CHAPTER 15

Evolution and Modern Behavioral Problems

The Case of Addiction

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Is addiction simply a state of mind, a genetic process, an evolved characteristic of our species, part of an emotional system found in all cultures? Is it strictly speaking a biological issue at all? Is it all biological? Can it ever be adaptive? Is it psychologically maladaptive? Can certain personalities be predicted to be vulnerable to particular types of addiction? Is addiction culturally specific? Could our early ancestors have found anything to be addicted to? How do cultural values and ideologies and friendships and family relationships and expectations create patterns of behavior that increase or decrease the likelihood of addictions? Lende offers a remarkably thorough beginning point that plots out a systematic methodology for answering some of these questions. Similar to Worthman's discussion of sleep, he uses an integrated ecological and developmental model framed by evolutionary thinking to describe a methodology to study addiction that forces us away from peripheralizing the components around which it is constituted in favor of a conceptual perspective that identifies addictive behaviors as being part of an otherwise expectable response at least to certain psychological dilemmas, circumstances, or contexts. Interestingly, Lende's discussion leads us to understand how addictive sequences often mimic "normalcy" but are instead expressed to a degree that rather than looking "normal," the behavior hovers on one or the other end of a behavior continuum. Certainly, for treating those addicted, and for lessons in how to study and interpret addiction, Lende eliminates easy categorical boundaries. He gives us some tools to appreciate the manner in which the human personality can come to positively interpret and even enjoy the very behavior by which it is victimized. It is an important therapeutic insight.

INTRODUCTION

Using the case study of addiction, this chapter addresses how to build a research-based approach to behavioral psychopathology using evolutionary theory. The chapter charts a middle ground between evolutionary psychology and behavioral ecology, while further developing the evolutionary mismatch approach. Taken together, this synthesis provides for a robust approach to modern behavioral problems that proves complementary to research in psychiatry, neuropsychology, and medical anthropology.

After summarizing the problem of substance abuse, the chapter presents some general assumptions for research, covers central steps to building an evolutionary approach, and finally considers how to translate this approach into method. Throughout, substance abuse will provide the relevant example, but the theoretical map itself is applicable to a broad range of problems such as overeating, compulsive behavior, and gambling. This is a how-to guide for studying these problems, derived from the challenges of actually doing such research on substance use and abuse.

BACKGROUND

Several reviews of how evolution applies to addictive behavior already exist, including a comprehensive chapter on the basic Darwinian approach to substance abuse in the first edition of this volume (Smith 1999). Other general reviews include Lende & Smith (2002), Nesse & Berridge (1997), and Saah (2005). Specific topics have also been analyzed, including the phylogenetic roots of substance abuse (Dudley 2000, 2002; Levey, 2004; Panksepp et al., 2002; Sullivan & Hagen, 2002), life history theory (Hill & Chow, 2002; Lende & Smith, 2002), animal models (Gerald & Higley, 2002; Panksepp et al., 2002), related problems like smoking (Pomerleau, 1997) and gambling (Spinella, 2003), and evolutionary discordance (Pani, 2000). Several articles that have focused on reward and decision making in substance abuse are also considered here (Kelley, 2004; Lende & Smith, 2002; Nesse & Berridge, 1997; Newlin, 2002; Pani, 2000).

Despite this growing body of research, most researchers focus either on animal models or on proposing how adaptive models help us make sense of addictive behavior. In particular, these models offer analyses that show how characteristics of addiction can be consistent with the theory of natural selection. At present, there is a need for a research program that systematically addresses the interconnected issues in addiction. In the remainder of the chapter I will outline the basic steps that were utilized in my research on adolescent drug use and abuse in Colombia (Lende, 2003, 2005). The overall study included a broad anthropological analysis of substance use and abuse, using both epidemiological and ethnographic methods. As such, the evolutionary component of this research was conceived as being complementary to a wider biocultural view of substance abuse (see also Hruschka et al., 2005).

The general anthropological basis of my research required a reworking of core proposals of evolutionary psychology and human behavioral ecology. Both bodies of theory present specific research programs based on derivations of modern evolutionary theory (Cosmides & Tooby, 1997; Daly & Wilson, 1999; Smith, Borgerhoff Mulder & Hill, 2000; Winterhalder & Smith, 2000). The problem for addiction, as for many modern

behavioral problems, is that these theoretical approaches are simply not applicable. Behavioral ecology, highly reliant on optimality theory and evolutionary stable strategies,[1] does not provide the necessary insight into the very costly, even pathological problem of substance abuse. With evolutionary psychology, there is no "universal module" for addictive behavior of the sort that evolutionary psychologists generally propose. These modules are generally seen as solving adaptive problems in past environments. Given the phylogenetic novelty of concentrated psychoactive substances, there is no past adaptive problem that substance users directly solve by taking drugs in large quantities. The theoretical problems of both behavioral ecology and evolutionary psychology are related to their particular derivations of evolutionary theory (e.g., optimality and universal modules). As shown here, a return to general evolutionary theory—the processes of natural selection and descent with modification that Darwin originally proposed—proves important for developing an evolution-based approach to modern behavioral problems.

