The Evolutionary Bases of Substance Use and Abuse

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Conventional Theories of Substance Use and Abuse

The abuse of psychoactive substances is a pattern of maladaptive and self-destructive behavior that, seemingly, offers little or no advantage to the substance user. Traditional explanations (whether they be psychosocial, behavioral, or neurobiological) of substance abuse focus on the pleasurable effects inherent in many psychoactive substances. According to these theories, use of psychoactive substances is rewarded with pleasure, while discontinuation is punished via painful withdrawal symptoms [1].

Mismatch Theory

The seemingly maladaptive nature of substance abuse makes it difficult for evolutionary theories of human behavior to explain. Despite this difficulty, several theorists have proposed evolutionary explanations for substance abuse, most of which focus (like traditional explanations) on rewards and punishments [2, 3, 4]. In this case, however, rewards and punishments are associated with fitness. Behaviors that encourage survival and reproductive success are rewarded through positive emotions, whereas behaviors that are likely to decrease overall fitness are punished via negative emotions [5]. What psychoactive substances do, in effect, is override the brain's natural reward and punishment centers. The large pleasurable effects of drugs lead the user to believe that drug-use confers fitness advantages; also, these drugs block negative emotional states, preventing the brain from providing accurate information on the decrease in fitness resulting from substance abuse [3].

This theory is supported by the traditional neurobiological model of addiction which emphasizes the role of the cortico-mesolimbic dopamine system (dopaminergic neurons that project from the ventral tegmental area of the midbrain to the nucleus acumbens of the forebrain) in producing pleasure when a person engages in a fitness-enhancing behavior (eating, sexual activity, etc.) [2]. Psychogenic substances act on the cortico-mesolimbic dopamine system, causing an increase in dopaminergic transmission in the nucleus acumbens and providing pleasure that reinforces the drug use [2,6]. Thus, drugs become associated with fitness advantages, instead of fitness decreases because humans did not evolve in an environment that included frequent exposure to psychoactive substances, and these substances co-opt a natural reward system designed to encourage adaptive behaviors such as eating and engaging in sexual activity.

This view of substance abuse is based on mismatch theory which suggests that human bodies, brains and behaviors evolved over millions of years in an ancestral environment free from modern environmental variables (like widespread and powerful psychoactive substances). Human behaviors, therefore, are adaptive, given an ancestral environment, but as humans encounter modern environments, for which we may be ill-adapted, behaviors can appear maladaptive. There is a mismatch between evolved human behavior and modern environmental demands. Thus drug users, associate drug use with fitness advantages, instead of fitness decreases because humans did not evolve in an environment that included frequent exposure to psychoactive substances, and these substances co-opt a natural reward system designed to encourage adaptive behaviors such as eating and engaging in sexual activity.

Unfortunately, as Sullivan, Hagen, and Hammerstein (2008) note, mismatch theory makes two assumptions which do not appear to be borne out by evidence [7]. One of these assumptions is that psychoactive substances are modern phenomena that did not influence human evolution leaving the modern human brain inherently vulnerable to psychoactive substances [3, 4]. The other is that drugs of abuse are inherently rewarding [3, 7].

Problems with Mismatch Theory

The view that humans' ancestral environments were drug free has long been an assumption of evolutionary psychology, but has recently come into question. One criticism of this notion is the fact that if exposure to psychogenic substances is a novel environmental stimulus, humans should not have evolved processes designed to counter these substances. There is, however, substantial evidence that humans have evolved mechanisms to counter the effects of both alcohol and plant neurotoxins (e.g.: caffeine, nicotine, THC, codeine, cocaine, etc.) [7, 8]. These plant neurotoxins are, in fact, evolutionary adaptations designed to prevent threats to the plant from herbivorous animals. By imitating mammalian neurotransmitters, such as acetylcholine, serotonin, dopamine, and norepinephrine, these allochemicals interfere with central nervous system functioning [6, 7, 9]. Mammals, in their turn, have evolved enzymatic countermeasures that metabolize these toxins. The fact that these enzymes are not unique to humans, but are present in a variety of herbivorous mammalian species, suggests that exposure to plant neurotoxins has been a consistent environmental variable throughout human evolution [7]. Similarly, humans' ability to catabolize ethanoll via alcohol dehydrogenase (ADH) and acetaldehyde dehydrogenase (ALDH) lends support to an evolutionary history with alcohol.

