Hoarding all of the chips: Slot machine gambling and the foraging for coins

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Abstract

Predictions made by the "incentive hope" hypothesis account for overconsumption in unpredictable food environments. However, when applied to uncertain gambling situations, there are several areas where this theory falls short. Most notably, it has trouble explaining why, in slot machine gambling, players are motivated by extended play to spend time trying to resolve uncertainty, rather than hoarding monetary gains.

When food is scarce and unpredictable, animals such as small passerines tend to increase their foraging, caching, and consumption of food, resulting in weight gain. In their interesting article, Anselme & Güntürkün (A&G) argue that this uncertainty-driven rise in motivation is the result of "incentive hope." That uncertainty in the size, frequency, and delay with which food will be encountered enhances the value of the large and immediate rewards that the animal sometimes encounters and instills hope that these large rewards will once again be attained in the near future. The generation of such hope in the face of uncertainty thereby promotes and intensifies food seeking.

A&G argue that although this theory does not replace that of incentive salience, it provides a complement for it and helps explain many of the findings surrounding uncertainty for which incentive salience makes false predictions. Most notably, they argue that the incentive salience hypothesis would predict that increases in motivation seen around conditions of reward uncertainty (Anselme et al. 2013) are the result of some intrinsic attraction for uncertainty itself. However, they point to evidence that in a free-choice task, animals fail to prefer uncertain over certain reward conditions (McDevitt et al. 2016) and can instead be made to choose suboptimally when the less advantageous choice contains conditioned stimuli (CSs) that provide predictive information regarding the outcome of that choice (Stagner & Zentall 2010).

A&G argue that incentive hope is the product of evolutionary pressures for animals to survive in harsh and unpredictable environments, but that like many other evolutionary predispositions, it might be hijacked under changing environmental conditions and result in problematic behaviors including drug addiction, obesity, and disordered gambling. Notably, the overconsumption and hoarding of food seen in animals at risk of starvation could be seen as a precursor to compulsive eating and overconsumption if unpredictability remained (e.g., surrounding economic stability) but the availability and food type (more fat- or sugar-rich foods) changed. Whereas this is a plausible explanation for the growing obesity epidemic, it is somewhat unclear how this would translate to gambling. In the case of animals, unpredictable environments predict the overconsumption and hoarding of food, where food is the unconditioned stimulus (UCS) reward. However, in gambling, one must assume that the UCS is money, especially given A&G's argument that uncertainty in itself is not rewarding. Players would therefore be largely inclined to seek and hoard monetary gain, which might explain behaviors seen in casual gamblers and with lottery ticket gambling, but appears to encounter certain problems when attempting to explain slot machine gambling. For example, incentive hope would suggest that problem gamblers would begin to hoard the monetary reward (e.g., earnings from gambling). However, instead, it appears more and more that as gambling problems develop, what players are hoarding is play itself (Dow Schüll 2012): specifically the ability to remain in the zone and carry on playing (Dixon et al. 2014), which requires spending rather than hoarding of money. Players report spending several hours gambling in front of the same slot machine, and gains are seen as the opportunity to further extend the duration of play rather than the chance to turn a profit. As a result, players might typically end a gambling stretch when they run out of money, rather than when they manage to hoard a large enough economic return. Therefore, in contrast to what might be predicted by incentive hope, the development of a gambling problem suggests a growing motivation to being in contact with and under the influence of uncertainty, rather than generating an urge to diminish and resolve it.

A&G highlight this need to resolve uncertainty by pointing to experiments using contrafreeloading, where animals choose and work harder under unpredictable conditions, because this is the way of countering the adverse effects of uncertainty. The motivation generated through incentive hope is born out of a "need to know" and extract exploitable information from an unpredictable environment. The authors go on to argue that the reason people gamble in casinos is because the venues are similar to autoshaping chambers under uncertain reward conditions, where players are enclosed in an environment in which outcomes are uncertain. Here, A&G seem to assume that, similar to animals in a research lab, humans are confined to the entrails of a casino and have no other choice than to attempt to resolve the uncertainty within as a means to survive or escape. This fails to explain an individual's initial and recurrent motivation to enter and remain within a casino for long stretches of time. If increased motivation is an attempt to counter the adverse effects of uncertainty, and individuals prefer certain over uncertain situations under free choice, it is hard to see how gambling would ever develop as a problem, because the heightened uncertainty of a casino would presumably be avoided when given the choice.

Nonetheless, maybe individuals, as A&G suggest, are not in fact attracted by uncertainty or even by the amount of reward that can be obtained. Instead they are attracted to and track the reliability of CSs – an ability that the authors argue is crucial for survival in the wild. This might explain the increased motivation to gamble generated by the advent of losses disguised as wins (LDWs) in slot machine gambling (Dixon et al. 2010). LDWs occur when players are given the chance to make several small bets on more than one row in a multiline slot machine, creating the possibility for the slot machine to provide an individual with a win (and all its celebratory lights and sounds) that is less than the total amount wagered, making it in effect a loss. Increasing the number and frequency of wins, despite often decreasing their size, would increase the reliability with which certain cues predict a rewarded outcome. This would explain why players report that they prefer games that contain LDWs, and it suggests that in this case incentive hope possesses some predictive validity of its own.

