Drug use and addiction: evolutionary perspective

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Drug use creates a significant amount of harm in modern societies. From an evolutionary perspective, the pervasive use of drugs and the ongoing risk of drug addiction can be explained in terms of the action of drugs on evolved motivational–emotional systems. Addiction arises through interaction of these evolutionarily ancient systems, designed to promote the pursuit of natural rewards, and contemporary environments where purified and potent forms of drugs are readily available. This evolutionary analysis is extended to account for developmental patterns in problem drug use, and to explain the existence of behavioural addictions, such as problem gambling. The paper concludes by considering some of the clinical and public policy implications of the evolutionary perspective presented.
Key words: addiction, behavioural addictions, drug use, evolution, life history theory.

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The use of drugs is a pervasive feature of human cultures throughout history. Recipes for beer appear in Mesopotamian clay tablets >5000 years old [1]; the earliest written record of opium is dated to 3400 BCE [2]; and the early use of other psychoactive substances such as cannabis, coca, betel and a variety of hallucinogens is well documented [3,4]. The ubiquity of drug use prompted Baron Ernst von Bibra, in his classic monograph *Plant Intoxicants,* to suggest the following [5].

> *…the enormous numbers of drug users just cited demonstrate the paramount importance these substances have for the human race, since there exist no people on the Earth that fails to consume one or another of these dainties, which I have subsumed under the name 'pleasure drugs'. There must therefore exist a deeper motive, and the notion of fashion or the passion for imitation cannot be applied here.*

The 'deeper motive' alluded to in this quote can be plausibly construed in terms of basic, evolved, human tendencies that promote drug use and render humans vulnerable to drug addiction.

Over the last decade or so there have been a number of attempts to understand drug use and addiction from an evolutionary perspective [6–14]. In the present paper we provide an overview of this literature, focusing on how an evolutionary perspective can help us to understand the phenomenon of drug addiction. We also extend this analysis to a discussion of 'behavioural addictions', and tease out some of the implications of an evolutionary approach for treatment and public policy responses to drug use.

Why do people use drugs?

Problem drug use causes a significant amount of harm to users in modern societies, without any clear and reliable benefits in terms of survival or reproductive success. From an evolutionary perspective drug abuse and drug addiction would appear to be maladaptive [or, on balance, selectively neutral). The use of drugs, of course, can also

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be beneficial in some contexts: stimulants such as caffeine and nicotine reduce fatigue and suppress appetite; alcohol can relieve anxiety and reduce stress; and opiates are highly effective in alleviating pain. The extensive comorbidity between drug use and other mental disorders [15,16] can be partly explained in terms of the capacity for drugs to alleviate some negative symptoms of these disorders [17]. These beneficial characteristics of drug use have led some researchers to suggest that humans may have evolved specific adaptations that motivate individuals to consume psychoactive substances [14].

Sullivan and Hagen argued that there has been a long co-evolutionary relationship between humans (and our hominin and mammalian ancestors) and plants with psychoactive properties [14]. This relationship opens up possibilities for the adaptive exploitation of the chemicals produced by plants. The synthesis of neurotransmitters such as serotonin and dopamine require the consumption of food products that provide the relevant chemical precursors. 'Substance seeking', Sullivan and Hagen suggested, 'evolved to alleviate these constraints on brain-signalling processes' [14]. By consuming plants that provided essential neurochemicals directly, time and effort spent foraging could be reduced. Although plausible, there are several problems with the account developed by Sullivan and Hagen [14]. First, despite the ubiquity of substance use across cultures, it is unlikely that psychotropic plants were widely enough available in the environments of ancestral hominins for the evolution of specific adaptations underlying drug-taking behaviour. Second, it is not clear what the nature of the specific mechanisms underlying drug-taking behaviour would look like. Food preferences are guided by specific sensory and regulatory mechanisms [18], but with the exceptions of ethyl alcohol present in ripe, calorie-rich fruit [6,7], the consumption of psychoactive drugs is not clearly linked to any specific evolved gustatory or olfactory preferences.

