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 predict 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 like 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 – 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 or 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, resulting from 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. 2016; 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.

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