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How foraging works: Uncertainty magnifies food-seeking motivation

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Abstract

Food uncertainty has the effect of invigorating food-related responses. Psychologists have noted that mammals and birds respond more to a conditioned stimulus that unreliably predicts food delivery, and ecologists have shown that animals (especially small passerines) consume and/or hoard more food and can get fatter when access to that resource is unpredictable. Are these phenomena related? We think they are. Psychologists have proposed several mechanistic interpretations, while ecologists have suggested a functional interpretation: The effect of unpredictability on fat reserves and hoarding behavior is an evolutionary strategy acting against the risk of starvation when food is in short supply. Both perspectives are complementary, and we argue that the psychology of incentive motivational processes can shed some light on the causal mechanisms leading animals to seek and consume more food under uncertainty in the wild. Our theoretical approach is in agreement with neuroscientific data relating to the role of dopamine, a neurotransmitter strongly involved in incentive motivation, and its plausibility has received some explanatory and predictive value with respect to Pavlovian phenomena. Overall, we argue that the occasional and unavoidable absence of food rewards has motivational effects (called *incentive hope*) that facilitate foraging effort. We show that this hypothesis is computationally tenable, leading foragers in an unpredictable environment to consume more food items and to have higher long-term energy storage than foragers in a predictable environment.

1. Introduction

To explain animal behavior, functional but also causal interpretations are necessary (Tinbergen 1963). The former attempts to determine *why* (for which survival or reproductive purpose) specific actions are performed, while the latter tries to determine *how* (by which biological and psychological mechanisms) those specific actions are performed. In this article, we examine the counterintuitive, though well-documented, evidence that individuals (at least in birds and mammals, including humans) exposed to unpredictable food supplies have higher fat reserves and/or cache more food items than individuals exposed to predictable food supplies. We show that the evolutionary origin (the *why*) of that phenomenon is quite well understood, but that the causal mechanisms (the *how*) contributing to increase fat reserves or to stimulate hoarding behavior remain largely unquestioned and therefore unknown (Pravosudov 2007). Here, we suggest a causal theory inspired from psychology and neuroscience to explain the mechanisms leading food unpredictability to enhance food seeking, a behavior that may enable animals to find more food items and hence to get fatter or to cache more items when the available amounts of food remain sufficient (e.g., Pravosudov 2003). Our causal mechanism is viewed as an adaptive consequence of the selective pressures (notably starvation and predation risks) that justify the functional interpretation put forward by behavioral ecologists. Importantly, this inquiry has the potential to also uncover processes that may underpin apparently unrelated behaviors such as drug addiction (Robinson & Berridge 1993), pathological gambling (e.g., Linnet et al. 2012), and obesity problems (Nettle et al. 2017).

The words *uncertainty* and *unpredictability* are used interchangeably and simply mean that a trial (or attempt to get food) is rewarded or nonrewarded on a random basis in a specific environment, independent of the proportion of time spent in that environment relative to another environment. An animal may experience uncertainty over repeated sessions in a Skinner box, a situation in which the exact same number of rewarded and nonrewarded trials occurs on each session. In nature, not all foraging bouts (or sessions) are likely to be similarly rewarded, especially when food is scarce. Some foraging bouts may be unsuccessful because of unfavorable meteorological conditions, whereas others are more profitable. But overall, the animal also experiences uncertainty over repeated foraging bouts in the environment in which it is used to seeking food. In all cases, uncertainty or unpredictability results in this

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simple – but crucial – effect: *the individual's inability to predict whether the next foraging trial in a given environment will be rewarded or not*. The goal of this article is to describe how organisms psychologically deal with such an absence of predictive control at the trial level, in a way that fits the functional perspective on behavior.

In behavioral ecology, hundreds of publications report that animals, like small passerines and rodents, as well as humans, accumulate more fat reserves and/or hoard more food items when their food sources are unpredictable, that is, hard to obtain and sometimes unavailable (e.g., Bauer et al. 2011; Brodin 2007; Cresswell 2003; Cuthill et al. 1997; Ekman & Hake 1990; Foster et al. 2006; Gosler 1996; Hurly 1992; Lilliendahl 1998; Lundberg 1985; MacLeod et al. 2007; Nettle et al. 2017; Polo & Bautista 2006; Pravosudov 2003; Pravosudov & Grubb 1997; Pravosudov & Lucas 2000; Ratikainen & Wright 2013; Rogers 1987; Witter & Swaddle 1995). Functionally, this phenomenon acts as insurance against starvation, because temporarily inaccessible food items prevent animals from meeting their daily budget requirements. For example, Hake (1996) found that greenfinches (*Carduelis chloris*) with low social status carried larger body masses than higher-ranked individuals. This occurred because dominant individuals prevented them from accessing the most predictable food sites, increasing the risk of famine among subordinate individuals. If bad weather conditions increased that risk for dominants as well, they could temporarily put on more fat than subordinates. Extra fat plays a crucial role for survival. Fatter great tits (*Parus major*), for example, have a better survival rate than leaner individuals in the absence of beech mast during winter (Gosler 1996). Hoarding behavior also provides insurance against starvation, with the advantage of external storage of food. Thus, the animal avoids the costs associated with fattening, such as a higher predation risk (Witter & Cuthill 1993).

In behavioral psychology, unpredictability has not been shown to increase fat reserves, but is known to increase responding to conditioned stimuli (CSs). Specifically, a CS unreliably followed by food delivery often generates higher response rates than a CS reliably followed by food delivery (e.g., Amsel et al. 1964; Anselme et al. 2013; Boakes 1977; Collins et al. 1983; Gibbon et al. 1980; Gottlieb 2004; Robinson et al. 2014). Several mechanisms have been proposed to explain this effect at a causal level (Anselme 2015a; Hug & Amsel 1969; Pearce & Hall 1980), and there is strong evidence that food uncertainty recruits the brain reward system, in particular, the release of dopamine from the midbrain (de Lafuente & Romo 2011; Dreher et al. 2006; Fiorillo et al. 2003; Hart et al. 2015; Preuschoff et al. 2006; Tan & Bullock 2008). Accordingly, higher dopamine levels in the brain enhance the inclination to gamble both in animals and in humans (e.g., Dodd et al. 2005; Johnson et al. 2011; Joutsa et al. 2012; Tremblay et al. 2017). However, no functional perspective on this process has ever been discussed (e.g., Domjan 2005; Hollis 1997). In summary, two distinct research areas describe a similar phenomenon (enhanced responding to signals that food is uncertain), but one (ecology) approaches it from a functional perspective only, whereas the other (psychology) approaches it solely from a causal perspective.

Could the increase in fat reserves or in hoarding behavior observed under harsh environmental conditions (ecology) and the increase in responding to a CS in a Skinner box (psychology) be the consequences of a common underpinning mechanism? We think the answer to this question is *yes*. In this article, we provide a comprehensive review of the literature on the stimulating effects of food unpredictability, both in behavioral ecology and in behavioral psychology. We also discuss some neuroscientific data, because identifying brain correlates may help disentangle distinct mechanistic interpretations. On this basis, we suggest an integrative idea: Psychology and ecology describe the two faces (causal and functional) of the same coin. In other words, enhanced responding to unpredictable CSs in Pavlovian conditioning and the increased fat reserves or increased hoarding in response to unpredictable natural conditions should depend on the same causal mechanisms and therefore have the same functional purpose. From previous theoretical developments, we argue that uncertainty magnifies food-seeking motivation because, in this context, animals not only "want" to obtain rewards (Berridge & Robinson 1998), but also they come to "hope" for those rewards (Anselme 2015a; 2016). The word *wanting* refers to the propensity to approach and physically contact a reward or its predictive CS when available. Wanting is a synonym for incentive motivation. Our central claim is that *incentive hope* is an extension of incentive motivation in situations in which the *wanted* rewards are unguaranteed on a given trial and in which uncertainty cannot be avoided. We argue that the behavioral invigoration or lengthening observed under reward uncertainty reflects a survival requirement rather than so-called preference for uncertainty. How incentive hope is related to incentive motivation is explained, as is its behavioral consequence: increasing the willingness to spend time and effort to seek uncertain rewards – in comparison with certain rewards – and their predictive cues. This mechanism provides a new causal interpretation of how foraging works, bridging the gap between animal foraging (behavioral ecology), sign-tracking behavior (behavioral psychology), and reward motivation (behavioral neuroscience). We show that this mechanism is computationally tenable, enhancing consumption and increasing fat reserves in simulated foragers seeking (pseudo)randomly distributed food items.

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2. Ecology: Food unpredictability increases fat reserves and hoarding behavior

Food unpredictability causes an upregulation of body fat and/or an intensification of hoarding behavior, including humans and nonhuman mammalian species (Foster et al. 2006; Nettle et al. 2017), but most studies have focused on small passerines. For this reason, these bird species will be discussed as priority. Small passerines are characterized by a low body mass (6 g to approximately 100 g). Because of their unfavorable surface/volume ratio, these birds are subjected to a rapid loss of their internal heat when exposed to cold winter days. To maintain it, they have to eat large amounts of food, representing a gain of 7%–12% of their morning body mass (Haftorn 1992). Cold may partly explain why small birds become heavier (Cuthill et al. 2000), although they do not always put on more fat when held under cold temperatures in the laboratory (Helms 1968; King & Farner 1966; Pravosudov & Grubb 1998). The main reason for higher fat storage in winter is that food availability is more unpredictable, increasing the risk of starvation (e.g., Gosler 1996; for a description of the different models, see Brodin 2007). This phenomenon is not specific to winter conditions; it has also been observed in subordinate individuals (e.g., Ekman & Lilliendahl 1993), in individuals exposed to predation risk (MacLeod et al. 2007), and in poor foragers (Cresswell 2003) – whether in the field or in captivity. Importantly, experimental manipulations that make food deprivation unpredictable, independent of temperature and dominance, can also increase fat reserves or food hoarding (e.g., Hurly 1992; Pravosudov & Grubb 1997). This process of fat regulation has also been observed outside the field of behavioral ecology. In humans, words such as *shortfall* and *adversity* lead participants to consume more food items of high-energy value (Laran & Salerno 2013) and to express a desire to eat such items despite their absence and despite any effect on general appetite (Swaffield & Roberts 2015). Interestingly, the mere subjective feeling of lower socioeconomic status relative to others is sufficient to increase food intake and preference for high-calorie foods, irrespective of the absence of objective differences in access to financial resources (Cheon & Hong 2017).

Is food less abundant or of lower energy value in winter, or is it just different (seeds rather than insects) from that found by birds in summer? Often enough, the concept of food unpredictability used by behavioral ecologists is a subjective interpretation based on a human perspective instead of the result of a predictive measurement made in advance. However, we think it is justified. It is likely that the kinds of food available differ between winter and summer, especially with respect to the presence of insects. It is also possible that the seeds collected in winter contain more fat than the insects collected in summer, although the amounts of fat in larval stages can be elevated (up to 60%) in comparison with those in adults (up to 15%; Kouřimská & Adámková 2016). But seeds are also present in summer, and certainly in greater amounts than in winter. Thus, the energy value of food may be similar in winter and summer, but the opportunities to become fatter in winter are reduced because the kinds of food available (insects and seeds) are less abundant.

Of course, fattening in a harsh, unpredictable, or unsafe environment implies that food is present in sufficient amount. For example, food insecurity in humans is associated with obesity only in high-income countries. In low-income countries, food-insecure people want to be fatter but cannot get the calories to put on weight (Nettle et al. 2017). However, "in sufficient amount" does not mean that it can easily be found (see sect. 2.2). Surviving a harsh, unpredictable, or unsafe environment implies that animals cannot reject opportunities to eat to minimize the risk of starvation – despite increased risk of predation. Indeed, fatter birds are exposed to a higher predation risk because they are slower and less agile in response to attacks (e.g., Gosler et al. 1995; Houston et al. 1993; King & Farner 1966; Krams 2000; Kullberg et al. 1996; Lehikoinen 1987; Lima 1986; McNamara & Houston 1990). In contrast, surviving a rich, predictable, or safe environment implies that animals reject opportunities to eat to minimize the risk of predation (and other risk factors related to injury, reproduction, and so forth; see Witter & Cuthill 1993) because there is no risk of starvation.

2.1. Fattening: A multifactorial process

Climate, seasonality, and body size all affect fat regulation in unpredictable environments. In large passerine birds exposed to temperate climates, such as crows (*Corvus corone*) and magpies (*Pica pica*), there is a loss of – rather than a gain in – body mass when environmental conditions are unpredictable (Acquarone et al. 2002; Cucco et al. 2002). Indeed, their fat reserves are a longer-term insurance against starvation compared with smaller passerine birds; food unpredictability does not constitute an immediate danger (see Abreu & Kacelnik 1999; Orduna & Bouzas 2004). But not all situations make larger birds indifferent to unpredictability. Corvid species living at higher latitudes, like the Siberian jay (*Perisoreus infaustus*), are fatter when food is unpredictable (Ratikainen & Wright 2013). This result suggests that corvid species that live and have evolved in temperate regions have no need to increase body fat under food unpredictability, because they are large and can survive without food for a while. But if similar sized birds live and have evolved in colder regions, they are likely to put on weight under food unpredictability. It is also worth noting that crows and magpies were studied in spring (Italy), when temperature and day length were increasing, whereas jays were studied early in autumn (northern Sweden), when temperature and day length were decreasing. Such seasonal and geographical differences may contribute to generate distinct patterns of fat regulation among corvid species, as observed for food hoarding in parids (Pravosudov 2006). To summarize, putting on more fat reserves under harsh environmental conditions seems to be a general rule for both avian and mammalian species. But the surface/volume ratio of the individuals and the environment in which their species has evolved together determine the degree of harshness of the environment.

2.2. The origins of fat deposition

There is good evidence that the increase in body mass under food unpredictability is essentially due to fat deposits in small passerines (Cornelius et al. 2017; Gosler 1996). But the mechanisms underpinning fat production have remained largely unquestioned (Pravosudov 2007), essentially because functional models can fruitfully predict the dynamics of fat regulation (Sherry & Mitchell 2007). Identifying the causal mechanisms that control foraging decisions is necessary to understand how foraging works (e.g., McNamara & Houston 2009; Pravosudov & Smulders 2010; Shapiro et al. 2008; Stephens 2008).

Counterintuitive, but reasonable, is the hypothesis that fat reserves increase because birds eat more when their access to food is unpredictable. Some studies reported increased consumption in harsh environments (Bauer et al. 2011; Dolnik 1967; Haftorn 1976; King & Farner 1965; Pravosudov 2003; Pravosudov & Grubb 1997; van Balen 1980). But other studies reported that fattening can occur independently of food consumption (Bednekoff & Krebs 1995; Cornelius et al. 2017;

Cuthill et al. 2000; Dall & Witter 1998; Fokidis et al. 2012), suggesting that other factors, such as environment-induced changes in metabolic rates, can play a role in fat production. Small birds can decrease their metabolic rate notably by reducing body temperature and general activity (e.g., Carpenter & Hixon 1988; Dall & Witter 1998; Pravosudov & Grubb 1997).

The fact that fat deposition does not always result from increased food intake in an unpredictable environment does not, however, mean that animals can be lazy, seeking food unfrequently. The risk of starvation is real. Small birds have to seek food items more intensively and/or for longer durations, because locating them is a difficult task (Lovette & Holmes 1995; for studies of other species, see, e.g., Daunt et al. 2006; Hiraldo & Donázar 1990; Kramer & Weary 1991; Shettleworth et al. 1988; Tamms 1987). As already shown, in some species, the individuals may limit their immediate consumption and cache most items for later use (Bartness et al. 2011; Cabanac & Swiergiel 1989; Hurly 1992; Lucas 1994; Pravosudov 2003; Shettleworth et al. 1995). But, whatever the strategy used, food unpredictability boosts foraging activity – with the potential consequence of increasing consumption when food is present in sufficient amounts.

3. Psychology and neuroscience: Food unpredictability promotes seeking behavior

In psychology, the invigorating effects of food unpredictability on behavior have long been noted. Here, we review the main findings obtained in some Pavlovian (autoshaping) and instrumental (free choice) procedures, and we discuss their traditional causal interpretations.

3.1. Sign-tracking, motivation, and dopamine

In Pavlovian autoshaping, an animal learns that a conditioned stimulus (CS) is predictive of the delivery of an unconditioned stimulus (UCS), such as food. Briefly, a CS is presented for a few seconds, and its termination is immediately followed by limited access to food. The animal is rewarded on every trial, whatever it actually does. What the animal does during the CS presentations is a measure of its learning and motivation to react to the CS. When a physical interaction with the CS is possible (e.g., a lever or a key, as opposed to a light or a sound), two distinct phenotypes emerge in the responses produced (Beckmann & Chow 2015; Meyer et al. 2014). Some individuals come to approach and interact vigorously with the CS when it is available (rats press and nibble a lever and pigeons peck at an illuminated key) – they are called sign-trackers (Hearst & Jenkins 1974). In contrast, other individuals come to approach and interact vigorously with the food dish during the CS presentations – they are called goal-trackers (Boakes 1977).

These intraspecific phenotype differences reflect individual brain differences, particularly with respect to the release of dopamine in the nucleus accumbens. The nucleus accumbens is a mesolimbic structure that receives part of the dopamine produced by the ventral tegmental area, which is located in the midbrain. It is homologous in mammals and birds, deriving from a common ancestor that lived more than 300 million years ago (Durstewitz et al. 1999; Reiner et al. 2004). Sign-trackers release more dopamine in the nucleus accumbens than do goal-trackers (Flagel et al. 2007; 2011a; 2011b). Because dopamine in the nucleus accumbens is known to control the motivational salience of rewards and their CSs (Berridge 2007; Berridge & Robinson 1998), sign-trackers appear to "want" rewards more than goal-trackers, causing a greater attractiveness ("wanting") of their CSs as well (e.g., Blaiss & Janak 2009; Day et al. 2006; Meyer et al. 2012; Robinson & Berridge 2013; Rose et al. 2013; Saunders & Robinson 2012; Tindell et al. 2009). The differences between sign- and goal-trackers are basically unrelated to the question of uncertainty processing, but we will show that they are important in understanding the mechanism underlying an animal's responses to reward uncertainty (e.g., Anselme et al. 2013; Gottlieb 2005).

3.2. Sign-tracking and uncertainty

Since the work of Amsel and Roussel (1952), psychologists have found that Pavlovian responses are magnified when cues are unreliable predictors of reward. In Pavlovian autoshaping, sign-tracking often comes to reach a higher asymptotic level when a CS is unsystematically followed by a UCS than when a CS is always followed by a UCS (Amsel et al. 1964; Anselme et al. 2013; Boakes 1977; Collins et al. 1983; Crawford et al. 1985; Gibbon et al. 1980; Gottlieb 2004; 2006; Robinson et al. 2014; 2015; Swan & Pearce 1987; Torres et al. 2016). The effect is easy to replicate, although some studies failed to obtain it (e.g., Papini & Overmier 1984; 1985; Rescorla 1999). These results suggest that animals unconsciously learn an averaged pattern from their past experience to represent the predictive accuracy of the CS, as an artificial neural network could do (Bechtel & Abrahamsen 1991). At the session level, a 50% chance of reward appears to be a probability value without any particularity, and nothing of interest could be predicted with respect to response rates. But at the trial level, a 50% chance of reward means that the individual cannot expect rewards more than non-rewards; uncertainty is maximal with respect to a specific CS. Animals seem to use this information to control the strength of their sign-tracking responses on the next trial. But which psychological process can account for this effect? At first sight, the elevated asymptotic performance under uncertainty is difficult to explain in terms of incentive salience: Why would animals be more motivated to approach and interact with a CS that fails to predict food on each trial? Several causal mechanisms have been proposed to account for this effect. These explanations invoke mechanisms of frustration, attention, or motivation. We now dwell on these hypotheses and argue that the motivational perspective is the best option to fully account for sign-tracking responses under partial reinforcement.

3.2.1. Frustration

An influential view is frustration theory (Amsel 1958). Frustration is assumed to develop when there is a violation of an expected reward and to produce some behavioral reactions to the absence of reward (Amsel 1958; 1992). Initially directed to the food dish (unconditioned frustration), frustration can be learned and directed to the CS (conditioned frustration). Here, a frustration drive develops and magnifies the dominant responses, for example, sign-tracking. Over training, conditioned frustration can then be gradually counterconditioned by the occasional delivery of reward, a process known to convert avoidance into approach behavior. In this section, we are not criticizing frustration theory as such, but only its prediction that enhanced responding under uncertainty would result from the frustration drive or from the counterconditioning of conditioned frustration. First, we think that reward uncertainty does not make room for a frustration drive to develop. Experiencing frustration involves the violation of a strong expectation, as in extinction and successive negative contrast, in which the amount or concentration of an expected reward is suddenly decreased. However, there is no strong expectation under a 50% probability of reinforcement, because, as noted earlier, reward cannot be expected more than non-reward on each trial (Anselme 2015a). Second, this theory does not clearly tell us how counterconditioning could increase partially reinforced responses at a higher level than the continuously reinforced responses. Counterconditioning can eliminate ("counter") the frustration associated with the anticipation of non-rewards. But counterconditioning does not provide "extra fuel" to boost performance when avoidance is reduced to zero, that is, when partially reinforced individuals come to respond like continuously reinforced individuals. Torres et al. (2016) found that massive lesions of the dorsomedial striatum eliminate the higher asymptotic performance under uncertainty, but have no effect on performance in extinction or after successive negative contrast. This result suggests that reward uncertainty is processed differently from reward omission and reward devaluation, which are more likely to result in frustration experience.

3.2.2. Attention

Another important theory of the behavioral effects of reward uncertainty is that unreliable CSs attract attention more than reliable CSs (Pearce & Hall 1980; Pearce et al. 1982). An orienting attentional response occurs when the actual outcome does not fit the expected outcome, in order to favor learning. This view has been supported by a number of findings (e.g., Collins et al. 1983; Kaye & Pearce 1984), and we are not trying to call it into question. But we think that the attentional response is a correlate rather than the cause of enhanced behavioral responses. In their model, Pearce et al. (1982) suggested that sign-tracking is controlled not only by the associative strength of a CS with a UCS, which is lower under uncertainty, but also by an orienting attentional response, supposed to be higher under uncertainty. The combination of the two processes is hypothesized to increase performance with unreliable CSs. A weak point of the theory is that it does not tell us how associative strength and the orienting response interact to control sign-tracking, so that whether the orienting response is sufficient to compensate for the decreased associative strength resulting from reward uncertainty cannot be predicted (Collins & Pearce 1985). Another problem is the difficulty in understanding how (and why) attention itself should influence behavior. Although attention has a focus, it is a nonspecific process in the sense that attention can be allocated to any stimulus – whether it is appetitive or aversive. Therefore, how could the same nonspecific attentional process explain, for example, that animals approach and interact with a CS+ (rewarded), while leading them away from a CS– (nonrewarded)? Uncertainty is likely to recruit attention more intensely than certainty, but we think that attentional arousal in this context can only be the consequence of a more basic process capable of explaining both the directedness and the strength of behavioral responses.

3.2.3. Evidence for a motivational process

Some findings suggest that the "basic process" in question is related to incentive motivation. For example, rats trained under reward uncertainty will sign-track on a lever CS located at a longer distance from the food dish than rats trained under reward certainty, suggesting that the CS has acquired a higher motivational salience (Robinson et al. 2014). The uncertainty effect on asymptotic performance is maintained, even after reducing the uncertainty level to which the rats were initially exposed, suggesting that uncertainty sensitizes the brain reward circuit in a similar way to dopaminergic drugs (Robinson et al. 2014). Such a long-lasting effect of uncertainty training was also observed after changing the initially trained CS or the initially trained reward contingency from uncertainty to certainty (Gottlieb 2006). Accordingly, reward uncertainty generates a larger number of sign-trackers and stronger sign-tracking responses than reward certainty, and elevates sign-tracking in a similar fashion to amphetamine, a dopamine agonist-like drug (Robinson et al. 2015). Also, uncertainty and dopamine have facilitating effects on each other in behavioral tasks (Singer et al. 2012; Zack et al. 2014). In addition to these behavioral facts, it is worth noting that many neurophysiological studies reveal that mesolimbic dopamine release is higher when the unreliability of a CS is maximal (de Lafuente & Romo 2011; Dreher et al. 2006; Fiorillo et al. 2003; Hart et al. 2015; Preuschoff et al. 2006; Tan & Bullock 2008). The fact that lesions of the dorsomedial striatum – with its abundance of dopamine receptors – specifically cancel the adjustment to reward uncertainty (Torres et al. 2016) may suggest that a motivational process related to incentive salience controls uncertainty processing.

Of course, it is not satisfactory to say that reward uncertainty enhances the motivation to sign-track without providing an original mechanism that is compatible with – though, partly different from – the incentive salience hypothesis. This mechanism is discussed in section 4. Importantly, for instance, we are not trying to suggest that reward uncertainty is attractive in (or sought for) itself. A number of studies indicate that animals may prefer a probabilistic option to a certain option when given a free choice (Belke & Spetch 1994; Dunn & Spetch 1990; Gipson et al. 2009; Laude et al. 2014; Mazur 1991; Pattison et al. 2013; Spetch et al. 1990; Stagner & Zentall 2010; Vasconcelos et al. 2015). But in most of these studies, the animals choose the probabilistic option only if it is associated with reliable CSs in the terminal link (e.g., if the white CS turns red, then 100% chance of reward; if the white CS turns green, then 0% chance of reward) and the surer option with unreliable CSs in the terminal link (e.g., if the white CS turns yellow or blue, then 75% chance of reward; for an excellent review, see McDevitt et al. 2016). Preference is reversed when reward contingencies are reversed, and indifference is shown when the two options contain reliable CSs (Chow et al. 2017; Smith & Zentall 2016). In other words, animals are not attracted by uncertainty or even by the amount of food that can be obtained; they track the reliability of CSs – an ability that is crucial for survival in the wild. Thus, we draw the conclusion that uncertainty-induced motivation in autoshaping cannot be equated with a preference for uncertainty.

Incentive salience is sufficient to explain choice behavior in probabilistic schedules, because animals are simply attracted by design elements with incentive salience – the reliable CSs. However, this view is unlikely to explain "contrafreeloading," the well-documented fact that animals may prefer earned over free food (Inglis et al. 1997). For example, gerbils spend more time foraging and consume more items from a bowl containing 200 seeds mixed with sand than from a bowl containing 1,000 seeds without sand (Forkman 1991; 1993). Here, the earned-food option is not associated with any attractive elements that could motivate preference. In addition, contrafreeloading is more frequent when food deprivation is low, suggesting that more than incentive salience is required to account for it. Current evidence supports the information primacy model (Inglis 1983; Woodworth 1958), which posits that contrafreeloading results from a "need to know" aimed to reduce uncertainty (Inglis et al. 2001). Indeed, contrafreeloading is observed only when the unprofitable/earned-food source is hidden (in sand, under lids, etc.) or changed in location over the trials; if it is visible or unchanged, the more profitable/free food source is preferred (Bean et al. 1999; Forkman 1996; Havelka 1956). Contrafreeloading experiments indicate that animals do not like uncertainty, as also suggested by the incentive hope hypothesis. Here, they choose to work harder in the uncertain option not because it is associated with attractive elements, as in the case of probabilistic choice schedules, but because this is the natural way of countering the adverse effects of uncertainty – similarly to rats trained under partial reinforcement in a Skinner box. Incentive hope for exploitable information might be an appropriate expression to characterize this "need to know."

3.3. Sign-tracking as a predictor of exploratory activity

Animals use various CSs in their environment to predict the presence of food, for example, the holes of earthworms, the odor of fruits, and the sounds of flying insects (e.g., Feenders & Smulders 2011; Heppner 1965; Wenzel 1968). Often enough in nature, however, CSs are only imperfect predictors of food because they may persist long after a potential prey is gone (e.g., earthworms' holes) or because they are associated with an unpalatable or a dangerous prey (e.g., the sound of a flying hornet), causing repeated failures in the attempts to obtain prey.

Can the propensity to sign-track depend on the reliability of CSs? It is reasonable to argue that the more unpredictable the food items, the more sign-tracking behavior makes sense. Indeed, an animal should not reject opportunities to eat in this unfavorable context and should track all potential food sources. This is in accordance with the evidence that more rats become sign-trackers and provide stronger sign-tracking responses under uncertainty (Robinson et al. 2015). Because the motivational salience of a CS is computed independent of its predictive value (e.g., Flagel et al. 2007; Robinson & Berridge 2013; Robinson & Flagel 2009), animals can potentially seek CSs more quickly and/or for longer periods under uncertainty, even if they learned that those CSs are not reliable. If enhanced sign-tracking responses under uncertainty reflect such natural conditions, a positive correlation between the propensity to sign-track and exploratory activity should therefore be expected. Indeed, there is a positive correlation between sign-tracking behavior and novelty place preference (Beckmann et al. 2011), as well as with the propensity to travel in an open field (Dickson et al. 2015). Flagel et al. (2010) reported a strong sign-tracking propensity in rats selectively bred to be high responders (bHRs) to novelty compared with rats selectively bred to be low responders (bLRs). Interestingly, bHRs had a greater density of dopamine D2 receptors in the striatum and showed more spontaneous dopamine release in the core region of the nucleus accumbens than bLRs. In short, sign-tracking as an index of incentive motivation might also be a reliable index of exploratory activity.