It is unlikely that humans have evolved specific adaptations that motivate drug use. The widespread attraction, however, of psychoactive substances may plausibly reflect their action on more domain-general motivational and emotional systems. These systems are likely to be phylogenetically ancient and conserved across a variety of animal species given that there is abundant evidence that non-human animals will readily consume psychoactive substances in both natural and laboratory contexts [19–23]. Drugs, then, have the capacity to alter affective and cognitive functioning in ways that many humans (and non-human animals) find attractive [11,24]. Importantly, drugs can generate positive, and alleviate negative, emotional states. Drugs generate positive emotions, argued Nesse, by effectively short-circuiting mechanisms that have evolved to signal positive, fitness-enhancing experiences such as the consumption of food; sex; and social relations [11]. 'Drugs of abuse' Nesse and Berridge suggested, 'create a signal in the brain that indicates, falsely, the arrival of a huge fitness benefit' [12]. Drugs have this capacity, it is argued, because they act on natural reward pathways in the brain. The neural basis of reward critically involves the mesocorticolimbic dopamine system. This reward circuit involves pathways from the ventral tegmental area to the nucleus accumbens, amygdala and prefrontal cortex [25,26]. All drugs of abuse activate this system by either directly or indirectly increasing levels of dopamine [27–29], although it is also widely recognized that other neurotransmitters, such as opioid peptides, play a role in the experience of drug reward and may be important in mediating the experience of pleasure or liking in response to a rewarding stimulus [25,28].

It is unlikely that the brain systems implicated in the rewarding effects of psychoactive drugs have evolved specifically for the ingestion of such drugs. Rather, these systems have been selected for because they generate positive emotional states that are linked to stimuli in the world that do have survival and reproductive relevance for the organism, such as food, sex, and positive social relations [22,30–32]. In essence, the reward system can be conceptualized as a signalling system that flags the importance of stimuli likely to promote reproductive fitness. From an evolutionary perspective, part of the reason that people take drugs is because they have the capacity to generate positive emotional states, and the reason why they have this effect is because they reliably act on evolved reward systems in the brain. Of course, it needs to be recognized that drug initiation, use, and desistance are shaped by the complex interaction of the psychobiological effects of drugs on users and the social context in which drugs are used [9,33,34].

Drug addiction

The evolutionary reward model provides a useful partial explanation for drug use. But drugs may be used initially even though they produce aversive rather than pleasurable experiences and there is no simple correlation between the pleasure induced by drugs and their addiction potential [10]. Moreover, individuals who become addicted to psychoactive substances typically experience relatively less pleasure in response to drug use over time, but their craving for and loss of control over drugs increase. Although the physiological processes of tolerance and withdrawal are important in understanding addiction, drug addiction is essentially a disorder characterized by behavioural compulsion and a related problem in self-regulation or impulse control: individuals become motivated to seek out and

consume drugs, at the expense of other activities, despite significant problems that arise from their drug use [35].

In order to understand why some individuals become addicted to drugs, we require a detailed understanding of the functional properties of the systems underlying motivational behaviour. Why have these systems evolved and how does repeated drug use affect these systems in ways that lead to drug addiction? It is fairly easy to understand the evolutionary function of motivational systems: organisms that are motivated to seek out food, water, mates, and other evolutionarily beneficial stimuli, and to avoid predators and other dangerous environmental situations, are going to be at a selective advantage and hence such systems will evolve. Indeed, the core features of the mesocorticolimbic dopamine reward circuit appear to be evolutionarily ancient [36], and they are recruited to promote a wide range of adaptive behaviour in different species, including feeding, sex, positive social relations, and infant attachment [25,30,37]. In order for motivational–emotional systems to steer behaviour into selectively advantageous channels, four important things have to happen: (i) stimuli that have evolutionary relevance for the organism (e.g. water, food, sexually receptive mates) need to be imbued with special significance (they need to stand out from other stimuli that have less evolutionary relevance); (ii) organisms need to be motivated to seek out these stimuli; (iii) organisms need to learn the specific environmental contexts associated with these stimuli in order to better predict their occurrence; and (iv) stimuli need to able to be ranked in importance depending on the specific internal state of the organism and the particular environment that they find themselves in. In other words, organisms need to be able to regulate their pursuit of rewards depending on the environmental context.

