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Review Paper

Assessing value representation in animals

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Among all factors modulating our motivation to perform a given action, the ability to represent its outcome is clearly the most determining. Representation of outcomes, rewards in particular, and how they guide behavior, have sparked much research. Both practically and theoretically, understanding the relationship between the representation of outcome value and the organization of goal directed behavior implies that these two processes can be assessed independently. Most of animal studies essentially used instrumental actions as a proxy for the expected goal-value. The purpose of this article is to consider alternative measures of expected outcome value in animals, which are critical to understand the behavioral and neurobiological mechanisms relating the representation of the expected outcome to the organization of the behavior oriented towards its obtention. This would be critical in the field of decision making or social interactions, where the value of multiple items must often be compared and/or shared among individuals to determine the course of actions.

Contents

1. Introduction

Among all factors modulating our motivation to perform a given action, the ability to represent its outcome is clearly the most determining. Anticipation or representation of outcomes, rewards in particular, and how they guide behavior, have been the topic of numerous studies and concepts in experimental psychology (see for review: Berridge, 2004; Balleine, 2011). Not only humans but also animals have outcome expectancies and are able to form flexible representations of goals or rewards (Dickinson and Balleine, 1994; Clayton and Dickinson, 1998; San-Galli et al., 2011; Janmaat et al., 2011, 2013). Nevertheless, nature and content of such outcome representations remain elusive. At least, they might contain incentive and affective properties to drive behavior (Berridge, 2004; Robbins and Everitt, 1996; Dickinson and Balleine, 1994). But, how do animals actually perceive an expected reward, and do they assign any subjective value to this representation?

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Assuming that animals can form a representation of the goal-value and use that representation to guide action, understanding the relation between these two processes (evaluation and action) is critical. Studying the interaction between evaluation and action would be greatly facilitated if these two processes could be measured independently. In that sense, it is necessary to measure the value of the expected reward independently of the action needed to obtain it. Practically, the value of the representation of an action's outcome refers to its affective and hedonic attributes, conscious or not, and proper to each individual. Intuitively, based on introspection, the evaluation of an outcome and its possible influence on action is obvious. For instance, we are daily exposed to situations in which we need to consider several options and their respective expected values, without necessarily acting. In that sense, human studies usually record both ratings (measure of value) and choices (measure of action) (Lebreton et al., 2009). Since we do not have any declarative or verbal measures, subjective value is difficult to address in animals, especially when it relates to an anticipated reward that is not currently happening but for which the animal must have a mental representation. As animals do show appetitive reactions and manifestations of pleasure when they consume the reward itself, it seems justified to extrapolate a form of subjective evaluation from humans to other species, and presumably even more justified when the species are closely related (Berridge and Kringelbach, 2008).

At this point, we could question the meaning and the function of such affective and hedonic representation in motivation: processing the outcome incentive value (i.e. the facilitating effects on acting) could be sufficient to account for most of goal-directed behaviors. Thus, in what sense is it adaptive to add a subjective component to the outcome representation? In other words, what is the advantage of representing outcome value independently from its influence of action? There might be reasons for which this feature has emerged and has been selected across evolution. We suggest that subjective value of an expected outcome can be crucial for theoretical and unobservable choices (e.g. intertemporal choices). Practically, in situations where several options are evaluated successively before one of them is selected, having a reliable measure of the value attributed to these options would enhance our understanding of the impact of these values on behavior (action selection and production) and its neuronal underpinnings. Assessing the value of a possible reward independently of the action is also pertinent for social interactions, where this information can be exchanged between individuals. Thus, it could have a role in social communication, whatever goal-directed (voluntary) or more reflexive (e.g. sharing information about upcoming food with facial expressions showing pleasure or disgust, Masi et al., 2013; Van Schaik et al., 2013).

