

## **Distinguishing between candidate efficient coding objectives in subjective valuation**

### **Abstract**

The scheme(s) by which the values of options in economic choices are encoded in the brain promise to elucidate all sorts of outstanding questions in neuroeconomics, for example, why and in what contexts choice biases exist. Efficient coding is a well-grounded theoretical paradigm that stipulates that stimuli (e.g., options in a choice set) are represented in the brain in some quasi-optimal way, given constraints on neural resources. What defines “optimality” (or, “efficiency”), though, is subject to interpretation, and the choice of an efficiency objective may yield different predictions for choice behavior. Here, I present two papers that find support for different efficiency objectives in the encoding of subjective value and discuss how their conclusions might be reconciled.

### **Introduction**

The efficient coding paradigm stipulates that stimuli (e.g., options in a choice set) are represented in the brain in some quasi-optimal way, given constraints on the neural resources available to support the representation (Barlow 1961). According to this paradigm, “irrational” choice behavior can be accounted for as fringe cases where neural constraints on encoding force performance to deviate from optimality. We have seen in class an example of how one incarnation of this paradigm, applied to representations of subjective value in economic choice, can explain coarse patterns in neural activity in brain areas associated with valuation (e.g., range adaptation; Rustichini et al. 2017).

However, there are several possible notions of “efficiency,” and therefore several competing schemes that could be seen as optimally governing encoding. For example, the neural machinery involved in encoding subjective value may be optimized to retrieve estimates of the values of the stimuli it encodes that are minimally different from true values (i.e., encoding may be efficient in that it maximizes accuracy). This case gives the form of the encoding objective classically considered to be at play in early sensory areas, where the mutual information between the raw sensory input and the representation is maximized (e.g., Laughlin 1981). By contrast, encoding may be optimized in such a way as maximizes one’s expected reward in the choice between options; notably, a reward objective may make meaningfully distinct predictions from those of an information objective because, for example, the accuracy of the agent’s discrimination between option values matters less to the agent’s overall reward when option values are more similar.

Distinguishing between these candidate coding objectives has proved elusive. In fact, two recent papers, both seeking to describe the encoding of subjective value, have found support for both coding objectives: Rustichini et al. (2017) for reward and against information, and Polanía, Woodford, & Ruff (2019) for information. Here, I present the experimental approach of each paper and outline how its results support its conclusions about encoding. Finally, I discuss how these results might be reconciled.

**Rustichini et al. (2017) (RCCP)**

RCCP measure the encoding of subjective value in the orbitofrontal cortex (OFC) of rhesus monkeys. In the task, monkeys were made to choose between two kinds and quantities of juice. In each trial, two offers were projected on opposite sides of a screen, and the monkey was trained to perform a saccade to the side corresponding to their choice. Offers were presented iconically by a number of colored squares: for each offer in a trial (i.e., on each side of the screen), the color of the squares indicated the identity of the juice and the number indicated the quantity. An indifference point describing the relative subjective values of the two juices was determined for each monkey by varying the quantities of each juice between trials and measuring choice frequency; by convention, juice A is preferred. The activity of “offer value cells” in the OFC, which have been shown to encode the subjective values of individual options in a choice set, formed the basis for the paper’s analysis.

For each kind of juice, an average tuning curve for offer value cells preferring that kind of juice (i.e., whose activity increase monotonically with the number of offered units of that kind of juice) was determined; this was done by binning together trials with the same number of units of the juice of interest and averaging the firing rates of cells preferring the juice within each bin. According to the maximum entropy principle and as demonstrated by Laughlin (1981), encoding is optimized with respect to an information objective if the tuning curve of the cells that represent the value of interest is in proportion to the cumulative probability density (CDF) of the distribution of stimulus values (i.e., the prior). Therefore, by comparing the tuning curves to the CDFs of stimulus values, it was possible to assess the compatibility of neural data with an information objective. As RCCP illustrate in their Fig. 1 (e and h), tuning curves are approximately linear despite nonlinear CDFs, thereby supporting the conclusion that encoding does not maximize mutual information. RCCP demonstrate that the observed tuning curves maximize expected reward in that they are subject to range adaptation, thereby maximizing the agent’s ability to discriminate between offers, subject to a limit on the dynamic range of neural firing rates. Though the authors were unable to demonstrate that the specific (linear) shape of these tuning curves (that are subject to range adaptation) adapts to maximize reward in each session, they show that offer value cell responses maximize the reward objective assuming a uniform joint distribution of offers.

