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EVOLUTIONARY MISMATCH, NEURAL REWARD CIRCUITS, AND PATHOLOGICAL GAMBLING

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Evolutionary mismatch theory has been applied to disorders of self-regulation such as maladaptive eating patterns and drug abuse. Modern gambling represents a refinement of the elements of risk and chance, which draw upon the faculties of judgment and novelty-seeking. A set of neuroanatomical structures, including prefrontal-subcortical systems and associated limbic structures, have been implicated in the processing of reward and punishment, including gambling-related situations. Neurobiological systems guiding choice and behavior have evolved to maximize chances for survival under hunter-gatherer conditions, and modern gambling represents an abrupt departure from these circumstances, sometimes resulting in pathological gambling.

Keywords addiction, evolutionary mismatch, neurobiology, pathological gambling

At face value, gambling can appear a paradoxical behavior. People engage in it despite knowing that the long-term odds for success are against them. While gambling may seem reasonable within certain limits, many people engage in it to an extent that causes significant personal and financial loss. Studies estimate that *5%* of gamblers exhibit problem gambling, and that 1% engage in it to a more severe,

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pathological degree (van Es, 2000). Pathological gambling appears to be increasing in prevalence, particularly in geo-graphical areas where gambling becomes more available (Ladouceur et al., 1999). While different criteria exist for what constitutes patho-logical gambling, the core feature is an over-reliance on gambling, manifesting as several possible maladaptive behaviors, and persistence in gambling despite negative consequences (American Psychiatric Association, 2000). Gambling can become a behavioral addiction, equal or worse in severity to drug addiction.

An evolutionary perspective has shed light on many seemingly illogical or paradoxical behaviors. This article applies evolutionary mismatch theory to pathological gambling in order to explain its origins and mechanisms.

Evolutionary Mismatch Theory

Evolutionary mismatch theory carries great heuristic value in providing a parsimonious explanation for many seemingly paradoxical behaviors, traits, and illnesses (for review, see Nesse & Williams, 1994). The core concept of evolutionary mismatch involves behaviors that were optimized over multiple generations by natural selection to best fit the environmental conditions present during most of human evolution. The majority of human existence has involved a hunter-gatherer lifestyle, and many behaviors and traits have adapted to maximize chances for survival and reproductive success in that context.

However, when a relatively rapid change occurs in environmental conditions, it can leave deeply ingrained behavioral tendencies at odds with the present circumstances. The demands of the environment for an organism's success shift, making behaviors that were once optimal now suboptimal and sometimes pathologically maladaptive. In particular, the advent of agriculture and industrialized civilization has rapidly changed the way in which most humans live, but the vestiges of our evolutionary past still have an important influence on our behavior.

Evolutionary mismatch has been applied to several areas. For example, changes in dietary choices and availability brought on by agriculture have led to a shift toward greater consumption of

carbohydrates and saturated fats (Eaton & Konner, 1985). This departure from the typical paleolithic diet has direct implications for the prevalence of diet-influenced illnesses such as diabetes mellitus and cardiovascular disease.

The same evolutionary mismatch logic has been applied to drug abuse and addiction (Pani, 2000). The ability to highly refine drugs from plants (e.g., cocaine from *Erythroxylon coca),* synthesize novel drugs (e.g. methamphetamine), and deliver them to the brain in a rapid and thorough manner (e.g., smoking freebase or alkaloidal drugs) has led to a significant increase in the intensity of their effects. As a result, modem humans have a greater variety of psychoactive drugs available to them and with more dependence liability than has ever been encountered in human history. Consequently, drug abuse and addiction have become severe and common problems.

Pani (2000) has pointed out that current evolutionary mismatch theory lacks a definition of the underlying neural substrates that mediate the behaviors or disorders of interest. He makes a convincing case for the dopaminergic system of the brain, and how environmental mismatch specifically involving this system can impact conditions such as addiction, stress, chronic emotional disorders, and sleep deprivation.

Critical Elements of Gambling: Risk and Chance

While gambling takes many forms, all arguably involve two essential elements: (1) chance, or an element of unpredictability, and (2) risk, or the possibility for loss and gain.

Chance

Many gamblers become experts in their games of choice, learning the rules and strategies in great detail, even gaining proficiency in the statistical aspects of the games. However, it is the element of chance that likely sustains interest in gambling. By necessity, games cannot pay more than they collect, so something other than financial reward must sustain interest. From a behavioral perspective, this would be expected to extinguish participation in gambling were it not for the unpredictable nature of the outcome. When losses are

too frequent, interest in a game wanes, but with random and intermittent reinforcement, anticipation is piqued and interest is sustained.