The presence of enzymes that metabolize these neurotoxins also serves to counter the hypothesis that the human brain is inherently vulnerable to drugs. This belief is based to a large degree on the notion that the cortico-mesolimbic dopamine system would be easily activated by drugs because drug exposure would not have occurred throughout human evolution.

The notion that drugs are inherently rewarding is also problematic in that it fails to account for the generally poor correlation between the pleasurable effects of a drug and drug-taking [10, 11, 12]. Several drugs (e.g.: nicotine, betel nut, etc.) produce a variety of unpleasant effects (e.g.: sweating, coughing, dizziness, nausea, etc.) to the new user while offering little in the way of experienced pleasure [9]. Also, for most addicts, drug-taking behavior appears to increase even as pleasure decreases [11]. This calls into question the notion of the cortico-mesolimbic dopamine system as a reward or pleasure center. The incentive salience hypothesis resolves these problems by viewing dopamine as influencing how salient (or demanding of attention) an object is, rather than how rewarding (pleasurable) it is [11, 12]. Thus dopaminergic action influences wanting and seeking, not reward and pleasure.

The problems with the mismatch theory of substance abuse must, by necessity, lead to the development of evolutionary theories of substance abuse that address these issues. One promising approach would be to integrate a paleobiological approach to diet with the handicap principle and life-history theory of evolutionary psychology.

Integrative Evolutionary Theory of Addiction

The Human Diet: A Paleobiological Approach

Rejecting the notion that humans have encountered psychotropic substances only recently (less than 50,000 years ago) in our evolutionary history necessitates an examination of the historical roots of the human diet. This paleobiological approach offers new insights into the evolutionary basis of addiction.

Drugs as Food: Domestication of crop species and agriculture first appeared in the fertile crescent of southwest Asia in approximately 8500 BCE [13]. Until that time, humans likely foraged a considerable amount of their diet from local plants, several of which were likely to contain at least low concentrations of psychoactive substances [14]. The betel nut (*Areca catechu*) has been chewed in Timor since 11,000 BCE, and in Thailand since 8700 BCE. Khat (*Catha edulis*), an ephedrine-like substance, had been used in Ethiopia and Northeast Africa long before the arrival of European colonists. Cocaine (*Erythroxylum coca*) has been in use by Native South Americans in Ecuador since 3000 BCE and in the Western Andes since 5000 BCE. Australian aborigines used nicotine from both the pituri plant (*Duboisia hopwoodii*) and *Nicotiana gossel* before the arrival of Europeans, as did Native Americans (from native *Nicotiana tabacum* and *Nicotiana rustica*) [6, 9]. Several of these plants have since been domesticated for a variety of purposes.

Plants with psychoactive properties were likely first consumed (and later domesticated) as a food source. Given that the gathered plant material likely formed a large portion of the ancestral diet, it is reasonable to assume that early hominids would treat nearly any edible plant as food. Indeed, in many pre-industrial cultures, plants containing psychoactive substances are still primarily regarded as food today [9]. Similarly, ethanol likely entered into the diets of early humans as a food source.