This research also required a more critical application of evolutionary medicine. Evolutionary medicine often uses a discordance model, which focuses on how modern environments change the functioning of adaptations (often in negative ways). However, consuming drugs has not provided a consistent adaptive benefit or cost over evolutionary time, which means that addiction is not an evolutionary problem in itself. Thus, a simple discordance model does not work well. For example, several researchers propose that drugs provide "false" fitness benefits due to their evolutionary novel impact on brain structures (Nesse & Berridge, 1997; Panksepp et al., 2002). These benefits are then assumed to account for the problem of addiction. In this approach, addiction is reduced to the novel effects of drugs alone. This type of analysis misses out on the numerous ways that evolutionary theory can be applied to the *behaviors* involved in addiction. These researchers also overlook the significant sociocultural aspects of substance use and abuse, from difficult family relations to the important role that friends play in drug use (Compton et al., 2005).

Thus, alongside basic evolutionary processes such as natural selection and descent with modification, a sophisticated consideration of the present-day environment is central to understanding modern behavioral problems. In today's world, many sociocultural and environmental processes and contexts that powerfully affect our behavior simply did not exist during evolutionary time. The impact of these environmental factors places a considerable demand on the evolutionary approach to work with other bodies of knowledge, such as sociocultural anthropology. This synthetic approach offers the possibility to produce more robust explanations of modern behavioral problems by attending to the multiple facets inherent in these behavioral problems.

ADDICTION: OUTLINING THE BEHAVIORAL BIOLOGY

A crucial step in developing this evolutionary approach is a clear description of current understandings of addiction. Too often, evolutionary theory confines itself to what initially appears as theoretically relevant, without engaging the actual complexity of the problem under consideration (e.g., the false fitness benefit model discussed earlier). This section aims to rectify this problem by outlining the biological and behavioral aspects of addiction (see Table 15-1).[2]

TABLE 15-1 Behavioral Biology of Addiction.

Function	Reward and liking	Seeking and desire	Habitual action	Association learning	Stress	Self control and cognitive biases
Relation to drug use	Positive sensations linked to drug use	Urge to seek out drugs and wanting to use drugs	Routinized searching and using behaviors	Environmental cues get linked to liking and wanting drugs	Heightens sensitivity to drug cues, reduces self-control	Inability to stop seeking or using, focus on benefits of use
Brain areas	Nucleus accumbens, substantia nigra	Mesolimbic dopamine system, ventral tegmental area, orbitofrontal cortex	Dorsal striatum, caudate-putamen	Hippocampus, amygdala	Hypothalamus, prefrontal cortex	Prefrontal cortex

[a] *This table summarizes those aspects of behavioral biology discussed throughout the chapter. The "related brain areas" serve as a rough guide, for the actual neurobiology is not so localized and is more interconnected. Certain neuropsychological processes that are relevant to addiction are not included, such as long-term potentiation in memory and management of attention in the prefrontal cortex. Withdrawal, central to some drugs, is also not included, as it can be substance specific (e.g., alcohol) while also creating aversive states similar to stress (Koob & Le Moal, 2005). Topics discussed later can also be linked to the behavioral biology. Ritualized behavior has links with the category "habitual action," and the importance of meaning involves the prefrontal cortex (indeed, Everitt and Robbins [2005] argue that the prefrontal cortex plays a central role in "post hoc commentary" on sensory perceptions linked to drug use).*

Two core behavioral patterns define addiction. First, over time the individual transitions from intermittent substance use to compulsive involvement with drugs (Everitt & Robbins, 2005; Koob & Le Moal, 2004). This amplification of one activity (drug use) with neglect of other areas of life (e.g., social responsibilities of family and work) is central to substance abuse. Second, addiction is also defined by "relapse," which means a reversion to the intense engagement with substance use (DeJong, 1994; McLellan et al., 2000). This return to old behavioral patterns can happen months or years after an individual has stopped using drugs, and thus is not always directly related to withdrawal from drugs.

Thus, "intensification" and "reinstatement" are two defining behaviors for substance abuse. It is in this sense that addiction is often defined as a chronic, relapsing disorder (Leshner, 1997; McLellan et al., 2000). Three often-used diagnostic criteria provide a more concrete view of the specific individual problems related to these behaviors (American Psychiatric Association, 2000; Deroche-Gamonet et al., 2004): (1) high motivation for drugs, with everyday activities focused on obtaining and using drugs; (2) difficulties in stopping or limiting drug use, and (3) continued use despite high personal and social costs (e.g., medical and family problems). In general terms, substance abuse is marked by heightened desire for and engagement in drug-related behaviors, compromised ability to control drug use and/or switch to other activities, and altered views of the costs and benefits of drug use.

