Anchors, scales and the relative coding of value in the brain
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People are alarmingly susceptible to manipulations that change both their expectations and experience of the value of goods. Recent studies in behavioral economics suggest such variability reflects more than mere caprice. People commonly judge options and prices in relative terms, rather than absolutely, and display strong sensitivity to exemplar and price anchors. We propose that these findings elucidate important principles about reward processing in the brain. In particular, relative valuation may be a natural consequence of adaptive coding of neuronal firing to optimise sensitivity across large ranges of value. Furthermore, the initial apparent arbitrariness of value may reflect the brains’ attempts to optimally integrate diverse sources of value-relevant information in the face of perceived uncertainty. Recent findings in neuroscience support both accounts, and implicate regions in the orbitofrontal cortex, striatum, and ventromedial prefrontal cortex in the construction of value.

Introduction
Can a restaurant seduce you into buying an expensive wine by offering similar but more expensive alternatives? Does the wine taste better if you pay more for it? Does the taste improve when tasted alongside lower-quality alternatives? That the answer to such questions is often ‘yes’ suggests that human value systems are unlikely to be the impartial critic that economists have traditionally assumed [1], and poses important questions for how the brain constructs value from the information available to it.

Phenomena such as this are increasingly sparking interest among behavioral economists, and these and related effects have begun to make their way to the lab (Figure 1). Indeed, many imaginative experiments have illustrated just how easily primes, anchors and contexts can bias preferences and prices. For instance, students’ interest in hearing their professor recite extracts from Walt Whitman’s acclaimed ‘Leaves of Grass’ anthology, for free, was found to be strongly influenced by whether they had previously be asked to pay, or receive payment, to attend [2*] (Figure 1). The initial question, although subsequently irrelevant, appeared to prime people towards thinking that the recital was either a privilege or a sufferance. But although the initial valuation was malleable, subsequent behavior was far less so: once a student has come to doubt their professor’s poetic prowess, they recognised that 5 min of it would be much less painful than 10 [2*]. Many of these experiments display what has been termed ‘coherent arbitrariness’ [3], which describes the apparent consistency of behavior that occurs once otherwise arbitrary baseline values have been set.

This leads to two related accounts of how humans generate estimates of the value of goods in transactions. The first is largely algorithmic, and posits that humans lack stable, long-term representation of the magnitude of value, and judgments are made purely by pair-wise comparisons in an ordinal dimension. This can be formalized by relative judgment models [4,5] and related theories (e.g. the stochastic difference model, multi-alternative decision field theory, adaptation level theory, and range frequency theory [6–9]), and draws support primarily from psychophysical observations. Humans are inherently bad at making absolute judgments about the intensity of various sensory stimuli (such as the loudness of a tone), despite being very good at discrimination (e.g. [10]). Applying the relative judgment model to value, would suggest that initial experience with goods and prices generate the anchors against which subsequent experience is judged. For example, if we are led to believe a new wine from Greenland typically retails $50 a bottle, we will jump at the chance to buy a bottle for $30, simply because in relative terms it must be a good price. When extended to choice, decisions are determined by the rank position of an item in a sample rather than absolute value [11**]. That is, decisions then depend on the sample people are cued to retrieve so that if one is cued to think of wines in general, the $30 Greenland wine seems expensive and may be rejected; if cued to think of Greenland wines, it seems cheap and is eagerly chosen [11**].

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the information presented. Informative and circumstantial cues are thereby exploited for any clues they might harbor regarding the true underlying worth of an option. This view is closely related to theories of perception [12,13], and is well illustrated in vision. For instance, if you catch a glimpse a small round object on the ground in the middle of an orchard, you are quite likely to perceive it as an apple. If you spot the same object on a tennis court, you are more likely to perceive it as a ball. In each case, the prior distribution of beliefs strongly biases the subsequent perception. A similar mechanism might well exist for value. This would predict, for example, that wine actually tastes better when said to be the ‘best’, or ‘expensive’, because there is a strong prior belief that such characteristics offer reasonable evidence indicating quality.

Recent neuroscience research on judgment and decision-making in humans and primates has the capacity to provide evidence of the implementation of these models, and as we show below, evidence exists for both accounts.

**Relative coding of value**

The orbitofrontal cortex has a well-studied role in reward processing, and neuronal activity correlates well with the motivational value of a reward, over-and-above its sensory properties [14]. For example, activity declines for a reward (or cues that predict a reward) when an individual (human or monkey) is sated with that reward [15,16], just as it does subjectively. Initial evidence for relative coding came from a classic experiment by Tremblay and Schultz [17], who presented monkeys with variously preferred juice rewards, and recorded from orbitofrontal neurons while presenting each juice, presented in blocks with one other juice. Critically, neuronal activity depended on whether or not the juice was the preferred in that block, rather than its absolute value (Figure 1). Thus, neurons fired if juice B was presented in blocks in which a less preferred juice (A) was also presented, but not if the alternative was more preferable (juice C). Comparable findings have also been found in human medial orbitofrontal cortex, using an analogous design in an fMRI scanner [18].