We are not aware of any studies analyzing autoshaping-like situations in the wild, although we have provided some evidence that both might be related (see also Suzuki 1986). But autoshaping is in line with a general principle of behavioral ecology that, in nature, food items are encountered sequentially rather than simultaneously (Shapiro et al. 2008; Stephens 2008; Stephens & Krebs 1986). In serial autoshaping, the trials (CS and food delivery) are indeed presented one after the other, interspersed by an intertrial interval. Autoshaping is certainly an oversimplified procedure in many respects (e.g., Stephens & Anderson 2001; Stephens et al. 2004), but Shapiro et al. (2008) found that the best predictive model of foraging performance is achieved by what they call the sequential choice model (see also Freidin et al. 2009; Vasconcelos et al. 2010). Thus, it is predicted that autoshaping measures a real phenomenon and gives us some relevant pictures of animal foraging in the wild.

3.4. The crucial importance of delays for food

Despite the importance of CSs in driving animal behavior, the delays for food are also crucial in determining the ability to survive. When two rewarded options are tested separately (no-choice trials), the option that generates a lower response latency is often that selected preferentially when both are presented simultaneously (choice trials; Shapiro et al. 2008). This means that an animal will attempt to reduce the delay to obtain a "wanted" food item. Similarly, a reward delivered after a short delay is more attractive than the same reward delivered after a longer delay (e.g., Cardinal 2006; Estle et al. 2006; Mazur 1987). According to Mazur (1987), a reward loses attractiveness as a function of the time elapsed between a response and reward delivery (temporal discounting), and this phenomenon can be represented by the hyperbolic equation $v = a/(1 + kd)$, where v is the subjective value of the delayed reward, a is the amount of that reward, k is a slope adjustment factor, and d is the delay value (Fig. 1). The activity of dopamine neurons reflects temporal discounting, with shorter delays being associated with stronger dopamine release (Day et al. 2010; Hariri et al. 2006; Kobayashi & Schultz 2008; Roesch et al. 2007).

When animals are given a choice between a constant-delay and a variable-delay option, they prefer the variable delay (Kacelnik & Bateson 1996), and even an unpredictably variable delay to a predictably variable delay (Bateson & Kacelnik 1997). The reason for that preference is well accounted for by temporal discounting:

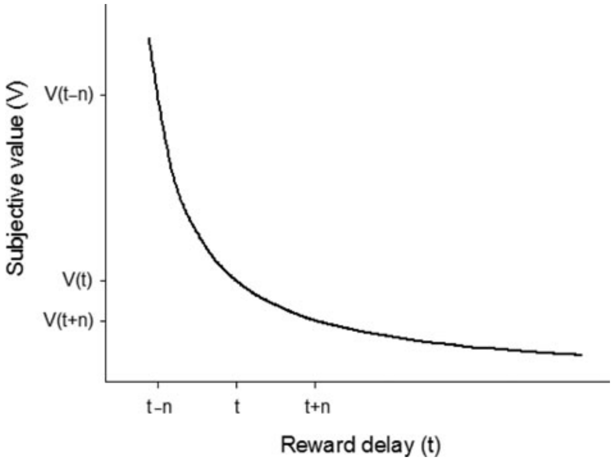

Figure 1. The subjective value V of a delayed reward decreases in a hyperbolic fashion as the delay (or time t) before receiving that reward increases. As a result, a variable-delay schedule (reward after $t - n$ or $t + n$) is preferred over a constant-delay schedule (reward after t) equal to its mean. Here, $V(t)$ is smaller than the mean subjective value between $V(t + n)$ and $V(t - n)$ – a property called *Jensen's inequality* – because of the high attractiveness of immediate or rapid rewards (received at $t - n$) in comparison with more delayed rewards (received at $t + n$).

Variability occasionally allows a quicker delivery of food (Fig. 1). A preference for variability over constancy is also often observed with respect to the ratio of responses to provision of food, an option that potentially combines smaller effort and shorter delay. Some studies even report a preference for variable ratios when variability is associated with lower gains or greater effort than constancy (e.g., Ahearn et al. 1992; Field et al. 1996; Johnson et al. 2011), suggesting that the assessment of delays is of primary importance during foraging. Also, there is more chance for a random-ratio schedule to be preferred to a fixed-ratio schedule if the mean number of responses required for food is elevated (Madden et al. 2005), because in that case, the items quickly received make a clear-cut difference with the fixed option. Dopaminergic drugs may increase the preference for variable-ratio over fixed-ratio schedules (Johnson et al. 2011; see also Anselme et al. 2018), probably because these drugs increase the motivational salience of immediate rewards while having almost no effect on delayed rewards.

Overall, the attractiveness of shorter delays for food is compatible with the incentive salience hypothesis that animals should "want" a quick food item more than a delayed one. In fact, animals always prefer quicker food, even if food delivery is not associated with variability (e.g., Lea 1979). This indicates that variability is not sought for itself. Preference for variable delays is comparable to that of probabilistic outcomes, discussed earlier (sect. 3.2.3), although the event that controls preference is different: In both cases, variability is unimportant as such; animals are just tracking properties that favor their survival (short delay or CS reliability). Functionally, organisms prefer rapid, easy rewards for at least two reasons: (1) They provide energy in case an emergency or a good opportunity occurs, and (2) delayed, costly rewards are less likely to be obtained because of intraspecific and interspecific competition. So, exploiting the immediately available resources is often an optimal strategy, even if those resources are in small amounts. Delays are perhaps even more important than CSs because long delays (scarce food) associated with reliable CSs are likely to imperil survival to a larger extent than short delays (abundant food) associated with unreliable CSs.

4. Uncertainty and food-seeking motivation: Causal and functional implications

We saw that psychologists developed mechanistic (causal) theories that account for behavioral invigoration under reward uncertainty. However, some of those theories have a series of shortcomings, suggesting that they are at best incomplete. In this section, we propose a mechanistic theory, initially restricted to autoshaping situations, to explain the psychological underpinning of this behavioral effect (Anselme 2015a; 2016). We show how it can be extended to natural environmental conditions, with the functional effect of regulating fat reserves and/or hoarding behavior in foraging individuals. Briefly, we argue that increased foraging activity under uncertainty reflects a stronger motivation to seek food. It is assumed that this psychological mechanism (called *incentive hope*) was shaped by natural selection as an insurance against starvation.

4.1. Chronic stress and its motivational correlate

Unpredictable food might be one of the numerous stressors animals encounter in their environment (Gosler 1996; Jenni-Eiermann et al. 2008; Marasco et al. 2015; Pravosudov et al. 2001; Strochlic & Romero 2008). In this section, we briefly discuss the physiology of stress and consider its impact on motivated behavior. Chronic stress activates the hypothalamus-pituitary-adrenocortical (HPA) axis, leading to the increased production of glucocorticoid hormones such as corticosterone and cortisol (Cabib & Puglisi-Allegra 2012). Although some studies failed to show an increase in plasma corticosterone levels in small birds exposed to unpredictable food access (Bauer et al. 2011; Partecke et al. 2006), others established a positive correlation between these two parameters (Jenni-Eiermann et al. 2008; Marasco et al. 2015; Pravosudov 2003; Reneerkens et al. 2002), but changes in body mass were not systematically observed (e.g., Marasco et al. 2015; Reneerkens et al. 2002). Specifically, glucocorticoids contribute to boost foraging activity. For example, corticosterone treatments increase locomotion in a novel – but not in a familiar – environment in rats (Sandi et al. 1996) and extend home ranges in territorial white-crowned sparrows (Breuner 1998). Higher levels of corticosterone speed up exploration in zebra finches (Martins et al. 2007) and facilitate food-caching behavior and food consumption in mountain chickadees (Pravosudov 2003).

In other words, moderate elevation in baseline levels of glucocorticoids relative to food uncertainty might enhance exploratory activity and feeding (Reneerkens et al. 2002). This phenomenon can be understood as stemming from the well-documented fact that glucocorticoids boost dopamine release from the ventral tegmental area (Barrot et al. 2000; Piazza et al. 1996; Rougé-Pont et al. 1998), increasing dopamine levels mainly in the shell region of the nucleus accumbens (Cabib & Puglisi-Allegra 2012). As already discussed, mesolimbic dopamine enhances an individual's incentive motivation (or "wanting") to approach and physically contact rewards and their associated CSs (Berridge & Robinson 1998; Flagel et al. 2007; Robinson & Berridge 2013; Tindell et al. 2009). Given that sign-tracker rats have higher corticosterone levels than individuals for which the CS was unpaired with food delivery (Tomie et al. 2002; 2004), it is conceivable that, rather than glucocorticoids, dopamine pharmacologically controls exploratory activity. Indeed, Piazza et al. (1996) found that peripheral administration of corticosterone increased extracellular concentrations of dopamine and locomotion in rats. These effects were more pronounced during a rewarding activity such as eating and drinking than in the absence of rewards. However, corticosterone-induced locomotion was suppressed following massive lesions of the dopamine neurons in the nucleus accumbens by means of the neurotoxin 6-hydroxydopamine. Accordingly, a number of studies indicate that there is a strong interaction between stress hormones and rewards, including food, sex, and drugs of abuse (e.g., Bronson & Desjardins 1982; Fuller & Snody 1981; Honma et al. 1984; Krieger 1974; Oswald et al. 2005; Peciña et al. 2006). It should also be noted that high-anxiety rats sign-track more under reward uncertainty than their low-anxiety counterparts, and more than high-anxiety rats trained under reward certainty, although dopamine and corticosterone levels have not been measured (Hellberg et al. 2018). Based upon this analysis, we suggest that the motivational consequences of glucocorticoids on dopamine release (rather than stress itself) boost foraging performance. In the next section, we characterize the type of motivation required to potentially increase food consumption and/or food hoarding in unpredictable environments.

4.2. The incentive hope hypothesis

The concept of incentive hope was originally used to explain behavioral invigoration under uncertainty in Pavlovian autoshaping (Anselme 2015a; 2016). But we think that this autoshaping-based effect is only part of the whole story, and therefore the use of this concept should be extended to animal foraging in general. After briefly describing the concept of incentive hope, we show that the uncertainty of food availability in natural environmental conditions may recruit the same brain mechanisms as the probabilistic uncertainty of food in autoshaping.

4.2.1. The concept of incentive hope

In its canonical form, the incentive salience hypothesis does not make any prediction about the effects of reward uncertainty on behavioral performance. Also, if reward uncertainty just increased incentive salience, it should be wrongly predicted that uncertainty is sought for itself and preferred as such over certainty in a concurrent reinforcement task. Thus, a new concept, encompassing (but not reducible to) that of incentive salience, is required to account for the motivational properties of reward uncertainty. Elsewhere, one of us suggested that animals exposed to uncertainty are not only attracted by rewards (as they are under certainty) but, in a sense, also "hope" for their delivery (Anselme 2015a; 2016). Initially, this concept was purely descriptive: Having a motivation for an unguaranteed reward is exactly what hope means. But it is also explanatory and predictive, as shown further. The rationale behind that concept is similar to that behind the concept of "wanting" proposed by Kent Berridge and Terry Robinson in the 1990s. "Wanting" is the core motivational process that controls our conscious desires, except that its occurrence does not involve any knowledge or any subjective feeling (Anselme & Robinson 2016; Berridge 1999; 2007). It denotes what motivation-without-cognition/consciousness is. Accordingly, "wanting" and conscious desires have the same behavioral properties: They lead individuals to approach and contact rewards, as well as their predictive cues. Relying on "wanting," incentive hope is related to conscious hopes in exactly the same way: Organisms exposed to uncertainty behave as if they explicitly hoped for a reward, but for that, they do not have to experience hope in its full psychological (human) sense. Glucocorticoid-induced dopamine release is assumed to be the ground on which incentive hope adds its motivational effects to those of "wanting," causing a faster approach and a more vigorous interaction with the CSs and the rewards, when available. In autoshaping, for example, partial reinforcement increases responding to a CS because animals hope that the trial will be rewarded – in other words, that the CS will be reliable. Incentive hope basically means that an animal is in a state of motivational excitement for possible good news (rewards) when bad news (non-rewards) is likely.

The incentive hope hypothesis focuses on rewards to come, whereas frustration theory focuses on lost rewards. Given that frustration is likely to be a cause of stress, introducing glucocorticoids (a neurobiological marker of stress) as a ground on which incentive hope can develop may appear surprising (see sect. 4.1). However, the two phenomena seem to have distinct effects on dopamine release. Frustration generates some avoidance of the CS, and this should induce a decrease in mesolimbic dopamine levels, as described in rats subjected to a successive negative contrast procedure (Genn et al. 2004; see also Leszczuk & Flaherty 2000). This effect occurs when a strong expectation of reward is violated. But we suggested that non-rewards are processed differently under uncertainty, because there is no strong expectation of rewards on a given trial (see sect. 3.2.1). Many situations in which we experience stress are related to the uncertainty of an outcome (taking an exam, having an appointment, talking in public, having a medical examination, etc.). In those situations, uncertainty is not a source of frustration; instead, we hope for passing the exam, being at the appointed time, giving an interesting talk, having no medical problem, and so forth. Thus, dopamine levels are assumed to increase (rather than decrease) as a motivational consequence of uncertainty (e.g., Fiorillo et al. 2003; Hart et al. 2015). Accordingly, food uncertainty increases glucocorticoid levels (Coover et al. 1984), while stimulating approach behavior (e.g., Anselme et al. 2013; Gottlieb 2004).

Does incentive hope require learning? Detecting some uncertainty in reward distribution requires learning something about reward contingency, just as the attribution of incentive salience to a CS is only possible only if the animal learned to associate its presentation with food delivery (e.g., Fiorillo et al. 2003; Sunsay & Rebec 2008). But what has been learned about an event does not control the strength of approach or even whether the event will be approached; only incentive salience modulates that behavior (Berridge 2012; Robinson & Berridge 2013; Tindell et al. 2009; Zhang et al. 2009). The same is true of incentive hope as a motivational process: Uncertainty-induced dopamine release – a non-learning process in itself – is assumed to be the ground on which incentive hope can develop. Reward uncertainty must somehow be learned, but only the motivational effects of uncertainty (incentive hope) are assumed to modulate foraging activity. In short, we recognize the primary importance of learning in an organism's *ability* to develop incentive hope, but understanding how incentive hope relates to behavioral performance does not require any direct reference to learning mechanisms.

As discussed earlier, it is important to realize that incentive hope does not motivate animals to "want" unpredictable situations; incentive hope only motivates animals to seek food more intensively and/or for longer (to work harder) *when unpredictability is unavoidable,* such as in autoshaping and in real environmental conditions. If unpredictability is avoidable, as in a free-choice task in which an animal must choose between an unreliably signaled 50% and a reliably signaled 100% chance of reward, our hypothesis predicts that the animal will prefer the predictable option – why hope for something unguaranteed if that something can be obtained for sure? (At best, the 50% and 100% options will generate a similar number of responses because of counterconditioning in the 50% option; see Anselme 2016.) As already explained, current evidence supports this view: When variable-delay and probabilistic outcomes are chosen in free-choice tasks, they are chosen for reasons unrelated to their lack of constancy (such as reliable CSs and short delays). Because of this, the concept of incentive hope is fully compatible with optimal foraging theory. Incentive hope is an adaptive process – shaped by natural selection – allowing animals and humans to deal with unavoidable uncertain outcomes, reducing their negative effects on survival through invigoration or lengthening of seeking behavior. Of course, in autoshaping, responding more to an unreliable CS does not allow the animal to collect more rewards. The animal is simply exploiting a behavioral strategy put in place by evolution, urged by the presence of reward uncertainty.

It could be argued that the concepts of incentive hope and prediction error (Schultz 1998) make identical predictions with respect to dopamine release. This is true, but error theory does not predict an increase in conditioned responding under uncertainty, because enhanced dopamine is assumed to reflect incomplete learning (and to inform the brain that more should be learned) rather than to control a motivational process. If dopamine is a teaching/learning signal, animals should perform less under reward uncertainty, as predicted by the Rescorla-Wagner model of learning (Rescorla & Wagner 1972). Finally, incentive hope is likely to recruit brain structures not directly related to incentive salience, such as the dorsomedial striatum (Torres et al. 2016). Although more research is required, incentive hope might be closely related to goal-directed behavior – for the processing that requires the dorsomedial striatum (e.g., Everitt & Robbins 2005; Yin & Knowlton 2006). Such a difference between incentive salience and incentive hope, and their respective brain structures, appears logical: The former process controls simple approach behavior for a goal reward, but the latter process might be involved in the search of a goal reward that is not there. Hope is unnecessary to approach a stimulus, but it may be necessary to seek it (Fig. 2).

4.2.2. Beyond autoshaping: Extending incentive hope to natural context?

Incentive hope is not only about CSs, but also about rewards – just as incentive salience is. So, this process must be sensitive to reward density, a factor possibly more important than CS-related probabilities for animals living in the wild. Here, we are not interested in food density in itself, but rather in one of its major effects: A low density of food makes the variability in delays crucial for survival. When food density is high, the average delay to obtain a reward is short (Fig. 3A). Thus, the risk of starvation is low, and animals are not expected to produce incentive hope for quicker food. In contrast, when food density is low, the average delay to get rewarded is longer, causing a higher risk of starvation (Fig. 3B). Here, any delay shorter than the mean value offers more insurance for survival, so that a foraging individual is expected to develop incentive hope for quicker food. In a sense, a low density of food looks like Pavlovian autoshaping under partial reinforcement, because there is a possible absence of reward (many trials in a foraging bout may be unsuccessful) and uncertainty is unavoidable (no other environmental option exists). An example of food scarcity is the presence of grazing lawns in Africa. Grazing lawns are traditionally believed to be locally abundant and relatively permanent. But they are not permanent. Grazing lawns are predictable in space, but not in time, because the weekly pattern of rainfall is a stochastic process (Bonnet et al. 2010). For this reason, herbivores cannot develop a perfect knowledge of the available resources, delaying food consumption in an unpredictable way. In this context, animals are likely to develop a high motivation for food obtained following short delays.

It is assumed that the unpredictability of short delays when food density is low stimulates food seeking similarly to the probabilistic uncertainty of reward delivery in autoshaping; developing incentive hope for quicker food and CS reliability under a low density of food should therefore lead to an intensification of seeking behavior (leading to a reduction in potential delays and to a track of CS reliability) and to a longer search (increasing the chance that the effort deployed is profitable). Thus, the survival advantages of incentive hope are more visible in natural settings than in autoshaping, where the effort deployed has no functional consequences.

The idea that variability in delays in the wild may produce incentive hope does not contradict the suggestion that variable-delay schedules are preferred to constant-delay schedules because of quicker food delivery in the lab (see sect. 3.4). Incentive hope is not impossible with those schedules (animals may hope for quicker food), but it is less likely because the conditions of its occurrence are not fully met: There is no real uncertainty. The individual is rewarded on each trial, whether the constant or the variable option is chosen. This situation differs not only from natural context, but also from partial reinforcement in autoshaping, where a significant proportion of trials are not rewarded. In most choice schedules, the incentive hope hypothesis is superfluous because it makes the same prediction as the incentive salience hypothesis: Animals prefer variability only if it is associated with relevant properties – whether they hope or do not hope for those properties. A noticeable exception might be contrafreeloading, where animals under low food deprivation work to reduce environmental uncertainty – they seem to hope for exploitable information. But the predictions of the two hypotheses basically differ when variability is unavoidable, as in serial autoshaping and in the wild, because here the incentive salience hypothesis has to presuppose that behavioral invigoration or lengthening is due to the attractiveness of variability. But this contradicts the evidence that, in choice schedules, variability is not attractive in itself (e.g., McDevitt et al. 2016). This means that incentive salience is not fully appropriate to explain behavior when uncertainty is unavoidable. Figure 4 summarizes the conditions maximizing the chance that incentive hope is produced.

As with probability, uncertainty in delays when food density is low might cause some stress in foraging animals, but it also enhances food seeking and food consumption compared with exposure of less motivated individuals to a safe environment. On the assumption that this view is correct, it may have strong functional implications for behavioral ecology. Our view suggests that the low motivation to forage when food is in safe density is an adaptation to remain fast and agile to escape from predatory attacks. By contrast, the higher motivation to forage when food is unpredictable is an adaptation to get the energy required to stay alive. This approach to fat regulation is in agreement with the functional interpretations proposed by behavioral ecologists, while shedding light on the causes that may underpin foraging.

5. Incentive hope can increase fat reserves: Computational evidence

To formalize our theoretical ideas, we developed the computer model of a small bird foraging on bugs in lawns or in clearings. This model had already been used to test the effects of several parameters (handling costs, rest periods, food quality, initial fat reserves, and predation risk), as well as the effects of incentive hope, on food consumption and fat accumulation in a safe and an unpredictable environment (Anselme et al. 2017). This set of simulations showed that a higher motivation to forage can lead foragers to survive longer, increasing food consumption and fat accumulation only within certain limits when the environment is unpredictable. In this article, the model is used to illustrate a point discussed earlier: The fat reserves of highly motivated foragers exposed to an unpredictable access to food will increase only if food is available in sufficient amounts.

In the model, a single forager followed a pseudorandom trajectory at a constant speed in a two-dimensional environment that contained CSs associated with food items UCSs (CSs+) and

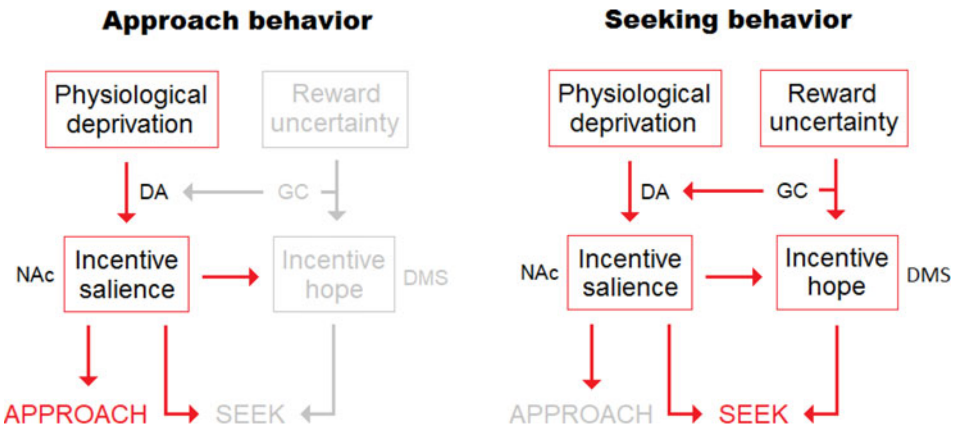

Fig. 2. Interaction between incentive salience ("wanting") and incentive hope. The left side depicts a situation where no uncertainty is present (the food items are predictable or accessible). Approach behavior results from incentive salience processes (involving the release of dopamine in the nucleus accumbens), while seeking behavior remains subactivated and, hence, prevented. The right side represents what happens when the animal is subject to food uncertainty (unpredictable access). The animal comes to produce not only incentive salience, but also incentive hope. Although approach could potentially be produced, its expression is canceled to the detriment of seeking, because the former behavior receives less activation than the latter. Of course, if uncertainty is temporarily abolished, then seeking is prevented and the stimulus is approached. This simple schema suggests that approach and seeking are differently processed while depending on the same motivational basis. It shows how a change in reward uncertainty can mechanically convert approach into seeking, and vice versa. DA = dopamine, GC = glucocorticoids, NAc = nucleus accumbens, DMS = dorsomedial striatum.

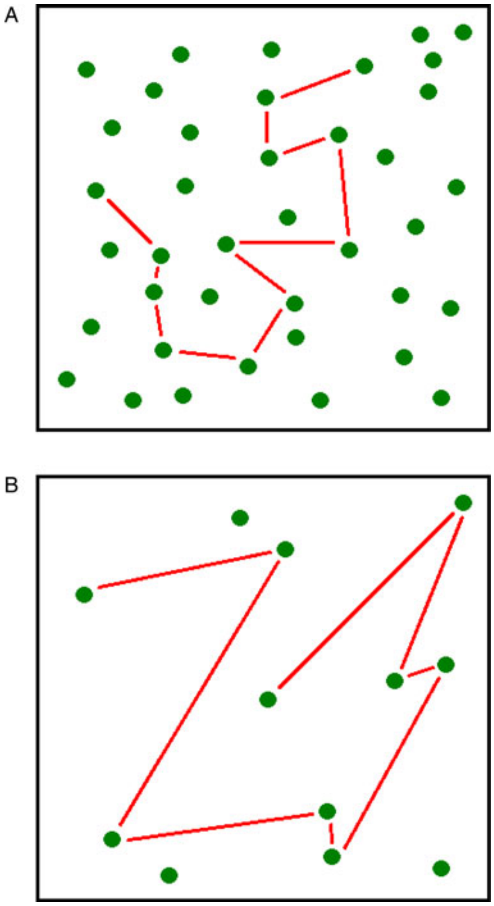

Fig. 3. (A) When food is abundant, there is no risk of starvation because the mean delay (the straight lines) to find edible items is short. (B) When food is scarce, there is a risk of starvation because the mean delay (the straight lines) to find edible items is longer. In such an environment, animals should hope for delays shorter than the mean and act accordingly.

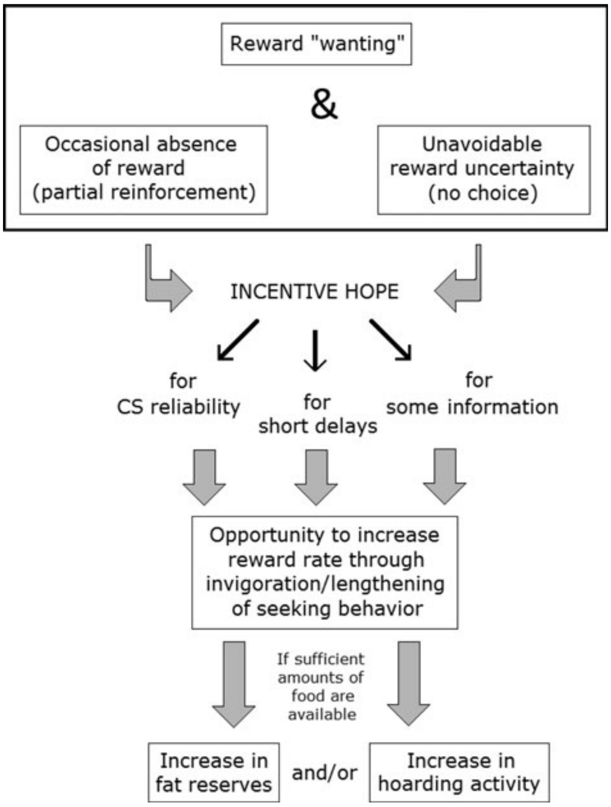

Fig. 4. The incentive hope hypothesis. On top, the three conditions required for the development of incentive hope, which can be shown for different survival-related parameters (especially CS reliability, short delays, and additional information). Incentive hope is believed to increase food-seeking behavior and, when food is in sufficient amounts in the environment, food consumption as well. As a result, the animals seeking food items whose uncertainty is unavoidable have the opportunity to increase their fat reserves and/or to hoard more items. Autoshaping consists of a special case, in which incentive hope is only produced for CS reliability, and the experimental procedure does not allow the animal to increase reward rate. CS = **conditioned stimulus.**

might also contain CSs alone (CSs–). The CSs+ and the CSs– had pseudorandom distributions in the environment, which offered 0.25 million possible locations (500 × 500) –the large majority of which were empty (without CS+ or CS–). The forager was able to detect CSs from a distance shorter than or equal to a detection radius (whose maximal value was fixed in advance) and to approach them with a probability higher than for any other direction once detected (whose maximal value was also fixed in advance). This meant that the forager could locally modify its direction to reach the detected CS. Because of space limitations, we present a nontechnical description here. A full description of the forager's properties (as well as the code used for its implementation) is available as an online supplement.

Briefly, in a safe environment, the forager could encounter some CSs+ while traveling. Environmental safety meant that all of the CSs were fully predictive of food and that there was no risk of starvation – the amount of food UCSs was equivalent to a predefined safety threshold (for details, see the online supplement). A food UCS was consumed when the forager came to occupy the same *x*, *y* coordinates as its CS. A consumed UCS (and its CS) disappeared and a new CS+ reappeared somewhere else in the environment, to maintain food uncertainty and density constant. The energy value of the item was temporarily stored in a short-term storage system ("stomach and gut") and then transferred at a constant rate to a longer-term energy storage system ("fat reserves"). Fat reserves decreased constantly and gradually over time, because of the energy costs related to traveling, but also to prey handling, CS inspection, and rest periods. The energy (fat) level resulting from this trade-off between consumption and energy expenditure controlled the forager's hunger-induced motivation (or "wanting"): High fat reserves caused a low "wanting" value, and lower fat reserves caused a higher "wanting" value. These motivational fluctuations had a direct impact on food seeking through an alteration of CS detectability and approach behavior. "Wanting" had the effect of increasing the forager's detection radius and of increasing the probability of approaching a detected CS; "wanting" increased CS attraction.