Preference for activities involving chance is related to the personality trait of novelty-seeking. While behavioral routines improve skill and efficiency through repetition and familiarity, seeking novelty also carries benefits. For example, seeking novelty and variety in foods would be more likely to produce a nutritionally balanced diet. Thus, adaptive behavior involves an optimal and context-appropriate balancing of novelty and routine. It is the aspect of chance that endows gambling with novelty.

Risk

Risk provides the allure of gambling, introducing the possibility for gain or loss, which is often financial. Thus, the element of risk necessarily engages emotional and cognitive arousal systems in order to evaluate the risks and make appropriate decisions. In many, this elevates mood and focuses attention, making gambling a pleasurable activity. Some pathological gamblers describe this state as outright euphoric, and may use it maladaptively to manage their mood, such as to alleviate depression, stress, or anxiety.

Most human activities carry some inherent level of risk. Thus, adaptive behavior must involve the ability to recognize risks, to weigh probable costs against the benefits, and to choose a course of action accordingly. There is considerable intra-individual variability in aversion or predilection for risk. While excessive risk-taking typically leads to reckless and dangerous behavior, a predilection for risk is not always a pathological trait. Arguably, either extreme in risk taking will result in maladaptive behavior. Appropriate risk-taking can lead to opportunities for gain when applied rationally (e.g., financial investing). Thus, adaptive behavior involves both engaging and refraining from risk in a manner that optimizes benefit.

Environmental Engineering in Gambling

Gambling environments vary greatly, but the culmination of environmental engineering occurs in casinos. The design and functioning of casinos represent deliberate attention toward manipulation of

sensory and cognitive influences on gamblers. On a sensory-perceptual level, intense visual and auditory stimuli are present. Lights and sounds pervade the casinos and are used to saliently signal wins and rewards. Casinos typically do not have windows or clocks readily displayed in order to minimize cues signaling the passage of time spent gambling. Such cues could be used by gamblers to limit their amount of time spent gambling. Further, alcohol is frequently consumed in casinos, and often given as a compensation for gambling. Alcohol has direct neurochemical effects that lead to altered judgment and increased risk-taking (Mongrain & Standing, 1989; Mitchell, 1985).

Neural Reward Circuits and Gambling

In recent years, there has been elaboration of neural circuits that underlie reinforcement and reward, with great implications for addictive behaviors (see Table 1). The reward system in the brain involves functional and anatomical circuits, including prefrontal-subcortical circuits and the limbic system. Evidence implicates orbitofrontal medial and prefrontal cortex (e.g., anterior cingulate cortex), ventral striatum/nucleus accumbens, ventral pallidum, and mediodorsal thalamus (Hollermann et al., 2000; Tzschentke, 2000; Kretschmer, 2000; Meunier et al., 1997). Interconnected and functionally related limbic structures such as the extended amygdala and hippocampus have also been implicated (Koob, 1999; Tabuchi et al., 2000).

The dopaminergic system in the brain has strongly been implicated in various forms of reward and addiction. Prefrontal-subcortical and limbic structures are innervated by dopaminergic projections from

TABLE 1. Neuroanatomical structures implicated in reward

Cortical	Orbitofrontal cortex/ventromedial prefrontal cortex Medial prefrontal cortex (anterior cingulate, subgenual) Hippocampus
Subcortical	Ventral striatum/nucleus accumbens Ventral pallidum Mediodorsal thalamus Extended amygdala

See text for references.

the mesencephalic ventral tegmental area (Tzschentke, 2001). Dopamine is believed to exert a context-dependent, neuromodulatory feedback signal, enhancing signal-to-noise ratio in response to contexts of reward and novelty (DeFrance et al., 1985, Kischka et al., 1996). Serotonin also plays a role in reward, influencing impulsivity and tolerance for delayed rewards (Bizot et al., 1999). Interestingly, pathological gamblers have been shown to discount delayed rewards (Petry, 2001a).

Thus, monoamine interactions with prefrontal-striatal and limbic circuits entrain associations between salient contextual stimuli and internal reward processes (Spanagel & Weiss, 1999). The activity of these prefrontal-striatal and limbic circuits encode decision-making and motivational processes. Thus, the rules and strategies for behavior are physiologically entrained in these structures by reward-related signals from monoamine neurotransmitters (Dehaene & Changeux, 2000).

