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Commentary

The problem with value

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ABSTRACT

Neural correlates of value have been extensively reported in a diverse set of brain regions. However, in many cases it is difficult to determine whether a particular neural response pattern corresponds to a value-signal per se as opposed to an array of alternative non-value related processes, such as outcome-identity coding, informational coding, encoding of autonomic and skeletomotor consequences, alongside previously described "salience" or "attentional" effects. Here, I review a number of experimental manipulations that can be used to test for value, and I identify the challenges in ascertaining whether a particular neural response is or is not a value signal. Finally, I emphasize that some non-value related signals may be especially informative as a means of providing insight into the nature of the decision-making related computations that are being implemented in a particular brain region.

1. Introduction

Interest in the neurobiological substrates of value-learning and value-based decision-making has surged in the past decade, following the emergence of nascent disciplines such as the fields of neuroeconomics and decision-neuroscience (Camerer, 2008; Fehr and Camerer, 2007; Glimcher and Rustichini, 2004; Levy et al., 2010; Montague and Berns, 2002; Sanfey et al., 2006). The prevailing assumption in these domains is that the brain encodes a representation of the expected value or utility of stimuli and/or of actions, and that in decision-making situations, those representations are used to guide choice such that actions are taken to maximize future expected rewards. Consistent with this proposed framework, experiments in humans using neuroimaging methods, and in animals using neurophysiological recordings, have uncovered evidence for value-related neuronal activity in a wide array of neural structures during learning and decision-making tasks. These findings suggest that a diverse network of brain regions participate in the encoding of value, and have led to proposals that some of these structures participate directly in the decision-process whether over goods (or stimuli) or over actions linked to selection of those goods.

However, ascertaining whether a neuronal response truly corresponds to a value or subjective utility signal is a rather challenging endeavor. Here I outline some of the problems in inferring that a particular neuronal response pattern encodes a value signal per se or else a number of other non-value related processes. A point that has frequently been made before is that reward-related responses may be confounded with attentional mechanisms, sometimes also referred to as "attention", "motivation" or "salience" (Horvitz, 2000; Leathers and Olson, 2012; Maunsell, 2004; Roesch and Olson, 2004). I will consider this possibility here, but also identify other less often highlighted but equally problematical confounding signals to a valuation account. These include differential encoding of sensory information about an outcome, informational signaling of an outcome, and representation of behavioral responses. I then consider viable steps to determining whether a particular neuronal response truly corresponds to a value signal. Finally, I argue that even if signals hitherto presumed to correspond to value turn out to represent something else, such signals should not be ignored but instead properly categorized as they might still play an important and perhaps even critical role in the processes of learning, value computation and choice.

2. Summary of different types of putative value signals:

Before embarking on consideration of the type of signals that may confound value, it is worth briefly first considering how value can be defined, and then summarizing the different types of value signals that have been reported in the brain.

2.1. What is value?

There are multiple approaches to the definition of value. Here I discuss a variety of approaches:

One approach is to define value as some function which pertains to the relative attractiveness of a particular good at the time of

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choice, and which is maximized as a result of the decision process (Rangel et al., 2008).

A related approach, is to adopt the notion of utility as used in economics and to apply this to the definition of value in neuroscience. In economics, "utility" is a function that describes a set of preferences an individual has over a set of goods. If the individual prefers good A over good B, then by definition good A will have a higher utility than good B. Translating this to neuroscience, we might expect that some neural process encoding utility would show an ordered relationship in its responses (such as for example by changes in average firing rates), to the stimuli presented to the animal, such that the neuronal responses are greater for a good that is more preferred by the animal compared to a good that is less preferred. Here, utility/value is inferred directly from behavior, and neural representations of this function are assumed to reflect behavioral preferences (Dean, 2013).

Another strongly related approach to the preference approach in economics arises from the behavioral neuroscience literature, and that is to define value in terms of the motivating properties of a stimulus for instrumental action (Rolls, 2007). The degree to which an animal is prepared to work (i.e. perform some kind of effortful action) to obtain a stimulus, relates to the degree to which the animal finds that stimulus rewarding.

Yet another approach is to define value is in terms of the subjective "pleasure" that is engendered by a particular stimulus. The experienced utility of a good, is the pleasure or happiness that arises from its consumption (Bentham, 2007; Kahneman et al., 1997). The challenge in using such a definition in experimental work is that it is very difficult to access such subjective "pleasure" states, particularly in animals, although some have argued for the existence of clear behavioral proxies for such subjective evaluations even in animals (Berridge, 1996). In humans, one can simply ask participants to verbally or otherwise rate their subjective pleasure. However this does require adopting the assumption that human participants have reliable insight into the nature of their affective disposition.