A similar pattern occurs with aversive outcomes: if a neutral outcome is presented alongside an electric shock, orbitofrontal neurons respond to the neutral outcome precisely as they do to juice reward presented alongside the neutral outcome [19]. That is, in both studies, stimul
activate orbitofrontal neurons only when better than their alternative.

More recent studies have shed light on the time course that prescribes the context that provides relative scales. In the previous studies, options were presented individually, with its paired alternative occurring during an individual block of trials (i.e. one block will contain either juice A or B, and another might contain juice B or C). However, if pairs are presented interleaved (i.e. a trial of juice B and C will appear immediately after a trial of A and B), orbitofrontal neurons code absolute value throughout [20]. In other words, the relative coding of reward seems to exist only between, and not within, blocks.

**Adaptive scaling**

Recording how much better an outcome is in the context of others is clearly useful, and indeed a fully coded version of this is analogous to the prediction error, a key learning signal thought to update values as a consequence of trial-and-error experience [21]. There is good evidence that dopamine projections from the midbrain to the striatum carry this signal [22–25], and striatal activity in humans recorded using fMRI concurs with primate data [26–29].

But theories of relative judgment also suggest that values should scale to match the relevant range of magnitudes. Tobler *et al.* [30] found that just this property was exhibited in dopamine neurons. They conditioned monkeys to predict varying quantities of fruit juice. When they presented cues that predicted two possible, equiprobable amounts, they showed (as expected) that dopamine cell activity coded the relative value of the outcomes (more precisely, the value prediction error), with larger volumes eliciting phasic activations and smaller volumes resulting in deactivations, independent of absolute magnitude. Critically, however, the difference between the activity associated with the higher and lower magnitudes were essentially constant, despite the fact that the volume ranges were substantially different. Thus, the apparent gain, or sensitivity, adapts to the range of magnitudes expected. That such scaling was not seen to the cues themselves, the order of which was unpredictable, suggests that the cues set the scale on each occasion, on a trial-by-trial basis.

**Expectation, inference and placebo effects on value**

In relative judgment models, contexts may provide anchors to establish scales in determining the relative positions of an option. However, in expectation and ‘perceptual’ models, they actually provide information that influences the experience of it. Expectation effects are well studied in behavioral, psychophysical and economic studies, in both the appetitive and aversive domain. Studies on the latter, which are slightly more extensive, have shown that placebo effects can be reliably induced by either implicit or explicit suggestions that a painful stimulus is less intense than it actually is (or more intense, as in the ‘nocebo’ effect). Human neuroimaging studies show that brain areas associated with the perception of unpleasantness, the anterior insula cortex and anterior cingulate cortex, show a pattern of activity that reflects the reduced aversive experience induced by expectation despite no change in the actual stimulus, suggesting that the representation of aversiveness is adapted in the brain [31,32].

Placebo effects also exist for rewards. De Araujo *et al.* [33] gave subjects isovaleric acid (which has a cheese-like odor) to subjects in an fMRI scanner, and accompanied it with the words ‘cheddar cheese’ or ‘body odor’, exploiting the disconcerting similarity between the two. They found that not only did subjects greatly prefer the scent when labelled ‘cheddar cheese’, but that activity in medial orbitofrontal cortex and rostral anterior cingulate cortex coded this subjective experience. Presumably had they been given the option, they would have paid more money to receive the cheddar cheese smell (or paid to avoid the smelly socks).

A more common setting for influencing expectancies occurs with brand names, which imply different degrees of quality. Indeed, both fMRI and lesion studies suggest that knowledge of brand influences subjective preferences for cola drinks via the ventromedial prefrontal cortex, in a region that connects strongly with, and abuts, the medial orbitofrontal cortical surface [34,35].

Not only can direct suggestions of quality influence subjective experience, but so can prices. Baba Shiv, Dan Ariely and their colleagues studied how the efficacies of products, either an energy drink or an over-the-counter analgesic, yield their behavioral effects depending on their apparent price [36,37]. They found that energy drinks helped sustain concentration, and analgesics relieved pain more, if they were thought to be more expensive, despite the fact that both products were in fact placebos. This is consonant with the observation that purely sensory judgments are to some extent uncertain, and that subjects use cues (in this case prices) to improve inference.

Recently, this neurobiological basis of this effect has been studied in people. Plassmann *et al.* [38] gave subjects several wines, and provided them with information regarding the retail price of each. Subjects tasting wine they believed to be expensive found it significantly more pleasant than the same wine labelled as being cheap. Neural responses in medial orbitofrontal cortex correlated with the experienced pleasantness, rather than the identity of the wine (Figure 2).
Taken together, these studies show that not only does the subjective experience of a product depend strongly on cues and contexts, be they relevant or irrelevant, but so too does the basic representation of reward value in medial orbitofrontal and ventromedial prefrontal cortex.

Equating value in transactions

Transactions of any sort involve establishing whether the value of obtaining something compares favorably with the value of losing something else. Since firing rates may not be negative and decreases from baseline firing offer limited resolution, losses and gains may be best encoded by separate populations of neurons. Indeed, this as has been shown in both the orbitofrontal cortex and striatum [39–41].