Ethanol consumption, in low levels, likely entered into hominid diets through ripe and overripe fruits. Humans, like most primates, are frequent consumers of fruits. In fact, with the exception of mountain gorillas, all apes are primarily frugivorous. Fruit offers a number of advantages to food gatherers: it is high in caloric content and sugar, seasonably abundant, and predictable. It is also, however, a likely source of ethanol. Yeasts are one of the primary agents of fruit decay, they are often found on and within ripe fruit, and fermentation of fruit sugars by yeast is likely to yield ethanol [8, 15]. Recent research investigating the ethanol content of wild tropical fruit found amounts ranging from 0.01 to 0.6% depending on fruit type and ripeness [8]. In all cases, ripe fruits were found to have both higher sugar content and a higher percentage of ethanol than unripe fruits. It is possible that a preference for alcohol may have evolved as choosing fruit with higher ethanol content (possibly via smell or taste) led to greater caloric intake [15]. Indeed, the ability to associate the smell of alcohol with ripe fruit may have led early hominids to additional sources of food by following the smell of fermenting fruit.

Neurotransmitter Depletion and Drugs: In addition to their use as food sources, psychoactive substances conferred other fitness advantages. Sullivan and Hagen (2002) suggest that substance-seeking behavior may have been selected for due to a lack of quality food necessary for the manufacturing of neurotransmitters [9]. Serotonin, dopamine, norepinephrine, and acetylcholine require adequate nutrition for their manufacture. As plant allochemicals mimic the structure of these neurotransmitters, they can serve as substitutes for the neurotransmitter during periods of privation. Indeed, as plants like tobacco, coca, and betel nut can be dried and stored, they may provide a ready source of neurotransmitter analogs during dry or winter months when game and fruit are scarce. It is unsurprising that the regions (deserts, mountains, and rain forest) in which early drug use was common are all prone to such periods of scarcity [9].

The central nervous system is quite susceptible to dietary effects on neurotransmitter manufacture, such that provision of neurotransmitter precursors (i.e.: tryptophan, choline, and tyrosine) stimulates neurotransmitter formation [16]. Conversely, modern dieting behavior has been demonstrated to reduce serotonin precursor availability and impair central nervous system serotonin function [17]. As serotonin depletion has been demonstrated to lead to food-seeking behavior of foods rich in precursors, it is possible that plants which provide serotonin analogues could be the subject of these cravings [18].

***Neurotransmitter Depletion and Stress*:** Stress is an adaptive reaction to adverse environmental conditions (including drought, nutritional scarcity, extreme weather conditions, and intergroup hostility). If stressful conditions persist, however, prolonged stress can have a detrimental effect on health and behavior including depression, fatigue, headaches, cardiovascular problems and even death. Neurotransmitter depletion may exacerbate, or even cause the negative behaviors that result from chronic stress exposure [9, 19]. By consuming plants which contain neurotransmitter analogues, early hominids may have been able to stem off the negative effects of chronic stress. Similarly, modern humans attempt to mitigate the effects of stress through the use of such substances as tobacco, caffeine, and cocaine.

Hormesis and Exposure to Psychoactive Substances: Hormesis is a favorable reaction in an organism to low doses of otherwise harmful toxins. Hormetic dose-response relationships are often such that at low doses, exposure to a substance is both stimulatory and beneficial to the organism, whereas higher dosages cause stress and harm [20]. There is considerable evidence to suggest that moderate alcohol use conveys hormetic benefits. It is well established that light to moderate alcohol consumption confers cardiovascular benefits, reducing the risk for coronary artery disease and stroke [21]. Additionally, some research suggests that light to moderate alcohol consumption may confer psychological benefits including increases in positive mood, stress reduction, improved social integration, reduced social anxiety, and reductions in depression [21, 22].

Psychostimulants, including caffeine, nicotine and cocaine, may also demonstrate hormetic benefits for light to moderate users. Moderate caffeine consumption has been demonstrated to confer cardiovascular benefits through a wide variety of processes including anti-platelet activity, decreasing insulin resistance, diuresis, increased fat metabolism, and antioxidant activity [23]. Additionally, caffeine confers psychological benefits at low doses 38-400 mg/day). These include increased positive mood, improved alertness and cognitive performance, and increased resistance to exhaustion [24]. It is likely that light to moderate use of other psychostimulants may confer similar physical and psychological advantages.