Multiple brain systems underlie these different aspects of abuse. Although by no means delineated with clarity, mesolimbic dopamine systems play a central role in facilitating

wanting and seeking of drugs (Hyman, 2005; Kelley & Berridge, 2002) and the prefrontal cortices mediate aspects of control (Kalivas & Volkow. 2005).[3] The alteration of costs and benefits relate both to drug-specific effects (e.g., opiates on opioid systems) and to neural systems that produce sensations of pleasure or "liking" in the brain (Berridge & Robinson, 2003; Hyman, 2005; Kalivas & Volkow, 2005). A main point of this discussion is that addiction involves multiple brain systems, and it is the interaction of these brain systems with environments and drugs that plays a formative role in developing substance abuse.

Given this behavioral interaction of drugs and individual, addiction is not a genetic problem per se. The vast majority of people who try drugs do not end up addicted to them (Anthony et al., 1994). Studies indicate that some variation in the vulnerability for drug abuse can be genetic, and genetics should not be overlooked as an important component of substance abuse (Young et al., 2006). However, it is equally clear that environmental circumstances can create these same vulnerabilities (Drake et al., 2002; Piazza & Le Moal, 1996). Thus, both having alcoholic parents (genetics) and growing up with alcoholic parents (environment) contributes to the risk for substance abuse (Newlin et al., 2000). Since genetics and environment play a role in substance abuse, the function of the proximate mechanisms (such as brain systems) offers the means to understand how these different sources of vulnerability interact during an individual's development.

In terms of drugs and their pharmacological impact on the brain, psychoactive drugs have three types of effects (Kelley & Berridge, 2002; Nesse & Berridge, 1997). First, they can provide natural rewards through intrinsic reinforcement within the brain (such as pleasure and/or relief of stress). Second, psychoactive drugs alter the functioning of the brain, for example, generating new connections between neurons or creating tolerance to the effects of certain neurotransmitters. Finally, drugs—given their purity and their availability—provide evolutionarily novel impacts. In the modern world people can ingest highly concentrated drugs and they can do so frequently. During our evolutionary history, this sort of access to drugs simply did not exist. In summary, it is the combination of purity with the mimicking of natural reward and the altering of functioning that can play such havoc with brain systems.

Finally, it is important to mention a central issue related to costs and benefits. Addiction has been linked to psychosocial stress and to the management of negative affect (Cooper et al., 1995; Koob & Le Moal, 2005). Indeed, in many ways, the functional use of drugs provides an important behavioral guide to understanding why individuals decide to use drugs (Boys & Marsden, 2003; Quintero & Davis, 2002). Individuals' reasons for using drugs are crucial and can be linked to both internal states (emotions, feelings, and the like) and social contexts and cultural norms (Boys & Marsden, 2003; Moore, 2004)). Thus, desire, control, and costs and benefits should be understood in relation to how individuals view drugs and what drugs can do for them, and not simply as a manifestation of hard-wired brain circuits.

FIVE STEPS FOR EVOLUTIONARY-BASED RESEARCH ON BEHAVIORAL PROBLEMS

The remainder of this chapter presents five steps that, taken together, provide a framework for how to conduct evolution-based research on problematic modern behaviors like substance abuse. The first step presents some basic assumptions for research, summed up

as "the human organism point of view." The next three steps are adaptive analysis, phylogenetic comparison, and discordance and malfunction. The final step focuses on methods, particularly how the conjunction of adaptive analysis and an embodied view of behavior offer important insights into how to carry out evolutionary based research. All five steps are summarized in Table 15-2.

TABLE 15-2 Evolutionary Analysis of Modern Behavioral Problems.