Again, how an expected reward is evaluated and mentally represented can be captured easily in humans, but it is far more difficult in animals. In the past, most of animal studies essentially addressed this question by using instrumental actions as a proxy for the expected reward value (Dickinson and Balleine, 1994; Killcross and Coutureau, 2003; Padoa-Schioppa and Assad, 2006). By definition, these measures reflect the incentive value of the expected reward (i.e. attributes energizing the behavior), which can be distinguished from its hedonic value (Berridge, 2000a,b). The conceptual framework developed by Berridge and colleagues focuses on the distinction between hedonic processes, especially related to the consumption of a pleasant item, and the incentive effects of rewards on behavior, both goal directed actions and simple approaches (Berridge, 2004). Our purpose here is slightly different: we want to assess value representation, either hedonic or incentive, but distinct from the goal-directed action. Such independent measures would allow to compare value with voluntary action and to further investigate how they interact. This distinction might be relevant in the framework of model-free vs model-based learning, but learning adds another level of complexity and it is beyond the scope of this article (Doll et al., 2012). The problem raised here is in line with earlier ideas on the contribution of goal-evaluation on instrumental action in animals or on the interaction between Pavlovian and Instrumental responses, Dickinson and Balleine, 1994; Dayan et al., 2006). Our goal, however, is not to discuss the possible interaction between Pavlovian vs Operant training procedures in animals but to assess possible measures of outcome value independently from goal directed action. These action-independent measures of goal-value representation in animals should fulfill several criteria. Such measures need to be appetitive (as long as we are talking about reward), instinctive (not goal-directed) and to reflect the value of the representation of a reward, not when the reward is present or being consumed. We suggest that a set of appetitive behaviors including facial expressions or approach, which can be regarded as Pavlovian responses in classical laboratory settings, can be appropriate for assessing value of reward representation. Since these responses not only appear in classical conditioning but in operant tasks as well, they could be put in regard of voluntary actions for a better understanding of how value representation drives animals' goal-directed behavior. First, we will briefly review the literature to circumscribe the notion of representation of reward value and then we will discuss a set of specific behaviors that could be used to measure it in animals.

2. Reward and representation concepts

2.1. Reward before (and without) value: drive reduction

In the history of reinforcement learning, people first thought that to be "rewarding", a reinforcer had to reduce drive (Hullian theory, 1943). A drive is an excitatory state produced by a homeostatic disturbance, an instinctual need that has the power of driving behavior. For instance, when we are hungry, we are in a state of drive that activates behavioral responses (actions) for food. Food, when eaten, reduces that hunger drive, and in that sense is rewarding. Because they were so intuitive, homeostatic drive concepts in which rewards were conceived exclusively as drive reducers, influenced psychology for decades (Hull, 1943). Nevertheless, empirical evidences against drive theories started to emerge in the 1960s (Miller and Kessen, 1952; Epstein and Teitelbaum, 1962; Turner et al., 1975; see Olds, 1973, for brain stimulation reward). For example, dogs intravenously fed the full amount of nutrients they would ordinarily eat still consume their normal meals by mouth, even after becoming overweight (Turner et al., 1975). Satisfying appetite is not merely a matter of physiological drive reduction. And current studies still argue in that sense. It has been shown recently that rats develop craving for saccharin after self-administration training, in the same way as for sucrose (Aoyama et al., 2014). Given that saccharin does not have any post-ingestive caloric consequence but only sensory properties (sweet taste), there might be another reason than drive reduction to explain its irresistible desire. Further studies in the 60s actually highlighted a critical role of goal-expectation, affect and sensory pleasure in animals' motivation (Pfaffmann, 1960; Epstein, 1982; Stellar, 1982). Thus, concept of hedonic reward became central in motivation theories. As attested by affective reactions to the reward, underpinned by conserved brain machinery across phylogeny, pleasure sensations and hedonic experiences are thought to occur in several non-human species (Berridge and Kringelbach, 2008). Rewards should be able to exert a direct control on behavior without going through homeostasis or physiological state regulation (Stellar, 1982).

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