It remains largely unknown how the brain integrates and compares gain and loss information. Knutson et al. [42] have shown that when an explicit trade-off is made between a stated price and an every-day good, there appear to be separate representations of the value of the item to be gained (in nucleus accumbens), and lost (in insula cortex). This leaves open the question of how the trade-off is made. Plassmann et al. [43] have shown that subjects’ willingness to pay for goods correlates with orbitofrontal cortical activity, consistent with the equation of a common currency of value in this area (since the amount offered will be lost). The fact that the brain area (i.e. the medial orbitofrontal cortex) involved in willingness-to-pay broadly co-localizes with that involved in placebo effects on value, and in the establishment of context-related scales, reaffirms the challenge in understanding exactly how setting up such currency trade-offs proceeds.

The artifacts of the comparison process may be quite striking. That scaling occurs in some form of another is not surprising, and it would be remarkable if neurons encoded accurately the value of goods such as a lunchtime sandwich and the price of a new house on the same scale. If they do indeed adapt, then comparisons across scales might be hazardous. This could offer insight into a classic experiment described by Tversky and Kahneman [44], who asked people whether they would spend 20 min to cross town to save $5 on a $15 calculator, or on $125 jacket. Subjects were far less inclined to do so for the jacket than the calculator, which is clearly absurd, since the absolute amount saved is identical. Clearly, the benefit of adaptive scaling weighs heavily against the inability to integrate across transactions in separate contexts in an individual’s daily life.

Discussion

Neurobiological studies are beginning to provide key insights into why the values people ascribe to goods, and the price they are prepared to pay for them, is often so

Anchoring of values in the VMPFC. Human subjects were given three wines to task while undergoing brain scanning (indicated by colors in the top plots). Indicated preferences were modulated by the stated price of the wine (top-left), but were consistent when no price information was given (top-right). The different in subjected preference was mirrored in the fMRI responses in the VMPFC (bottom). Adapted from [38].
susceptible to manipulation. First, in given contexts, the brain sets relative scales against which the ordinal position of goods is set. Second, the brain uses available and additional information to help refine judgments of value. Thus, object or price anchors can act in two distinct ways to influence trade decisions. First, they can establish the boundaries and sensitivity (or gain) of a value scale, such that a given transaction will appear relatively good or bad. Second, they can appear to provide information about the true worth of a product, and lead the individual to change the judgment and experience of a product.

However, many questions are left open. First, it remains unclear whether absolute value judgments may exist somewhere in the brain. That relative judgements of value are found to exist is not in itself a strong argument that it represents a fundamental characteristic of value encoding, since many related functions, in particular choice, might reasonably be predominantly concerned by how much better or worse one option is to another. Indeed, the striatum has an important role in guiding choice, and hence relative coding and adaptive scaling seen here might occur downstream of absolute value coding elsewhere. However, that relative coding is seen in orbitofrontal cortex is more important since this region has a well understood role in basic value coding, although it will be important for future studies to establish whether scaling, in addition, is also a feature of neuronal activity.

Second, evidence that hedonic perception is subject to perceptual priors does not necessarily imply that these influence subsequent decisions (transactions). One of the key insights from behavioral neuroscience to economics has been the realization that there are many interacting value systems that determine behavior [45]. This raises important questions, and limits the generality of conclusions about the findings from existing experiments. Notably, dopaminergic responses are thought to be central to cached Pavlovian and habit like actions, but appear to be less involved in more cognitive, ‘goal-directed’ action [46,47].

Third, despite good evidence that point predictions provided by cues can seemingly act as inferential priors in hedonic perception, the effect of referential anchors on value within the same modality remains unclear. That is, if you taste a medium quality wine, does this make a subsequently tasted wine taste better or worse? According to a simple Bayesian account, if there is temporal correlation between values, previous stimuli should act as relative attractors. In the absence of this, however, they might be expected to act as repellents, as sometimes seen in adaption effects in other modalities, for instance in color constancy and tilt illusions [48]. Beyond this, priors might operate at a higher level if, for instance, the brain actually learns distributions over values, and uses individual events to learn the parameters of these distributions.

Independent of this, a more straightforward prediction of Bayesian accounts is that certainty or confidence should control the magnitude of expectancy effects. In the appetitive domain, there is some behavioral data indicating that the strength of influence of prior knowledge depends on the amount of experience [49], but the neural basis of this effect has not been established. Recent data from the aversive domain does suggest that greater confidence in prior expectancies results in a greater impact on perception, an effect correlated at a neural level with aversive representations in anterior insula [50]. Whether confidence controls placebo effects in markets, either behaviorally or neurally, remains to be tested.

In summary, the way that the brain processes value-related information leaves it vulnerable in many modern day situations. While this is good news for marketing consultants, inspiring various inventive marketing tricks, it is bad news for economists schooled in traditional notion that willingness to pay for goods reflects the inherent, known, and stable values that people ascribe to them.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


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