

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,