In an unpredictable (or unsafe) environment, the CSs+ were pseudorandomly mixed with CSs– and there was a risk of starvation – the amount of food UCSs was lower than the predefined safety threshold (for details, see the online supplement). Contrary to CSs+, which could disappear and reappear anywhere else once inspected and the associated food consumed, the inspected CSs– maintained their pre-inspection location throughout. Because the foragers had a greater risk of energy shortfall here, foraging motivation depended on fat-related "wanting" and also on incentive hope. In the model, incentive hope was a consequence of CS unreliability (a CS might or might not be associated with a food item), delay variability, and food density (see Eq. 4 in the online supplement). Incentive hope magnified the effects of fat-induced "wanting," increasing the forager's detection radius and the probability of approaching a detected CS. Motivational strength had no effect on the forager's traveling speed.

Here, we compared eight foragers seeking food in three distinct environments. First, the *safe* environment contained 800 CSs+ and 0 CSs– (then referred to as S-800). Second, the *moderately unpredictable* environment contained 200 CSs+ and also 200 CSs– (U-200). Third, the *highly unpredictable* environment contained 60 CSs+ and 60 CSs– (U-60). The safety threshold value was 800 in each environment. Thus, relative to the safety threshold of 800 CSs+, the two unpredictable environments were suboptimal in the sense that they contained significantly fewer CSs+ (4 times fewer in U-200 and 13.3 times fewer in U-60) and also contained CSs– that could attract the foragers without providing them additional energy. Each forager traveled a distance of 3,000 steps (one step = distance from one location to the next) in an environment that was 500 steps long and 500 steps wide. Figure 5 represents the portion of each environment traveled by the foragers. As predicted, they explored smaller portions of a safe environment (19%) than of an unpredictable environment (68% in U-200 and 56% in U-60). In doing this, the foragers increased their chance of finding food items, just as real birds travel longer distances to find food in the harsh winter (e.g., Daunt et al. 2006; Hiraldo & Donázar 1990; Lovette & Holmes 1995). All of the foragers were exposed to prey-handling costs and to mass-dependent predation risk (see the online supplement), which could force them to rest at certain times (for additional simulations, see Anselme et al. 2017).

All of the foragers started in the middle of the environment with the same level of fat reserves. Fat reserves remained relatively stable over the 3,000 steps in the S-800 environment, they gradually increased in the U-200 environment, and they gradually decreased in the U-60 environment (Fig. 6A). This result indicates that there was a limit from which food unpredictability could not be adaptively countered, even if moderate decreases in the safe density of food had positive effects on the ability to store fat. In winter, fatter foragers have a higher survival rate than leaner foragers (Gosler 1996), and our simulation was in accord with this fact; in particular, fatter foragers were able to travel a longer distance than leaner foragers in case of a prolonged period of famine (Fig. 6B). Our model revealed that, compared with those in the S-800 environment, the foragers in U-200 stored more fat ($F(1,21) = 23.554$, $p = 0.000$) and consumed more food items ($F(1,21) = 25.645$, $p = 0.000$), while the foragers in U-60 stored less fat ($F(1,21) = 116.972$, $p = 0.000$) and consumed fewer food items ($F(1,21) = 138.093$, $p = 0.000$; Figs 6C and 6D). The effect sizes were very large (fat reserves: $\eta_p^2 = 0.85$; food consumption: $\eta_p^2 = 0.87$). Figure 6E illustrates that a higher motivation to seek food was effective only when the reduced density of food remained within an acceptable range; extreme (probably unrealistic) motivational values could not compensate for a too low density of food. Finally, compared to the foragers in S-800, the foragers in U-200 were more exposed to mass-dependent predation risk and the foragers in U-60 were less exposed (Fig. 6F; U-200: $F(1,21) = 27.378$, $p = 0.000$; U-60: $F(1,21) = 36.786$, $p = 0.000$; $\eta_p^2 = 0.86$). But the energy lost because of the frequent rest periods induced by a higher predation risk did not prevent the foragers in U-200 from consuming more food and accumulating more fat reserves.

By design, motivational strength was systematically higher in the unpredictable environments. What we have tried to demonstrate here is that a higher motivation in an unpredictable environment is theoretically sufficient to allow animals to consume more food and to store more fat reserves than when the environment is safe. This is not a trivial claim because it is not guaranteed in advance that motivation can compensate for a significant reduction in food probability and density. In other words, our simple simulation suggests that interpreting fat regulation in motivational terms is a plausible scenario.

6. Major predictions of the incentive hope hypothesis

Until now, the incentive hope hypothesis has been discussed on the basis of the existing data that may support it. However, the hypothesis can be satisfactory only if it is empirically testable by means of new

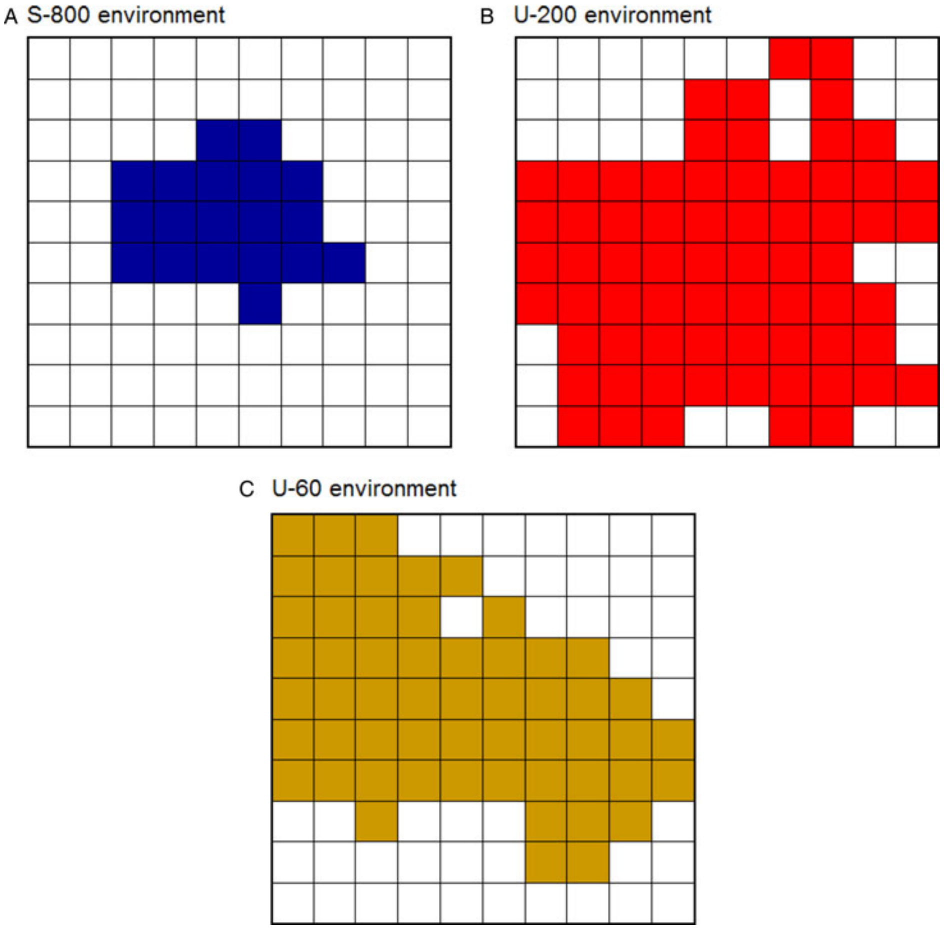

Fig. 5. Portion of an environment traveled depending on its density of food. (A) Safe environment. (B) Moderately unpredictable environment. (C) Highly unpredictable environment. The safe environment was less explored than the two unpredictable environments. In each environment, the colored squares represent the total number of squares crossed by the eight foragers (a square was colored when at least one of the eight foragers entered, and consisted of a surface of 50 steps × 50 steps).

predictions. In this section, we present a few predictions related to autoshaping or based on other methods of investigation, whether they refer to the lab or to the field. The new predictions are contrasted with those from other theories when possible.

1. *The injection of a dopamine antagonist into the dorsomedial striatum should abolish the higher asymptotic response rate under partial reinforcement, but have no effect on (or amplify) the expression of negative contrast.* However, frustration theory predicts that both types of responses (asymptotic rate and negative contrast) are related to frustration, so that a dopamine antagonist should affect them in a similar fashion.
2. *Animals with a higher dopamine release should show higher asymptotic response rates under partial reinforcement and no negative contrast, whereas those whose brains release less dopamine should not evince higher asymptotic response rates under partial reinforcement but should express negative contrast.* Strains of rats that differ motivationally or emotionally could be used here (e.g., Flagel et al. 2010; Sanna et al. 2017). Frustration theory predicts that the two types of responses will be obtained in one strain, but not in the other.
3. *Individuals maintained under unpredictable deprivation periods in their home cage should show a higher break point in a progressive-ratio schedule than individuals that receive constant amounts of the same food every day in their home cage.*
4. *Late in training under partial reinforcement, the increase in responding should be observed whether the previous trial was rewarded or not (because the hope for reward on the next trial is independent of what was received just before).* In contrast, frustration theory predicts that the increase in responding should only occur after a nonrewarded trial (because of frustration drive).
5. *In small passerines, corticosterone-implanted birds should have higher dopamine levels in the nucleus accumbens and increase the intensity and/or the duration of their foraging bouts, compared with saline-implanted birds.*
6. *In small passerines, higher dopamine levels in the nucleus accumbens should boost food consumption and/or food-caching behaviors when the available amounts of food are sufficient.*

These predictions are in keeping with the next priorities in the study of food seeking in animals. There is a vast literature on autoshaping, and a growing number of studies examine the neuronal basis of this process (e.g., Flagel et al. 2011a; 2011b; Hart et al. 2015; Saunders & Robinson 2012; Sunsay & Rebec 2014; Torres et al. 2016). In this context, it is important to test theoretical views that could help understand animal foraging in the wild, especially through an investigation of the neuronal correlates of response invigoration relative to ambiguous CSs. It could also be valuable to determine the behavioral effects that pretraining under uncertainty autoshaping may have on foraging behavior in more realistic ecological conditions. Conversely, understanding the motivational, emotional, and cognitive aspects of animals foraging is paramount (e.g., Bateson & Kacelnik 1995; Cabanac 1992; Dukas & Kamil 2000; McNamara & Houston 1985; Pravosudov & Smulders 2010). These psychological mechanisms must complement, not replace, the

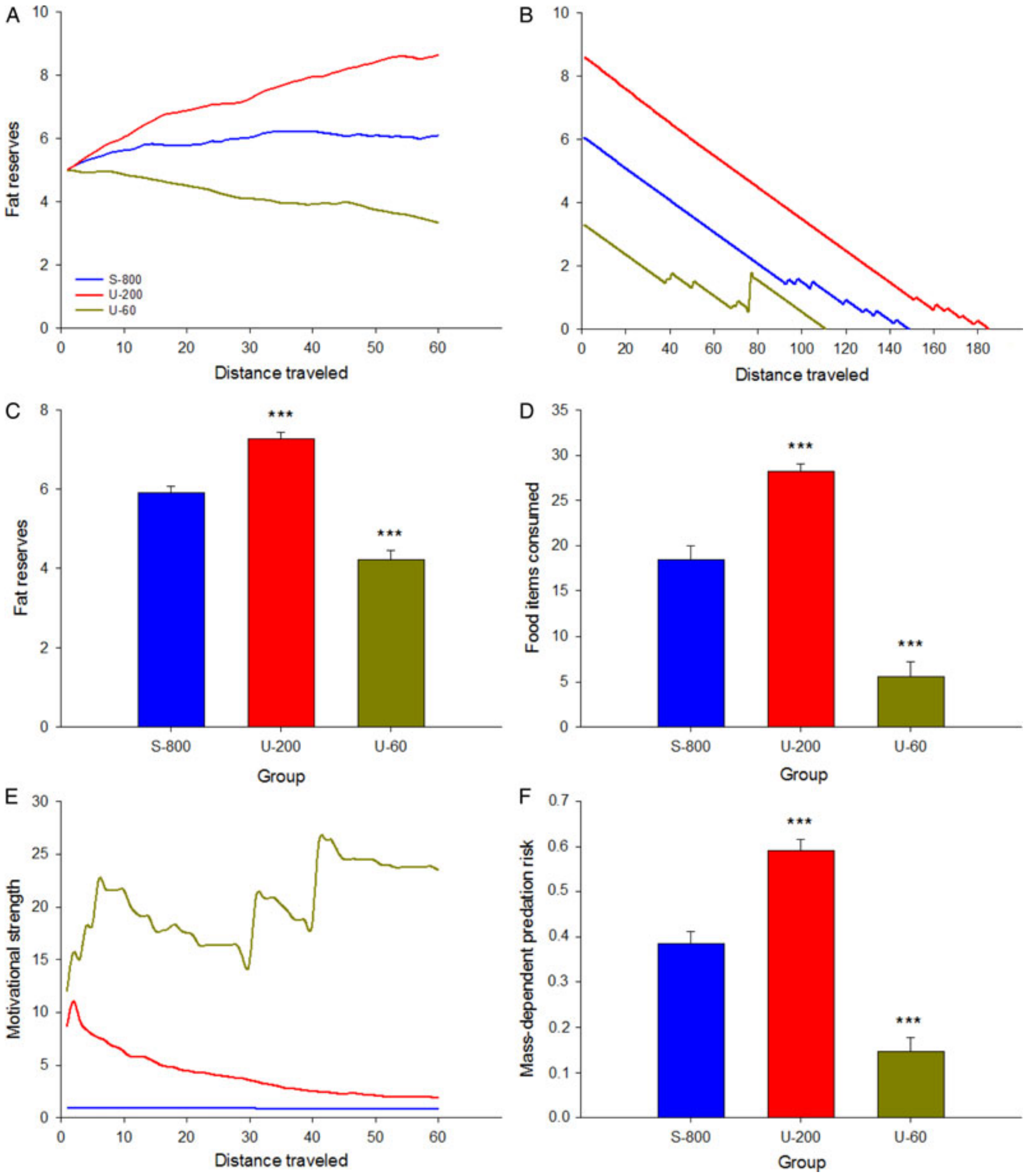

Fig. 6. The beneficial effects of increased food seeking imply that food amounts remain within a biologically acceptable range. (A) Compared with foragers exposed to a safe environment (group S-800), more fat is stored over time in group U-200, but there is a gradual loss of initial fat reserves in group U-60. (B) When food is not available, the ability to survive for longer periods = is proportional to the amount of fat stored. (C) Overall group comparisons indicate that fat reserves were higher in U-200 and lower in U-60 compared with S-800 foragers. (D) The number of food items consumed was higher in U-200 and lower in U-60 compared with S-800 foragers. (E) Motivational strength in seeking food was higher in U-200 than in S-800 foragers, but it even reached a greater intensity in U-60 foragers. (F) Mass-dependent predation risk was higher in U-200 foragers (because they gained weight) and lower in U-60 (because they lost weight) compared with S-800 foragers. Each data point on the abscissa must be multiplied by 50 to obtain the number of steps actually traveled (total: 60 × 50 = 3,000 steps).

functional views suggested by behavioral ecologists and be compatible with the biological findings (e.g., about hormones and fat deposits) revealed by physiologists.

7. Implications of the incentive hope hypothesis

Modern Western societies are very demanding, in terms of both professional successes and social status. The demands are difficult to achieve because many people have to compete for short-term contracts of employment and have salaries that do not always reflect how hard the work is. As a result, successes in life depend partly on chance. This situation strongly contributes to the reasons so many people suffer from stress problems. As shown, stress favors the release of mesolimbic dopamine through an elevation of glucocorticoid levels in rodents (Barrot et al. 2000; Piazza et al. 1996; Rougé-Pont et al. 1998), a process also assumed to occur in birds, and incentive hope could result from utilization of the extra dopamine. We think that this process may help explain a number of pathologies such as drug addiction, problem gambling, and obesity. We show how the causes of uncertain-reward seeking (leading to adaptive responding in nature) may have maladaptive implications beyond the context in which natural selection operated initially, because of the disappearance of their functional relevance.

7.1. Drug addiction

Animal and human research indicates that social and environmental stresses make individuals more vulnerable to the addictive properties of drugs of abuse and also more prone to attribute motivational salience to CSs (Beckmann & Bardo 2012; Diaz et al. 2013; Lomanowska et al. 2011; Nader et al. 2012; Pattison et al. 2013). Also, developmental stress boosts locomotor activity in starlings (O'Hagan et al. 2015), though not their speed to respond to ambiguous stimuli (Bateson et al. 2015). Our view suggests that incentive hope is an adaptation shaped by natural selection to reduce the risk of starvation when food is in short supply. Incentive hope can be a product of evolution because it is effective in the wild, allowing small birds to cache more food and/or to store more fat. The human environment meets the conditions for the recruitment of incentive hope (reward "wanting," occasional failures, and unavoidable uncertainty). But this motivational process may fail to do its job here, because the ability to escape from the stressful contexts is often independent of the individual's willingness to change the situation (e.g., poverty, repeated bad luck, constraining work conditions). A higher sensitivity to drugs of abuse under chronic stress might be a response to the apparent need for more dopamine. Dopamine's stimulating effects may indeed lead to actions and biased perceptions that give the impression of greater opportunities to control the events of one's life. In traditional societies, when shamans fall into a trance after taking some drugs, they call on supernatural powers to solve stressful situations such as curing disease and defeating the enemy. Local people are convinced that this strategy will help them deal with adversity. However, this response turns out to be maladaptive in modern Western society, because most of the problems encountered cannot be "solved" that way: Taking drugs repeatedly often has the effect of degrading (instead of improving) the individual's socio-professional life.

A more effective strategy consists of engaging in activities that reorient attention toward new, stress-free objectives. For example, drug-dependent rats reared in a socially enriched environment and/or an environment that contains opportunities to do various activities significantly reduce their drug consumption and even stop showing neural sensitization of their dopamine neurons (Bardo et al. 2001; Cosgrove et al. 2002; Lespine & Tirelli 2015; Nader et al. 2012; Solinas et al. 2008). The incentive hope hypothesis provides an original view of neural sensitization, which is viewed as an adaptive strategy of the brain to make dopamine neurons more responsive to situations in which stress persists a long time. In a natural context, this process increases the chance of managing those situations, while its "hijacking" to face modern Western-society problems is no longer effective and contributes to the development of addictive behaviors.

7.2. Pathological gambling

The link between human gambling behavior and dopamine release has been empirically established (Joutsa et al. 2012; Linnet et al. 2012), but the causal and functional explanations of this process remain unknown. Like drug addiction, problem gambling may be the consequence of chronic stress in a demanding societal context. For example, electronic gambling machines, which are associated with potentially large payout after a short delay on each trial, are the favorite game of problem gamblers who try to escape stressful situations in their life (Nower & Blaszczynski 2010; van Holst et al. 2010). Compared with non-gamblers, they are not interested in lotteries at all, which involve delaying gratification, and they are strongly motivated to earn additional incomes (Nower & Blaszczynski 2010). They also differ from other categories of gamblers, such as horse racing and casino gamblers, who attempt to replace feelings of boredom with higher levels of arousal (van Holst et al. 2010). In electronic machine gamblers, the gradual sensitization of corticosterone-induced dopamine release over repeated exposure to gambling opportunities should have contributed to the development of incentive hope more than in non-gamblers and occasional gamblers. It is predicted that electronic machine gamblers will report higher hopes for money than non-gamblers and occasional gamblers before a trial or before placing a bet. It is also predicted that hopes will be higher than any negative effects such as frustration and stress. Why do people gamble, then, if, as suggested earlier, uncertainty is not sought for itself? The reason is that casinos act similarly to autoshaping boxes: they consist of a confined environment in which any outcome is uncertain. Such an environment favors incentive hope in vulnerable individuals and hence invigorates and lengthens the propensity to seek (monetary) rewards. The fact that a casino is an artificial environment (just as an autoshaping box is) does not abolish seeking behavior, which is genetically fixed in our mammalian brains – for the same reason, captive passerines may downregulate their fat reserves despite the absence of actual predators (Verdolin 2006). We hypothesize that pathological gambling is the consequence of a behavior that was adaptive for our ancestors (increased reward seeking when the environment was unpredictable) but has ceased to be adaptive in our modern Western societies (Anselme & Robinson 2013).

7.3. Obesity problems

Today, many people suffer from overweight. The genes that control fat storage were also present in our ancestors, but their expression came to be problematic only very recently. The reason is that fat-rich food is cheap and easy to access, allowing people to eat more than they really need (Bodor et al. 2010; Hill & Peters 1998). However, food consumption is also partly associated with food insecurity in women with a low-economic status living in rich countries (Nettle et al. 2017). This means that economic uncertainty (irregular, low incomes) in a demanding society may lead to behaviors that favor the accumulation of fat reserves in humans, as observed in small passerines and other species. Fat accumulation was certainly adaptive in ancestral human societies, in which rich food (meat, honey, etc.) was rare and required a lot of work to be obtained. But this situation leads to overweight in modern humans, for whom junk food can be found at every street corner. Sinha and Jastreboff (2013) pointed out the influence of glucocorticoids and corticotropin-releasing factor (CRF) on dopaminergic transmission, which may increase motivation for highly palatable food and consequently may promote changes in body fat mass (see also Corwin 2011). The incentive hope hypothesis is compatible with this view and provides a theoretical framework to explain the very nature of uncertainty-induced motivation. To reduce its maladaptive consequences, a first direction to follow should be to decrease the risk that people experience adversity in life, for example, through education, employment security, good salaries, and well-being at work. But more practically, having fixed feeding routines should increase the feeling of food security and contribute to maintain appropriate fat reserves (Nettle et al. 2017). A second direction to follow would be to reduce the temptations, which bias the perception of what people really need. For example, the development of local shops – as opposed to large shopping centers – points in this direction.

8. Conclusion

In this article, we argued that fat regulation essentially depends on how much animals are motivated to consume food. In addition, we showed that this mechanistic approach is computationally tenable. The concept of incentive hope may account for the evidence that birds and mammals respond more to reward-related cues in situations in which uncertainty cannot be avoided. Incentive hope is related to incentive motivation, but irreducible to the concept of incentive salience for at least two reasons. First, the incentive salience hypothesis does not capture the motivational effects of reward uncertainty and therefore cannot explain them. Second, if incentive hope was only some additional incentive salience under uncertainty, animals should prefer an uncertain or variable option over a certain or constant option in a free-choice task. But we showed that uncertainty is not attractive in itself. Incentive hope is also different from frustration and prediction error. This new concept may have profound implications for the understanding of animal (and perhaps human) behavior, in the sense that many aspects of reality are uncertain in essence. Nevertheless, more thorough investigations are necessary with respect to the psychology and neuroscience of animal foraging. Outstanding questions might be the following: Does the activity of dopamine neurons sustain the duration and the intensity of foraging? Which are the respective roles of the ventral and dorsomedial striatum in foraging? How do CSs impact foraging? What is the relative importance of CSs and food density in controlling foraging activity?

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Open Peer Commentary

Food seeking and food sharing under uncertainty

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Abstract

We propose an elaboration of Anselme and Güntürkün's research that considers individuals' foraging behavior as part of group efforts to cope with uncertainty. We discuss different possibilities for the interaction between individual and group mechanisms for risk reduction in uncertain environments, and we raise some open questions for future research.

Anselme and Güntürkün (A&G) propose a theoretical model for foraging behavior under uncertain and unpredictable environments that links increased foraging with increased fat and dopamine levels. In this commentary, we elucidate another common strategy used by animals and humans alike in face of environmental uncertainty: the collective strategy, which entails collaborative foraging efforts and food sharing. Previous sociobiological and anthropological studies have shown that food sharing with non-kin is common for both human and non-human societies, from small animals such as vampire bats (Wilkinson 1990; Winterhalder 1986) to apes (de Waal 1989) and human hunter-gatherer societies (Gurven 2004; Gurven et al. 2000).

Researchers have proposed several social benefits of sharing resources, including *costly signaling* (Bleige Bird et al. 2001; Hawkes et al. 2001), and *tolerated theft* (Bird 1997; Blurton Jones 1987). However, the most prominent explanation of the collective strategy is the *social insurance hypothesis*. According to this explanation, by joining groups and sharing foraged outcomes, individuals can benefit from the law of large numbers, thereby decreasing the effect of uncertainty. That is, group members decrease the variability of their individual outcomes by aggregating and distributing the collective foraged amount. This hypothesis is supported by anthropological studies (Gurven 2004; Gurven et al. 2000; Kaplan et al. 1985) and controlled laboratory experiments, which have demonstrated a causal relationship between (monetary) outcome variability and the tendency to join groups (Bone et al. 2004; Charness & Genicot 2009; Kaplan et al. 2012; Suleiman et al. 2015). Suleiman et al. (2015) found that the tendency to share resources in the face of risk existed even in one-stage interactions and was more pronounced when group-joining was framed as a way to avoid losses (as opposed as a way to make gains).

A&G make an important contribution by integrating two separate lines of research on individual risk reduction mechanisms – the psychological and the ecological. Because foraging efforts in small-scale human societies and non-human species are often pursued in groups, we propose to extend A&G's research by considering not only individual risk reduction mechanisms, but also the collective risk-sharing mechanism.

One approach is to view the two mechanisms as mutually exclusive. According to this approach, when faced with environmental uncertainty, individuals make a choice between foraging alone and joining groups to share their foraging outcomes with others. Evidence from experimental studies seems to support this approach. Suleiman et al. (2015) gave participants the choice to participate in a gamble as individuals and gain the gamble's outcome or to join a group of a given size, pool the individual outcomes, and distribute them equally between the group members. A higher percentage of participants chose the group over the solitary gamble, particularly in gambles that were high risk (higher variance). Moreover, when under high risk, participants opted for larger groups over smaller groups, a tendency not observed under low risk. However, in another study, when participants were offered an alternative, individual mechanism for reducing variability (i.e., making multiple gambles) that is equivalent to increased foraging, the tendency to join groups disappeared (Suleiman et al. 2015).

The decision between foraging alone and as a group may depend on the type of resource. The individual strategy discussed in the target article might be optimal for some types of food, while a collective strategy might be optimal for others. Anthropological studies lend support to this conjecture by demonstrating that resources that are shared most among non-kin are those characterized by high outcome variability – such as meat – compared with collected goods, the supply of which is more stable (Gurven et al. 2000; Kaplan et al. 1985). Another factor that may affect the choice of risk-reduction strategy is the level of trust between group members. Jimenez and Pietras (2018) reported that when the probability of reciprocation was low, individuals engaged less in sharing.

Another approach concerning the conjunction of individual and group strategies for risk reduction is that increased individual foraging and collective resource sharing are *complementary* rather than mutually exclusive mechanisms. According to this view, when faced with environmental uncertainty, only *some* members of the group engage in increased foraging and share their outcomes with the rest of the group members. This conjecture could be tested by examining whether the surplus of foraged goods after increased foraging is more likely to be shared (because of group solidarity) or less likely to be shared (because of individual hoarding). In line with A&G's model, which links foraging under uncertainty with *increased* body fat, we expect that increased collective foraging (as part of a sharing effort), as opposed to increased individual foraging, will be associated with a *decrease* or no change in body fat.

Finally, pursuant to A&G's proposal that dopamine levels are correlated with individual motivations for seeking more food under uncertainty, research should address the physiological and neurological correlates of the motivation to form risk-sharing groups and sustain cooperative foraging behavior. Based on previous research, we suggest that food sharing is associated with increase in the level of the neuropeptide oxytocin, which is reported to elicit trust and cooperative behavior in humans (De Dreu et al. 2010; Kosfeld et al. 2005; Madden & Clutton-Brock 2011). Indeed, a recent study reported an increase in urinary levels of oxytocin following food sharing (Wittig et al. 2014).

To summarize, we argue that the theoretical model proposed by A&G and the literature on the social insurance hypothesis can benefit each other by revealing a larger picture of human behavior under environmental uncertainty. Conceptualizing individuals as part of a group could explain not only the amount of foraging, but also the scope and range of foraging by different members in the group.

A neural basis for food foraging in obesity

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Abstract

Poverty-related food insecurity can be viewed as a form of economic and nutritional *uncertainty* that can lead, in some situations, to a desire for more filling and satisfying food. Given the current obesogenic food environment and the nature of the food supply, those food choices could engage a combination of sensory, neurophysiological, and genetic factors as potential determinants of obesity.