	Specific steps	**Application to addiction**
1: Human Organism Point of View	(a) Focus on how people actually behave, with consideration of proximate mechanisms and positive and negative outcomes (b) Take a biocultural view, where evolutionary and cultural explanations work together in explaining behavioral problems	(a) Addiction can be highly costly, where the behavioral biology plays a major role in explaining maladaptive outcomes (b) Drug use both biological (pharmacology) and cultural (subcultures of use)
2: Adaptive Analysis	(a) Critical assessment of biomedical and sociocultural approaches (b) Proximate mechanisms reveal the outcome of natural selection (not a priori modules) (c) Present benefits and costs shape behavior, along with sociocultural factors	(a) Addiction not simply driven by "hard wired pleasure" or cultural learning of expected drug effects (b) Address "reward" as an evolutionary problem related to foraging and reproduction, and shaped by the limitations of past environments (c) Drug-using lifestyle can reinforce drug use, e.g., through sexual behavior often considered as a "risk" factor
3: Phylogenetic Comparison	(a) Proximate mechanisms (e.g., neuropsychological processes) appeared in different phylogenetic periods (b) Use animal models and research, while still maintaining a biocultural view	(a) Addiction involves the interaction of ancient limbic motivational systems and the more recent prefrontal cortex (b) Wheel running provides a model for compulsive use, with the understanding that cage environments significantly shape animals' behaviors
4: Malfunction and Discordance	(a) Malfunction reveals functioning of particular proximate mechanisms that work together to produce behavior (b) Discordance can focus on how modern environments promote malfunction—what specific factors encourage nonadaptive behavior? why are specific people vulnerable?	(a) Mechanisms for "seeking" excessively active due to drug use (b) Sexual and competitive benefits associated with use reinforce drug use, while drug availability and stress promote involvement in drugs due to heightened vulnerability and short-term focus
5: Methods	(a) Focus on specific experiences and behaviors (b) Engage the viewpoint of the individual—what does the behavior accomplish from their perspective? (c) Use an epidemiological approach to examine factors that impact maladaptive behavior, including both evolutionary and cultural hypotheses	(a) Subjective experiences of "wanting" and "seeking" drugs significant predictor of being addicted (b) Shift away from painful subjective states important reason to use (c) Compulsive involvement and endorsement of cultural models differently related to addiction and poly-drug use

Step One: Guiding Assumptions—"The Human Organism Point of View"

For an evolutionary approach to be complementary with other fields of inquiry, two main assumptions are crucial: (1) that human nature is essentially biocultural, for it involves the interaction of culture and human biology, and (2) the individual point of view provides a unique perspective for applying evolutionary theory. Evolutionary theory often proceeds from a theory of inclusive fitness and/or optimality. Neither of these approaches is biocultural at its core. However, human evolution is (Fuentes, 2004; Richerson & Boyd, 2005). Local behavioral traditions such as those demonstrated by chimpanzees likely predate our hominid lineage (Wrangham et al., 1994), tool manufacture and use dates back at least 2 million years (Klein, 1999), and symbolic activity (such as bead making) dates back at least 100,000 years (or approximately 4000 generations) (Vanhaereny et al., 2006).

The corollary of this assumption is that many modern behaviors are not good candidates to be broken into biological parts that can be categorized as phylogenetically ancient and cultural parts that are a recent veneer. In the past, eating was presented as the result of either Paleolithic tastes (Eaton & Konner, 1985) or recent cultural history (Harris, 1986). However, recent analyses highlight the interaction of biology and culture in eating (Goodman et al., 2000; Rozin, 1996). With addiction, biocultural interactions also play a role, such as the previously mentioned "reasons to use." Another biocultural aspect of addiction that deserves further analysis is ritual-like behavior (i.e., repeated stereotypical actions). Substance abusers can display these sorts of behaviors in the precise steps they take while preparing and consuming drugs (Lende, 2003). Ritual-like behaviors have roots in animal behavior (Eilam et al., 2006), and recent cultural analyses of ritual are amenable to behavioral analysis (Bell, 1997). Human ritual has also been analyzed from an evolutionary point of view (Donald, 1991; Boyer & Lienard, in 2006). Thus, the links between the evolution of ritual and the behavior of ritually preparing and using drugs represents one way in which a biocultural approach could be made more explicit in the analysis of addiction.

Inclusive fitness and maximization both take perspectives that limit their view of how organisms develop, negotiate their environments, and engage in successful or unsuccessful behaviors. Maximization, with its emphasis on an ideal solution for all individuals in a population, does not focus sufficiently on the particular mechanisms and processes by which organisms (or individuals) accomplish specific ends, nor does it consider how individuals might vary in these mechanisms. Inclusive fitness, by emphasizing the role of genetics and inheritance, also leaves little room for an understanding of how a specific organism actually goes about living a life (e.g., how it makes choices about what sorts of things to eat). Put differently, between the population-level rationality of optimality and gene-level adaptive modules, the point of view of the human organism—of actual people—is often lost.

The human organism point of view is addressed at different points in this chapter, from the actual biological mechanisms involved in addiction to understanding people's intentions. The thread that ties these areas together is the consistent focus on building an understanding of how organisms (in this case, people) actually function on the ground. Optimality and adaptive modules posit theories for how organisms *should* behave. The organism point of view presents the challenge of building an evolutionary understanding based on how people actually behave. For this chapter that means the focus on people who engage in extremely costly and repetitive consumption of drugs.

Step Two: Adaptive Analysis

With a concern for both adaptive design and behavior, evolutionary theory can provide a critical assessment of some biomedical portrayals of substance abuse as well as improvement of neuropsychological theories of decision making. Beginning with research by Olds (1958) on the self-stimulation of the brain in rats, there is a long history of biomedical research that views substance abuse as the result of the overwhelming pleasure produced when hard-wired brain circuits are stimulated (either by electrical current or by drugs of abuse) (Blum et al., 1996).