The involvement of these processes in human reward is not just theoretical. While the above work provides clear evidence in non-human species, there have also been human functional neuroimaging studies that convergently implicate the same systems. Many studies even have employed actual monetary reward (e.g., Thut et al., 1997; O'Doherty et al., 2001). O'Doherty and colleagues (2001) have further shown that magnitude of orbitofrontal activation correlates with the magnitude of rewards and punishments. Monetary rewards are associated with activation of the midbrain and ventral striatum, and monetary punishment activated the hippocampus (Elliot et al., 2000). Further, Berns et al. (2001) showed that reward-related activity in orbitofrontal cortex and nucleus accumbens is maximal when rewards are unpredictable, highlighting the importance of chance and novelty in the activation of reward systems. Similar activations occur in these structures with many other forms of pleasurable activity, including drug-induced euphoria, listening to enjoyable music, and eating appetizing food (Kilts et al., 2001; Blood & Zatorre, 2001; Small et al., 2001).

A ventromedial sector of prefrontal cortex (vmPFC) has particularly been associated with decision-making and weighing risks versus benefits (Bechara et al., l994). People with lesions of vmPFC show impairment on Bechara's gambling task, and similarly show

poor judgment in naturalistic decision-making. A functional neuroimaging study of drug abusers performing Bechara's gambling task confirms the role of vmPFC and the amygdala for optimal decision-making in this task (Grant et al., 2000a). Further, a recent study has shown that subjects with comorbid drug abuse and pathological gambling tend to perform poorly in this task (Petty, 200 1b).

Implications for Pathological Gambling

Evolutionary mismatch and the existence of specific reward circuits in the human brain has direct implications for pathological gambling. As we learn more about the functioning of the reward system, its role in gambling becomes clearer. Further understanding also suggests ways in which the system can be inappropriately engaged in pathological gamblers. The reward system described here plays a definite role in representing the reinforcing value of environmental stimuli and experiences. These same structures are involved in decision-making, risk assessment, and planning of behaviors accordingly. Neurochemical activity in these circuits entrains the structures to respond preferentially to pleasurable and novel situations, and to exert impulse control when waiting for rewards. While the reward system may be appropriately engaged in most individuals, it becomes apparent how variability in the function of these systems can produce a behavioral addiction as in pathological gambling.

The operating characteristics of the reward system are a consequence of anatomical connections, physiological regulation, and neurochemical sensitivity. Most of the research in this area has focused on the neurochemical aspect, particularly on dopamine receptors. Genetic studies reveal that the Taq Al variant of the human DRD2 gene has been associated with drug addiction, impulsivity, and pathological gambling (Comings et al., 1996; Comings et al., 1997). More recent work has also implicated receptor genes for other neurochemical systems including serotonergic, noradrenergic, and glutamatergic systems (Comings et al., 2001).

The genetic underpinnings of the reward system would have adapted to maximize survival and reproductive success throughout human evolutionary history. Thus, its neuroanatomical, neurophysiological, and neurochemical configurations would be best suited to manage

risks and rewards under conditions most typical of a hunter-gatherer existence. However, modern gambling represents an abrupt departure from risk-taking in this context. In modern gambling, the contingencies for reward and punishment are intentionally calculated and adjusted to maximize gambling: the element of chance inherent in naturalistic situations has been refined into games of chance. Environmental conditions are carefully manipulated to intensify the impact of experience. Alcohol is supplied to alter judgment and risk- taking tendencies, and to minimize impulse control.

In the evolutionary context, the losses and gains provided by risk taking were often more immediate and tangible, affecting one's food availability, mating opportunities, and physical safety. In contrast, the losses in modem gambling are abstract and delayed, represented by symbolic chips and numerical digits. Their relation to material items is only through associative conditioning. When other factors are equal, abstract and delayed rewards tend to have less of an impact on conditioning, and may be perceived as less of a realistic threat. The beginning of Internet gambling poses a greater danger in this respect. It makes gambling almost ubiquitously available and entirely abstract, where money is wagered in credit card accounts.

This is not to suggest that all gambling is an addiction or that gamblers will inevitably become addicted. Many gamblers do so on a budget, and stop before they have exceeded it. Rather, the environmental mismatch perspective provides some explanation as to why the activity is so appealing despite having so many unappealing features. It also sheds light on how a subset of the normal population is more susceptible to its appeal and become pathological gamblers.

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