The proposed "incentive hope" hypothesis is highly relevant to the global obesity epidemic and its accompanying adverse consequences on population health (GBD 2015 Obesity Collaborators 2017). In the present commentary we expand and bring in alternative views from two perspectives, (a) the socioeconomic perspective and (b) the physiological perspective, including neurological and genetic factors. Both can have a role in the development of obesity.

It is plausible that poverty-related food insecurity represents both economic and nutritional *uncertainty.* Such uncertainty, in some situations, could lead to a desire for more energy-dense, filling, and satisfying foods. The foods' reward value could be mediated by individual genetic programming and variation (Qasim et al. 2018).

Although obesity is far more prevalent among populations with lower education and incomes and living in more deprived neighborhoods, middle-income groups and even high-income groups are not totally spared (Hruby & Hu 2015). In other words, obesity and type 2 diabetes also occur among groups of higher socioeconomic status (SES) where material deprivation or lack of resources to purchase nutritious foods is not at issue (Chan 2016).

This access to economic resources by higher-SES groups removes food uncertainty as understood in the context of the animal studies discussed in the target article (i.e., need to forage or hunt). What does characterize food choices of lower-SES groups is the selection of low-cost foods that are typically rich in energy but can have minimal nutritional value (Pechey et al. 2013). In general, the widespread availability of palatable low-cost, energy-dense foods has been associated with rising obesity rates both in high-income and in low- and middle-income countries and societies. The reward value of energy-dense foods can have a strong neural component.

Preferences for high-energy-density (high-ED) foods are a strong determinant of food choices, mostly linked with fatty and sweet taste preferences present from birth (Chmurzynska & Mlodzik 2017; Mennella & Bobowski 2015). In addition, overconsumption of particularly high-ED foods (e.g., processed, extracaloric snacks, meals, and desserts) could respond to an *evolutionary discordance*, that is, a poor adaptation to detect calories in foods that have a historically unusual (high) ED (Brunstrom et al. 2018). This may be because, as early humans, we adapted to discriminate between low (e.g., plants)- and high (e.g., meat)-ED foods to make foraging more cost-effective, thanks in part to basic taste characteristics. However, in the current *hyper*-caloric food environment, this level of discrimination is not sufficient and leads to the consumption of extra calories (Ziauddeen et al. 2018).

In addition to sensory attributes potentially misleading our food choices, food decisions may be driven by negative processes occurring at the neuropsychological level, ranging from executive function impairment, expressed in deficient inhibition and cognitive inflexibility, to behaviors including implicit motivation and impulsivity (Medic et al. 2016). In the selection of convenient food choices, not only prefrontal regions, but also the neural communication between the lateral hypothalamus and corticostriatal regions determined by the metabolic state, are functionally relevant (Huerta et al. 2014). The dopaminergic system in particular may play a key role in reward-related food intake and with behaviors necessary for feeding to maintain survival (Suzuki et al. 2012), but also with motivation (Salamone et al. 2015) and risk-taking behavior (Arrondo et al. 2015).

These traits, which typically occur in overweight individuals, combined with a "temptations-loaded" food environment, are likely to be determining factors for the development of obesity among higher-SES groups. There is also a higher level of control that is related to keeping long-term goals not found in animals, for example, a concern for body image (Yiu et al. 2017).

Overall, energy homeostasis depends on energy intake and expenditure, which are regulated by exogenous (e.g., food availability and environmental conditions) and endogenous (e.g., there are genes regulating appetite, taste, and olfaction) factors. Furthermore, the neuroendocrine balance is influenced by an individual's genetic variant and polymorphisms, which could produce different responses regarding reward behavior, impulsivity, and instincts related to food-seeking motivation (Martinez et al. 2014; Qasim et al. 2018).

In summary, the incentive hope hypothesis may partially explain some of the consequences of economic and nutrition insecurity on excessive food consumption leading to higher obesity rates. However, the economic insecurity hypothesis is less viable for high-income countries and higher-SES groups. Here, the current obesogenic environment and the associated influences on taste preferences, genetic variation, and neurobehavioral factors are likely to play a more prominent role.

Foraging extends beyond food: Hoarding of mental energy and information seeking in response to uncertainty

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Abstract

When an environment is uncertain, humans and other animals benefit from preparing for and attempting to predict potential outcomes. People respond to uncertainty both by conserving mental energy on tasks unrelated to the source of the uncertainty and by increasing their attentiveness to information related to the uncertainty. This mental hoarding and foraging allow people to prepare in uncertain situations.

Anselme and Güntürkün (A&G) show that uncertainty about food leads to changes in foraging behavior, including more eating, weight gain, and hoarding. We propose that humans also engage in an analogous sort of hoarding of mental energy when confronted with uncertainty. The present commentary draws parallels between the research discussed in A&G's article and research on uncertainty in humans to demonstrate that uncertainty increases conservation of diverse resources and that information seeking extends beyond food.

Conserving mental energy

Previous research has indicated that uncertain individuals avoid expending precious mental energy on situations unrelated to the source of the uncertainty. Participants who were asked to think about an issue about which they were uncertain completed significantly fewer anagrams than participants in a control group (Alquist et al. 2018). Participants who were left uncertain about the kind of music they would soon hear were less likely to choose an educational article to read than participants who knew the kind of music they would hear (Milkman 2012). We also have performed unpublished studies indicating that being uncertain about a potentially bad outcome (might have to give a speech) causes participants to perform more poorly on an unrelated task than being certain of a bad outcome (definitely have to give a speech).

Lack of mental effort in such situations is unlikely to be due to an inability to expend mental effort, but is instead the result of conserving mental effort for future tasks. Muraven et al. (2006) reported that when mental energy is low, participants avoid expending all of their energy on one task to perform better on an anticipated following task. A&G's model demonstrates that fatter animals (who have stored up food) are better able to survive in uncertain environments. Individual differences in people's likelihood of conserving mental energy may similarly predict their success in uncertain circumstances. In the same way that many species respond to food uncertainty by storing additional food, humans also respond to uncertainty more broadly by conserving their mental energy on tasks unrelated to the uncertain situation.

Resolving uncertainty

A&G also discuss research on information seeking in response to food uncertainty. Although people conserve mental energy on tasks that are unrelated to the experienced uncertainty, they may demonstrate increased mental effort and attention toward the source of the uncertainty itself.

A&G's model proposes that although animals will not typically choose an uncertain reward over a certain reward, they are more responsive when rewards are not guaranteed. Research on humans with non-food rewards has also revealed evidence of both a preference against uncertainty and increased attention to uncertainty. When given the choice between a certain and an uncertain situation, even if both are positive, people typically prefer the situation with more certainty surrounding it (Kurtz et al. 2007; Wilson et al. 2005). People even sometimes value a smaller reward of certain value (a lottery for $50) over a reward that could be the same amount or larger (a lottery for $50 or $100; Gneezy et al. 2006; Simonsohn 2009).

Although people do not prefer uncertain situations, they do, however, seem to attend more to uncertain situations over certain situations when the uncertain situation is unavoidable. People remain happier longer if there is some uncertainty surrounding a reward they have received (Kurtz et al. 2007; Wilson et al. 2005). This is due in part to the participants' thinking more and remembering more about the situation when it is uncertain than when it is certain (Wilson et al. 2005). Other research has indicated that when participants are assigned to utter phrases indicative of uncertainty ("I don't get it"), they report greater curiosity than when they are assigned to utter phrases indicative of certainty ("That makes sense"; Bar-Anan et al. 2009). As with finding food in an unpredictable environment, expending effort in uncertain situations may be worthwhile in the service of understanding and predicting the situation better in the future.

A&G provide an excellent overview of the research showing that animals become more reward sensitive and exhibit more hoarding behavior when food is uncertain. Broader uncertainties, such as not knowing what to expect next in a situation, have a less clear path for preparation. Nonetheless, people respond to uncertainty by conserving the mental energy available to them and becoming more sensitive to information related to the source of the uncertainty, fostering a sense of all-purpose preparedness. Such an approach would seemingly maximize one's ability to cope with the impending unknowns.

Full appreciation of uncertainty may require advanced metacognition, at least insofar as one has to recognize the limits and gaps in one's knowledge. Nevertheless, we extrapolate from the combination of human and animal findings to speculate that there may be a broadly adaptive default response to uncertainty: Conserve all resources, and heighten alertness.

Simulating exploration versus exploitation in agent foraging under different environment uncertainties

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Abstract

For artificial agents trading off exploration (food seeking) versus (short-term) exploitation (or consumption), our experiments suggest that uncertainty (interpreted information, theoretically) magnifies food seeking. In more uncertain environments, with food distributed uniformly randomly, exploration appears to be beneficial. In contrast, in biassed (less uncertain) environments, with food concentrated in only one part, exploitation appears to be more advantageous. Agents also appear to do better in biassed environments.

We simulate the behaviour of artificial agents foraging for food in toroidal environments consisting of 400×400 cells, over 10,000 repeated experiments, each consisting of 300 iterations or sequences of observation-action-reward, similar to the architecture described by Chmait et al. (2015; 2016a; 2016b). This number of iterations makes it possible for artificial agents to discover a fraction of the environment space, and therefore this number of iterations models the agents' short-term foraging behaviour. Rewards in the range [0,1] can have different spatial distributions (Fig. 1). A cell reward of 0 indicates unavailability of food in that cell, whereas food density is maximum at 1.

Agents can only see their eight neighbouring cells (equivalently, a Moore's neighbourhood with $n = 1$), allowing for more flexible navigation across the environment in comparison to Anselme & Güntürkün (A&G). In each experiment, agents are initialized with different starting cell positions and evaluated in environments comprising different percentages of food. At any time step, we arbitrarily assume that an agent eats 0.1 worth of reward once it lands on a cell that contains ≥ 0.1 food reward. An agent's score is calculated as its average reward over the 300 iterations. To mimic natural environments, we introduce some stochasticity by allowing environment cells, with a very low probability, to gradually produce or deplete food. When the food resources are uniformly randomly distributed (e.g., Figs. 1a and 1b), the uncertainty of an environment with food distribution probability p will – by symmetry – be equal to that of an environment with food distribution probability $(1 - p)$ (Boulton & Wallace, 1969). As such, we will only experiment with environments with $p \leq 0.5$.

Efficient foraging requires a trade-off between two operations (Bartumeus et al. 2016; Mehlhorn et al. 2015): exploration, which aims to locate resources, and exploitation, which aims to maximize the amount gathered from each resource. These two operations can occur in separate phases (Green et al. 2014; Paperin et al. 2011) and require a balance between the time allocated to each. The percentage of resources in the landscape is crucial to the above trade-off.

We note in passing that, if cells are arranged in a two-dimensional grid, with a random scatter of cells containing resources, then there is a critical percolation density ~0.592746 (Newman & Ziff 2000) above which most of the resource cells become connected into a single "giant component" (Green et al. 2006; 2014; Paperin et al. 2011). That is, when ~59% of cells contain resources, a phase change occurs and the resource transforms

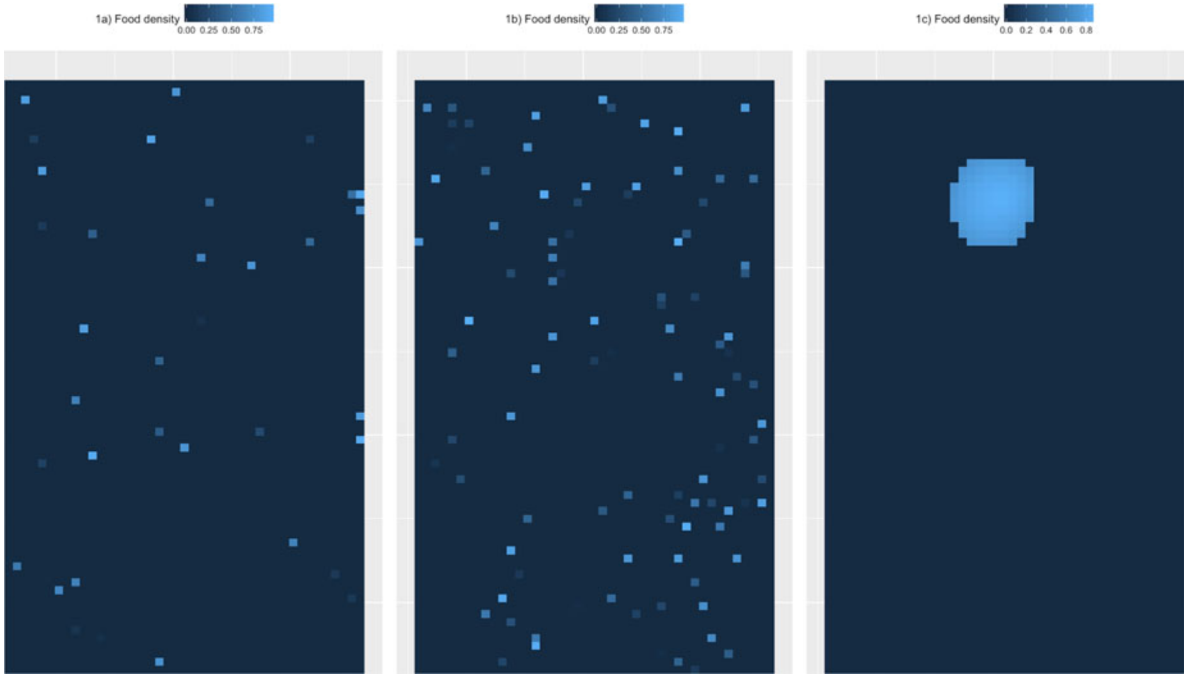

Figure 1. (Chmait et al.) Examples of possible environments with different distributions and percentages of rewards (food) and reward densities. The first two plots (1a and 1b) show rewards distributed uniformly randomly across the environment (with food more abundant in environment 1b), whereas plot 1c (on the right) has a biassed distribution of food that is concentrated in one part of the environment.

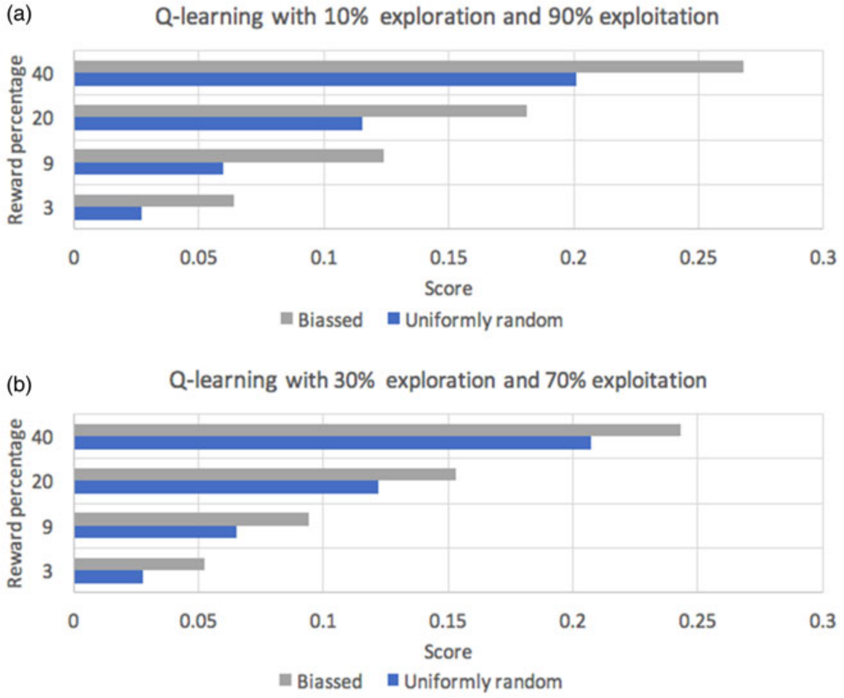

Figure 2. (Chmait et al.) Q-Learning algorithm scores in environments with different percentages of biassed and uniformly random distributed food across the environment space.

from being random, scattered items to a single, connected resource.

In our experiments, a reinforcement Q-learning algorithm was evaluated under different exploration-exploitation trade-offs across environments with biassed and uniformly randomly distributed food. Our Q-learning agents learn an action-selection policy where an action consists of taking a step in any of the possible directions, leading into one of the neighbouring cells (Chmait et al. 2016a; 2016b).

Results illustrated in Figure 2 (both 2a and 2b) suggest that Q-learning performs better in environments with biassed reward distributions, even when relatively abundant with food (e.g., 40% of cells contain some density of food). In such cases, a Q-learning algorithm seems to better learn a policy (or the sequence of

Figure 3. (Chmait et al.) Q-learning agent behaviour under different exploration-exploitation trade-offs in biassed and uniformly random reward-distributed environments.

actions) leading to the food source, and then spends time exploiting rewards around this source.

We now suggest this to be perhaps a special case of something more general in terms of (algorithmic) information theory. If we encode environment cell-rewards as a vector of 0's and 1's denoting the availability and absence of food in these cells, respectively, we expect the agents' scores to be lower in environments of high Solomonoff-Kolmogorov complexities (Boulton & Wallace 1969; Wallace & Dowe 1999), even across different percentages of reward in the environment.

Noteworthy is that the ratio of the scores (of the biassed divided by the uniformly random distributions of rewards) in Figure 2 (both a and b) seems to be monotonically decreasing with the percentage of food available in the environment, giving a bigger ratio in a food-scarce environment. For instance, in an environment space similar to that depicted in Figures 1a and (especially) 1b, reward patterns are seemingly of high randomness relative to environment spaces similar to that in Figure 1c. Thus, as the reward pattern becomes closer to (uniformly) random, learning seems of less importance/relevance to the agent's score. Nevertheless, further controlled experimentation is required to assess the above premise, across different food-density distributions (under 50%), time periods (long-term behaviour) and types of foraging agents (among other factors) (Chmait et al. 2016a; 2017; Hernández-Orallo et al. 2017). Moreover, in multi-agent foraging, the trade-off can involve balancing the allocation of agents to exploration and exploitation.

Figure 3 illustrates the same results as in Figure 2, but instead contrasts the Q-learning agent scores under different exploration-exploitation trade-offs. We observe that, when food is uniformly randomly distributed across the environment space (in turn making the environment of higher uncertainty), more exploration of the environment (food seeking) seems to increase an agent's overall food. This is in contrast to environments where food is concentrated in only one part (lower uncertainty, e.g., Figure 1c), in which more exploitation was beneficial, and exploring different portions of the environment diverted the agents from the only consistent food source available.

The contrast between Figures 3a and 3b supports the hypothesis of A&G that uncertainty magnifies food seeking.

Unpredictable homeodynamic and ambient constraints on irrational decision making of aneural and neural foragers

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Abstract

Foraging for nutritional sustenance represents common significant learned/heritable survival strategies evolved for phylum-diverse cellular life on Earth. Unicellular aneural to multicellular neural foragers display conserved rational or irrational decision making depending on outcome predictions for noise-susceptible real/illusory homeodynamic and ambient dietary cues. Such context-dependent heuristic-guided foraging enables optimal, suboptimal, or fallacious decisions that drive organismal adaptation, health, longevity, and life history.

Anselme and Güntürkün (A&G) develop intriguing data-persuasive hypotheses on the emergence of irrational decision making in animal foragers that illustrate common phenomena associated with phylogenetically diverse cellular life on Earth. According to A&G, animals experiencing conditions of uncertain food distribution and access become controlled by classically conditioned "incentive hope," a nontrivial motivational state whereby animals increase their food seeking, hoarding, and/or consumption behaviors to stave off starvation risks. This sort of ecoevolutionary strategy exemplifies superstitious or irrational decision making because animals choose ecological trade-offs that favor performance of (corporally) riskier energy-depleting foraging when unreliable cues for nutritional supplies imprecisely signal life-sustaining food abundance or life-threatening food scarcity. A&G contend that the biological bases of these sign-tracking animal behaviors is mediated largely by brain dopamine-reward systems important for conditioned incentive motivation and by metabolic changes in high-caloric body-fat reserves. Although dopamine-reward systems likely serve a central role in expression of animal incentive hope, similar context-dependent irrational strategies leading to generational/transgenerational adaptive or maladaptive outcomes may be observed for aneural single-celled and multicellular foragers ranging from bacteria to protists to plants (cf. Beekman & Latty 2015; Cao & Goodrich-Blair 2017; Clark 2010a; 2010b; 2010c; 2012; 2013a; 2013b; Dussutour et al. 2010; Hillesland et al. 2009; Latty & Beekman 2011a; 2011b; López Garcia de Lomana et al. 2017; Trewavas 2003). Such cross-taxonomic findings, regrettably unacknowledged in A&G's presentation, strongly indicate that irrational decision making, including fallible learned/heritable heuristic-guided foraging, is well-conserved across phylogeny, being mediated through assorted fuzzy somatic, epigenetic, and genetic systems responsive to real/illusory stochastic homeodynamic and/or ambient processes capable of driving organismal adaptation, health, longevity, and evolved life history (Anreiter et al. 2017; Clark 2012; Jobson et al. 2015; Lumey et al. 2011; Meyer et al. 2017; Reichert et al. 2017; Trewavas 2003; Vaiseman 2014; Wolf et al. 2005).

To conquer limitations of A&G's animal-centric hypotheses, one must better characterize the ubiquitous influence of stochastic processes on context-dependent generational/transgenerational adaptive or maladaptive foraging choices irrespective of phylum-specific forager anatomy and physiology. Such efforts, employing instances of kingdom-invariant ecoevolutionary game contexts ignored by the authors, identify variable detection sensitivity of perfect or fallible decision makers to real/illusory homeodynamic and/or ambient environmental cues, critically exposing generalizable scenarios where irrational gambling fallacies and other probabilistic consequences of noiseless/noisy signal-detection constraints elicit judged/misjudged win-shift, lose-shift, win-stay, and lose-stay foraging strategies (Dussutour et al. 2010; Latty & Beekman 2011a; Jobson et al. 2015; Lumey et al. 2011; Meyer et al. 2017; Trewavas 2003; Vaiseman 2014; Wolf et al. 2005). Notably, regardless of selective foraging biomechanisms and occurrence of real/illusory enteroception and exteroception, aneural, and neural organisms differentially apply absolute and comparative valuations of nourishment quality and diet balance when seeking, hoarding, and/or consuming foods during periods of famine or feast. Distinguishable linear divergence in food availability/quality magnitude and bioenergetics status results in rational optimal foraging decision making regulated by accurate representativeness or availability heuristics. However, when signal-detection noise distorts perception of homeodynamic and/or ambient environmental pressures, aneural and neural organisms begin to execute error-prone learned/inherited irrational heuristic-guided decisions consistent with uncertainty-forced incentive hope – findings that extend the external validity and power of A&G's conjecture. If stochastic processes emerge in less challenging game scenarios (e.g., unpredictable food availability and predictable food quality), win-stay or lose-shift selective foraging strategies, such as the hot hand fallacy, yield comparatively smaller ecoenvironmental advantages or disadvantages for individuals and populations of parents, progeny, and grandprogeny. On the contrary, lose-stay or win-shift choices, such as the gambler's fallacy manifesting from harder foraging dilemmas (e.g., unpredictable food availability and quality), may confer more profound positive or negative context-dependent effects over the life spans of individual organisms and across many generations, such as hunger-induced, robust or compromised phenotypic variations supporting survival and reproductive successes (Anreiter et al. 2017; Jobson et al. 2015; Lumey et al. 2011; Reichert et al. 2017; Trewavas 2003; Vaiseman 2014).

Thus, despite differences in biological bases of information acquisition, modification, representation/storage, and transmission (i.e., aneural vs. neural processing), predictability of internal and external dietary cues fundamentally determines rational or irrational foraging, with unreliable cues tending to compel directly proportional irrational goal-directed choice behavior. In many respects, this evidence-backed conclusion should be unsurprising to experimentalists and theorists, because the hypothetical construct of rationality is founded on and scaled to categorical and probabilistic traits of either natural or formal logic systems (Busemeyer & Bruza 2011; Clark 2012; Eisenstein & Eisenstein 2006; Nisbett & Ross 1980; Tversky & Kahneman 1974). Maybe a deeper, trickier question to answer is whether irrational foraging decisions, such as those accompanying hot hand and gambler's fallacies, and possibly similar public-/private-goods decisions made by aneural and neural hunters and farmers (Gowdy & Krall 2016; Werner et al. 2014), might counterintuitively generate dependable adaptive outcomes on organismal health, longevity, and life history. A&G's exposition of animal incentive hope suggests the appearance of just that kind of positive ecoevolutionary "irrational rationality" for metabolically compensatory foragers, where irrationality-causing life costs are reconciled or surmounted by changes in body-fat storage and utilization. Examples and exceptions to those types of generational/transgenerational trajectories in animals are well reported for fluctuating and persistent nutritional stress linked to developmental periods (Anreiter et al. 2017; Jobson et al. 2015; Lumey et al. 2011; Reichert et al. 2017; Vaiseman 2014). Nonetheless, much remains unknown about conservation of learned/heritable irrational rationality for aneural organisms engaged in foraging or other vital tasks. The arguably best instance involving microbes may be extrapolated from a game scenario called Parrondo's paradox, a set of indeterministic conditions imposing prospective lose-stay winning plays that advance transitions to stable optimal ecoevolutionary strategies (Wolf et al. 2005). Under such unpredictable homeodynamic and/or ambient constraints, microbes, very similar to taxonomically recent animals, irrationally produce dependable learned/heritable adaptive survival strategies capable of improving and protecting the health and longevity of individuals belonging to extant and future generations, reinforcing provocative notions that universal computational/informational/physical principles structure expression of irrationality and rationality in foragers, and perhaps predators and cultivators, independently of aneural and neural systems (Bekenstein 2004; Clark 2010a; 2010b; 2015; Clark & Hassert 2013; Gödel 1931; Ladyman et al. 2007).

Hope, exploration, and equilibrated action schemes

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Abstract

The concepts *want, hope*, and *exploration* cannot be organized in relation to a single type of motive (e.g., motive for food). They require, in addition, the motive for acquiring and maintaining a stable scheme that enables reward-directed activity. Facing unpredictability, the animal has to seek not only reward, but also a new equilibrated state within which reward seeking is possible.

In one of the classics of behavioral psychology, *Schedules of Reinforcement*, Ferster and Skinner (1957) reported how changing the contingencies that link an animal's response to reward can change the rate and pattern of responses. After sufficient exposure to a fixed contingency of reinforcement, the animal's rate of response tended to reach a steady state. After the regularity changed, response rates also changed, typically increasing at first. In the case of a new regular contingency, the animal's performance could eventually reach a new steady state. We could interpret the findings of Ferster and Skinner in terms of reward-seeking behavior and its sensitivity to changes in the schedules of reinforcement. Alternatively, we could consider their results in terms of two distinct motives: the motive for the reward (i.e., food) and the motive to acquire the ability to predict environmental contingencies (Kelly 1963; Piaget 1937). These two motives correspond, respectively, to observations on a smaller timescale (e.g., a single response) and observations on a larger timescale (e.g., increased rate of response vs. reaching steady state). We believe that Anselme & Güntürkün's (A&G's) proposal would benefit from a similar emphasis on the second type of motive that corresponds to patterns of behavior along relatively larger timescales.

Consider Joe, an office worker, who buys a cup of coffee from the same coffee shop every morning before going to work. One day, after arriving at the coffee shop, he is faced with a "closed" sign at the door. He goes to work, and he finds himself thinking about the coffee shop several times during the day. He might even visit the shop a few times. Even though he finds the coffee shop open in the afternoon, he remains concerned. His preoccupation is not only because he wants his daily dose of caffeine, but also because he wants to know whether his access to the source of coffee is restored, stable, and reliable. Visiting the shop, even prior to encountering the closed sign, served two purposes: (1) getting coffee and (2) confirming Joe's implicit knowledge of his own action and the rewarding outcome. After facing the closed sign, Joe was deprived of both coffee and the ability to predict access to coffee. Receiving a cup of coffee in such a circumstance would address the first need, though addressing the second need would require repeated exposure to the new environmental contingency. Presumably, being deprived of the ability to predict access to reward is unpleasant. Therefore, Joe might increase the frequency of his visits to the coffee shop, to shorten the process of reaching the ability to predict the new environmental contingency.

Goal-directed activity is typically nested within an understanding of the context in which the activity takes place. The term *action scheme* (Piaget 1937) refers to the implicit understanding of the context in which an animal engages in an activity, including learned action-outcome associations (e.g., walking toward the coffee shop means, among other things, one is getting closer to a cup of coffee). An action scheme, thus, involves an implicit understanding of the environment in which movements can serve goals. It is on the basis of that understanding that the animal is capable of expecting certain outcomes. Indeed, in the absence of any ostensible reward, simply perceiving an expected action outcome can serve as a reward, presumably because it serves to confirm the animal's action scheme (Eitam et al. 2013; White 1959). Therefore, when the primary reward of a given activity becomes inaccessible, it is not merely the reward that is taken away. What is also taken away is the reliability of the action scheme.