Humans have likely had a long evolutionary history with psychoactive substances, and indeed, it is likely that ingestion of these substances, in moderation, conferred survival advantages. It is likely that limitations in the natural environment kept consumption at moderate to low levels. Naturally occurring ethanol in fruit, for example, is at a level well below that found in modern alcoholic beverages, and while Sullivan and colleagues (2008) argue that the most commonly used drugs today (coffee, tea, tobacco, betel nut, khat, cannabis, coca, and cola nut) are no more potent than those encountered by our ancestors, it is likely that pre-agricultural environments would limit the availability of these substances, thus making heavy use and abuse unlikely [7, 8]. After the advent of agriculture, these substances likely became available in higher quantities, and for some substances (such as alcohol) higher potencies, as well. At this point, substance abuse becomes more likely. The hormetic nature of these substances demonstrates itself in decreased overall fitness for heavy users. This leads to the question, then, as to why humans would engage in heavy use and abuse of psychoactive substances if it decreases their chances of survival.

The Handicap Principle and Substance Abuse

It is important to remember that not all adaptations improve personal survival. There are sometimes good reasons for an organism to decrease its likelihood of survival in exchange for increased likelihood that its genetic offspring will survive. This is illustrated by the female killdeer. Killdeer are small wading birds common to North and Central America. The females build nests on open ground, frequently on gravel, where their speckled eggs are well-camouflaged. If a possible predator (such as a fox) nears the nesting area, the female will use a distraction display, feigning a broken wing to lure the predator from the nest site. The sight of an apparently injured bird induces the predator to follow, leaving the nest site protected at the expense of an increased risk to the female killdeer. Admittedly, the fact that the female killdeer is only feigning a broken wing and can easily fly away should the predator get too close puts her at only mild risk, but it demonstrates the fact that some adaptations increase individual risk to decrease risk to offspring.

This sacrifice of personal survival benefits for the sake of offspring can also be seen in the males of many species. In these cases, the male is not sacrificing personal survival to ensure the survival of offspring, but rather for the chance to breed and possibly produce offspring. As Darwin (1874) noted, evolution operates by two different selection pressures: survival and sexual [25]. While Darwin noted that female preferences shaped the evolution of a variety of male characteristics that appear deleterious to survival (for example, brightly colored plumage and long, ornate tail feathers in peacocks), he did not explain why females would prefer such traits. Indeed, from a survival standpoint, female peahens should prefer drab, camouflaged male peacocks with smaller tail feathers, as these traits would likely increase the survival value not only of the male, but of any male offspring produced by that male. Despite the advantages that might be conveyed by drab males, clearly female preference has leaned towards elaborate, brightly colored male peacocks. The more elaborate the peacock, the greater the likelihood of breeding and the greater the likelihood that the next generation of peacocks will continue to be brightly colored.

Zahavi (1975) proposed a hypothesis, termed the handicap principle, to explain this apparent female preference for disadvantaged males [26]. All animals need to develop ways of signaling to potential mates that they will be good choices for mating. In species that invest at least some time in child-rearing, it is the male that does the majority of the conspicuous advertising. While males appear willing to mate with any available female, females tend to be choosier. This is likely due to the relative costs of mating. The male may be able to mate multiple times with multiple females leaving many offspring to be raised by various females, whereas the female invests considerably greater time and energy into the processes of reproduction and child-rearing. Females, therefore, can bear far fewer offspring than males can sire, so it is in their best interest to mate only with males who are likely to provide high quality offspring.