This approach has all the makings of an adaptive just-so story (Gould & Lewontin, 1979), a speculative account without necessary analysis (Lende & Smith, 2002). Initially the story might have sounded plausible. However, subsequent research has shown that not all animals respond equally to stimulation and that the quality of the environment (e.g., enriched cages with other things to do besides self-stimulating) plays a central role in rates of stimulation (Wurbel, 2001). Furthermore, the reduction of reward (in the psychological sense of how animals respond to the environment) to pleasure does not make adaptive sense. To use the example of food, nutritional quality shapes food choices as well as pleasurable tastes (Goodman et al., 2000). With drugs, having friends who use drugs can be as important as the drugs themselves in rates of substance use and abuse (Beyers et al., 2004; Lende, 2005).

A growing number of researchers have become interested in understanding how reward works through a sophisticated combination of neurobiological, behavioral, and computational analyses (Redish, 2004; Schultz, 2000; Wise, 2002). This research breaks down reward into separate components (such as wanting/seeking and liking/consuming) (Berridge & Robinson, 2003). It also pays attention to the idea of "natural rewards," or how appropriate responses can lead to enhanced survivorship or reproduction (not simply pleasure) (Kelley & Berridge, 2002). Nevertheless, this research paradigm retains its experimental focus on how animals respond (e.g., whether rats prefer sugar or cocaine), rather than a theoretical focus on how decision making affects fitness.

This problem hampers the application of the reward paradigm to addiction, for it places undue emphasis on drugs as the cause of addiction—drugs as sensitizing neurological systems (producing maladaptive responses like substance abuse) and/or providing exceedingly high reward to individuals whose genetic variability make them susceptible. An evolutionary approach would also look at the design of decision-making systems in relation to the structure of past environments (Lende & Smith, 2002). In the past, foraging and reproduction have consisted of two general phases: finding food or partners and then engaging in eating or sex. The two phases of decision making correspond to the different components of wanting/seeking and liking/consuming that neurological research has outlined (Robinson & Berridge, 2001, 2003). The design perspective can further elaborate the seeking phase. In past environments there was a relative scarcity of food and sexual partners (Lende & Smith, 2002). This limitation indicates that there was no selective reason to build a system that automatically self-regulates (i.e., to prevent eating too much or having too much sex). For humans, this sort of design places much greater emphasis on higher levels of cognitive control, which are generally compromised in substance abusers.

The emphasis on drugs as reinforcers also limits our understanding of evolutionarily important sources of reward in present environments. Drug-related behaviors can lead to

adaptive outcomes, such as enjoyable sexual situations and positive outcomes to dominance or competitive interactions. In other words, from an evolutionary point of view, sexual behavior can be a potent reinforcer. In the substance abuse field, however, sex and violence are generally cast as dangerous "risk behaviors." Research rarely examines how environmental and behavioral links between drug use and "sex and violence" might actually encourage further use. In summary, these proximate reinforcers can help explain why people maintain certain lifestyles (a topic developed further later in this chapter), even if from the biomedical point of view these individuals are putting themselves at risk.

In summary, the adaptive analysis proposed here focuses on both adaptive design and behavior with an emphasis on the proximate level. Rather than attempting to come up with a module that matches a proposed adaptive problem, an adaptive analysis considers research on neuropsychological mechanisms as revealing the outcome of evolutionary processes. These outcomes can then be analyzed to understand how adaptations developed in the past and how today's environment shapes the adaptive functioning of neuropsychological systems.

Step Three: Phylogenetic Comparison

A robust evolutionary approach to behavioral problems can also draw on the strengths of phylogenetic and comparative cross-species analysis. This approach leads to greater understanding of substance abuse by drawing on the vast research on animal models of abuse (Berridge, 2003; Cardinal & Everitt, 2004; Deroche-Gamonet et al., 2004; Kelley & Berridge, 2002; Olmstead, 2006). Today it is evident that the dopamine systems involved in substance abuse are among the most ancient that we possess. Dopamine receptors appeared before the split of vertebrates and invertebrates (Cravchik & Goldman, 2000), and there are invertebrate models of dopamine function (Wolf & Heberlein, 2003). Thus, the typical approach of identifying the Pleistocene as the "environment of evolutionary adaptedness" (the time when psychological adaptations were formed) is mistaken because many core brain systems that mediate motivation and emotion emerged far earlier in evolutionary time (see Panksepp & Panksepp, 2000, for a more elaborate version of this argument).

At the same time, as mentioned earlier, the prefrontal cortices have been implicated in substance abuse (Kalivas & Volkow, 2005). These have emerged over the last 1.6 millions years of human evolution (Semendeferi et al., 2001; Streidter, 2006). Thus, addiction involves the interaction of phylogenetically recent and ancient brain systems, which appears common to many behavioral health problems (Bechara et al., 2000; Cardinal et al., 2002; Davidson et al., 2000). This model highlights the necessity for sophisticated phylogenetic thinking about how brain systems interact and what roles they play in modern behavior.