The first three of these functional properties of motivational–emotional systems correspond to the three major components of reward outlined by Berridge and Kringel [22]. The first component is 'liking' and describes the conscious and/or unconscious experience of pleasure in response to a rewarding stimulus. The hedonic experience becomes a way of marking out certain experiences as evolutionarily relevant. The second component is 'wanting'. This comprises the attribution of incentive salience to rewards and the corresponding motivation to seek them out [38]. The third component is 'learning' and involves the development of associations and predictions based on past experiences. An organism, for instance, will learn that rewarding experiences are associated with certain features of the environment and the presence of those features may trigger motivational behaviour. The fourth component recognizes that motivational behaviour needs to be regulated depending on internal states of the organism (e.g. hunger and thirst) and appropriate environmental contexts (e.g. presence of predators or conspecifics). This may involve a trade-off between the pursuit of immediate rewards and the control of behaviour in order to obtain greater rewards (relative to costs) in the future. In many animal species, and perhaps especially in humans, the social context also plays an important role in modulating relevant motivational behaviour. Whether the pursuit of rewards is likely to promote reproductive fitness will depend, in part, on the presence of conspecifics and their response to the reward-seeking behaviour.

By virtue of their psychopharmacological effects, repeated drug use can alter these motivational–emotional systems in ways that give rise to the characteristic features of addiction. As noted here, drugs can generate strong positive emotional experiences because of their action on natural reward systems in the brain, essentially signalling that they are the kind of stimuli that the organism should be paying attention to. One prominent theory of drug addiction also highlights how repeated drug use results in the alteration of brain systems underlying incentive salience, leading to pathological wanting to use drugs [25,38]. Stimuli associated with drug use (e.g. needles, pipes, drug-using locations) also become imbued with special significance because they are associated with and predict the delivery of drug reward. These drug-related cues can become powerful triggers for relapse in individuals who have been addicted to drugs, probably through the activation of the motivational systems related to wanting [39,40], subjectively felt by the individual as craving.

One important characteristic of drug addiction is the pursuit of drugs at the expense of other (normally rewarding) activities despite adverse consequences. This suggests that the reward value of drugs becomes magnified to the extent that it displaces other rewards, and that the individual's ability to accurately assess the adverse consequences of drug use (or at least to act on this assessment) is severely compromised. Koob and LeMoal argued that addiction results in an increase in brain reward thresholds such that normally rewarding activities result in less hedonic pleasure [28]. This confers an ongoing vulnerability to relapse, as individuals use drugs to alleviate negative emotional states. Chronic drug use also may affect an individual's ability to regulate behaviour through changes in the function of the prefrontal cortex [38,40–42]. It is widely recognized that the prefrontal cortex plays a critical role in the regulation and control of behaviour. The orbitofrontal cortex also appears to be involved in coding the stimulus value of rewards [42,43]. Changes in these brain regions as a result of repeated drug use may result in both the pathological elevation in the value of drug rewards and the diminished capacity to regulate drug-seeking behaviour, despite harmful consequences.

The role that self-regulatory systems play in addictive behaviour also highlights the importance of the environmental context in the development of addiction. Although repeated drug use might result in the pathological wanting of drugs, whether drugs are taken ultimately depends on a social context that facilitates drug use [9]. Historical and cross-cultural patterns in drug use clearly implicate the importance of environmental context: when drugs are readily available and social norms (and legal contexts) support the use of drugs, prevalence rates increase [34,44,45]. This is almost certainly the main reason why addiction to nicotine and alcohol is much more prevalent in Western societies than addiction to all other drugs [46]. Of course, many individuals continue to use drugs even when they are difficult to attain and the environment (both social and legal) strongly discourages drug use, highlighting the extreme motivational salience that drugs have attained in the individual's life.

In sum, drug addiction can be conceptualized as a pathology or disruption in the evolved physiological mechanisms that underpin motivational behaviour [25, 36,41]. The fact that repeated drug use can fairly readily have adverse effects on evolved motivational systems suggests that drug addiction is largely a recent phenomenon. Although drug use has a long history and may well have been a feature of human populations for at least the last 10 000 years [4,34], the ready availability of purified and potent forms of drugs and mechanisms for delivering them are extremely recent phenomena [45]. With the possible exception of genes that protect some individuals from alcoholism [6], there simply has not been enough time for the factors that promote addiction to be selected out of the population. Moreover, because the motivational–emotional systems that underpin addiction clearly have important adaptive functions, selection against drug use would need to target specific drug-related metabolic processes rather than the underlying neural mechanisms that drugs act on. In sum, because the motivational–emotional systems that are affected during drug addiction are phylogenetically ancient and clearly adaptive in most environments, humans are likely to remain vulnerable to drug addiction given the ready availability of drugs and social contexts that facilitate use in contemporary environments.