Although these definitions of value differ, by and large we would expect them to make similar predictions about when a particular stimulus would be deemed valuable or not, as well as to make similar predictions about the expected pattern of neural responses tracking value. However, under some situations, the definitions may lead to divergent predictions. Most notably, under situations where behavior becomes habitized, an action can be selected resulting in attainment of a good that is not actually preferred by the animal (Dickinson, 1985; see below for further discussion of habits). Under those conditions, both the revealed preference and work motivation operationalizations of value would yield an inference that this particular good has high value for the animal, because that is what is reflected in the action-selection behavior. However, once the good is actually attained by the animal as a result of the habitual action(s), the animal would not actually consume the good. Some have also proposed that the motivation to work for a good or "wanting" can be neurally and sometimes behaviorally dissociable from its subsequent evaluation (or "liking") (Berridge, 1996). Thus, it is clear that how one defines value, has non-trivial implications for how one interprets value-signals in the brain.

3. Different types of value signals

Now I will consider the existence of different types of value signal as they have been described in the brain:

3.1. Outcome value codes

Valuation responses that are presumed to occur in response to the receipt of an outcome, have been referred to as an experienced value or outcome value (O'Doherty, 2004). Many studies have reported neuronal responses to the receipt of rewarding or aversive stimuli in the literature, in both human neuroimaging studies and in animal neurophysiological recordings. As I will consider later, probably only a subset of these can unambiguously be ascertained to correspond to experienced value per se.

3.2. Predictive value codes

We now consider value codes that are elicited on the basis of predictions about the value of future outcomes. I will call these collectively predictive value codes. This type of signal can be further subdivided into a number of unique forms of valuation code:

One form of predictive value-signal is Pavlovian values – these correspond to a representation of the value of an expected outcome signaled by a discriminative stimulus. Such signals have been widely reported in the orbitofrontal cortex and amygdala as well as the ventral striatum in both rats, monkeys and humans (Gottfried et al., 2002; Paton et al., 2006; Schoenbaum et al., 1998).

Another class of predictive value-signal corresponds to what are variously described as "offer values", "stimulus values", or "goal-values" – these correspond to the expected value of a prospective outcome or goal as this goal is being evaluated at the point of choice, typically under situations where other prospective outcomes or goals are also available. Such signals have been reported in the monkey central orbitofrontal cortex, as well as in human ventromedial prefrontal cortex (Padoa-Schioppa and Assad, 2006; Plassmann et al., 2007).

Yet more value signals arise when an animal or human must render a choice over different actions in order to obtain a goal outcome. Collectively these signals can be called "action-values". Action-value signals have been reported in a number of brain regions including the striatum, lateral intra-parietal cortex and supplementary motor cortices (Lau and Glimcher, 2007; Platt and Glimcher, 1999; Samejima et al., 2005; Sohn and Lee, 2007; Sugrue et al., 2004; Wunderlich et al., 2009).

Finally, post-decision value signals have been reported corresponding to the value of the option that is ultimately chosen in a decision-task, particularly in medial and central orbitofrontal cortex (Hampton et al., 2006; Padoa-Schioppa and Assad, 2006; Wunderlich et al., 2009, 2010).

I will now consider competing explanations for different value signals.

4. Outcome identity coding vs. outcome valuation

Any outcome whether a rewarding, aversive or affectively neutral event, has perceptual properties: attributes that distinguish it from other stimuli in the world. Thus, any difference found in neural activity in response to different outcomes might reflect these sensory properties as opposed to the underlying value of those outcomes. This problem is particularly stark under situations where outcomes differ in their sensory modalities such as for example by comparing responses to juice reward vs. a painful cutaneous stimulation as a means of determining rewarding vs. aversive responding outcome values. However, the problem is not overcome even when using reward stimuli in the same sensory modality by e.g. comparing a sweet vs. a salty taste, and is not unique to appetitive vs. aversive comparisons, as it is equally evident even when comparing responses to two different rewarding stimuli (such as a more vs. less preferred reward).

One way to attempt to circumvent this difficulty would be to use the same stimulus (such as a particular juice reward), and instead manipulate the intensity or magnitude of the outcome provided. However, once again, any variation in outcome magnitude or