Here it helps to return to the animal research. It is important to emphasize the individual variation that can result from these ancient systems (Cravchik & Goldman, 2000)—while universal, these systems should not be considered "uniform." With respect to addiction, it is clear that there are animal lines that respond more to certain substances than other genetic varieties (e.g., mice that like to drink alcohol) (Crabbe, 2002). At the same time, the comparative view highlights the role of environmental conditions in encouraging the repetitive use of drugs, even in the studies taken as paradigmatic (e.g., cocaine-using rats neglecting food and water until near death) (Badiani & Robinson,

2004; Garner & Mason, 2002; Wurbel, 2001). First, these animals need to be trained to exhibit this behavior, and second, there needs to be a nearly complete lack of other behavioral options (i.e., an unenriched cage, even if food and water are available, is not a behaviorally rich environment, something that most zoos have finally realized). Thus, the animal research points to addiction as a more complex disorder than is commonly appreciated. An evolutionary analysis, therefore, cannot simply rely on proposals about "false fitness benefits" or reward systems gone awry due to drugs.

An interesting animal model exists for a comparative approach to modern abnormal behavior—wheel running by rodents (Rhodes et al., 2003; Sherwin, 1998). This is a behavior not exhibited in the wild (similar addiction); nonetheless, some animals will spend an extraordinary amount of time and effort doing this. Wheel running can even displace drug consumption as a preferred behavior (Cosgrove et al., 2002)! Sherwin (1998) and I agree—a behavior-based approach is crucial to understanding these sorts of obsessive activities. Each behavior is related both to the activity itself (wheel running or drug taking) and to the surrounding environment (the cage or a drug lifestyle that reinforces use). For humans with their enlarged cortices, there is an added level of complexity due to the meaning drug use can have for people (e.g., "reasons to use"). For example, the shifts in wanting and attention related to changes in dopamine activity have corresponding interpretations by the person (Lende, 2005). In my research, an adolescent girl with a troubled home life spoke of how drugs put her into a "video" that she contrasted with her life at home.

In summary, drawing on an understanding of brain evolution and the use of animal models is central to developing an evolutionary medicine of behavioral disorders. Researchers who do not take this step run the risk of reverting to simplistic and often mistaken proposals about adaptive benefits, rather than building on the wealth of knowledge that already exists on the comparative biology of behavior.

Step Four: Malfunction and Discordance

Evolutionary medicine's concern with malfunction provides the field with a considerable advantage over evolutionary psychology and human behavioral ecology. Both of these approaches generally assume optimal design, but malfunction can reveal adaptive function just as well. As I show below, this approach proves particularly fruitful in illuminating the function of proximate components that are often glossed over in assumptions about optimal modules or behaviors.

Berridge and Robinson (2003) discuss how reward can be parsed into at least three components: learning (including associative conditioning and cognitive processing), affect and emotion (implicit "liking" and conscious pleasure), and motivation (wanting and seeking). For over a decade, Robinson and Berridge (1993, 2001, 2003) have argued that pathological functioning in the brain components mediating wanting and seeking is central to drug abuse. Drugs, given their pharmacological impact on the mesolimbic dopamine systems of the brain (the wanting system), can produce sensitization, a progressive amplification in neuronal responding. This sensitization leads to extremely strong desire and searching for drugs. The process can happen even as the pleasurable rewards provided by drugs decline due to tolerance in the "liking" system. Thus, there is a relative dissociation of wanting and seeking from pleasure, with heightened seeking a core problem in addiction.

Other research supports this view of the mesolimbic dopamine system. Salamone et al. (2003) examined the role of dopamine in responsiveness to conditioned stimuli and the activation of behavior (for example, searching for food at the sound of a bell). Their research indicated that dopamine mediates the amount of effort put into reaching a goal (particularly in vigorous responding by mice and rats, such as climbing barriers to reach food). Similarly, Cannon and Bseikri (2004) showed how the lack of dopamine leads to deficits in goal-directed behavior. Finally, Redgrave et al. (1999) argued that dopamine plays a central role in switching animals' attention to unexpected and behaviorally important environmental stimuli. In summary, overinvolvement in wanting and seeking drugs and heightened sensitivity to conditioned cues that signal environmental availability of drugs (so as to start seeking them) represents a core "malfunction" at the heart of addictive behavior.