"How Foraging Works": Let's not forget the physiological mechanisms of energy balance

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Abstract

Anselme & Güntürkün propose a novel mechanism to explain the increase in foraging motivation when experiencing an unpredictable food supply. However, the physiological mechanisms that maintain energy homeostasis already control foraging intensity in response to changes in energy balance. Therefore, unpredictability may just be one of many factors that feeds into the same dopaminergic "wanting" system to control foraging intensity.

We agree wholeheartedly with Anselme & Güntürkün (A&G) that it is important not only to understand the functional explanation for why animals should gain more weight (carry more fat reserves) when food is unpredictable, but also to understand the mechanisms that drive this phenomenon. In the target article, A&G try to bring together functional explanations from behavioural ecology with the mechanistic explanations from behavioural psychology and behavioural neuroscience. Specifically, they speculate about a novel mechanism that they call "incentive hope," which works alongside (and interacts with) the well-established "incentive salience" mechanism, which they equate with the "wanting" system *sensu* Berridge (Fig. 2 in the target article; Berridge et al. 2010). This "wanting" mechanism is physiologically represented by the dopaminergic innervation of the nucleus accumbens (NAc) by the ventral tegmental area (VTA). The implication of this proposed mechanism is that the increased foraging that leads to increased eating, increased fat reserves, and, in some species, increased food hoarding (a "seeking" response), only occurs once the incentive hope system is activated but not following activation of the "wanting" system alone.

We believe that the wanting system is broader than A&G propose, with a complex interplay of factors that influence it. Berridge et al. (2010, p. 47) stated that the wanting system is activated "when a food cue is encountered in a mesolimbically primed state (*or if cues are vividly imagined then*)" (emphasis added). Clearly, "wanting" can be activated to search for food, not just in the presence of food. This is also how the late Jaak Panksepp conceptualized the same system, which he called the SEEKING system (his capitalization), which drives intensive exploration and searching for resources upon release of dopamine in the NAc (Alcaro & Panksepp 2011; Ikemoto & Panksepp 1999). This implies that the wanting system can be activated in the absence of direct food cues, which leads to active searching for said food (and, indeed, active searching for other resources, such as sexual partners, water, and even a way to escape danger). Therefore, the wanting system, as typically conceptualized, controls not only the consummatory, but also the appetitive, phase of feeding behaviour, in other words, foraging itself.

Indeed, situations other than unpredictable foraging success lead to an increase in foraging, eating, and hoarding. In particular, food restriction or food deprivation leads to increased foraging and hoarding in hamsters (Bartness & Clein 1994; Keen-Rhinehart et al. 2010). This response seems to be initiated by homeostatic regulatory hormones and neuropeptides. Experimental peripheral administration of leptin decreases foraging and hoarding in both hamsters (Buckley & Schneider 2003) and titmice (Henderson et al. 2018). Leptin and insulin also directly inhibit the VTA, while ghrelin, an appetite-stimulating hormone in mammals, activates it (Palmiter 2007). In hamsters, at least, we also know that intracerebroventricular injection of the hypothalamic neuropeptides – agouti-related protein (AgRP) and neuropeptide Y (NPY) – increases food intake, foraging, and hoarding (Day & Bartness 2004; Teubner et al. 2012), but at different timescales. Whereas NPY seems to respond to short-term food shortages and induce immediate, but relatively short-lived, increases in foraging and hoarding, AgRP is more responsive to chronic food restriction and leads to much longer-lasting changes in foraging and hoarding (Thomas & Xue 2017) of the kind one would expect to occur in small birds when confronted with ongoing winter conditions. Indeed, AgRP neurons reduce their activity the moment food is detected (Ferrario et al. 2016), while activation of AgRP neurons in the absence of food leads to clear foraging behaviours (Dietrich et al. 2015). Less is known about the role of AgRP and NPY in foraging in wild birds. However, in birds in general these neuropeptides show strong evolutionary conservation with mammals in terms of their amino acid sequences, the neuroanatomical arrangement of the neurons synthesising them in the hypothalamus, and the sensitivity of their gene expression to nutritional state (Boswell & Dunn 2017). In red junglefowl, as in rodents, AgRP expression is more sensitive to chronic food restriction, whereas NPY is more responsive to acute food restriction (Lees et al. 2017), suggesting that the same dichotomy may exist in birds as well.

Therefore, when we return to Figure 2 in the target article, "physiological deprivation" does not just lead to increased consumption. Chronic food deprivation, signalled in mammals through respective decreases and increases in circulating concentrations of the metabolic hormones leptin and ghrelin, leads to increased AgRP synthesis, secretion, and neuronal activity, which controls foraging behaviour. It is very likely that this increased foraging driven by AgRP is, in turn, at least in part regulated by the mesotelencephalic dopamine system (Dietrich et al. 2012; Roseberry et al. 2015). The wanting system is therefore enough to mediate these effects on appetitive behaviours without the addition of a new motivational system to the model.

So what is going on under unpredictable foraging conditions? Firstly, we agree with A&G that unpredictability is likely to lead to