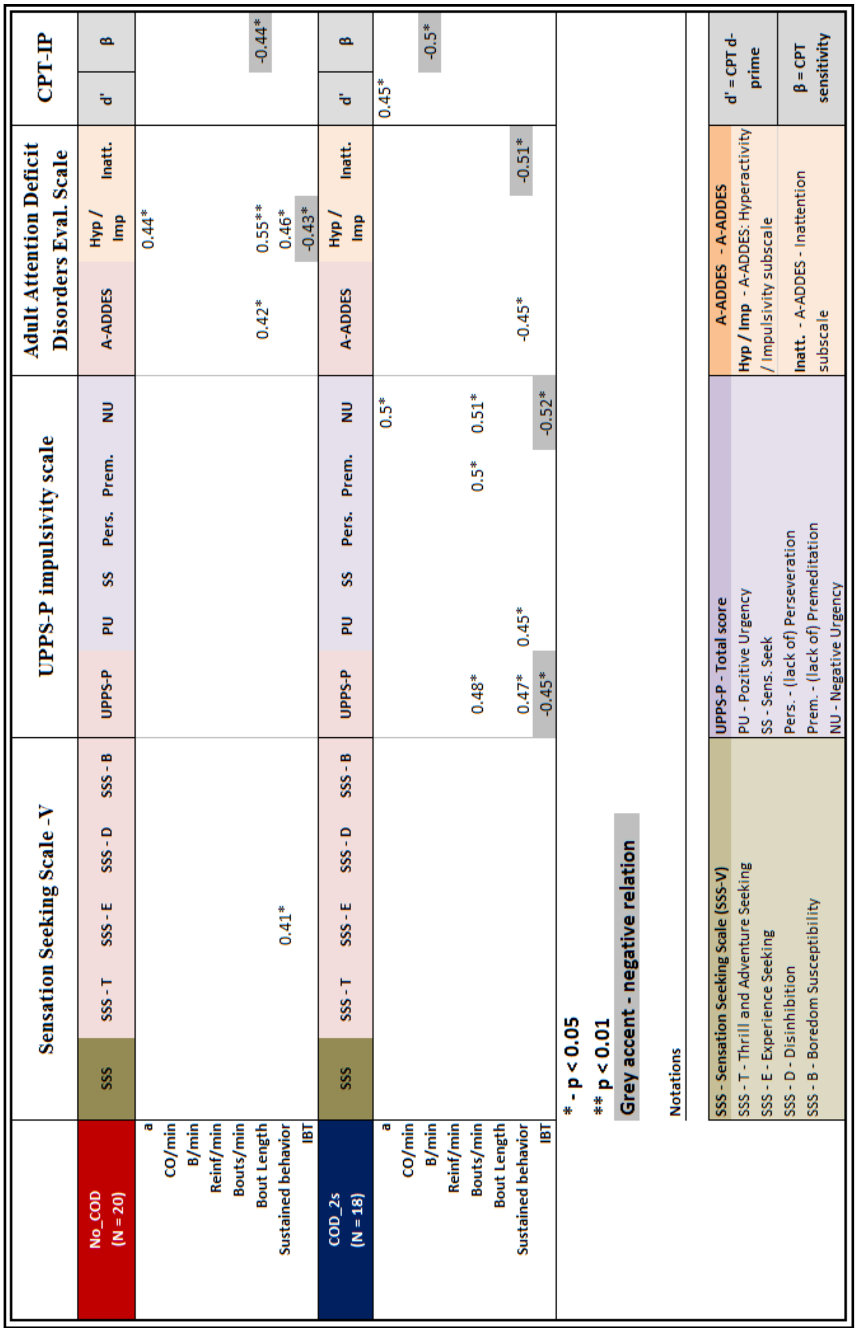


*Figure 14.*The figure depicts proportions of sustained behavior (top panels) and the average Inter-Bout Time (IBT; bottom panels). The left panels depict results produced by the Evolutionary Theory at various HD_{COD} values. The right panels depict results produced by college students when the duration of the changeover delay was zero seconds ("No_COD") and two seconds ("COD_2s"). The error bars represent standard errors of the mean (*SEM*). Asterisks indicate significant differences between conditions (* $p< 0.05$).