Obviously, if males are advertising to females in order to mate, it is in their own best interests to lie or exaggerate their qualities as a mate and father. Just as the female killdeer lies to the fox about having a broken wing, male animals are likely to lie to females in order to gain sexual access. It becomes imperative, then, that females focus on characteristics that give honest appraisals of the male's genetic worth. The handicap principle suggests that costly traits and behaviors are selected for by females because they serve as honest indicators of a male's genetic worth [26, 27, 28, 29]. Inferior males cannot afford to maintain behaviors and structures that impinge upon their survival abilities. A parasite-prone peacock, for example, is more likely to be discovered by a discerning peahen because parasite infestation demonstrates itself as damage to plumage (which is more noticeable given the peacock's bright coloration). Also, brightly-colored peacocks that are not capable of avoiding predators (through speed, intelligence or other desirable traits) will either be eliminated prior to breeding, or will likely be attacked during their conspicuous breeding displays. Only superior peacocks (fast, smart, and parasite-free) will be chosen for mating. The handicap principle, in effect, acts as a test of the male's genetic worth.

Humans are animals that invest considerable time and energy into child-rearing, and, unsurprisingly, women are choosy about potential sexual and parental partners. As such, the handicap principle is likely to be operating in human mate selection. Men, therefore, are likely to put themselves at a survival disadvantage (either through behavior or structure) in order to gain sexual access to females. Females, in their turn, are likely to select these disadvantaged males, provided that the male can triumph over adversity. A wide variety of behavioral handicaps are available to humans, indeed nearly any behavior that is either costly or dangerous can be used to increase a male's sociosexual status.

Substance Use as Handicap: Drug and alcohol use certainly fit the requirement of being dangerous behaviors. In fact, several aspects of drug and alcohol use make this behavior ideal for demonstrating superiority. First, as discussed above, new users of many substances experience negative reactions. Novice betelnut chewers, for example experience tremors, facial flushing, sweating and nausea [7]. Adolescent smokers report that their first cigarette led to dizziness, nausea, and headache [30]. Inexperienced drinkers may pass out, vomit, or demonstrate disgust at the bitter tastes of common alcoholic beverages (beer, wine, scotch, gin, vodka, tequila, etc.). A male who can withstand the negative experiences associated with substance exposure demonstrates his strength, potency, and endurance, especially when compared against peers who are overcome by the substance's effects.

In addition to first use, there is also the issue of dosage as handicap. The ability to consume larger quantities of a substance (compared to a rival) without obvious impairment may represent an honest test of health and endurance. This is clearly illustrated in alcohol use through drinking contests, binge drinking, and the ability to "hold one's liquor." Unfortunately, this aspect of the handicap principle is likely to lead to heavy use and abuse.

With regards to alcohol, the well-known impairments in coordination, reaction time, and vision represent another handicapping phenomenon. Men who are able to engage in potentially dangerous behaviors despite alcohol impairments (i.e.: drinking and driving, physical fights, etc.) demonstrate superiority to those men who are injured or killed in such activities. Disturbingly, they may also demonstrate superiority to those men who do not engage in such risky behaviors, as men who do not engage in risky behaviors do not put their quality to the test.

Life History Theory

The handicap principle applies specifically to males of a species, as such; any handicapping behavior (such as risky substance use and abuse) should be greater in men than women. Moreover, as the handicap principle applies to sexual selection, handicapping behaviors should be present more often in men who are at a point in their life when they are concerned about sexual access to females (unmarried adolescents and young adults). Life history theory suggests that behavior is best understood within terms of the maturational and reproductive aspects of the lifespan. From the standpoint of life history theory, risk-taking behavior, including risky substance use and abuse, is related to an individual's age, gender, and environmental characteristics that impact upon survival or sociosexual status.

Risk-Taking: Risk-taking behavior serves an adaptive function for men. Choosy behavior on the part of females has a number of implications for male mating. It results in high variability with regards to mating (some men mate frequently with multiple partners, others may not mate at all), and in high dependence upon competition (men must compete with rival males in order to mate). Females do not demonstrate the same level of variability or competition – females may compete for high quality males, but most females mate with some degree of frequency until the point of child-rearing. These differences encourage risk-taking on the part of men [31].