A&G discuss the function of intensified foraging along two dimensions: (1) seeking what is valued and (2) uncertainty. These lead them to characterize the phenomena in terms of *hope*, which they define as wanting without certainty. Their characterization is not inconsistent for the two types of motivation – an animal can "want" food in the presence of a stable or reliable action scheme, but an animal can only "hope" for food in the absence of a stable or reliable action scheme. It might, however, appear that the motivation to pursue a scarce or unpredictable resource is the same type of motivation underlying the pursuit of an abundant or predictable resource. We suggest drawing a distinction between two kinds of motivation, one of which is directed at the valued resource. The other motivation is directed toward retaining or updating an action scheme for the pursuit of the resource. Drawing the distinction is somewhat counterintuitive, because the two kinds of motivation do not necessarily correspond to separate sets of activities.

Why does the rate of action increase in the case of a scarce and unpredictable resource? The animal in such a circumstance may work toward a new equilibrated action scheme. Uncertainty regarding access to food is aversive, and therefore, shortening the period of uncertainty would require that the animal expend more effort on building an action scheme. Hope is implied in the attempt to achieve a stable action scheme. After all, acting *as if* the contingencies will eventually become predictable is a prerequisite for trying to learn about them. Increasing the rate of responding (i.e., sampling the environment), in the form of intensified foraging, may generate a tentative action scheme. If the scheme is effective in reducing prediction error, the animal's activity will reach equilibrium. In any case, working to acquire a stable action scheme is not the same as hoping for the valued resource.

Returning to the example of Joe, it is possible that after checking the coffee shop a few times, he learns about the new opening hours, thus acquiring a new reliable action scheme in relation to his morning coffee. It is also possible that he widens the scope of his sampling, exploring the neighborhood for other coffee shops. Exploration is the basis for learning action schemes (Gozli & Dolcini 2018). That is, the purpose of exploration is not merely acquisition of reward, but also the acquisition of new action schemes that provide the animal with sensorimotor mastery and stable access to reward over relatively large timescales.

Mechanistic models must link the field and the lab

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Abstract

In the theory outlined in the target article, an animal forages continuously, making sequential decisions in a world where the amount of food and its uncertainty are fixed, but delays are variable. These assumptions contrast with the risk-sensitive foraging theory and create a problem for comparing the predictions of this model with many laboratory experiments that do not make these assumptions.

Anselme & Güntürkün (A&G) present a mechanistic model of foraging that makes functional sense. All models are simplifications of the complex world inhabited by an organism. Here, we highlight some of these simplifying assumptions made by A&G and point out how these assumptions contrast with previous attempts at understanding the effect of uncertainty and why exploring these assumptions is important.

Firstly, they A&G focus on variation in delays until food is obtained rather than amounts of food. Secondly, they focus on sequential as opposed to simultaneous choice. Thirdly, they assume that uncertainty is fixed over time.

Let us examine the assumption of variability in the delay until food is obtained. In this context, A&G see a functional account as a general explanation of preference for variability. This is at odds with the conclusion reached by Bateson and Kacelnik (1997), who argue that a mechanistic account is required. In general, food rewards can vary in delay, amount, or both. Variation in amount is analysed by the theory of risk-sensitive foraging (RSF). As we now discuss, there are places where A&G would benefit from closer links to the RSF theory.

Under RSF, if one assumes that the organism must reach a critical level of reserves at the end of a foraging period (i.e., foraging is *interrupted*), it can be shown that the organism should be risk averse if food is plentiful and risk taking if food is scarce. This is the famous *daily energy-budget rule* (Stephens 1981; tests reviewed by Kacelnik & El Mouden 2013). The rule is relevant to this quote from A&G: "food unpredictability does not constitute an immediate danger (see Abreu & Kacelnik 1999; Orduna & Bouzas 2004)" (sect. 2.1, para 1). It is not clear that the cited articles show what is claimed. These lab studies are not about the danger of starvation. They are arguing against the energy-budget rule as an explanation of behavior.

Existing RSF theory is also relevant to this statement: "So, exploiting the immediately available resources is often an optimal strategy, even if those resources are in small amounts" (sect. 3.4, para. 3). Unlike most of the target article, this point is about variation in amount. Assume that an animal sequentially encounters prey items that differ in energy and handling time. Houston and McNamara (1985) report that if there are no interruptions to foraging, then survival is maximised by eating everything that results in a gain of energy (i.e., the energy content of a prey item is greater than the energy spent handling). If there is a day-night cycle, then the optimal decision depends on energy reserves and time until nightfall (Houston & McNamara 1985). This shows that the optimal strategy depends on the ecology of the forager, a point emphasised by Houston (1991), McNamara and Houston (1992), and Houston and McNamara (1999). How will the approach of A&G perform when faced with simultaneous choice between options that vary in amount?

The model of A&G also assumes that the level of uncertainty remains fixed over time (an organism is either in an S-800, U-200, or U-60 environment). In an ecologically realistic situation, the availability of food will vary over time. A model that assumes variation in uncertainty might make very different predictions about the psychological factors that affect the consumption of food (cf. McNamara 1996). For example, when the uncertainty of the environment is autocorrelated, the current state becomes informative (e.g., Fawcett et al. 2014; Mallpress et al. 2015) and might be used to regulate the level of consumption. Similarly, if the animal can choose how much effort to devote to foraging, the optimal decisions depend on the degree to which the environment fluctuates (Higginson et al. 2012).

Examining these assumptions and their role in model predictions is crucial from another perspective. A functional model is based on a particular ecological context and consequently does not necessarily need to explain an animal's behavior outside this context (Houston 2009; Houston & McNamara 1989; McNamara 1996). However, a mechanistic model, such as that proposed by A&G, must also explain behavior during laboratory experiments. This makes two of the three assumptions that we have highlighted above – sequential rather than simultaneous choice and variability in delays rather than amounts – problematic for A&G's account. Many lab experiments use simultaneous choice between options that vary in amounts (see the articles discussed by Kacelnik & Bateson 1996; Kacelnik & El Mouden 2013). A mechanistic account, such as that of A&G, must be general enough to explain behavior in these contexts. A related point is that A&G have produced a spatially explicit model. This is a complication that is not required to evaluate the model using data from laboratory experiments, and a simpler model that looks at choices and energy reserves will have a smaller set of assumptions and be more tractable for examining predictions in the laboratory.

If the spatial component is retained, it could be used to investigate behavior when there is a spatial correlation between items (see Fawcett et al. 2014).

To conclude, it would be interesting to develop a synthesis of optimal levels of energy and RSF. Fat regulation is based on mass-dependent costs (Houston et al. 1997). Most models of RSF do not include these costs (for an exception, see Bednekoff & Houston 1994). A general model would predict both fat levels and choices between variable options.

Extending models of "How Foraging Works": Uncertainty, controllability, and survivability

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Abstract

We argue that *How Foraging Works* sketches a good foundational model, but it needs expanding to incorporate hierarchical and multiscale conceptions of uncertainty and to incorporate inference of environmental controllability. Most pressingly, its algorithmic implementation needs to be better justified in terms of its functional forms and, ultimately, to be more heavily constrained by survival optimality.

Why and how animals increase energy reserves in uncertain environments has been overdue wider attention. We applaud the effort of Anselme & Güntürkün in synthesizing a novel theory seeking to unify several distinct literatures. We comment along three frontiers: the normative, the controllable, and the algorithmic.

How Foraging Works (HFW) is predicated on evolutionary assumptions, whereby energetic uncertainty should promote foraging policies that minimize starvation risk. This line of theorizing is welcome, but would benefit from more rigor. Their definition of uncertainty (sect. 1, para. 2) is that a trial or food acquisition attempt is rewarded on a random basis, independent of the time spent in that environment. They state that this uncertainty yields an inability to predict whether the next trial is rewarded (sect. 1, para. 2) and that this uncertainty is maximal when that probability is 0.5 (sect. 3.2, para. 1). First, the time independence is a questionable clause to insert into a definition of uncertainty, in that in many settings, foraging actions do interact with future probabilities of food acquisition (e.g., as finite resources are depleted). Perhaps this aspect of the definition is better considered a simplifying assumption than a definition. Second, the deeper issue we have with this treatment of uncertainty is that it is too narrow. Ecologies are causal networks with hierarchical structure, evolving over multiple timescales. The intelligent agent has to evolve, grow, and update its own hierarchical generative model of this environment to deploy the foraging decisions necessary for it to stay alive. For instance, to maximize reward rates, such an agent needs to compute expectations, variances, and labilities of reward variables over multiple timescales. Suppose patch #1 affords a mean energetic rate of 5 calories per hour and the probability of reward is 0.5 on any single foraging encounter (e.g., with a conditioned stimulus). The agent will be unable to predict the next outcome of the next encounter, yielding uncertainty over trials as defined above. Despite this trial-level uncertainty in the outcome, the intelligent agent can still compute precise expectations with respect to the mean energetic rates over longer timescales. This would be a form of expected uncertainty, in which reward rates are predictable over longer timescales, but unpredictable over short timescales. By contrast, consider patch #2, which comprises highly predictable cues, that currently delivers the same mean energetic rate but with a reward probability of 0.9 (i.e., by delivering less energy per reward). Suppose that the agent has a less precise estimate of the mean energetic rate, which, because of its volatility, jumps above and below the agent's minimal metabolic needs. This would be a form of unexpected uncertainty, in which outcomes are relatively predictable over short timescales but unpredictable as energetic rates over longer timescales. Given that patch #1 yields a higher cumulative survival probability, it has a higher fitness value than patch #2. Thus, all else being equal, the agents should normatively prefer to occupy patch #1. If the agent was unable to control which patch it occupies, what should it do with respect to their foraging vigor and consumption while within these patches? Because of its volatility, the agent should increase its foraging efforts and consumption in patch #2, but not in patch #1, even though patch #1 is the more uncertain and less predictable patch, under the HFW definition. The problem is that unless one is more nuanced about the hierarchical structure and multiple timescales of ecological uncertainty, one becomes easily tangled in these apparent contradictions. Ultimately, this hierarchical and multiscale uncertainty must be scored by something deeper than the narrow uncertainty articulated in HFW. This exercise is potentially important, because without a deeper conception of uncertainty, the model presented in HFW is vulnerable to being "falsely falsified" by empirical observations such as these, even though, at the deepest level, we think it merits remaining as a candidate theory for the field.

Another fundamental dimension missing from HFW is the inference of environmental controllability. Increasing foraging effort is only advantageous if the effort is likely to be profitable over life-relevant timescales; otherwise it wastes energy and shortens the odds on starvation. Complex organisms are typically able to estimate whether their foraging policies are hopeless, and thus whether they are better off conserving energy through inaction, until greater control is (hopefully) restored.

The functional forms of the HFW model appear to be ad hoc, or at least no deeper justification is provided. So for instance, linking wanting to energy level is described in Equation 1 (Online Supplement) as a power law. But why a power law? The concavity of this function is biologically implausible. For instance, for each unit loss of energy, the marginal increase in wanting decreases. This is the opposite of what should be expected if motivation is to optimize survival. As you get closer to the boundary of death, you need motivation to marginally increase, not decrease, in line with the fact that the fitness costs of losing each unit of energy are marginally increasing as energy reserves decrease.

Likewise, in Equation 4 (Online Supplement), there is no specific justification for its functional form, above the plausible justification that wanting, uncertainty and scarcity all matter to incentive hope. Without justification, the reader is left wondering whether the observed behaviors are specific to this seemingly ad hoc formulation or whether they are general to a particular class of function. We are not against using simplified assumptions where necessary to make a model work; however, there are several equations that seem fundamental to the meaning and rationale of the theory, but that seem to be arbitrarily contrived or without deeper justification. This speaks to the broader point of designing the model to optimize survival. Consideration of survival optimality could provide crucial constraints in choosing the functional forms of the equations, because for any given survival probability function linking energy state to survival, there will be specific (potentially unique) wanting and foraging motivation functions that are survival optimal. Indeed, the HFW model has approximated a very simple environment in which this normativity analysis could be quite tractable. We look forward to seeing future foraging models inspired by HFW that can address these challenges.

Beyond uncertainty: A broader scope for “incentive hope” mechanisms and its implications

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Abstract

We propose that food-related uncertainty is but one of multiple cues that predicts harsh conditions and may activate “incentive hope.” An evolutionarily adaptive response to these would have been to shift to a behavioral-metabolic phenotype geared toward facing hardship. In modernity, this phenotype may lead to pathologies such as obesity and hoarding. Our perspective suggests a novel therapeutic approach.

Anselme and Güntürkün (A&G) provide a thought-provoking and insightful synthesis of ideas from traditionally disparate fields. We largely endorse it, but suggest that the evolutionary scope in which “incentive hope” mechanisms are adaptive is far broader than proposed by A&G: Food-related uncertainty is but one of multiple factors that may trigger incentive hope. Their common characteristic is the anticipation of harsh conditions, in which it would be adaptive for an organism to shift to behavioral and metabolic phenotypes that prepare it for hardship, such as food shortage. Expanding the theory’s scope leads to novel predictions regarding human behavioral ecology, cognition, and mental health.

From a behavioral ecology perspective, at least two types of cues, beyond food uncertainty, may signal that fat reserves would be beneficial in the near future: (1) reliable predictors of an impending food shortage, such as the decrease in light hours as winter approaches (Heldmaier et al. 1982; Williams et al. 2014), and (2) occasional correlates of food shortage. The latter include experienced stress and predictors of stress, such as changes and disruptions to physiological cycles, conspecifics’ pheromones from a disease-related response, or stress-indicative behavior of conspecifics. During evolution, it would have been adaptive for incentive hope mechanisms to be triggered in such cases. Thus, the general trigger for incentive hope is *anticipated hardship* (not only food uncertainty), which may modify behavior, cognition, and physiology.

For an individual, expectations about the near future can be optimistic or pessimistic, for which it would have been adaptive to opt for different behavioral or metabolic phenotypes. For example, optimism might promote investment of resources and effort in reproduction or attainment of social status, and pessimism might promote preparation for hardship, for example, by accumulating reserves. In contemporary human society, the evolved mechanism of anticipated hardship and its physiological and cognitive effects might be triggered by any stress-related cue, such as pressure at the workplace, irregular sleep, a perception of instability or insecurity of the environment, or the lack of social support and insecure attachment (Coyne & Downey 1991; Mikulincer & Shaver 2012). This is due to an evolved association between such cues and anticipation of hardship.

Unfortunately, the “pessimistic phenotype” might no longer be predominantly adaptive for humans in general, while remaining “evolutionarily hardwired” in our brain and physiology. This observation accounts parsimoniously for behaviors and physiologies that can lead to the development of psychopathologies and medical conditions (Harvey et al. 2011; Kalanthroff et al. 2016; Snyder & Hankin 2016), including major depressive disorder, hoarding disorder, obsessive-compulsive disorder (OCD), and abnormal attentional processes, all of which can be understood as extreme expressions of behaviors that might have been adaptive when expecting hardship during our evolutionary history. It also extends the range of possible causes of conditions that A&G discuss, namely, obesity, drug addiction, and gambling (Logan et al. 2017; Spiegel et al. 2009). Importantly, extending A&G’s theory may produce novel insights and therapeutic interventions for these pathologies.

Our extension of A&G’s framework provides an explanation for a range of observations. One example is the well-established correlation between lack of sleep (or fragmented sleep) and obesity (Gileles-Hillel et al. 2016; Hakim et al. 2015; Miller et al. 2015; Wang et al. 2014); a priori, this is unexpected, as obesity might be considered merely a diet-induced condition (as it was for many years). However, it is now clear that disturbed sleep leads both to altered metabolism and to behavior that influences calorie intake and expenditure in a manner that promotes accumulation of fat (Chaput et al. 2011; Spiegel et al. 2009; Wang et al. 2014). Proximate mechanistic explanations for this link have been proposed (Gileles-Hillel et al. 2016; Hakim et al. 2015; Miller & Cappuccio 2007); in comparison, we offer an ultimate explanation, which highlights possible evolutionary and ecological underpinnings of the link between disturbed sleep and obesity. It suggests that disturbed sleep induces stress, which in turn triggers the "pessimistic phenotype" and expectation of future hardship, shifting the individual's behavior and metabolism to focus on resource retention, at the expense of alternative utilization of time or energy. Similarly, we suggest that stress may induce seemingly unrelated behaviors that may become pathological, such as hoarding and OCD. Although such a link has been suggested (Kalanthroff et al. 2016; Paterson et al. 2013; Raines et al. 2015), it is not well studied; our account sheds light on its possible underpinnings.

Many medical conditions and psychopathologies are thus not cases of broken systems that need to be fixed. Rather, we suggest that they are extreme manifestations of historically adaptive mechanisms that switch between alternative behavioral-metabolic phenotypes. In the context of a modern society, switching to the pessimistic phenotype may lead to severely maladaptive outcomes: Behaviors and metabolic syndromes that manifest as hoarding or preference for high-fat and high-sugar foods ("junk food"), alongside reduced sociality and reduced exploratory thought processes, not only fail to help cope with hardship as they may historically have, but instead exacerbate initial stress factors. Pathological outcomes may not occur in all individuals but are expected for some, as a result of interactions between genetic and environmental factors. Unfortunately, high stress seems to be prevalent in many modern societies, particularly so in the perpetually insecure underclass (Eyer & Sterling 1977; Nettle et al. 2017; Wisman & Capehart 2010). The upshot of this observation is that the way to treat these pathologies (short of replacing the socioeconomic system that fosters them) is not by looking to remove the trigger that brought them about. Rather, treatment should focus on switching the individual to the "optimistic phenotype." Just as a range of factors can induce anticipated hardship, so there can be multiple cues that promote switching to the optimistic phenotype. One such trigger might be physical activity, which may have been evolutionarily associated with appropriate timing of phenotype switching, for example, at the end of hibernation and beginning of reproduction. Indeed, regular exercise benefits individuals diagnosed with anxiety and psychotic disorders, regardless of whether it was a factor in inducing the condition (Fentem 1994; Firth et al. 2018; Salmon 2001). Moreover, we hypothesize that explaining the reasoning behind such an intervention to the individual may render it more effective than exhortations for lifestyle changes.

Our ecological-evolutionary perspective may aid the development of interventions involving cues that over evolutionary time were predictors of near-future favorable conditions. These may be physiological, social, or psychological, for example, an increase in the ambient temperature, an extension of daylight hours, regular sleep that is associated with reduced stress, a switch to a diverse diet, social interaction with individuals in the optimistic phenotype state, or interaction with content infants. Many of these treatments make intuitive sense; our proposal provides a *causal* framework that links them with desired phenotypic switches. Conceptualizing the challenges in ecological-evolutionary terms allows informed reasoning about the drivers of pathologies and conditions and about potential remedies for them.

Complex social ecology needs complex machineries of foraging

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Abstract

Uncertainty is caused not only by environmental changes, but also by social interference resulting from competition over food resources. Actually, foraging effort is socially facilitated, which, however, does not require incentive control by the dopamine system; Zajonc's "drive" theory is thus questionable. Instead, social adjustments may be pre-embedded in the limbic network responsible for decisions of appropriate effort-cost investment.

Classic theories of optimal foraging behaviors assumed single individuals that maximize the long-term gain rate while foraging in highly uncertain environments (Charnov 1976a; Stephens & Krebs 1986). Because of their clear-cut arguments and fruitful sets of predictions, the optimality theories contributed not only to the behavioral ecology of animals, but also to the foundation of neuro-economics in humans (Glimcher 2003). In particular, the marginal value theorem proposed for optimal patch-use behavior (Charnov 1976b) has been considered to represent a highly realistic situation to study the neural and pharmacological bases of value-based decision making (Blanchard & Hayden 2015; Hayden et al. 2011; Matsunami et al. 2012). However, this is not enough. Most animals do not forage alone but do so in groups despite the enhanced competition over food resources.

In a group of foragers, as a result of the strong interdependence of consequences on each other's decisions, not one of the group of foragers can maximize the individual payoff (Giraldeau & Caraco 2000). Instead, evolutionarily stable strategies are assumed to represent the stable and adaptive Nash equilibrium of the game-theoretical situation. A typical example is found in a producer-scrounger game, in which the former (producers, *P*) search and find food, but must share their find with the latter (scroungers, *S*). Note that each one does not necessarily follow a fixed strategy *P* or *S*, but can flexibly switch between them. We may further assume a group of opportunists, which can produce and scrounge at the same time. As the social foraging increases uncertainty, it is highly challenging for studying what is the best foraging decision.

Social facilitation appears under the social foraging accompanied by an increase in uncertainty (Ogura & Matsushima 2011). When animals such as domestic chicks are placed in an

I-shaped maze with two terminal feeders at both ends, they start to actively shuttle between these feeders. Under the high level of uncertainty (i.e., the food supply is randomized at a low rate, and the subject is perfectly uncued), effort-cost investment is further enhanced if the subject is accompanied by competing foragers. Since systematically reviewed more than a half-century ago (Zajonc 1965), enhancement in behavioral performance in the presence of conspecifics has been referred to as *social facilitation*. As an account generalizable to a wide variety of animals including humans, Zajonc proposed the drive theory. He hypothesized that the presence of others increases general arousal or level of drive, which is meant to be a non-selective enhancer of behavior in the sense that Hull (1943) argued. However, the assumed "drive" has not been addressed with respect to its causal machineries. As the social facilitation denotes a commonly found phenomenon, it does not have to imply any unitary and general mechanisms. Actually, Clayton (1978) argues that this term can be used only descriptively, without specifying underlying causal processes.

The "incentive hope" hypothesis raised by the target article may sound like a renewed version of the drive theory by Zajonc, if the issues on the socially brought uncertainty are concerned. In this respect, we may reasonably predict that the dopaminergic system is involved in the social facilitation, which, however, was not true (Ogura et al. 2015). Dopamine-selective depletion by micro-infusion of 6-hydroxydopamine into the substantia nigra failed to suppress the social facilitation, even though a novel reinforcement learning was severely impaired. As the underlying neural substrates for the social facilitation, we would rather suggest the descending pathway from the limbic area in the telencephalon or the lateral part of the arcopallium (Arco) of domestic chicks (Xin et al. 2017b). On the one hand, Arco was initially assigned to be the avian counterpart of the mammalian amygdala (Phillips et al. 1972) and also to a part of the motor/premotor area responsible for orofacial control (Wild et al. 1985). On the other hand, lesions localized to Arco resulted in handling cost aversion in chicks (Aoki et al. 2006), suggesting a functional similarity to the mammalian basolateral amygdala or anterior cingulate cortex. Lesions localized to the lateral Arco suppressed social facilitation, while sparing the foraging shuttles in the isolated (nonsocial, but yet highly uncertain) condition unchanged. Note that even without additional food gains, socially facilitated effort-cost investment can be beneficial (Xin et al. 2017a). Chicks foraging in pairs achieved a better matching to the food supply ratio and a significantly longer-lasting memory of the more profitable feeder. We would argue that if a group of opportunistic foragers shared information on the food resource more efficiently, the facilitated effort-cost investment could be paid in the long run. The game-theoretical nature of the social complexities also gives us ecologically reasonable accounts for a paradoxically high level of choice impulsiveness under competition (Amita et al. 2010; Ogura et al. 2018). Behavioral adjustment to social foraging situations is supposed to be pre-embedded in decision mechanisms, allowing animals to flexibly change according to individual social and economic circumstances.

Considering these complexities in social foraging situations, it might be appropriate to assume a bit more complex machineries and processes than those assumed in the target article. The effort-control network is intensely intermingled with the social network responsible for conspecific perception, rather than (or in addition to) the incentive control network. To develop comprehensive views, it will be important to ask what sort of natural counterparts our psychological questions could have. By designing tasks in a manner that appropriately improves their external (or ecological) validity, we would more easily specify the internal processes underlying decision making.

Does the "incentive hope" hypothesis explain food-wasting behavior among humans? Yes and no

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Abstract

In this commentary, we discuss how the "incentive hope" hypothesis explains differences in food-wasting behaviors among humans. We stress that the role of relevant ecological characteristics should be taken into consideration together with the incentive hope hypothesis: population mobility, animal domestication, and food-wasting visibility.

In their target article, Anselme & Güntürkün posit that "incentive hope" serves as an evolutionarily shaped motivational mechanism that increases animals' foraging effort and food hoarding as insurance against starvation, especially in environments where food is scarce. The authors further suggest that the incentive hope hypothesis may be useful in explaining such human-related phenomena as addiction, gambling, and obesity. However, is incentive hope hypothesis alone able to explain human food-wasting behaviors? We posit that although it seems to be doing so effectively in industrialized societies, the incentive hope hypothesis should be complemented by ecological and cultural characteristics, such as *mobility, animal domestication,* and *behavior visibility*, to effectively explain food wasting in traditional societies.

Food wasting is a global problem that contributes to food crises (World Economic Forum 2016) and influences climate change (Vermeulen et al. 2012), deforestation (Houghton 2012), and water shortages (Chapagain & James 2011). Although in many countries, food wasting is conditioned by specific factors, no overarching theory is available that allows prediction of future patterns of food wasting among human populations. The incentive hope hypothesis may serve as a promising starting point for such theorizing.

According to the incentive hope hypothesis, human populations living in environments where food availability is predictable exhibit fewer behaviors associated with food hoarding. That should lead to a larger amount of food being wasted. Yet, although the incentive hope hypothesis might fit the patterns observed in industrialized societies (Secondi et al. 2015), it is not certain in the case of traditional societies. In industrialized societies, food wasting is associated primarily with the lack of peoples' behaviors aimed at utilizing the surplus of food (Quested et al. 2013). On the contrary, food wasting hardly ever takes place in traditional societies. Let's consider two examples.

The population of the Hadza hunter-gatherers from Tanzania is exposed to unpredictable access to food. Hadza foraging methods are quite representative of human evolutionary past: Women spend each day collecting wild plants, and men, hunting. In doing so, both men and women cover very long distances (Blurton-Jones 2016). After they make use of the surrounding natural resources, they move their camps to locations where food is more abundant. The incentive hope hypothesis predicts that the Hadza hoard food, yet it is not the case (Marlowe 2010). The Hadza do not store their food and do not have any hoarding methods because of their mobility. But they also do not waste the surplus of their food – they share it with the camp members. When a Hadza man hunts down a large animal, instead of leaving the surplus of meat for wild animals, he shares the food with other Hadza. This cultural norm works reciprocally, and the same hunter can expect other hunters to share their surplus with him (Marlowe 2004). Prevalent food-sharing behaviors among the Hadza minimize the effects of food unpredictability. Thus, Hadza mobility prevented the development of food-hoarding methods and resulted in a cultural norm of food sharing.

Not only did hunter-gatherers develop cultural adaptations that minimize food wasting, but recent study (Misiak et al. 2018) reported that two traditional populations – the Maasai from Tanzania (Endulen) and the Yali from West Papua – developed strong moral disapproval for food wasting. It serves as a cultural adaptation that motivates individuals to not waste the surplus of food. Both populations do not use any hoarding methods and do not deposit high levels of fat reserve. The Maasai of Endulen are seminomadic pastoralists, and the lack of hoarding behavior among this population stems from their mobility, similarly to the Hadza. The Yali, however, are horticulturalists, yet they do not use any methods of food hoarding either. The Yali do not waste the surplus of food: Instead, they feed the pigs and dogs – the only domesticated species in this population. Although feeding the stock and dogs is not a method of hoarding literally, it minimizes food unpredictability through raising of pigs for pork. Furthermore, the Yali use dogs for hunting, thus increasing their hunting outcome.

Except for *mobility* and *animal domestication*, another factor increases the prevalence of behaviors that minimize food wasting: *visibility*. In industrialized societies, food-wasting behaviors are far less visible than in traditional societies (Quested et al. 2013). Therefore, social norms aimed at influencing the management of food surpluses are not likely to prevent people from wasting food. High visibility of food-wasting behavior among traditional populations could reinforce the development of cultural norms.

The incentive hope hypothesis offers an attractive framework for understanding animal foraging behavior, and in doing so, it provides an interesting explanation for human-related phenomena. It also has the potential to explain and predict food wasting in human populations. That being said, we believe that the incentive hope hypothesis would benefit from accounting for such ecological characteristics as mobility, animal domestication, and behavior visibility, which informed cultural adaptations like food sharing and harsh moral judgments of food wasting. Enriched by moderating ecological factors, the incentive hope hypothesis could and should be examined in such traditional populations as Hadza; they form real-life cases that allow for testing the mathematical models presented in the target article.

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The value of uncertainty: An active inference perspective

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Abstract

We discuss how uncertainty underwrites exploration and epistemic foraging from the perspective of active inference: a generic scheme that places pragmatic (utility maximization) and epistemic (uncertainty minimization) imperatives on an equal footing – as primary determinants of proximal behavior. This formulation contextualizes the complementary motivational incentives for reward-related stimuli and environmental uncertainty, offering a normative treatment of their trade-off.