Even given the role of drugs in sensitizing the dopamine system, the overall malfunctioning is still environmentally shaped (Crombag & Robinson, 2004). Here is where a sophisticated understanding of modern environments produces a great pay-off in expanding how the discordance concept can be used. Normally, discordance focuses on the mismatch between past and present environments. For example, our evolved taste for salt makes evolutionary sense, for salt was an important but limited nutrient in past environments. Today the abundance of salt can lead to health problems such as hypertension. This mismatch is easy to recognize, and can be further developed by examining why certain people consume more salt than others and what sorts of environmental factors encourage salt consumption. This approach places emphasis on examining *how* modern environments shape the maladaptive responding of evolved traits. Turning to drug use, both the pleasurable effects of drugs and the proximate benefits associated with drug use help establish drug taking as a goal. Sharing drugs with friends, part of establishing social relationships and long-term reciprocities, should also not be overlooked as another way in which drug taking becomes established. These behavioral and environmental factors can favor the move from the initial goal of drug use to compulsive involvement with drugs (Everitt & Robbins, 2005; Hyman, 2005; Wise, 2002).

The discordance view highlights two other ways in which modern environments promote addiction—drug availability and psychosocial stress. Epidemiological research has shown the role that drug availability plays in increased rates of substance use (Compton et al., 2005), although availability on its own does not automatically promote drug use (indeed, an integrated suite of sociocultural factors can mediate against drug use even in environments where drugs are readily available, such as Colombia [Lende, 2003]). With psychosocial stress, behavioral biology has confirmed its importance in heightening vulnerability for drug use, in particular through heightened responsiveness to reward (Koob & Le Moal, 2005; Kreek et al., 2005; Weiss, 2005). Thus, from the discordance point of view, environments that share high availability and high stress are those most likely to promote drug taking and seeking. Inner city environments where drug selling is active can be particularly stressful (Bourgois, 2003). These types of environments often promote intense drug using. Similarly, families in which parents abuse drugs or alcohol present the same mix of availability and high stress for children, and this combination should be considered a major reason why substance abuse runs in families (alongside genetics) (Compton et al., 2005; Kreek et al., 2005).

What is ironic, and ultimately maladaptive, is that these same stressful environments promote risk-taking behavior and a focus on short-term benefits by the participants

(Lende & Smith, 2002). These are precisely the environments in which the pleasures of drugs, the proximate benefits of a drug-using lifestyle, and the importance of friends can help establish initial drug taking. Subsequent use can then be enhanced due to both the aversive costs of stopping (e.g., reduction in pleasure, increase in stress, physiological aspects of withdrawal— see Koob & Le Moal, 2005) as well as the conscious recognition by users that using drugs takes them away from the stresses and difficulties of their everyday lives (Lende, 2005).

Overall, modern environments play a central role in the establishment of drug taking and in the reasons individuals return to drug use. The discordance and malfunction views help amplify the understanding provided by adaptive analysis and phylogenetic comparison, producing a more comprehensive approach to substance abuse than any one type of analysis on its own.

Step Five: Methods

In turning the varied considerations of this chapter into a research paradigm, strategic choices need to be made. Given the complexity of substance abuse, a focus on key behavioral components represents one fruitful approach that is elaborated upon here, although the modern environment, the role of ritual, and the interaction of genetics and development represent other research possibilities.

Even after an initial choice of research focus, the step from evolved behavioral biology to research is not one of simple prediction and testing. Returning to our initial assumptions, it is important to rely on the "human organism point of view." This viewpoint—emphasizing what matters to the individual—places considerable emphasis on actual experiences and behaviors. In contrast, evolutionary psychology generally relies on judgments by informants (say, of attraction), rather than focusing on how and why individuals actually experience attraction. With abstract judgments, cultural symbolism and biases often shape how individuals respond. The obvious impact of culture opens up the evolutionary psychology approach to easy, repeated, and often vehement critiques (Buller, 2005; McKinnon & Silverman, 2005; Rose & Rose, 2000).

Human behavioral ecology faces a similar problem given its core question: Does the behavior match the theoretical prediction? This approach often does not consider what the behavior accomplishes from the viewpoint of the individual, something that ethnography can provide. Moreover, its theoretical aim is not always useful for research on health. Human behavioral ecologists rely on abstract "outcomes" that might be theoretically relevant (e.g., optimal foraging) but are not necessarily relevant to what shapes adaptive or maladaptive behavior (e.g., what environmental factors favor healthy eating). In contrast, an epidemiological approach offers the tools to analyze what factors are associated with unhealthy dietary habits or what risk factors predict substance abuse.

In my previous research, ethnography contributed to understanding participants' experiences of compulsive wanting and seeking (Lende, 2005). Psychometric techniques were used to develop a scale that examined "compulsive involvement" in substance abuse by focusing on these subjective experiences. This measurement proved to be an important predictor of addiction (Lende, 2005). Indeed, this approach—using ethnography to explore experiences and behaviors and then developing the interconnections between

these reports and the behavioral biology of substance abuse—represents an alternative way to do evolutionary analysis.