	Sensation Seeking Scale -V					UPPS-P impulsivity scale						Adult Attention Deficit Disorders Eval. Scale			CPT-IP	
No_COD (N = 20)	**SSS**	**SSS - T**	**SSS - E**	**SSS - D**	**SSS - B**	**UPPS-P**	**PU**	**SS**	**Pers.**	**Prem.**	**NU**	**A-ADDES**	**Hyp / Imp**	**Inatt.**	**d'**	**β**
a													0.44*			
CO/min																
B/min																
Reinf/min																
Bouts/min																
Bout Length												0.42*	0.55**			-0.44*
Sustained behavior			0.41*										0.46*			
IBT													-0.43*			
COD_2s (N = 18)	**SSS**	**SSS - T**	**SSS - E**	**SSS - D**	**SSS - B**	**UPPS-P**	**PU**	**SS**	**Pers.**	**Prem.**	**NU**	**A-ADDES**	**Hyp / Imp**	**Inatt.**	**d'**	**β**
a											0.5*				0.45*	
CO/min																
B/min																-0.5*
Reinf/min																
Bouts/min						0.48*				0.5*	0.51*					
Bout Length																
Sustained behavior						0.47*	0.45*					-0.45*		-0.51*		
IBT						-0.45*					-0.52*					

*** - p < 0.05**

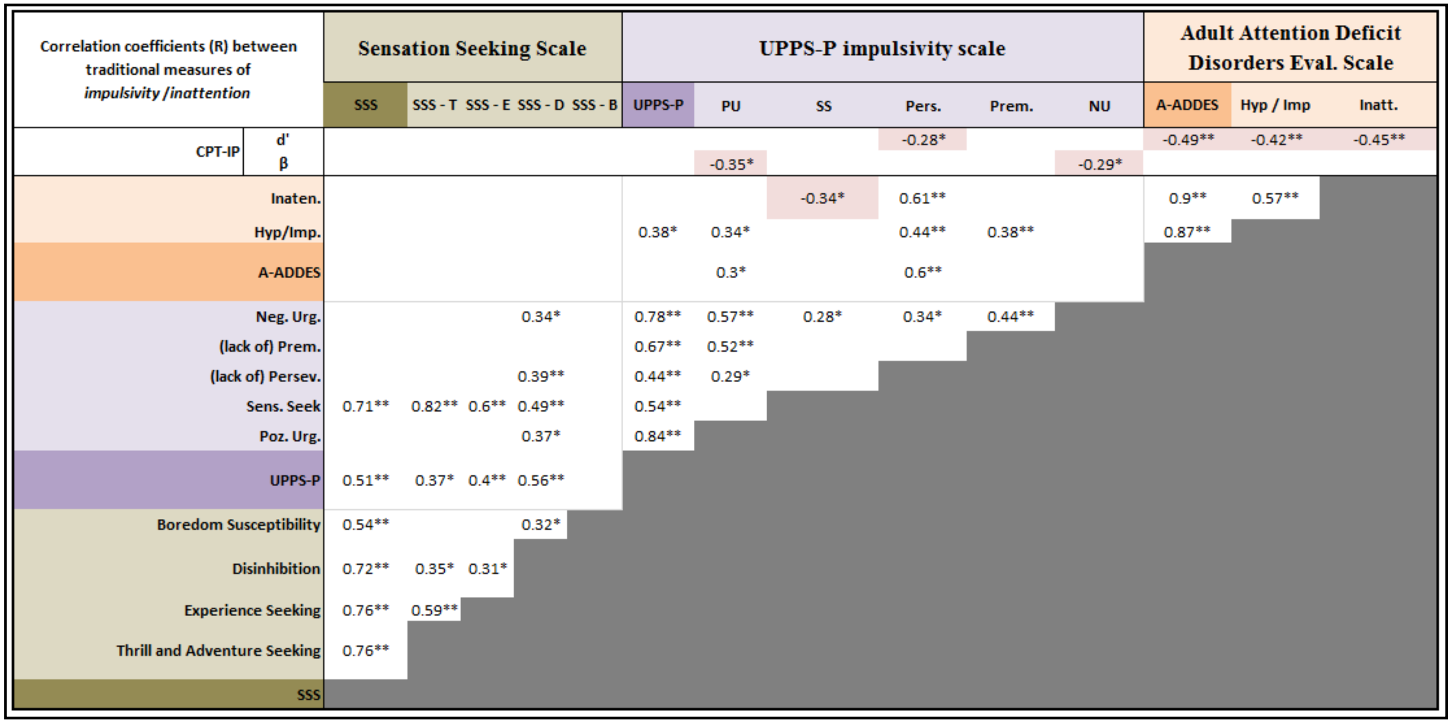
**** p < 0.01**

Grey accent - negative relation

Notations

SSS - Sensation Seeking Scale (SSS-V)	**UPPS-P - Total score**	**A-ADDES - A-ADDES**	**d' = CPT d-prime**
SSS - T - Thrill and Adventure Seeking	PU - Pozitive Urgency	**Hyp / Imp** - A-ADDES: Hyperactivity / Impulsivity subscale	**β = CPT sensitivity**
SSS - E - Experience Seeking	SS - Sens. Seek	**Inatt.** - A-ADDES - Inattention subscale	
SSS - D - Disinhibition	Pers. - (lack of) Perseveration		
SSS - B - Boredom Susceptibility	Prem. - (lack of) Premeditation		
	NU - Negative Urgency		