In terms of mating, men are faced with a situation that is both high-risk and high-gain. Men who are willing to take risks are more likely to successfully mate then those who play it safe. This tendency to take risks translates into a variety of male behaviors including physical aggression, criminal behavior, athletic competition, resource acquisition, and substance abuse [32]. Life history theory suggests that risky behaviors should be greatest in young, unmarried men. Indeed, marriage has long been known to decrease criminal and reckless behaviors in men [33]. While this has generally been explained as socialization effects of marriage and investing in a conventional life, it is exactly what would be predicted from an evolutionary life history perspective.

There is considerable evidence that risk-taking is greatest in young unmarried men. With regards to substance abuse, this is demonstrated in a variety of behaviors. Young men (between the ages of 15 and 29) demonstrate the highest rates of risky drinking [31]. Binge drinking is most common among males under the age of 35, and among college students males binge drink more frequently than females [34, 35]. Males between the ages of 18 and 29 are at the highest risk for drinking and driving [36]. Age of onset for alcohol abuse peaks between 15 and 29, and males are nearly four times more likely to abuse alcohol compared to females of the same age [31]. With regards to illicit drugs, persons between the ages of 16 and 29 were the most likely to have used illegal drugs in the past month, and males are about twice as likely as females to have used marijuana in the past month [37].

In contrast to marriage (which increases the likelihood of mating), environmental variables that decrease the likelihood of survival or impact negatively on sociosexual status are likely to increase risky substance use and abuse. Competition is generally greatest at the low end of the sociosexual hierarchy. Men who have fewer resources are at a disadvantage when seeking a mate, as such, they must compete to a greater extent than men with greater resources. Resources, from this standpoint, are not necessarily economic, but may include personality variables (i.e.: ambitious, outgoing, humorous, kind), intelligence, success in a valued domain (i.e.: academic, artistic, employment), attractive appearance, or athleticism. Demonstrated risk factors for substance abuse include unemployment, lower socioeconomic status, early aggression, shyness, and poor academic performance [37, 38]. Further, in environments in which mortality is in question (i.e.: neighborhoods with high rates of homicide), risk-taking is likely to be a more effective strategy than conserving resources for the future. Not surprisingly, young males in unsafe environments and little perceived chance of future success are at high risk for substance-related problems [39].

Summary

The origins and prevalence of substance use and abuse have long frustrated evolutionary attempts at explanation. Conventional mismatch theory suffers from three major problems that limit its utility as a viable theory of the evolution of substance abuse: evidence that suggests that human use of psychoactive substances are not a purely modern phenomenon, new views of the cortico-mesolimbic dopamine system as mediating incentive-salience rather than reward, and evidence that not all drug use is rewarding. Evolutionary theory, however, is able to account for the origin of substance abuse by unifying a paleobiological analysis of diet, the handicap principle, and life-history theory.

Paleobiological analyses of humans' ancestral diets reveal that early hominids had a long history with both psychoactive plant chemicals and ethanol from ripe and fermenting fruit. These chemicals confer a number of advantages in small doses: they can act as neurotransmitter substitutes in periods of deprivation, reduce the harmful effects of stress, and confer physical benefits including cardiovascular advantages. In the case of alcohol, the smell of ethanol may have led to greater concentrations of ripe fruit, allowing for increased caloric intake, as well as, conferring cardiovascular health advantages.

The handicap principle explains why overuse or abuse of a psychoactive substance occurs. As males attempt to impress potential mates, they utilize physiological and behavioral disadvantages to demonstrate honest fitness qualities. By placing oneself at a disadvantage relative to one's rivals (i.e.: binge drinking) and still being able to demonstrate superiority (i.e.: winning a bar fight), a male demonstrates a comparative advantage in terms of traits that may be attractive to females (i.e.: strength and stamina).

Life history theory suggests that the tendency to engage in risky behaviors (including risky substance use and abuse) is likely influenced by the individual's age, gender and sociosexual status. This predicts that young, postpubescent, unmarried males are the most likely to engage in risky drinking and drug use. Furthermore, males who view themselves as having little likelihood of surviving and thriving as adults are at greatest risk.

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