Several studies in behavioral ecology and psychology have found that certain forms of uncertainty (e.g., unpredictable access to food) promote and invigorate exploration, foraging, and food-related responses. Anselme & Güntürkün (A&G) argue convincingly that there is a motivational basis to this process. They propose that uncertainty produces an "incentive hope" that promotes exploration and seeking behavior, analogous to the ways the "incentive salience" (or "wanting") of specific stimuli such as food promotes approach behavior (Berridge 2004).

It may be instructive to revisit the idea of complementary motivational and incentive systems for reward seeking and uncertainty reduction, respectively, within current formulations of exploration-exploitation in computational neuroscience. The idea that forms of uncertainty should elicit exploratory actions is encountered in various models; yet these models differ in their specific implementations. For example, various proposals about "exploration bonuses" in reinforcement learning are related to the idea of "hope" in A&G – in the sense that the bonus essentially amounts to an optimism about visiting regimes of state-space that have not been explored (at least recently). This supplement to the utility function precludes excessive or premature exploitation (Christiansen et al. 1991; Dayan & Sejnowski 1996; Sutton 1990).

Other computational approaches, such as active inference, assume that exploration and exploitation are two aspects of the same imperative (to minimize expected free energy). This amounts to resolving uncertainty under normative considerations about the *epistemic* or *informational value* of exploratory actions (Friston et al. 2014; 2016a). Clearly, in active inference, uncertainty has no value per se (and indeed, animals do not seek out uncertainty when they have a choice). Rather, it is the potential *reduction* of uncertainty and the associated *information gain* that enable (future) goal-directed behavior – which is intrinsically valuable. Pursuing this sort of value through exploratory or curious behavior has thus a strong knowledge-seeking, motivational component, which has been variously called *intrinsic motivation, epistemic drive, value of information, Bayesian surprise*, and *salience* in different contexts (Baldassarre & Mirolli 2013; Berlyne 1960; Friston et al. 2015; 2017; Gottlieb et al. 2013; Oudeyer et al. 2007; Schmidhuber 1991; Singh et al. 2005).

A recurrent idea is that the ultimate reason to reduce uncertainty, or more broadly to pursue epistemic drives, is to facilitate subsequent pragmatic, utility-maximizing behavior. Yet, active inference agents consider both epistemic and pragmatic drives on an equal footing, during action (or policy) selection, and both can be primary determinants of proximal behavior. This is evident if one considers that active inference agents strive to minimize a quantity (a *free energy* functional) that explicitly includes two terms: the *pragmatic value* and the *epistemic value* afforded by actions or policies (Friston 2010; Friston et al. 2016b; Pezzulo et al. 2018; 2015). This is important because it equips rewards with an information measure and, conversely, means we can talk about the utility of information.

During sequential action or policy selection, the relative balance between pragmatic and epistemic imperatives depends on quantities that are inferred by the agent, such as the statistics of reward distributions and contextual uncertainty (without requiring ad hoc terms like bonuses). Limiting conditions, such as when the agent is fully satiated or has resolved all its uncertainty, advocate pure epistemic or pragmatic behavior. But between these two extremes, policy selection balances pragmatic and epistemic value, which may manifest as apparently suboptimal foraging (e.g., excessive seeking and foraging in uncertain situations), if one considers only utility maximization rather than the epistemic imperatives that are part and parcel of free energy minimization. Crucially, the balance between pragmatic and epistemic imperatives changes systematically with experience and varying environmental conditions. A progressive reduction of epistemic value reveals pragmatic (possibly habitual) policies, when environmental uncertainty resolves – or vice versa, when it suddenly increases (Friston et al. 2014; Pezzulo et al. 2016). On this view, there is no need to invoke any random exploration; in other words, there are always optimal epistemic moves to select from. Indeed, one can develop *epistemic habits* under active inference (Friston et al. 2016a).

This line of thinking is compatible with the information primacy hypothesis that reducing environmental uncertainties can be a primary determinant of proximal behavior (Inglis 2000; Inglis et al. 2001; Woodworth 1958). One implication of this view is that, because information gain is motivating per se, above and beyond reward, animals may have an incentive motivation to reduce uncertainty, or to collect valuable information, without necessarily being optimistic about the outcome of an uncertain event; for example, hoping to find reward when this is unlikely. Assessing the contributions of information gain and reward expectation (or hope) to foraging in uncertain domains is an important, open research question (Behrens et al. 2007; Daw et al. 2006; Gallistel & Gibbon 2001; Hayden et al. 2011; Schwartenbeck et al. 2013).

The motivational incentives associated with uncertainty may manifest beyond their effects on action selection. In the real world, exploration comes at a cost – not just the cost of abandoning or deferring exploitable rewards, but also, for example, the greater physical effort and energetic investment required for extensive foraging (Charnov 1976b). It thus makes sense that the same motivational incentives promoting exploration also have pragmatic energetic effects; for example, by decreasing the "costs of effort" during cost-benefit considerations (Iodice et al. 2017; Salamone et al. 2009; Walton et al. 2006). In turn, the lower inferred costs of acting promote higher activity rates and information-seeking behavior, whose benefits (e.g., increased reward rate) may become apparent, especially under conditions where rewards are occasional.

In sum, adapting to uncertain environments may require the convergence of cognitive, motivational, and bodily factors, which jointly conspire to make the animal fit to its niche. Exploratory and novelty-seeking behavior need not necessarily be treated in terms of "bonuses," "hopes," or other correctives of a quintessentially reward-seeking behavior, but emerge from normative considerations within belief-based approaches, namely, planning as (active) inference (Attias 2003; Botvinick & Toussaint 2012; Donnarumma et al. 2016; Friston et al. 2016b; Maisto et al. 2015; Pezzulo et al. 2013; Pezzulo & Rigoli 2011; Stoianov et al. 2015; 2018).

Considerations for the study of "incentive hope" and sign-tracking behaviors in humans

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Abstract

The amplification of reward-seeking behavior under uncertainty described by Anselme & Güntürkün is based on the animal literature. However, this phenomenon could provide valuable information for the understanding of several dysfunctional human behaviors such as overeating and gambling. Therefore, we formulated some considerations on how the "incentive hope" hypothesis could be tested on a human population.

The "incentive hope" hypothesis described by Anselme & Güntürkün suggests interesting mechanisms underlying the increase of reward-seeking behavior under uncertainty. We think that this approach could provide a valuable framework for the understanding of a variety of human behaviors that negatively affect well-being, such as overeating, pathological gambling, and substance addiction. Indeed, the uncertainty of the reward delivery seems to be a critical feature of many dysfunctional behaviors. A clear example occurs in the case of pathological gambling, where the uncertainty associated with reward expectations is a key factor in the persistence of the pathological behavior (Linnet et al. 2012). The incentive hope hypothesis thereby represents an interesting research line to pursue to investigate affective processes in humans. On that basis, we formulated some considerations on how the findings from the animal literature described by Anselme & Güntürkün could be translated to a human population.

The first aspect to consider is that the increase in reward-seeking behavior under uncertainty is a phenomenon observed in the realm of Pavlovian conditioning. Decades of behavioral and neuroscience studies in nonhuman animals have led to the proposal that there exists multiple types of behavioral control systems in the brain, among which there is the instrumental system and the Pavlovian system (O'Doherty et al. 2017). The Pavlovian system allows individuals to assign an outcome's affective value (an outcome could be, e.g., a highly palatable food, and it is typically called an unconditioned stimulus) to a neutral stimulus with which it has been systematically associated (e.g., a metronome sound, typically called conditioned stimulus). Pavlovian conditioning is one of the most fundamental forms of behavior that is widely present across the animal kingdom, and has a deep influence on complex forms of human behavior and cognition (O'Doherty et al. 2017; Pool et al. 2014). The instrumental system allows individuals to learn to perform specific yet arbitrary actions (e.g., pressing lever) that lead to a reward (e.g., food). Within the instrumental system, there is the possibility to select actions in a goal-directed manner, which requires a high level of cognitive resources to represent the states, actions, and available goals and to flexibly compute action plans (Balleine & O'Doherty 2010). It is important to note that instrumental and Pavlovian associations are governed by distinct mechanisms (Dickinson & Balleine 1994; Ostlund & Balleine 2008; Sennwald et al. 2017). Incentive hope does not seem to involve goal-directed mechanisms, but it rather appears to involve more primary Pavlovian mechanisms. This aspect is particularly relevant given that research investigating human affective processes often targets goal-directed mechanisms (Moors 2017). Therefore, experimental research aiming at testing the predictions of the incentive hope hypothesis on a human population should target Pavlovian paradigms rather than paradigms involving goal-directed processes.

The second aspect to consider with respect to potential translational research in humans is that the increase in reward-seeking behavior under uncertainty has been observed in a specific class of Pavlovian responses, namely, sign-tracking behaviors. The importance of the existence of multiple classes of Pavlovian responses has for a long time been underlined in the Pavlovian conditioning literature (Balleine & Killcross 2006). There is a classical distinction between two classes of Pavlovian responses: the "preparatory responses" (e.g., heart rate, blood pressure), reflecting the motivational properties of the outcome and the "consummatory responses" (e.g., chewing for a solid food outcome vs. liking for a liquid food outcome Konorski 1967), reflecting the sensory properties of the outcome. It has been suggested that there could be more than two associations between the Pavlovian stimulus and the different aspects of the outcome, for instance, by building associations with the hedonic or temporal aspect of the outcome in addition to the sensory, motivational aspects of the outcome (Delamater 2012; Delamater & Oakeshott 2007). Each of these associations could elicit a different class of Pavlovian responses within the same individual. The different classes of Pavlovian responses are executed in parallel and are underlain by distinct neuronal networks in both animals and humans (Balleine & O'Doherty 2010; Zhang et al. 2016). This suggests that Pavlovian learning is not a unitary process but rather involves a multitude of stimulus outcome associations triggering a multitude of Pavlovian responses. Crucially, these parallel Pavlovian responses can react differently to motivational manipulations: Some classes of Pavlovian responses might be more sensitive to changes in outcome values than others. Therefore, the class of Pavlovian responses measured while testing the effect of uncertainty on human reward-seeking behaviors appears to be fundamental. This highlights the relevance of using Pavlovian paradigms measuring sign-tracking behaviors on a human population.

Nonetheless, to date little research has investigated sign- as opposed to goal-tracking behaviors in humans (Garofalo & di Pellegrino 2015). In animals, sign- and goal-tracking behaviors are distinguished during presentation of the Pavlovian stimulus (e.g., a lever cue that has been associated with the delivery of food in a cup): Some animals approach and engage with the Pavlovian stimulus itself (e.g., approach the lever cue, sign-tracking), whereas other individuals approach the location where the food will be delivered (e.g., approach the food cup, goal-tracking). These inter-individual differences in Pavlovian conditioning are thought to reflect different learning styles that can predict impulsive behaviors and might represent a vulnerability to some mental disorders such as substance abuse (Joyner et al. 2018). Moreover, a consistent amount of research has shown that humans are also attracted to the Pavlovian stimuli themselves: For instance, human attention is very rapidly oriented toward the Pavlovian stimuli (Bucker & Theeuwes 2017; Pool et al. 2014). However, despite the potential contribution that sign- versus goal-tracking propensities could have for identifying risk profiles for substance addiction, the development of paradigms allowing measurement of these two classes of Pavlovian responses in humans is just beginning (Joyner et al. 2018). The development of such paradigms will be extremely valuable to research trying to translate the incentive hope" hypothesis from animals to humans.

In conclusion, we suggest that research testing the prediction of the incentive hope hypothesis in humans should aim at using Pavlovian paradigms and measuring a specific class of Pavlovian responses consisting of sign-tracking behaviors. Such a translational effort of the incentive hope mechanisms could provide valuable information for the understanding of several dysfunctional behaviors observed in humans such as overeating and gambling.

Food security and obesity: Can passerine foraging behavior inform explanations for human weight gain?

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Abstract

Commonly used measures of human food insecurity differ categorically from measures determining food security in other species. In addition, human foraging behaviors may have arisen in a divergent evolutionary context from nonhuman foraging. Hence, a theoretical framework based on food insecurity and fat storage in nonhumans may not be appropriate for explaining associations between human food insecurity and obesity.

Obesity is rising globally and in all regions of the world (UN Food and Agriculture Organisation et al. 2017). However, within countries, obesity is unequally distributed, with lower socioeconomic status often associated with higher prevalence of obesity. The inverse social gradient in obesity is not restricted to high-income countries in North America and Europe; it is also found in lower- and middle-income countries across all continents (Popkin & Gordon-Larsen 2004). Based on associations between food insecurity and high body weight, it has been argued that food insecurity could be a causal factor (Nettle et al. 2017). Anselme & Güntürkün (A&G) advance a theory compatible with this position, proposing mechanisms that might underlie the relationship between food insecurity and obesity. However, problems arise from the application of their model, based on animal behavior, to a human context.

It cannot be assumed that food security as represented in A&G's model is equivalent to routine measures of human food security. A&G use a quantitative measure relating to availability of food in the environment. However, widely used human measures such as the U.S. Department of Agriculture's Household Security Survey Module (Nord et al. 2009) require individuals to assess their qualitative experiences of having enough food to eat, as well as provide cognitive evaluation of their food situation (e.g., being worried about running out of food). Questions asking about actual (as opposed to perceived) food conditions still require explicit evaluation, introducing potential confounding variables between the objective food situation and the response.

While such measures provide insight into attitudes towards food availability, they do not necessarily reflect the same underlying variable as objective measures of food security in nonhuman models. Although this variable might be characterised as perceived food security for humans, it could reflect other (implicit or explicit) attitudes towards food. Implicit and explicit attitudes are not always consistent within individuals (Rydell & McConnell 2006), including in the context of food and eating (Hoefling & Strack 2008). Further, respondents' explicit evaluations of their food conditions are not always consistent with objective measures: A recent U.S. Department of Agriculture study found that experiential measures of food security did not match nutrition-based measures. More than two thirds of households that were undernourished in calories did not report experiencing food insecurity; conversely, around a third of households classified as being adequately nourished reported experiencing mild food insecurity (Broussard & Tandon 2016).

Potential discrepancies between quantitative and qualitative measures suggest that theories proposing food security as a causal factor must define their concept of food security and ensure that this is consistent with the evidence relied upon. Even so, A&G's model does not provide a satisfactory explanation for the positive association between human food insecurity and obesity, which applies only to women in high-income countries (Nettle et al. 2017). This is problematic for A&G's hypothesis, which is based on general psychological mechanisms and thus should be generally applicable. If food insecurity increases behaviors that lead to overeating, the hypothesis predicts that an association between food insecurity and obesity should be observed generally.

To evaluate the relevance of A&G's model to human obesity, we can refer to data that are more directly comparable with food security as it is defined in nonhuman contexts, such as their model of foraging behavior. For example, when food security is assessed by calories available per capita, global trends indicate that food insecurity is decreasing, with daily caloric supply increasing steadily in all regions since 1969 (Alexandratos & Bruinsma 2012). This is not consistent with A&G's hypothesis, which predicts that as food insecurity decreases, obesity should also fall. However, human obesity has been rising rapidly at the same time as food insecurity (when quantified in a manner analogous to that used by A&G) is decreasing.

Just as food security in A&G's model may not correspond to the notion of food security in human populations, the assumption that the simple foraging behavior represented in the model is applicable to humans may not be warranted. Humans possess a combination of relatively large brains, social structures, food-sharing behaviors, and complex foraging techniques not observed in other species (Hill et al. 2011; Schuppli et al. 2016), which may reflect changes in brain metabolism and diet hypothesised to have arisen with the evolution of the genus *Homo* (Leonard & Robertson 1994). Therefore, extrapolation from animal models of foraging to human behavior requires explicit justification, which A&G do not provide.

Today's foodscape differs dramatically from the food environment to which human foraging behaviors were, presumably, well adapted. Consequently, food-related human behavior today may diverge even further from patterns that can be explained by nonhuman models. For example, humans, in common with other species, can discriminate the energy density of foods that occur naturally (i.e., in unprocessed form) in the environment (Gibson & Wardle 2003). This ability is important for successful foraging (Brunstrom & Cheon 2018). Foods occurring naturally during early human evolution were typically low in energy density (<1.75 kcal/g). However in modern, industrialised food environments, common processed foods can be more than twice as energy dense; and when it comes to evaluating foods with an energy density that would have been unusually high historically, human ability to differentiate breaks down (Brunstrom et al. 2018). This suggests that although evolutionary thinking and recourse to psychological mechanisms might be helpful in explaining associations between the food environment and patterns of obesity, characteristics specific to humans and human foodscapes may need to be taken into account.

Although A&G's hypothesis may be useful for explaining foraging behaviors in passerines, the authors' extrapolation from an animal model to human food behavior is neither justified theoretically nor well supported by the patterns of food supply and obesity observed in human populations. To make progress in revealing potential relationships between food security and obesity, it will be necessary to determine precisely what the standard food security measures in humans represent, taking into account psychological processes alongside socioeconomic factors and characteristics of the food environment.

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 an increase in glucocorticoids and that this can also activate the mesotelencephalic dopamine system (Piazza et al. 1996). In that sense, we believe unpredictability is just one of a complex interplay of different inputs that regulate the dopaminergic wanting system. Secondly, it is difficult (at least under natural conditions) to separate unpredictable foraging from at least some form of food restriction, making it very likely that the AgRP-mediated mechanisms we have outlined above also play a role in the increase in foraging, eating, and hoarding under winter-like conditions.

Bringing the knowledge from behavioural psychology to ecological questions is therefore important, and we thank A&G for doing so. Even though we disagree with the details of how they think unpredictable foraging affects foraging motivation, the target article is thought-provoking and raises some very interesting questions that will allow us to better understand how physiological mechanisms have evolved to help animals survive periods of scarce and unpredictable food supply.

Food-seeking behavior has complex evolutionary pressures in songbirds: Linking parental foraging to offspring sexual selection

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Abstract

The target article addresses increased food-seeking behaviors in times of instability, particularly in passerines. We note that food instability might have intergenerational effects on birds: Nutritional stress during development affects song-learning abilities, associating parental foraging with offspring sexual selection. We explore the implications of these compounding selection pressures on food-seeking motivation during breeding, as well as the hormonal underpinnings of these behaviors.

In their broadly relevant target article, Anselme & Güntürkün (A&G) point out that animals, particularly small passerines, are remarkably responsive to unpredictable food sources, eating and storing more food when access to it is limited or unreliable. The authors convincingly link this behavior to an adaptive evolutionary strategy to prevent death by starvation, which would certainly impose a large fitness cost on animals of reproductive age or younger. Here, we aim to extend the argument of A&G by highlighting another potential fitness cost to food unreliability for small passerines, even if the birds survive. Oscine songbirds, a clade that makes up approximately 80% of passerine species, learn their song from an adult tutor, and females use the quality of a male's song to assess his potential as a mate (Byers & Kroodsma 2009; Catchpole & Slater 2003; Nowicki et al. 2002b). Importantly, reduced access to food early in development is linked to a reduction in song quality: When juvenile birds experience elevated stress levels because of food restriction or high parasite load, they produce lower-quality songs in adulthood, presumably because the stress has impeded development of the neural pathways underlying song learning (MacDonald et al. 2006; Schmidt et al. 2014; Spencer et al. 2005).

In addition, stress during development has been linked to reduced fitness, measured by increased mortality and decreased reproductive output (Blas et al. 2007; Gorman & Nager 2004). Taken together, these studies suggest that song-learning prowess in birds is linked to their access to food early in life, which, by extension, implies that learned vocalizations can be honest signals of fitness due to the effects of nutritional stress (Buchanan et al. 2003; Nowicki et al. 2002a) In this sense, food instability is particularly impactful when passerine birds are raising offspring. If birds raise their chicks in times of limited food availability, the resulting stress can make their offspring less sexually attractive even if food is subsequently becomes abundant and predictable. An increase in foraging behavior in such an environment may protect against this potential decrease in (offspring) reproductive fitness. Thus, adult birds that are particularly sensitive to the motivational effects of food instability, and enhance their food-seeking behaviors in response, could have more reproductively successful offspring. Therefore, in addition to the *natural selection* pressure on birds to respond to food unpredictability by increasing food-seeking behavior, there could also be a *sexual selection* pressure on these birds' offspring, with potential indirect fitness effects on parental behavior. In theory, the offspring with the best songs after seasons of food shortages – potentially those offspring whose parents were most active in food-seeking behaviors in times of instability – would be favored by sexual selection. Thus, the conceptual framework proposed by A&G has broad relevance to future studies in multiple evolutionary contexts.

The target article explores the causal underpinnings with respect to the direct fitness effects of food unpredictability on the individual level. We suggest that these mechanisms may be complicated when considering the intergenerational fitness effects of clutch rearing, modulated by both offspring sexual selection and survival. Adults tending to nestlings must temporarily dramatically increase their food-seeking behavior; food unpredictability during breeding causes an evolutionary dilemma regarding resource allocation to parents versus offspring. To maximize reproductive success of current offspring, parents should allocate resources overwhelmingly toward nest provisioning; however, depending on the parents' potential for future breeding success, it may be more advantageous to instead allocate all resources toward self-preservation.

As A&G note, food unpredictability is a known stressor; accordingly, the vast majority of studies on the subject of nest provisioning during harsh conditions have focused on the role of corticosterone, the homolog of human cortisol present in birds. In some avian species, experimentally and endogenously elevated baseline corticosterone levels have been correlated with moderate increases in parental investment, even when they increase the time spent away from the nest, consistent with increased foraging (Bonier et al. 2009; 2011; Kitaysky et al. 2001; Miller et al. 2009; Ouyang et al. 2013) This may be directly tied to demonstrated inverse relationships between levels of corticosterone and prolactin, the hormone linked to maintaining nest-attendant behavior. Paradoxically, reducing the drive to tend to a brood promotes the requisite departure from the nest to forage.

Any reproductive fitness benefit from elevated corticosterone during food instability, however, seems to have an upper limit, as high levels of corticosterone have resulted in reduced provisioning or complete abandonment of offspring (Kidawa et al. 2017; Silverin 1986). When the threat to survival is severe, it is evolutionarily advantageous for an adult to reallocate all resources away from offspring toward self-preservation. In this situation, corticosterone depresses prolactin enough to overcome nest attachment and facilitate nest abandonment (for a review, see Angelier & Chastel 2009).

Very few studies in birds have considered the role of dopamine in modulating reproductive behaviors during periods of food scarcity or in general (Angelier et al. 2016). Based on evidence from other animal taxa, dopamine may have an important and potentially context-dependent function in mediating foraging behaviors as they relate to reproduction. Studies in rodents have shown that dopamine promotes maternal attachment and that dopamine dysfunction can lead to abandonment of pups (for a review, see Dulac et al. 2014). We wholly agree with A&G's call for studies testing their predictions regarding dopamine and foraging behaviors in small passerines (sect. 6).

To complement the impressive contributions of the target article, we suggest that, in multiple ways, the discussion of food-seeking behavior is complicated by its link to reproductive success, particularly in passerine birds. Behaviorally, food-seeking behaviors in times of resource uncertainty can have an outsized effect on offspring fitness because the ability to learn song in oscine songbirds is affected by nutritional stress during development, thus linking parental foraging to offspring sexual selection. Extending from the authors' proposed topics of study, it is worth further investigating the interaction of dopamine and corticosterone and its evolutionary links to songbirds' foraging-mediated reproductive fitness.

Random isn't real: How the patchy distribution of ecological rewards may generate "incentive hope"

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Abstract

Anselme & Güntürkün generate exciting new insights by integrating two disparate fields to explain why uncertain rewards produce strong motivational effects. Their conclusions are developed in a framework that assumes a random distribution of resources, uncommon in the natural environment. We argue that, by considering a realistically clumped spatiotemporal distribution of resources, their conclusions will be stronger and more complete.

Science is advanced by identifying novel connections among disparate findings and by developing new theories (Jack et al. 2018). Anselme & Güntürkün (A&G) do both, integrating proximate neural mechanisms with evolutionary theories and extending the integration via mathematical modeling. Their thesis provides an impressive and timely connection between two disparate fields: the psychology of motivation and animal foraging. When bringing together separate bodies of literature, even the most scholarly integration can overlook important details (Fitzpatrick et al. 2018). We believe that the authors underappreciate a critical feature of natural environments – the spatial distribution of resources – and how profoundly the spatial distribution of food will affect selection on neural mechanisms and animal behavior, as well as the outcome of foraging models (Arditi & Dacorogna 1988; McIntyre & Wiens 1999; Pyke 2015).

Most laboratory trials are based on random reward schedules. In natural environments, food may be rare, but it is seldom distributed randomly in space or in time (Iwasa et al. 1981; Racey & Swift 1985). Given that a single plant produces many seeds, an animal finding one seed is predictive of finding another nearby. River valleys, tree fall gaps, and low-lying wet areas support a local abundance of plants that are otherwise rare across the landscape. Nests, burrows, and swarms often contain multiple edible prey. For most animals, then, the probability of finding food items is not independent of recent experience. As resources predict other resources nearby, local foraging is incentivized after finding an initial reward (Krebs et al. 1974). Expectation of enhanced rewards can be seen even in humans when finding one good restaurant causes people to anticipate other good restaurants in the area. By assuming an environment where the probability of reward is independent of previous events, A&G miss key dynamics inherent in natural contexts, particularly a likely explanation for the apparent overperformance of animals under conditions where reward is uncertain. Although the experimental paradigm for sign-tracking studies may be one of random reward, the neural circuits and behaviors that are tapped likely evolved under conditions where rewards were not truly random but changed in probability based on recent foraging experience. This nonrandom distribution of rewards in natural environments can explain increased attention when reward is uncertain, a phenomenon that has been previously explained using hypotheses including frustration and simple attention to unexpected outcomes.

The statistical distribution of food resources has important implications for proximate neural mechanisms and emergent foraging behaviors. A&G connect stress to elevated dopamine levels, which are in turn connected to increased exploration, risk taking, and gambling. If food is discovered after a stressful period of starvation, there is good reason for the animal to expend additional energy and incur additional risk if the probability of imminent success is higher than it has been. The fact that exploration and risk taking are particularly enhanced when a stressed animal is feeding or drinking further suggests that these pathways are well suited to helping organisms exploit local resource patches. Furthermore, dopamine is highest when uncertainty is greatest, increasing the salience of immediate rewards and promoting learning, potentially reinforcing a recently successful foraging strategy. Rather than elevated performance under uncertainty being something of an odd anomaly in need of explanation, it is likely to be incredibly adaptive in natural environments, allowing organisms to adjust their motivation and investment in response to the local probability of finding additional resources in the same place or time or using a similar foraging strategy. Even the use of the word *hope* in the concept of "incentive hope" underscores the way that one successful foraging event appropriately changes the expectation of success for additional attempts in a similar time and space.

If the phenomenon of incentive hope arises from the spatial and temporal distribution of food in evolutionary environments, the hypothesis predicts that some species should express incentive hope more strongly than others and that specific behavioral contexts can elicit incentive hope. For example, one prediction is that incentive hope will be more strongly expressed by species that experience patchy resources than by species that inhabit environments where resources are comparably rare, but are more evenly distributed across the landscape. Indeed, some of the species that have been most studied for sign-tracking and foraging behavior (such as rats and small passerines) have highly clumped food resources. During laboratory training, the expression of incentive hope may be exacerbated by supplying non-independent rewards (where animals experience runs of success and failure and thereby learn to respond more strongly after encountering a first successful response). The importance of these recent experiences could be tested in a sign-tracking paradigm where the reward is still delivered in 50% of the trials, but the probability of reward is contingent on the previous probability of reward. The evolved tendency to expect strings of rewards might also be revealed in people and other animals through slot machine scenarios that include near misses and "payouts" that are less than the cost of play (Harrigan et al. 2010; Scarf et al. 2011). Finally, the simulation developed by A&G is well suited for determining whether clumped resources increase the tendency and ability of organisms to gather and store resources over the scenario of random resource distribution.

A&G use the term *incentive hope* to indicate that the animal "is in a state of motivational excitement for possible good news (rewards) when bad news (non-rewards) is likely" (sect. 4.2.1, end of para. 1). A critical thing to note about incentive hope and foraging behavior is that, although bad news may be likely, once one food item is found, bad news is less likely than it was before.

Overlapping neural systems underlying "incentive hope" and apprehension

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Abstract

Positioning "incentive hope" in a general model of behavioral control systems removes artificial boundaries between mechanisms of incentive motivation in foraging behavior and other functions of the striatum and connected systems. Specifically, incentive hope may involve mechanisms of anticipation of both reward and threat, explaining why anxious individuals show stronger potentiation of incentive motivation under conditions of reward uncertainty.

Animal research suggests that neural systems are fundamentally organized to discriminate conditions of low resources and unmet energy needs from conditions of high resources and met energy needs and to regulate behavior, effort, autonomic function, and homeostasis accordingly (Schneider et al. 2013). Energy acquisition and storage are an important prerequisite for reproductive success. Thus, in most species, behavioral sequences are organized so that a period of eating and fattening often precedes mating and caring for offspring. This is particularly important in habitats where food availability fluctuates or is unpredictable (Schneider et al. 2013). Perceptions of having a surplus of resources and energy shift the regulatory focus from immediate, momentary concerns and harm prevention toward future-directed behavior and investments.