Life history theory and patterns in drug use and drug addiction

Although all people may be vulnerable to the development of substance use problems, the risk of developing a substance use disorder is not evenly distributed in the population. Understanding the individual difference factors that can help to explain risk for addiction has been an important focus in theories of addiction [47], and researchers have highlighted a number of biological, psychological, social, and cultural factors that are important in explaining these differences [33,48,49]. For instance, pre-existing neuropsychological vulnerabilities that limit self-regulatory capacities are an important risk factor for the development of substance use problems [50]. The oft-cited finding that the majority of Vietnam veterans did not continue with their opiate use after they returned to the USA also highlights the importance of social context and availability in the development and maintenance of addictive behaviour [51,52]. Another robust finding is that the prevalence of substance use problems varies in fairly reliable ways according to age, gender, and sociodemographic characteristics. For instance, the recent (last month or last year) use of illicit drugs tends to be higher for male than for female subjects and is higher for adolescents and young adults than for other age groups [53,54]. The 12 month prevalence of substance use disorders is also significantly higher among young adults (age 18–29), men, unmarried individuals, and individuals of lower socioeconomic status (as measured according to education and income) [55,56]. The broad patterns of risk found for substance use problems is also largely mirrored for a range of other risky behaviours including dangerous driving, risky sex, and problem gambling [57,58].

From an evolutionary perspective, these patterns can be explained in terms of the fundamental trade-offs that occur during different developmental periods, and gender differences arising from reproductive asymmetry. According to life history theory, organisms have finite resources and decisions must be made as to whether to invest more effort into survival, growth, current reproduction, or future reproduction [8,59,60]. How resources are allocated to these different tasks in order to most effectively maximize reproductive fitness will depend on the age and sex of the organism and the environmental context in which the organism finds itself.

Life history theory predicts that young men should be most prone to engage is risky behaviour and be most prone to discount the future. Because the competition for mates, status, and resources is greatest during late adolescence and young adulthood we should expect that young, unmarried men have the most to gain from risk-taking behaviour [61,62]. As men age they are more likely to develop long-term intimate relationships, accrue status, and have children. Therefore, we should see a decrease in risk taking as resources are diverted primarily to parenting rather than mating. Women, in general, should be less prone to engage in risk-taking behaviour because, in humans, women experience less variance in reproductive success and therefore have more to gain from focussing effort on parenting and avoiding situations that put their

survival at risk. We should also expect that risk taking is dependent, in part, on environmental circumstances. In highly unpredictable or impoverished environments where survival prospects are less certain, there is more to gain from engaging in risky behaviours. Put simply, when prospects for long-time survival are diminished there is less to lose and more to gain from pursuing immediately rewarding, but potentially dangerous activities [8,63].

This suggests that part of the vulnerability for developing a substance use disorder is related to developmental differences in the mechanisms underlying risk taking. The evolutionary importance of certain rewards is not uniformly distributed in the population. We should, for example, expect that the relative significance of immediate rewards, all other things being equal, is the greatest during adolescence and young adulthood and will be greater for men than for women. Individuals living in dangerous and unpredictable environments should also be more oriented to the pursuit of immediate rewards.

Recent research on neurodevelopmental processes can help us to flesh out our understanding of why adolescents and young adults are at a heightened risk for substance use problems and other behavioural addictions. Studies suggest that, although adolescents may accurately assess the risks of certain behaviours, they place greater value on the benefits or rewards of risky behaviour and hence seek out stimulating experiences [57,64–67]. The biological changes that can account for this change in reward salience, or the attractiveness of stimulating and risky activities, have yet to be fully elaborated. Recent findings indicate that they are probably related to changes in the activity of key reward circuits in the brain [64,68]. Rewarding, and often risky, activities thus seem to become more attractive to adolescents. The development of the pre-frontal cortex, however, a region of the brain that is implicated in impulse control, planning, and decision making, is not fully developed until the early 20s [67,68]. Biologically speaking, then, adolescence is a period where the rewards of risky behaviour become more attractive, but the capacity to control and regulate behaviour is still developing. These changes can be plausibly considered to reflect selection for an increase in risk taking during adolescence and young adulthood. The heightened risk for the development of substance use problems during this period of development can, thus, plausibly be understood in part as the result of the normal development of human motivational–emotional reward systems.