Similarly, rather than being focused on expected benefits about drugs (a judgment approach), this research looked at actual patterns of behavioral reinforcement of the drug-taking lifestyle. By asking how many times respondents had been involved in agreeable sexual situations and had won competitions or fights due to substance use, this research emphasized the significant differences between addicted and nonaddicted individuals (defined in Lende, 2005). Using a summary variable of evolutionary benefits (the sum of both sexual and competitive benefits), addicted individuals reported 2.76 total benefits versus 0.98 benefits for nonaddicted individuals ($p < 0.001$, two-tailed *t*-test).

This *experience-and-behavior* approach shares many similarities with an embodied view of human behavior. Embodiment refers to the central role that bodily states and interactions with the environment play in cognition and behavior, rather than abstract reasoning and symbolism (such as the computer model of the brain). Evolutionary psychology, based on an information-processing model, and human behavioral ecology, with its emphasis on assumed rationality, both contrast sharply with recent understandings of how organisms (including people) engage in successful cognition and behavior in specific environments. From understandings of how to build successful robots (and not just computer programs) (Clark, 1996) to the ecological view of psychology (Reed, 1996; Rosch, 1996) to embodied views of perception and neuroscience (Barsalou, 1999; Barsalou et al., 2003; Gibbs, 2006) to categorization and even philosophy (Lakoff & Johnson, 1999), this emerging approach is one that evolutionary theory can engage successfully, provided it remains rooted in the selectionist and phylogenetic analyses that are its main strengths.

Combining ethnography and epidemiology also permits the examination of other competing hypotheses to explain substance use and abuse. For example, compulsive involvement was not a significant predictor of poly-drug use even though it was for addiction (Lende, 2005). However, endorsement of a cultural model emphasizing social distance from the world of drug use was a significant negative predictor for poly-drug use, even though endorsement of this model had no significant statistical relationship with addiction (Lende, 2005).

Similarly, risk factors derived from other research paradigms can actually end up being quite complementary to an evolutionary approach. Previous epidemiological research in Colombia revealed the importance of friends' drug use and of experiencing violence as predictors of marijuana use (Brook et al., 1998). In my research, these two factors were major predictors of addiction alongside compulsive involvement (Lende, 2005). Friends' drug use provided both drug availability and an adaptive benefit (particularly given the importance of social relationships in the high-risk environments associated with using). Experiencing violence captured the extreme stress involved in compulsive use of drugs, which often takes place on the "street" in Colombian cities. This high-risk environment also accentuates short-term benefits such as positive sexual encounters and winning competitive encounters—respondents often reported feeling stronger and "crazier" due to drug use.

Thus, the evolutionary approach can be fully compatible with approaches developed in other fields, while also providing novel interpretations for how and why individuals

behave the way they do. From compulsive involvement and adaptive benefits to making sense of how modern environments can push individuals to engage in short-term behaviors, evolutionary medicine—drawing on an approach that begins with the experiences and behaviors of actual individuals—places itself in a position to provide novel understandings of modern behavioral problems like addiction.

CONCLUSION

This chapter highlights three important components in the evolutionary analysis of addiction. First, it is crucial to use adaptive considerations and phylogenetic comparisons when considering the behavioral biology that underlies problematic behavior. Particular processes, like wanting and seeking, can malfunction. This malfunction can be affected by specific adaptive benefits and/or vulnerabilities (from genetics and development to local environments, such as a drug-using family). This focus on malfunction and the factors that shape malfunction can apply to other behavioral problems, such as eating disorders. Obesity is a modern epidemic, and recent research (Berthoud, 2004; Kringelbach, 2004; Wang et al., 2004) is compatible with many of the points developed in this chapter.

It is also useful to consider the interaction between more phylogenetically ancient motivational systems and more recent systems of cognitive and symbolic control. Environments that are stressful and that encourage short-term behavioral strategies can sensitize phylogenetically older systems so they become overly reactive. At the same time, systems of inequality (which control local resources and access to long-term successful behavioral strategies) can reinforce this sort of immediate decision making, even as advertising and global economic development present a wealth of options to satisfy cravings.

Finally, modern lifestyles seem to bundle together evolutionarily relevant factors in ways that worsen compulsive involvement in behaviors. With friends, availability, adaptive benefits, and subjective escape all wrapped up into drug taking, this lifestyle has an immediate appeal and ease, especially in contrast to stressful environments with few available long-term options. This sort of lifestyle can be reinforced by the particular cultural scenes and attitudes that provide ways to further define a drug-using lifestyle. Overall, the parsing of lifestyles and environments in evolutionarily relevant ways (while maintaining a biocultural approach) represents a logical next step for research, given how evolutionary analyses already address the separate components of behavioral decision-making systems. This type of approach will significantly increase the validity and applicability of the discordance hypothesis in evolutionary medicine.

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