Figure 15.The figure depicts the correlation coefficients (*r*) that described the relations between continuous-choice characteristics (vertical) and scores on *impulsivity*/*inattention* inventories and CPT-IP measures (horizontal). The figure only retained the relations that were statistically significant (* *p*< 0.05, ** *p*< 0.01). The shaded values emphasize negative relations.



Correlation coefficients (R) between traditional measures of *impulsivity /inattention*		Sensation Seeking Scale					UPPS-P impulsivity scale						Adult Attention Deficit Disorders Eval. Scale		
		SSS	SSS - T	SSS - E	SSS - D	SSS - B	UPPS-P	PU	SS	Pers.	Prem.	NU	A-ADDES	Hyp / Imp	Inatt.
CPT-IP	d'									-0.28*			-0.49**	-0.42**	-0.45**
	β							-0.35*				-0.29*			
Inaten.									-0.34*	0.61**			0.9**	0.57**	
Hyp/Imp.							0.38*	0.34*		0.44**	0.38**		0.87**		
A-ADDES								0.3*		0.6**					
Neg. Urg.					0.34*		0.78**	0.57**	0.28*	0.34*	0.44**				
(lack of) Prem.							0.67**	0.52**							
(lack of) Persev.					0.39**		0.44**	0.29*							
Sens. Seek		0.71**	0.82**	0.6**	0.49**		0.54**								
Poz. Urg.					0.37*		0.84**								
UPPS-P		0.51**	0.37*	0.4**	0.56**										
Boredom Susceptibility		0.54**			0.32*										
Disinhibition		0.72**	0.35*	0.31*											
Experience Seeking		0.76**	0.59**												
Thrill and Adventure Seeking		0.76**													
SSS															

Figure 16.The figure depicts the correlation coefficients (*r*) between the various measures of *impulsivity/inattention*observed in the present sample (self-reported and CPT-IP), for all participants (N = 38). The figure only retained the relations that were statistically significant (* *p*< 0.05, ** *p*< 0.01). The shaded values emphasize negative relations.