Behavioural addictions

If certain drugs can affect evolved motivational–emotional systems in ways that result in addiction, then we might expect that other non-drug-related activities (especially those involving ‘natural’ rewards) can also result in addictive behaviour to the extent that they act on these reward systems. Whether or not the concept of ‘addiction’ can be extended to non-drug-related stimuli and activities remains a matter of substantial debate [69–71]. The DSM-IV includes the category ‘impulse control disorders not otherwise specified’, which includes a fairly heterogeneous group of disorders, including kleptomania, pyromania, pathological gambling and trichotillomania [35]. The defining feature of these disorders is the ‘failure to resist an impulse, drive, or temptation to perform an act that is harmful to the person or to others’ [35]. The DSM-IV also recognizes the diagnostic category ‘binge eating disorder’ and some have argued that we could also include other impulse control disorders such as ‘compulsive buying’, ‘compulsive sexual behaviour’, and ‘Internet addiction’ [69].

As Potenza outlined, most of these impulse control problems share some clear psychological and behavioural features with drug addiction: (i) they involve a psychological state of craving prior to the behaviour; (ii) they involve a loss of control over behaviour; and (iii) they involve engaging in behaviour despite adverse consequences [71]. There is also an emerging body of evidence that suggests that problem gambling, and perhaps other behavioural addictions, may be mediated by the same motivational–emotional systems in the brain that are involved in addiction to drugs [72–74]. Further evidence in support of the idea that behavioural addictions represent similar pathologies of motivational–emotional reward systems comes from research that has demonstrated the effectiveness of opioid antagonists, typically used in the treatment of alcohol and opiate dependence, on pathological gambling [75,76].

From an evolutionary perspective we should expect that the mechanisms underlying the signalling and pursuit of natural reward should be calibrated so as to bias some types of stimuli and activities over others. Organisms should be more motivated to engage in activities that increase their survival and reproductive success such as the pursuit of food and sex. We should perhaps expect, therefore, compulsive eating and compulsive sexual behaviour to be the most common addictions, given that they involve the pursuit of natural rewards. Food intake, however, is under the (imperfect) control of homeostatic regulatory mechanisms and compulsive sexual behaviour is also to some extent regulated by physiological limitations. Importantly, both regular food consumption and regular sex are normal activities that do not result in undue harm, whereas the regular use of psychoactive substances often can. This suggests that the addiction threshold for what constitutes problem eating

or problematic sexual behaviour may be higher than for problem drug use.

Moreover, the core mechanisms underpinning the motivational–emotional reward system appear to be remarkably conserved across species and thus have a very long evolutionary history [36]. They are probably not designed, therefore, to respond to highly specific stimuli. Rather, any activity that generates pleasurable hedonic states becomes the object of motivational salience. Drugs may also be different from natural rewards in several important ways [25,39]. First, they may simply produce more powerful hedonic states that more potently signal reward. Second, drugs may, through their specific pharmacological actions, disrupt normal reward systems by inducing excessive incentive salience. And, third, drugs may have other physiological effects, such as the production of aversive withdrawal states that further promote use.

Individuals, then, may be especially prone to pursue drugs in a compulsive fashion because they have very specific physiological effects on the brain. Potentially any rewarding activity, however, may become compulsive. An evolutionary analysis suggests that certain types of stimuli or certain activities are more likely to result in behavioural addiction. In particular, we suggest that the risk for addiction will be greater when (i) the activity or stimulus reliably generates strong and pleasurable emotional states (and thus activates motivational–emotional reward pathways); (ii) the activity or stimulus in its current form is relatively novel in evolutionary terms (and hence is not controlled by specific regulatory mechanisms); (iii) the activity or stimulus is available enough to support compulsive patterns of behaviour; and (iv) the activity or stimulus is under less formal (e.g. legal) and informal (e.g. social) control (and thus, is less likely to be self-regulated).