Based on this fundamental organization of neural systems, we recently proposed a neurobehavioral theory of predictive and reactive control systems (PARCS; Tops et al. 2014; 2017). PARCS integrates evidence of separate neural systems that control behavior, autonomic responses, and homeostasis in predictable, familiar, and stable environments versus unpredictable, unstable, and novel environments, respectively. PARCS suggests that a ventral, reactive control system evolved for the purpose of processing novelty and biological salience to control behavior in unpredictable as well as urgent and emergency situations. It responds in a feedback-guided manner to the immediate situation and focuses attention narrowly on the local situation. This system includes areas such as the anterior insula (AI), inferior frontal gyrus (IFG), amygdala, and ventral striatum. On the other hand, PARCS suggests that the dorsal, predictive control system engages in creating internal models that predict future outcomes through simulation and updates those models slowly during learning, in line with the idea that it responds to environmental predictability and familiarity. This system implements feed-forward action control and includes areas such as the posterior cingulate cortex, precuneus, dorsolateral prefrontal cortex, and dorsal striatum.

Learning of a novel task involves a ventral-to-dorsal shift in reactive-to-predictive (and eventually habitual) processing through corticostriatal neural loops, forming schemata and predictive internal models for efficient task performance (Tops & Boksem 2012; cf. Alcaro & Panksepp 2011). Based on the physiology and behavioral pharmacology of different parts of the striatum, it has been proposed that the ventral striatum responds to temporally unpredictable stimuli (which require interruption of ongoing behavior) and that the dorsal striatum responds to temporally predictable stimuli (i.e., stimuli that are so predictable that animals engage in behavior just prior to the stimulus; Nicola 2007). Similar to temporally unpredictable stimuli, reward uncertainty may activate the ventral striatum and require reactive control, because uncertainty of reward delivery produces prediction error signals that interrupt routinized responding.

Based on the above, we suggest that "incentive hope" reflects a type of anticipation that involves the activation of reactive control in unpredictable circumstances. This anticipation involves focused attention on the here and now. At first sight, this focus on the here and now sounds contradictory to "anticipatory." But it is central to reactive control: If the onset of an appetitive or aversive stimulus is unpredictable but potentially impending, then reactive control (i.e., focus on the here and now) is kept in ready mode (sustained attention, vigilance) for immediate feedback-guided responses to the stimulus. The resulting prolonged sense of immediacy is characteristic of anticipatory anxiety, which makes this anxiety condition aversive with intense responses to pain and other aversive stimuli. The prolonged sense of immediacy likewise invigorates responding to appetitive stimuli: The prolonged focused processing of a potentially impending food stimulus magnifies the motivational processes underpinning food seeking under uncertainty. Although this mode of response/appraisal readiness does not involve prospection based on predictive control and internal models, it is anticipatory because reactive control (in response to unpredictability and conditioned stimuli) puts goal, task, and target stimulus activations in a maintenance working memory buffer. Such functions of reactive system areas such as the IFG are well reported in the neuroimaging literature (e.g., Blumenfeld & Ranganath 2007; De Baene et al. 2012; Hampshire et al. 2009; Owen et al. 1999). For instance, the IFG may project back to the temporal lobe to keep representations active, allowing for stimuli and task set to interact when coming in sequentially (e.g., Assadollahi & Rockstroh 2008).

The state of readiness in anticipation of unpredictably timed or uncertain stimuli is also required in vigilance tasks that activate a set of mainly right-lateralized brain regions that may form the core network subserving vigilant attention in humans, including IFG, AI, and the temporoparietal junction (Langner & Eickhoff 2013). Moreover, often right-lateralized reactive system areas in the IFG and AI have been implicated in incentive motivation (Naqvi & Bechara 2009), anticipation of pleasant and aversive stimuli (Knutson & Greer 2008), and anticipatory anxiety (Carlson et al. 2011; Simmons et al. 2011). For instance, suggesting that the AI is preparing for the sensory and affective impact of the stimulus, the degree of activation in the AI during anticipation is correlated with experienced stimulus intensity and with the degree of activation in the caudate during stimulus processing (Lovero et al. 2009). Additionally, the AI shows sustained activation by unpredictable but not predictable threat (Alvarez et al. 2011).

Anticipatory processing in reactive control may be implicated in the potentiation of incentive motivation under conditions of reward uncertainty (hope) and punishment uncertainty (apprehension), both for uncertain delivery and timing. In obese subjects, AI revealed increased functional and effective connectivity in response to food cues, especially to striatal regions (Garcia-Garcia et al. 2012; Kullmann et al. 2013; Nummenmaa et al. 2012). In posttraumatic stress disorder, a disorder associated with the experience of decreased predictability and control, excessive anticipatory reaction of the AI to temporally unpredictable aversive stimuli related to greater perceived threat (Simmons et al. 2013). These examples illustrate that, through the overlap of incentive hope and apprehension in reactive control, PARCS theory may explain why anxious individuals show stronger potentiation of incentive motivation under conditions of reward uncertainty (Hellberg et al. 2018).

“Incentive hope” and the nature of impulsivity in low-socioeconomic-status individuals

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Abstract

Low-income environments have been associated with greater levels of impulsive behavior, which contribute to the higher debt and obesity rates that further perpetuate current wealth and health disparities. In this commentary, we describe how this might be explained by an appeal to “incentive hope” and the motivational drive toward consumption triggered by the future uncertainty these groups face.

Anselme & Güntürkün (A&G) present a mechanistic explanation for the enhanced foraging behavior observed in animals living under conditions of uncertainty. This commentary examines how their “incentive hope” hypothesis might also explain related phenomena based on behavioral observations in humans. In particular, we suggest that the greater rates of impulsive decision making associated with people in low-socioeconomic-status (SES) environments may stem from the relative resource scarcity they experience and the subsequent uncertainty of their future stability. We also describe some implications of this theoretical effort in addressing wealth inequality and promoting adaptive decision making in low-SES populations.

In modern society, impatience and impulsivity, where individuals pursue immediate gratification rather than long-term rewards, can have a significant impact on daily life decisions. Important examples include saving enough for retirement (Laibson et al. 1998), investing in higher education (Castillo et al. 2011; Eckel et al. 2013), buying on impulse and accruing credit debt (Meier & Sprenger 2010; 2013), and obesity (Courtemanche et al. 2015; de Oliveira et al. 2016). A growing amount of evidence indicates that impulsive decision making is more prevalent among people in low-SES environments and is connected to a constellation of negative outcomes. For example, societies with significant income inequality, that is, Gini coefficients greater then 0.5, have higher rates of obesity and type II diabetes (Wilkinson & Pickett 2011). There are also a greater number of low-income individuals taking out short-term, high-interest loans (Bair 2005). This characteristic pattern of impulsivity has been systematically studied in the laboratory. Participants who are experimentally induced to experience low-SES indicators in terms of income or job types choose foods with higher caloric intake (Cheon & Hong 2017), make riskier financial decisions (Burdick et al. 2013; Payne et al. 2017; Shah et al. 2012), and demonstrate greater impulsive spending (Yoon & Kim 2016). These findings introduce an apparent paradox: Why would individuals experiencing so much difficulty in their lives engage in greater amounts of impulsive behavior that *increases* their vulnerability?

One explanation for the greater levels of impulsivity found in low-SES groups is consistent with the incentive hope hypothesis, which focuses on the impact of resource scarcity in the surrounding environment. We believe that the life experiences and relative deprivation that people struggling with economic hardship face engenders a feeling of uncertainty and insecurity toward the future, which in turn motivates more impulsive resource-seeking behavior. The relationship between one’s future prospects and impulsive decision making has often been studied via temporal discounting tasks, in which participants are asked to choose between receiving a smaller monetary amount sooner or a larger amount later. Studies have shown that discounting rates, which could be interpreted as a measure of impulsivity, can change by making people think more about their future (Appelt et al. 2011; Brown et al. 2015; Hershfield et al. 2011; Weber et al. 2007). In general, people become less impulsive when prompted to think toward the future. However, future prospects are not equally bright for people in low-SES environments who face multiple challenges and ongoing struggles in their lives. Several studies have shown that poverty distorts an individual's mindset to be focused on the present and have distrust toward the future (Farah & Hook 2017; Haushofer & Fehr 2014; Shafir 2017; Shah et al. 2012). To directly test how having negative future prospects can change an individual's intertemporal choice, we recently conducted an experiment in which participants were primed with either a positive and promising or a negative and unstable future prospect in an economic, geopolitical, and environmental domain. We found that the negative future primes increased discounting rates relative to baseline measures, whereas no such effect was found with positive primes (Kwak et al. 2017). These results indicate that the way one's future is perceived can have a significant impact on how individuals trade off present and future consumption.

In the wild, the link between impulsivity and future uncertainty is most evidently shown under harsh environments; animals hoard and consume more food when exposed to an unpredictable food supply. A&G provide a mechanistic explanation for this, focusing on how the brain's motivational system changes when subjected to resource scarcity. Specifically, they describe how unpredictable access to resources enhances "incentive hope," which manifests as an increase in seeking behavior and a greater motivational drive toward consumption. In humans, individuals in low-SES environments may experience comparable circumstances that trigger a similar response – limited access to resources contributes to an overall sense of uncertainty about one's future prospects. Facing repeated hardship and unpredictability in this way may result in a similar shift in the brain's motivational system. Overall, this increasing motivational drive might manifest itself in terms of both an immediate increase in the consumption of resources and a cascade of problematic behaviors such as substance use and pathological gambling, which are both more prevalent in these vulnerable populations (Casswell et al. 2003; Hiscock et al. 2012).

Understanding the nature of impulsivity in low-SES groups in terms of incentive hope also helps motivate potential interventions that may help mitigate some of the negative consequences of impulsive decision making, ranging from financial debt to obesity and other addiction-related outcomes. Specifically, if the feeling of unpredictability or uncertainty toward the future is what triggers greater incentive hope and a maladaptive motivational drive, we can start by focusing on mediations that build trust and reliability. A recent real-world intervention study demonstrates that providing a supportive social environment by promoting community trust can reduce impulsive decision making in low-income individuals as measured through temporal discounting (Jachimowicz et al. 2017). These results are particularly intriguing as prior research indicates that low-SES individuals, in general, have less trust in society (Brandt et al. 2015; Sirola & Pitesa 2017). Future research should address ways to effectively enhance trust and reduce feelings of future uncertainty in our world's most susceptible groups. Increased focus on mechanistic explanations such as that proposed in the target article will, it is hoped, lead to more practical solutions to help mitigate the long-running wealth and health inequalities that societies face around the world.

Beyond "incentive hope": Information sampling and learning under reward uncertainty

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Abstract

Information seeking, especially when motivated by strategic learning and intrinsic curiosity, could render the new mechanism "incentive hope" proposed by Anselme & Güntürkün sufficient, but not necessary to explain how reward uncertainty promotes reward seeking and consumption. Naturalistic and foraging-like tasks can help parse motivational processes that bridge learning and foraging behaviors and identify their neural underpinnings.

Anselme & Güntürkün (A&G) propose a new mechanism, "incentive hope," inspired by both behavioral science and neuroscience, to explain how exposure to reward uncertainty could lead to increased reward-seeking effort and reward consumption. We agree with the authors that it is crucial to identify common motivational processes that bridge learning, decision making, and foraging behaviors. However, we cautiously suggest that their explanation, although sufficient, is not necessary. In other words, other motivating factors, not necessarily mutually exclusive with incentive hope, could lead to the same behavior.

In one-shot choices, animals should maximize expected reward, but in repeated gambles, animals ought to maximize long-term intake; this means actively sampling risky options if there is an opportunity to learn more about distributions (Daw et al. 2006; Pearson et al. 2009). Multiple factors contribute to uncertainty. These include variation in prey quality, variation in spatial and temporal distributions of prey (patchiness, density, etc.), stochastic prey quality, and rate of variation in environmental factors (volatility) (Stephens & Krebs 1986). Therefore, after a fresh encounter with a prey (or failure to find an expected prey), animals must assign credit; that is, they must decide which factor(s) contributed to the experience to update and infer (learn) a mental model of the environment and make predictions to guide future behavior (Noonan et al. 2010; Rushworth et al. 2011; Walton et al. 2010).

Building a mental model of the environment yields more successful decisions in the long run but requires sampling to gather information. Information sampling often comes in the guise of locally suboptimal decisions, such as exploration (Daw et al. 2006; Pearson et al. 2009). Numerous species can exploit complex environments rich with uncertainty (e.g., Bateson & Kacelnik

1997; Blanchard et al. 2014; De Petrillo et al. 2015; Kacelnik & Bateson 1997). Many organisms will forego primary reward to seek information that provides strategic benefits or satisfies curiosity (Blanchard et al. 2015a; Bromberg-Martin et al. 2010; Kidd & Hayden 2015; Wang & Hayden 2018). Animals appear to be aware of their own uncertainty; their proclivity to sampling information is affected by ambiguity of the information and their confidence in the estimation (Kiani & Shadlen 2009; Kornell et al. 2007; Pouget et al. 2016).

This information-seeking perspective offers an alternative explanation for some of the behaviors that incentive hope explains. For example, A&G argue that sign-tracking behavior is motivated by incentive hope. Alternatively, sign tracking could reflect incomplete learning (in the process of building a mental model of the environment, transitioning from model-free to model-based control), high ambiguity of new reward information, and/or low confidence in the current mental model, whereas goal tracking could reflect complete learning (model-based control), low ambiguity of new reward information, and/or high confidence in the current mental model. This means that the heightened reward-seeking behavior that A&G argued as being motivated by incentive hope could reflect sampling of information to form a better estimation of uncertain rewards or building a mental model of the task/foraging environment used in model-based reinforcement learning.

A&G use several findings about ventral tegmental area (VTA) dopamine neurons to make reverse inferences about motivations for behavior. However, recent empirical and theoretical developments on dopamine responses suggest that dopamine neurons interact with a vast network of striatal, orbitofrontal, and prefrontal regions that play a critical role in learning and represent the task state to build a mental model of the current task and guide behavior (Abe & Lee 2011; Behrens et al. 2007; Blanchard et al. 2015a; Boorman et al. 2011; Bromberg-Martin et al. 2010; Chang et al. 2017; Gershman & Schoenbaum 2017; Hayden et al. 2009; Langdon et al. 2018; Sadacca et al. 2016; Takahashi et al. 2017; Wang & Hayden 2017). This means that the dopamine response described by the authors as reflecting the motivational power of incentive hope could potentially reflect a learning signal that differentiates the various sources of environmental factors involved in reward uncertainty (cf. Bromberg-Martin et al. 2010).

We do not believe that all ostensible cases of incentive hope are really just cases of information seeking. We think the explanation proposed by A&G is often correct. Instead, we argue that neuroscientists need to move toward behaviorally rich but well-controlled tasks to disambiguate factors that can be intractable with traditional low-dimensional lab tasks (Kaplan et al. 2017; Pitkow & Angelaki 2017; Schonberg et al. 2011). For example, incentive hope and information seeking are hard to isolate and manipulate in traditional lab paradigms – yet an at least somewhat controlled laboratory environment is necessary for sufficient control of confounding variables.

Thus we propose that a valuable path forward will be seminaturalistic foraging-like decision paradigms. Careful analysis of behavior, along with consideration of the tenets of foraging theory, will be able to separate various motivational factors (Blanchard et al. 2015b; Calhoun and Hayden 2015; Hayden 2018; Mobbs et al. 2018). Such tasks can reveal deeper coding of task variables than conventional tasks and analyses can (e.g., Killian et al. 2012; Musall et al. 2018; Strait et al. 2016; Wirth et al. 2017). It is likely that large-scale, multiple-unit recordings will be necessary to take advantage of the likely rare occurrences of cognitively important events. We are especially sanguine about virtual reality settings, as these allow both full controllability and relatively immersive task environments (Kaplan et al. 2017; Minderer & Harvey 2016). Such tasks can focus on independent manipulation of a task's or foraging environment's richness, reward density, and patchiness, as well as the ambiguity and volatility of uncertainty reward.

How uncertainty begets hope: A model of adaptive and maladaptive seeking behavior

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Abstract

The "incentive hope" model creatively explains hoarding and fat accumulation by foragers under uncertainty and food seeking when food cues are present but food is not. The model has difficulty explaining why animals driven by cues fare better than animals driven by food reward itself, why human obesity exists when food is abundant, and why people enjoy gambling and care about winning.

Anselme & Güntürkün (A&G) introduce the concept of "incentive hope" to explain foraging in animals when food supply is uncertain. Uncertainty-induced dopamine release invigorates pursuit of cues signaling food availability, when the association between cues and food is unreliable (cf. Fiorillo et al. 2003). Incentive hope differs from incentive salience because it entails pursuit of remote rewards and is evoked specifically by uncertainty, whereas salience mediates approach of proximal rewards (Berridge 2007).

A&G advance several novel ideas. First, Pavlovian autoshaping is cited to explain how uncertainty promotes foraging. In autoshaping, animals persist in seeking a reward when a conditioned stimulus (CS) is present both when food (unconditioned stimulus [UCS]) is delivered and when it is withheld (Brown & Jenkins 1968). Autoshaped responses persist despite prolonged absence of reward, indicating they are under Pavlovian rather than instrumental control. A&G note that animals foraging under uncertainty hoard more food and store more fat than animals foraging when food is reliably available (Pravosudov & Grubb 1997). Thus, uncertainty-induced foraging represents an evolutionary advantage to individuals that do this most effectively. In autoshaping, these individuals are called *sign-trackers*, and their behavior differs reliably from that of animals whose seeking is more instrumental. The latter group, goal-trackers, use CSs primarily to facilitate access to food. In contrast, sign-trackers find CSs rewarding in their own right: They seek and interact with them more than UCSs that they signal (Robinson & Flagel 2009). Second, incentive hope entails the recruitment, during uncertainty, of glucocorticoids, which in turn activate dopamine

(Barrot et al. 2000). Much like a car's accelerator, glucocorticoids permit the transmission to work harder while signaling availability of fuel for expenditure when dopamine-mediated reward seeking occurs. Third, the incentive hope model asserts that invigoration of reward seeking during uncertainty is not subjectively reinforcing. It is strictly an adaptive response born of necessity. When predictable and unpredictable rewards are available, animals choose the former (e.g., Smith & Zentall 2016).

A&G extrapolate from foraging in animals under uncertainty to humans under unpredictable living conditions, suggesting that incentive hope may explain excessive-compulsive behaviors such as substance abuse, pathological gambling, and overeating and obesity. The correspondence with overeating is straightforward. The correspondence with substance abuse and pathological gambling is less so. In the case of gambling, the authors assert that casinos are essentially human autoshaping boxes. Like autoshaped rats, gamblers persist despite ongoing losses because of the presence of CSs (e.g., lights, bells), whose association with reward delivery is uncertain. Although most people gamble for some time and then quit, typically when their money runs out, a few persist despite ongoing losses, a behavior called "chasing" (Toce-Gerstein et al. 2003). These pathological gamblers have presumably fallen prey to autoshaping.

Incentive hope is a valuable extension of the incentive salience concept as it explains why animals pursue rewards that are physically absent. The linkage with autoshaping is novel and defines a potential mechanism to explain chasing in pathological gamblers. The putative facilitatory role of glucocorticoids helps explain how stress translates into reward seeking under uncertainty and aligns with empirical evidence of deficient basal cortisol transmission in pathological gamblers (Zack et al. 2015). Targeting neural substrates of autoshaping (e.g., dorsomedial striatum; Torres et al. 2016) may also improve interventions for maladaptive reward seeking under uncertainty in humans.

Along with these many strengths there are a few shortcomings. First, as A&G note, delay of reward may be even more important than uncertainty as a driver of food seeking (Mazur 1987). If an animal experiences a 1-week lack of food at exactly 2-month intervals, it may be more inclined to hoard and store fat than an animal that encounters food at irregular intervals of a few hours. Thus, of the two motivating factors, uncertainty and delay, fear of starvation may be a more important motivator than incentive hope. Second, the adaptive phenotype in A&G's model is a sign-tracker. Sign-trackers engage primarily with CSs, not UCSs (Robinson & Flagel 2009). Thus, sign-trackers may be more interested in, and interact more extensively with, a particular species of tree (CS) than with the eggs (UCS) that are likely to be nested there. Under these conditions, goal-trackers may fare better in evolutionary terms simply by following sign-trackers to a location where they can usurp the food. Third, incentive hope predicts maximally vigorous food seeking and fat storage under conditions of food uncertainty. This does not explain why copious food supply and reliable CSs for food (e.g., restaurants) coincide with the current epidemic of obesity (cf. Vucetic & Reyes 2010). Uncertainty of food predicts food seeking and hoarding in nature. This is not tantamount to uncertainty *in general* – the anxiety of modern society – as a driver of food seeking. At best, food seeking in this scenario is a form of displacement or adjunctive behavior rather than a direct response to unpredictable food. Fourth, the idea that reward seeking under uncertainty is strictly utilitarian does not translate well to gambling. Social gamblers willingly spend time, energy, and resources to access unpredictable rewards in casinos. They also display numerous behaviors indicative of pleasure. Players at a roulette table often display or verbalize intense anticipatory excitement (Goudriaan & Clark 2013). Similarly, slot machine gamblers report eager anticipation of winning (Ladouceur et al. 2003). These expressions of positive arousal may correspond loosely to 50-kHz vocalizations of rodents when amphetamine is injected into their nucleus accumbens (Burgdorf et al. 2001). In addition, pathological gamblers are strongly driven by the desire to win (Lee et al. 2007). They chase losses precisely because they hope for a win that will erase their losses, not because of an automatized Pavlovian response, although Pavlovian factors may be involved. A key reason why uncertainty is pleasurable in gambling, unlike foraging, is that the potential reward far outweighs any lost investment or opportunity foregone (Gainsbury et al. 2014). As long as a jackpot awaits, every trial is suffused with eager anticipation.

In sum, incentive hope provides a novel explanation for foraging. However, the factors that mediate foraging under uncertainty in nature do not correspond fully to excessive-compulsive behaviors in humans. Uncertainty is a powerful driving force in nature and in some human environments. I believe incentive hope is most useful as a heuristic to guide inquiry and that foraging under uncertainty in animals is an analogy rather than a direct counterpart to human excessive-compulsive behavior.

Authors' Response

Incentive hope: A default psychological response to multiple forms of uncertainty

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Abstract

Our target article proposes that a new concept – incentive hope – is necessary in the behavioral sciences to explain animal foraging under harsh environmental conditions. Incentive hope refers to a specific motivational mechanism in the brain – considered only in mammals and birds. But it can also be understood at a functional level, as an adaptive behavioral strategy that contributes to improve survival. Thus, this concept is an attempt to bridge across different research fields such as behavioral psychology, reward neuroscience, and behavioral ecology. Many commentaries suggest that incentive hope even could help understand phenomena beyond these research fields, including food wasting and food sharing, mental energy conservation, diverse psychopathologies, irrational decisions in invertebrates, and some aspects of evolution by means of sexual selection. We are favorable to such extensions because incentive hope denotes an unconscious process capable of working against many forms of adversity; organisms do not need to hope as a subjective feeling, but to behave *as if* they had this feeling. In our response, we carefully discuss each suggestion and criticism and reiterate the importance of having a theory accounting for motivation under reward uncertainty.

We gracefully thank the different commentators for their thoughtful and inspiring reflections on the concept of incentive hope. We had proposed this concept in our target article to explain foraging motivation when access to food is unpredictable. Many of the commentaries consist of positive attempts to enlarge the applications of our concept beyond the limited context in which we used it, that is, mainly food seeking in nonhuman animals. Other commentaries are more critical, suggesting that the concept accounts for less than it should or is reducible to other concepts. These reflections have been helpful to us in broadening the scope of incentive hope to a certain extent and also reinforce our argumentation regarding some criticisms.

Our target article generated discussions about uncertainty and behavior from many distinct research fields that reach from protistology (**Clark**) to social anthropology (**Aharonov-Majar & Suleiman; Misiak, Sorokowski, & Karwowski** [**Misiak et al.**]). Despite the breadth of these fields, the comments and criticisms can be grouped in a small number of directions. Thus, the response is organized according to the degree of agreement with our view. Section R1 is a response to commentators who suggest that the concept of incentive hope is unnecessary (other explanations work) and/or insufficient (requires other parameters) to account for behavior under uncertainty. Section R2 specifically discusses the relevance of the incentive hope hypothesis in shedding light on maladaptive behaviors such as gambling and pessimism. Section R3 is about the scope and the limits of our computational model and its relation to the theory itself. Finally, section R4 considers possible extensions of the concept of incentive hope beyond food-seeking behavior and describes why it is potentially applicable to phylogenetically distant species, too.

R1. Is incentive hope a useless concept?

Several commentators suggest that incentive hope is an unnecessary and/or insufficient concept to explain stronger foraging motivation in an environment that is sending signals that the available amounts of food are low. In contrast, we explicitly stress the importance of incentive hope here, while recognizing that it is not the whole story about food seeking.

R1.1. "Wanting" and fear

According to **Smulders, Boswell, & Henderson** (**Smulders et al.**), incentive salience (or "wanting") is not limited to approaching a present stimulus, and unpredictability is simply only one of its numerous modulatory factors. It is correct that "wanting" can be recruited whether a stimulus (conditioned or unconditioned [CS or UCS]) is present or absent, although a large majority of experiments refer to the direct perception of the stimulus. Our simplification aimed to suggest that organisms may differently process the predictable presence and the unpredictable absence of the stimulus, because unpredictability is only significant in its absence. We hypothesized that evolution shaped mechanisms that enhance food seeking under unpredictability because of potential negative consequences for survival. Unpredictability and its negative consequences cannot be determinants of "wanting." Actually, these two factors lead to a paradox between motivation and preference: If unpredictability and its negative consequences increased incentive salience only (as the higher response rates suggest), they should be preferred to predictability and positive consequences for survival. As shown, this does not happen. The goal of the incentive hope hypothesis is precisely to solve this kind of paradox while remaining coherent relative to the well-established concept of incentive salience. Thus, our concept appears necessary and may be revealed to be useful each time an uncertainty-induced behavioral paradox is found. In addition, without incentive hope, an increase in foraging activity should be interpreted as the consequence of a strong deprivation-related "wanting." However, intense food deprivation weakens the forager, causing slower movements and ineffective search. A process such as incentive hope, in which "wanting" is only a modulatory factor, can stimulate seeking behavior before the forager is close to starvation. We agree with Smulders et al. that a sophisticated neurophysiological machinery can have an impact on "wanting," but this does not demonstrate that "wanting" is sufficient to explain animal foraging under all environmental conditions. Psychological and neuroscientific investigations (e.g., partial reinforcement and contrafreeloading) indicate that foraging motivation requires more than "wanting." Distinct neurophysiological mechanisms may be correlated with distinct, complementary psychological processes. In particular, we believe that the interaction between dopamine and glucocorticoids (and perhaps corticotropin-releasing factor [CRF]) under reward unpredictability transforms "wanting" into "hope."

Severely food-deprived organisms might experience fear of starvation (**Zack**), a situation that is likely to be associated with high glucocorticoid levels. But evidence based on such a measurement often indicates that food unpredictability causes only mild stress (Bauer et al. 2011; Marasco et al. 2015; Reneerkens et al. 2002). In this case, glucocorticoid-induced dopamine release (motivation), rather than glucocorticoids themselves (stress), might control foraging performance (e.g., Sinha & Jastreboff 2013). For example, Lemos et al. (2012) reported that CRF-induced dopamine in the nucleus accumbens has appetitive properties, causing conditioned place preference in mice that received intra-accumbens CRF (500 ng) but not in mice that received 6-hydroxydopamine (6-OHDA) in addition to CRF. The CRF antagonist α-helical CRF also reduces approach to and exploration of a novel object. In contrast, severe stress abolishes these appetitive effects of CRF on dopamine release for long periods (> 90 days) after stress exposure (see also Inoue et al. 1994). The abolition of depression-like responses to stress was prevented by the glucocorticoid receptor antagonist RU486. Recently, Mascia et al. (2019) found that high dopamine outflows in the nucleus accumbens of rats occur in response to exposure to a variable-ratio (unpredictable) schedule for a saccharin reward, compared with rats exposed to a fixed-ratio (predictable) schedule. They did not observe any schedule-specific effects on response rates in these instrumental tasks. But the rats tested with the unpredictable schedule showed subsequent increase in locomotion after an amphetamine injection and responded at higher rates on a progressive-ratio schedule for amphetamine, obtaining more amphetamine than the rats tested with the predictable schedule. Such results are compatible with an interpretation of reward-seeking behavior in terms of motivation rather than stress or fear.