Problem gambling presents a particularly interesting case because gambling by its very nature is the pursuit of an evolutionarily novel, but in contemporary societies, universal reward: money. Compulsive eating and compulsive sexual behaviour, as noted in the previous section, may be less common than other behavioural addictions, but the ready availability of intensely hedonic food (rich in fats and sugar) and pornographic sexual material will increase the risk for the development of these behavioural addictions.

Implications for clinical practice and public policy

An evolutionary perspective on addiction shows the inevitability of both voluntary and compulsive engagement in substance use and hedonic behaviours within human populations, while at the same time aiding in the identification of environmental changes and clinical interventions likely to limit the extent of the problem.

In clinical settings a range of currently used interventions is compatible with the evolutionary perspective explored in the present paper. On the one hand, pharmacological agents that substitute for drugs of abuse or which seek to disrupt the rewarding effects of substances or compulsive behaviours highlight the growing understanding of the neurochemical and neurophysiological underpinnings of addiction. Psychological and social interventions such as cognitive behavioural therapy and 12-step programmes, on the other hand, seek to weaken cued associations, strengthen response inhibition, and consciously increase the salience of negative consequences of use.

Broader lifestyle change may also facilitate recovery. The literature on natural recovery, for instance, highlights the importance of life experiences in desistance from problem drug use [77]. A more positive approach to treatment that promotes the pursuit of ‘natural rewards’, or what Ward and Stewart term ‘primary goods’ such as friendship, agency, and community [78] may contribute to relapse prevention through reducing the relative reward salience of drugs and increasing the perceived costs of use.

The recognition that adolescence is a period of heightened vulnerability for the development of substance use problems, in part due to the developing nature of the adolescent brain, should promote initiatives that enable families and communities to act as ‘surrogate frontal lobes’ that can temper risk-taking proclivities. Equally, improving the prospects of marginalized youth may reduce the propensity towards risk taking, a strategy which may be seen to straddle individual treatment interventions but which also has wider societal and policy implications.

An appreciation of the collision between ancient evolved mechanisms for habit formation and the very recent emergence of manufactured or naturally occurring but now cultivated and concentrated substances leads to a heightened appreciation that substances of abuse and gambling are ‘no ordinary commodities’ [79], a caution that applies equally to licit substances (such as alcohol, for which the term was coined) as it does to illicit substances. In their seminal work, Babor *et al.* made a powerful argument for the dangers of a *laissez faire* policy approach to the licit substance alcohol, arguing instead that harm limitation is best achieved by having robust control over availability, affordability and promotion, while also maximizing the chances of negative consequences for hazardous use in the form of drink driving [79]. Equally, in the area of illicit drugs the twin approaches of demand reduction and supply limitation are seen as essential co-contributors to harm minimization [80]. The recognition that drugs are inherently attractive substances that can readily disrupt evolved

motivational–emotional systems in ways that promote compulsive use, should also encourage policy makers to recognize that the use of illicit drugs is primarily a public health issue that is unlikely to be satisfactorily addressed through overly punitive criminal justice sanctions. This should not of course be taken as an argument for the legalization of currently illicit substances; rather, it needs to be recognized that attraction of drug use and the compulsive nature of drug addiction are likely to negate any marginal deterrent effects that could arise through the implementation of harsh criminal penalties for drug use. Indeed, the idea that substances of abuse are 'no ordinary commodities' suggests that the ongoing regulation of illicit substances is an essential component of an effective policy for reducing drug-related harm.

An evolutionary perspective suggests that humans will remain attracted to the lure of psychoactive drugs and other rewarding activities. The development of compulsive patterns of behaviour arises through an interaction of evolutionarily ancient motivational–emotional systems designed to promote the pursuit of natural rewards and contemporary environments that allow (and sometimes encourage) problematic levels of use. Strategies for reducing the harm caused by addiction to drugs and other behavioural compulsions can be effective through a combination of targeting the mesocorticolimbic reward pathway with pharmacological agents, enhancing self-regulatory capacities, and through restructuring of the social environment to regulate availability and promote increased levels of social control.

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