R1.2. Learning and exploration

As pointed out by some commentators, cognition plays a crucial role in reward seeking; information, learning, and the development of new action schemes are proposed to be sufficient bases for exploration. Effective reward seeking may indeed require cognitive abilities. But we have the impression that several authors see cognitive processing (in particular, expectations) as the motivation to forage itself. **Pezzulo & Friston** suggest that information gain is rewarding per se – an organism explores its environment (epistemic dimension) to be able to exploit the information collected (pragmatic dimension). Nobody would disagree with this exploration-exploitation principle, which approximately corresponds to the distinction between goal-directed behavior and habit (e.g., see Yin & Knowlton 2006). What these authors call "active inference" requires an expectation-based motivational process controlling instrumental actions, while incentive hope is assumed to operate via Pavlovian processes, as does incentive salience. We think that foraging motivation is basically related to incentive processes rather than expectations leading to instrumental actions, even though those actions could indirectly be influenced through Pavlovian-to-instrumental transfer. How? Dopamine release in the nucleus accumbens core predicts both the cueing effect (Peciña & Berridge 2013) and the strength of lever presses in rats during Pavlovian-to-instrumental transfer (Wassum et al. 2013). With unreliable CSs, something similar could happen – except that infrequent, ambiguous CSs should enhance instrumental actions through incentive hope. Without Pavlovian-to-instrumental transfer under incentive hope, we could speculate that the higher strength of goal-directed foraging actions in winter would be difficult to explain because the action-outcome contingency is degraded (effort is less often rewarded) in comparison with the summer period. As long as the paradox between motivation and preference persists (propensity to respond vigorously to an uncertain situation versus preference for a more favorable situation), incentive hope is believed to maintain seeking activity at a high level – not only with respect to Pavlovian approach, but also indirectly to instrumental (goal-directed) actions. To return to the link between motivation and expectations, some colleagues might believe that expectations have a motivational or an emotional component, because we tend to expect events with some motivational or emotional salience (e.g., salary increase, next holidays, a big bill to pay). However, producing expectations is a cognitive process without intrinsic motivational power (modern robots can do that without having to be motivated by their tasks). Thus, expectation-based information gain cannot be attractive per se; it becomes attractive only if incentive properties are (potentially and subcognitively) associated with the information in question. Reducing uncertainty in an apparently useful context is a source of motivation to get those incentive properties.

Gozli & Gao note that uncertainty-induced behavioral invigoration can make the unpredictable more predictable – by shortening the delays for food – and can promote the learning of new action schemes. They see no need to hope for rewards to acquire a new, stable action scheme. We think that, like **Pezzulo & Friston**, they interpret exploration only as an expectation-based (cognitive) process. Given that an expectation is not motivation, what does motivate the production of new action schemes? There is probably no simple answer to this question. But incentive hope may indirectly contribute to acquiring action schemes through behavioral invigoration, forcing organisms to be more vigilant and to explore vaster spaces for longer durations. In a similar cognitive perspective, **Wang & Hayden** insist on the importance of mental models in driving behavior and mention that many organisms decide to "forego primary reward to seek information that provides strategic benefits or satisfies curiosity." We agree, but it is important to know what is meant by "strategic" here. Very often, the strategy in question is the consequence of an evolutionary adaptation of which the organisms may have no awareness. For example, it is noticeable that the decisions made by mammals and birds exposed to free-choice procedures involving a fixed option and a variable option do not differ from the decisions made by bees and wasps in similar situations (Anselme 2018a). The decision to contrafreeload might also depend on incentive properties acting below any conscious control. Wang & Hayden also suggest that, in their attempts to build mental models, organisms sign-track when learning is incomplete and goal-track when learning is complete. However, learning mechanisms have been shown to be hardly plausible to account for the sign- versus goal-tracking distinction, whether uncertainty is present or absent (Anselme 2016; Berridge 2012). Current data indicate that sign- and goal-trackers have similar learning performance relative to their own CS (Meyer et al. 2012). Also, if goal-tracking reflects complete learning, why are goal-trackers sometimes observed under reward uncertainty (Gottlieb 2005)? In fact, sign-trackers appear to have low top-down (cognitive) control compared with goal-trackers, and their behavior simply reflects the strength of their cue-triggered motivation in Pavlovian autoshaping (e.g., Kuhn et al. 2018; Meyer & Tripi 2018; Paolone et al. 2013).

R1.3. Social behavior

In the target article, we focused our attention on the environmental incentives of foraging to the detriment of the social dimension, which is significant in some species. **Matsushima, Amita, & Ogura** note that the presence of competitors increases unpredictability in the access to food and increases foraging effort, as the incentive hope hypothesis predicts. However, they report that dopaminergic manipulations in the substantia nigra – which projects to the medial striatum – in chicks have no effect on socially facilitated foraging effort (Ogura et al. 2015). We could also add that the increase in foraging effort seems to depend only on the mere perception of a congener, not on competition for food: When two chicks are separated by a Plexiglas panel, the social facilitation of foraging effort occurs irrespective of whether the feeders at the two ends of an I-maze are separated or shared (Ogura & Matsushima 2011). These findings are incompatible with what the incentive hope hypothesis would apparently predict. But we see two reasons why social facilitation might *not* require incentive hope. First, there is possibly no paradox between motivation and preference here, because of the presence of secondary benefits associated with social foraging. In other words, an animal could increase its foraging effort within a group of congeners and also prefer foraging in group because of dilution and confusion effects and other predator-related advantages (e.g., Fernández-Juricic et al. 2004; Roberts 1996; Vásquez & Kacelnik 2000). Second, the presence of a congener might motivate behavior differently from food. For example, farm animals such as pigs tested under a progressive-ratio schedule are not ready to deploy a lot of effort to obtain access to a congener, while effort is adjusted to demand with respect to food (Keeling & Jensen 2002). The observed decrease in activity in the nucleus accumbens in the presence of a competitor supports this view (Amita & Matsushima 2014).

Social facilitation is a good example to illustrate that an increase in behavior under uncertainty does not necessarily call for an explanation in terms of incentive hope. We have provided other examples related to ratio and delay schedules in the target article; our concept is most likely to be useful when a motivation-preference (or behavior-preference) paradox exists. Sometimes, however, incentive hope could be recruited but remain behaviorally silent because of interfering factors. **Misiak et al.** say that the incentive hope hypothesis could explain food wasting in industrialized countries, in which food is abundant – presumably because abundance makes hoarding unnecessary. However, they indicate that hunter-gatherers such as the Hadza (Tanzania), the Maasai (Tanzania), and the Yali (West Papua) do not hoard or waste food – they share it in case of surplus. The authors argue that factors such as mobility, feeding of domesticated animals, and social visibility play an important role in explaining the absence of food hoarding and of food wasting among hunter-gatherers. We fully agree and would like to add that, even though incentive hope is expressed during hunting and gathering, its effects could be unobservable given a population's lifestyle and social norms. This might be different in sedentary populations of hunter-gatherers, known to store food (e.g., Testart et al. 1982).

R1.4. Human obesity

Another context in which incentive hope might have limited effects is human obesity, which essentially depends on the abundance and cheapness of food rather than uncertainty in Western countries (**Pool; Zack**). In most cases, human obesity is a consequence of incentive salience alone, even though incentive hope could have an impact on poor women living in high-income countries (see Nettle et al. 2017). Furthermore, we recognize possible inconsistencies in the assessment of food insecurity in humans and nonhumans and also the existence of human-specific characteristics of feeding behavior (Pool). People could also lack information on low- and high-calorie foods in modern environments (**Almiron-Roig, Pastor, Martínez, & Drewnowski** [**Almiron-Roig et al.**]). However, it is important to point out that food attraction, seeking, and consumption are under the control of homologous brain structures in all mammalian species, including humans. Many people probably know that a hamburger is more caloric than a salad, but they prefer consuming hamburgers because of deep-rooted evolutionary biases leading us to find energy consumption delightful (Pankseep 1998). Putting on an equal footing our modern feeding habits and adaptive strategies we have inherited for hundreds of thousands of years is somewhat unconvincing. The main difference between our Pleistocene ancestors and us is that we are exposed to needlessly high caloric food, causing overeating and maladaptive fat storage. With respect to food seeking, it is also interesting to note that anthropological studies have revealed common features in many animal species and human hunter-gatherers (Bettinger et al. 2015; Raichlen et al. 2014). Almiron-Roig et al. are right to point out that poverty is not the unique cause of human obesity; genetic and neurodevelopmental factors are crucial for the development of obesity in people with a high socioeconomic status (SES). But those factors are likely to act as modulators of cue-triggered "wanting" for food-related stimuli, just as abundance, cheapness, and uncertainty do (e.g., Robinson et al. 2015b; Soussignan et al. 2012).

R2. Phenotypic traits leading to maladaptive behavior

R2.1. Sign-tracking and pessimism

According to **Zack**, our hypothesis implies that sign-tracking, but not goal-tracking, is the adaptive phenotype. Sign-tracking is indeed supposed to be the adaptive phenotype, but only in an environment in which food is scarce, because sign-trackers should explore and inspect the surroundings more than goal-trackers. However, although there is a genetic basis for these two behaviors (e.g., Flagel et al. 2010), their expression is not immutable (Meyer et al. 2014), and uncertainty seems to favor the sign-tracking phenotype (Robinson et al. 2015a). Thus, many individuals could be sign-trackers under harsh environmental conditions.

Persistent harshness could therefore lead to a pathological propensity to track CSs. **Pool & Sander** claim that incentive hope through the study of sign-tracking in humans could help in understanding overeating, addiction, and pathological gambling. Many studies have already revealed the importance of cue-triggered "wanting" in drug and behavioral addictions. But it is a fact that not much attention has been paid to the role of unreliable cues in addictions, except with respect to gambling, of course. It would also be worth studying how incentive hope could affect anxiety and obsessive-compulsive disorders and could lead people to recover from depression.

In this respect, **Linkovski, Weinbach, Edelman, Feldman, Lotem, & Kolodny** (**Linkovski et al.**) suggest that adversity-predictive stimuli in the environment activate a pessimistic phenotype based on anticipated hardship, which could be at the origin of many pathologies in modern humans. Importantly, they argue that the trigger of incentive hope is anticipated hardship rather than uncertainty itself. This idea is interesting and should be pushed further. For that, however, some clarifications are needed. First, by uncertainty (or unpredictability) we mean that an organism cannot predict whether the next foraging or search trial will be rewarded or nonrewarded. The probabilistic definition of maximal uncertainty (50% chance of reward) is narrow and applicable only to Pavlovian autoshaping. In the wild, the probabilistic and temporal aspects of uncertainty are inseparable, the former having possibly more local (CS-related) effects than the latter (**Hulme & Kvitsiani**). Is our definition of uncertainty radically different from Linkovski et al.'s hardship? In our understanding, hardship simply means that finding rewards is difficult; that is, a significant number of attempts are unpredictably successful because of variability in the delays for food and in the reliability of its predictive CSs. Here, it is important to remember the definition of incentive hope: motivational excitement for rewards *when non-rewards are likely*, which suggests that uncertainty and hardship are relatively equivalent terms. Second, anticipated hardship is acceptable in a Pavlovian context only if "anticipated" refers to the predictive value of a stimulus independent of any cognitive assessment, for example, paramecia can learn Pavlovian associations while having not a single cognitive processing system (Hennessey et al. 1979). In other words, a 50% chance of reward in autoshaping must be learned as an *implicit regularity* rather than an explicit rule. The implicit predictive value of a CS is likely to contribute to incentive hope (as "wanting" × uncertainty), given that exposing people to adversity-related words or simulated low SES is sufficient to alter nutritional desires (Cheon & Hong 2017; Laran & Salerno 2013). Thus, anticipated hardship should somehow be related to this implicit predictive value, but not to motivational salience or "wanting." In consequence, the direct connection between incentive hope and pessimism suggested by the authors is unclear: Pessimistic individuals should be hopeless because of their high expectation of non-rewards (no uncertainty) and their apparent lack of motivation (no "wanting"), and hence not much inclined to seek and explore. In this view, we could see incentive hope as a sort of compensatory motivational response to anticipated hardship responsible for pessimism. But trying to replace the stimuli that cause anticipated hardship by others, which will activate a more optimistic phenotype – a strategy that should require no incentive hope – appears to be an excellent suggestion from these authors to cure a number of human psychopathologies.

R2.2. Pathological gambling

While recognizing the relevance of the incentive hope hypothesis in different contexts, two authors suggest that it might be inappropriate to account for pathological gambling (**Robinson; Zack**). One criticism is that gamblers seek money at casinos, but they do not hoard it – contrary to small birds storing fat or food items in winter (Robinson). In particular, slot machine players seem to play so they can obtain more coins to continue gambling. The pathological dimension of gambling could possibly alter the adaptive logic behind incentive hope. But we would like to note that hoarding (or fattening) does not necessarily follow seeking in nature; as shown in our computer model, organisms need the opportunity to accumulate reserves. In the case of gamblers, especially slot machine players who can place a lot of bets within short periods, the losses largely overcome the wins so that hoarding is virtually impossible. Of course, in comparison with recreational gamblers, it is likely that pathological gamblers would totally re-engage their considerable wins, which may occasionally occur. But even such big wins would probably not compensate for the money amounts previously placed. In this view, gambling represents an instance of foraging under extreme conditions, in which hard-earned coins must immediately be re-engaged to stay in the game. In foraging animals, that would mean that the food items found provide just enough energy to find new items and stay alive. Of course, we are not suggesting that gamblers chasing losses activate simple Pavlovian responses only (Zack). We simply mean that complex behaviors can, at least in part, result from basic processes. For example, "wanting" is not just a concept for rats in autoshaping boxes but is also likely to be at the origin of our human conscious desires (Anselme & Robinson 2016). The same reasoning applies to incentive hope with respect to gamblers.

In our target article, we argue that uncertainty is not attractive in itself and, thus, is not preferred to certainty (Anselme 2018a; Kahneman & Tversky 1979; McDevitt et al. 2016). Therefore, it may seem difficult to understand why gamblers take pleasure in recurrently going to a casino (**Robinson; Zack**). Is it because they can choose between going and not going to a casino? Why do they decide to spend their time and money there? First, it is important to realize that this choice is different from that made by individuals in an experimental context, where they have to decide between an uncertain reward and the same reward for sure. In contrast, the choice for gamblers is between uncertain money (casino) and no money for sure (e.g., staying at home) or losing money for sure (e.g., going to the cinema). Second, at least with respect to pathological gamblers, it is not certain that they have the opportunity to quit. Like many drug addicts, they may repeatedly try to avoid the events that cause their addiction without success. Third, given that uncertainty sensitizes dopamine neurons in the ventral striatum (e.g., Mascia et al. 2019), we agree that gambling activity is somehow desirable and, by extension, pleasurable. As said, uncertainty does not seem attractive per se. But casinos are confined environments full of attractive predictors of (uncertain) rewards that stimulate incentive hope as our ancestral motivation to forage (Anselme 2018b). Organisms are likely to find it desirable and pleasurable to express the behaviors for which they are adapted. A good example is that of caged animals that normally live and forage over a large range in the wild: Their confinement within small, impoverished captive environments causes the development of behavioral pathologies, such as stereotypies, despite receiving their food for free (see Eilam et al. 2006). Chasing is probably desirable and pleasurable for a lion, even if this often involves deploying a lot of effort for nothing. Similarly, gambling could generate positive feelings because this activity recruits seeking motivation and behaviors for which our Pleistocene ancestors developed adaptations (Anselme 2018b).

R3. Presuppositions in our computer model

Several contributors point out some limits of our definition of uncertainty. We will not repeat here our general definition, recalled earlier (see R2.1), but focus on more specific aspects. For example, **Hulme & Kvitsiani** describe a situation involving two patches that apparently contradicts our prediction: if patch #1 is unpredictable over short timescales ($p = 0.5$) but predictable over longer timescales, and patch #2 is predictable over short timescales ($p = 0.9$) but unpredictable over longer timescales, an animal should spend more time and energy seeking in patch #2 but should prefer patch #1. However, deciding which patch is more stimulating and which patch is preferred is rather difficult if we do not know *how often* the CSs are found. These authors define uncertainty only in probabilistic terms, while we consider two forms – one about CS reliability and one about delay shortness. For example, a CS-food association can be very frequent ($p = 0.9$) but the CSs scarce – any other combination also being possible. Our hypothesis predicts that delay uncertainty might have a stronger impact on the motivation to forage than probabilistic uncertainty.

Symes & Wheatley argue that the distribution of food in the environment is not random but patchy, so that one item found increases the probability of encountering other items. We agree that food patches may exist, although they are not as common as sometimes postulated (Arditi & Dacorogna 1988). But, contrary to a widespread presupposition since Charnov (1976b), food is not uniformly distributed within a patch; an animal is often forced to seek food items despite their relative abundance. Thus, we think that our argumentation remains unchanged. Our hypothesis and computer model describe trial-level randomness such as it could exist within a patch (e.g., a clearing), where some food items (e.g., bugs) are necessarily present, but their exact location unknown.

Just as we did not specify the size of our virtual environment, we did not allow uncertainty to fluctuate over time (**Houston & Malhotra**). The reason is that the model is assumed to measure phenomena occurring within relatively short intervals – no more than few hours. We can reasonably postulate that uncertainty remains stable under these conditions. **Hulme & Kvitsiani** rightly note that our model did not try to capture the inferential controllability of the environment (see also **Gozli & Gao; Pezzulo & Friston; Wang & Hayden**). Assuredly, expectations play an important role in animal foraging – at least in "higher" vertebrates. But here we had to demonstrate how motivation as a subcognitive process could affect foraging, without having to disentangle its effects from those of cognitive expectations. In winter, the high expectation of non-rewards on some days may lead a bird to reduce its activity, and our hypothesis predicts that this decision results from the absence of incentive hope for the opportunity to find edible items. Energy resources (fat reserves) are therefore conserved for later use (**Alquist & Baumeister**).

We agree with **Houston & Malhotra**, who suggest that our model is not adequate when applied to laboratory experiments, especially with respect to risk-sensitive foraging theory. Although we explicitly refer to temporal discounting to explain sensitivity to delays (a mechanistic rather than functional interpretation), this dimension is absent in the computer model and should somehow be included in subsequent research. It is also true that our model does not take choice and food amounts into account. Indeed, based on some findings, we postulated that wild animals encounter food items sequentially (they do not have to make choices; Shapiro et al. 2008) and are indifferent to variability in food amounts (variable, higher amounts do not stimulate sign-tracking more than fixed, lower amounts; Anselme et al. 2013). In fact, for reasons developed in the target article, choice between fixed and variable food amounts should not depend on incentive hope. Imagine that the fixed and the variable food amounts are equivalent on average. Because variability is different from real uncertainty (some food is always provided) and is not associated with any advantage (such as a shorter delay or more reliable CSs), the two options are likely to be preferred in a similar fashion, as often observed (Kacelnik & Bateson 1996). In other words, incentive hope plays no role, and incentive salience is equivalent in both cases. Now, if both options are not equivalent on average, the most profitable should be more attractive and preferred, in accordance with the incentive *salience* hypothesis (e.g., Real et al. 1982).

It is true that our equations are not fully justified in functional terms and should contain more factors whose fluctuation is dynamical rather than fixed in advance (**Hulme & Kvitsiani**). In the future, models based on a refinement of our ideas would be useful to examine the psychological underpinnings of animals foraging in poor environments in the absence of cognitive control. For example, **Chmait, Dowe, Green, & Li** propose a different approach to food predictability (large food amount in a specific location), which totally avoids any risk of starvation for a while once the food is detected. Their model shows that finding unpredictable resources requires more exploration and lesser learning capacities than finding predictable resources, as our hypothesis would predict.

R4. New horizons for incentive hope

Several commentators suggest that the concept of incentive hope describes a phenomenon that is, in fact, more general than considered in our target article. We focused our reflections on food seeking in birds and mammals because it is in these zoological groups that a parallel was logical to establish with Pavlovian autoshaping, for which the incentive hope hypothesis was initially formulated (Anselme 2015a). But, given that incentive hope denotes a core (unconscious) psychological process rather than a mental (conscious) state, it can potentially be applied to other zoological groups and to non-food-related contexts, as shown below. **Alquist & Baumeister** provide convincing evidence for mental energy conservation and alertness in humans having to deal with uncertain events. Like the preservation of fat reserves through activity reduction in small birds, conservation of mental energy may prepare people to cope with adversity. Energy *conservation* (whether physical or mental) is not a consequence of incentive hope, but may be necessary for energy *accumulation* (whether measured as fat reserves, experience, self-confidence, etc.) that results from enhanced performance in response to unfavorable events through incentive hope. We agree with Alquist & Baumeister when they postulate the existence of a "broadly adaptive default response to uncertainty." A non-food-related illustration of this idea could be religious faith, which is widespread and strong in countries with low per-capita incomes resulting from persistent existential insecurity and infrequent sources of gratification (Norris & Inglehart 2011). People experiencing adversity may come to endure the situation rather than trying to overcome the encountered difficulties (Oettingen & Chromik 2018) – in Alquist & Baumeister's terms, we could see the ability to endure as a way of conserving mental energy for other tasks. However, people rationally invest much of their time and energy in activities – such as prayer and attendance to religious services – that they perceive as more likely to be rewarding.

Another consequence of recurrent feelings of uncertainty and insecurity in low-SES people is the expression of greater impulsivity in their decision making (Pepper & Nettle 2017). Accordingly, **Walsh, Cheries, & Kwak** show that experimentally reducing those feelings in low-SES people decreases their propensity to be impulsive. As they note, this phenomenon is compatible with the incentive hope hypothesis, which predicts that scarce resources will generate a hope for short delays and reliable CSs, causing invigoration in the activity of seeking rewards. Based on this idea, they envision an interesting therapeutic perspective in reducing impulsivity in low-SES people. We add that, as in the case of psychopathologies (**Linkovski et al.**), incentive hope is not in itself responsible for maladaptive behaviors. Hope is associated with positive effects for many people (e.g., Snyder 1994). But hoping for unrealistic achievements in long-lasting unfavorable contexts, such as experienced by low-SES people, could be psychologically damaging. More secure or predictable environmental conditions (in terms of health, employment, governmental effectiveness, etc.) avoid keeping hopes up for nothing and should contribute to avoiding a number of irrational behaviors with potential pathological consequences (**Clark**).

Aharonov-Majar & Suleiman suggest extending incentive hope to human social contexts, reporting that people tend to form groups when variability in the chance of reward is high, because the redistribution of gains is a more profitable strategy than solitary gambling. They also report that making multiple gambles (increasing foraging) is a way of reducing uncertainty correlated with solitary gambling. These ideas fit well our interpretation of incentive hope as a mechanism of uncertainty reduction working in the absence of cognitive strategies. The psychological underpinnings of group formation are certainly diverse and unrelated to incentive hope in many cases. But we could imagine that this mechanism of the brain is sometimes recruited to motivate collective behaviors against environmental uncertainty – a positive effect of sociality also noted in bees (Schmickl & Crailsheim 2004). These commentators mention that the neuropeptide oxytocin is important in eliciting trust and cooperation in humans. Could uncertainty reduction in a social context emerge from cooperation, in which case incentive hope appears unnecessary? Or does cooperation itself require incentive hope, because cooperation is based on a desire to reach a goal without a guarantee that the goal will actually be reached or even that the others will collaborate? After all, if oxytocin reinforces trust and cooperation in general, it does not explain why we form groups to struggle against adversity. The answers to these question require further research. Incentive hope could have been particularly useful in hunter-gatherer societies because, as Aharonov-Majar & Suleiman point out, collective foraging combines foraging effort (maximizing food sharing) with decreased or unchanged body fat (caused by food sharing). In a sense, collective foraging and consumption would have functional consequences similar to those of hoarding behavior: increasing the available resources without having to store them directly in the body.

Tops proposes an integrative neurobiological view in which incentive hope could share neuronal systems with apprehension, explaining why uncertainty can motivate individuals. This view is in line with our suggestion that incentive hope – a dopamine-dependent motivational process – requires the release of glucocorticoids, which are typically involved in stress responses. We left open the question of whether other neurotransmitters or neural circuits play a role in its expression as well. Discovering brain correlates of behavior is important, but our main interest has been to explain behavioral facts. We need psychological concepts describing precisely what animals and humans do. For example, we can describe the brain activity of a rat running away from an aversive CS, but we can only understand what the rat is doing through the concept of fear. Incentive hope is conceptually compatible with the idea of an overlap between its neurobiological mechanisms and those of apprehension. But identifying neuronal processing systems does not eliminate the need for concepts to possibly shed light on distinct psychological components correlated with these systems (**Smulders et al.**). A good example is the idea that uncertainty might generate an error prediction signal in the brain that interrupts routinized responding (Tops) and favors learning (Schultz 1998): Understanding this process is difficult without an appropriate motivational concept. Interestingly, Laurent et al. (2018) recently found that a rat's motivational state determines the positive prediction error signal for appetitive excitors; motivation is required to generate the error on which learning is subsequently computed.

Clark indicates that organisms without a nervous system may respond to unpredictability similarly to taxonomically more recent animals, and, therefore, that incentive hope is appropriate for describing their behavior. Although largely studied in mammals, Pavlovian conditioning has indeed been observed in protozoa (Hennessey et al. 1979) and risk sensitivity in pea plants (Dener et al. 2016) – aneural organisms. Of course, noticeable differences necessarily exist in the physiological mechanisms involved among species so phylogenetically distant, but it is a fact that most organisms share the same functional purposes – notably approaching rewards and avoiding uncertainty. For example, in the absence of rewards, common woodlice, *Porcellio scaber,* exposed to random visuotactile patterns show enhanced rearing-up – exploratory – activity than when exposed to regular patterns (Anselme 2015b). Woodlice act as if they hoped for more opportunities to escape when the environment is less predictably unrewarding. In the same vein, there are good reasons to suspect the existence of a "wanting" system in insects, even though octopamine rather than dopamine is sometimes its main brain correlate (Perry & Barron 2013; Søvik et al. 2015). Clark also suggests that the concept of incentive hope could explain the origin of irrational behaviors. Incentive hope may certainly lead organisms to take some risks. For example, if an animal's decision to forage harder is unable to compensate for the investment in the task (because food is too scarce), this should cause a rapid loss of energy reserves and a high risk of starvation. Incentive hope may lead people living under precarious conditions to work hard to keep their jobs, but working hard for the jackpot in casinos may cause a rapid loss of considerable sums. It is unclear to us whether incentive hope could be the origin of any kind of irrational behavior, such as suboptimal decision rules identified in the brainless, unicellular, slime mold, *Physarum polycephalum* (Latty & Beekman 2011a). But the evidence that unpredictability may distort perception and lead to error-prone decisions in neural and aneural organisms supports the idea of universal decision rules and behaviors in living beings.

In our target article, we suggest that incentive hope is a brain mechanism designed by natural selection because of its ability to reduce starvation risk in an unpredictable environment. **Snyder & Creanza** think that incentive hope could also have implications for the sexual selection of song in songbirds. Indeed, better-fed offspring will develop better singing, causing greater reproductive success and better transmission of their genes. So, the propensity of the parents to forage harder to feed their offspring increases the offspring's fitness, in addition to increasing the chance that the genes controlling the ability to forage harder will be transmitted as well, and so forth. We like this idea, even though this example might be an isolated case where sexual selection contributes to shape incentive hope. This process should be particularly crucial in poor environments, such as semidesert regions, but also in richer environments for young birds that hatch too early in the year, when insects are not yet abundant. Snyder & Creanza rightly note that our hypothesis does not account for the parental dilemma that consists of having to choose between favoring their own survival and that of their offspring. Answering this question is important, but it would involve a clear understanding of the evolutionary decision rules underpinning animal motivations; such decision rules are likely to be independent of incentive hope per se. According to the selfish gene hypothesis (Dawkins 1976), genes rather than the individuals (their vehicle) attempt to maximize their survival, that is, their propagation over generations. If correct, we could speculate that genes can favor the parents or their offspring (which have half of their genes) depending on the most likely adaptive effectiveness of one or the other strategy. Although this explanation does not provide any genetic or neuronal mechanism, it suggests that genetic control could orient incentive hope toward distinct beneficiaries according to circumstances.

R5. Conclusion

Interdisciplinary articles may easily lead readers to various misunderstandings of what the authors attempt to say, but we were delightfully surprised to see that this was not the case here. Few commentators think that incentive hope is not useful to account for behavior under reward uncertainty, giving us the opportunity to clarify and refine our arguments. However, most commentators perceived the interest of our hypothesis and even tried to extend it to issues not discussed in our target article – such as social foraging, decision making in invertebrates, and sexual selection in songbirds. Although more facts have to be collected about predictions of the incentive hope hypothesis, many commentaries contributed to amplifying and diversifying the applications of our hypothesis beyond food seeking in "higher" vertebrates, including original therapeutic approaches for psychopathologies and maladaptive behaviors possibly associated with too much insecurity in life. They also contribute to suggesting the existence of a common, ancestral mechanism put in place by evolution, allowing very distinct organisms to deal with uncertain, significant events.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

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