**Polanía, Woodford, & Ruff (2019) (PWR)**

RCCP find evidence against an information objective in the encoding of subjective value in monkeys, but PWR find support for such an objective in humans. In their experiment, participants performed two tasks: a value-rating task and a choice task.

First, in the value-rating task, participants gave subjective ratings of the same set of food items several times, without knowing that they would rate the same items repeatedly (thereby not skewing any natural trend in rating variability). Participants were familiarized with the range of food items and the scale on which they would be rating them before the task began; this ensured that the rating scale could be used effectively from the very first trials, thereby rendering rating consistency between phases a meaningful measure. Though the value-rating task included some additional rating phases with slightly different conditions (i.e., varying presentation times; discrete v. continuous rating scale; value rating complemented by confidence rating), it is most important for the purposes of this discussion that participants rated each food item multiple times. The authors fit the parameters of an

efficient-coding model (prior, noise parameters, “true” subjective values of each option) for each participant as those that maximize the likelihood of the ratings that participant gave.

Following the rating phases, participants were asked to choose between two food items that they had already rated. Choice sets were generated by picking pairs of food items whose ratings were separated by a given margin (the “rating-difference level”). The authors incentivized participants to make their choices carefully by (a) asking them not to eat or drink anything for 3 hours before the experiment began, and (b) promising to reward them at the end of the experiment with one of the food items that they chose in the choice task.

The key analyses that the authors use to support of their information-maximizing coding model involve: (1) the consistency of ratings between rating phases, and (2) choice frequencies as a function of the relative subjective values of the options. Rating consistency was assessed for each option as the variance in the ratings of the same option between rating phases. The authors’ efficient coding model predicts that the variability in a participant’s rating of the same option is a function of the option value, due to noise introduced in the encoding and estimation steps. Using model fits, it was possible to predict rating variability as a function of the “true” subjective value of the option; as the authors illustrate in their Fig. 2 (b and c), there is excellent agreement between the observed rating variability and the model’s predictions. Furthermore, the model’s predictions agreed better with the rating distribution than those of an alternative model that simply assumes constant noise in the estimation step. Using the efficient-coding model fits, the authors could also predict choice frequencies in the choice task as a function of the relative subjective values of the options. Here, too, there is excellent agreement between observed choice and the model’s predictions as a function of rating-difference (Fig. 2, g and h).

## Discussion

Both RCCP and PWR report evidence for an “efficient” coding scheme for subjective value, but RCCP find support for a reward objective (and against an information objective) governing efficiency, while PWR find support for an information objective. Though these conclusions may seem incompatible, there are several important differences between the studies that may be reconcile their findings.

First, RCCP and PWR use importantly different participant cohorts. In principle, it may be reasonable to suppose that disagreement between their conclusions may result from an actual difference in efficient coding objectives between monkeys and humans. However, each encoding objective should in theory be possible in monkeys and humans, since they both have been evidenced in neural data in a much simpler organism: the blowfly (Laughlin 1981; Schaffner et al. 2021). Why a particular encoding scheme would be optimal in one species and suboptimal in another closely related one would need some motivation beyond “humans are more cognitively complex than monkeys.”

Additionally, RCCP and PWR differ in the nature of their data. Whereas RCCP support their conclusion using neural data, PWR use behavioral data (subjective estimates and choice behavior). Though PWR do not consider an alternative efficient-coding objective than information, even if they had their data may have been too noisy to distinguish effectively between two candidate objectives; it may be that their behavioral data is consistent with both objectives. Related to this, PWR’s approach to model selection is not nearly exhaustive enough. Importantly, they have not compared the performance of their information-based efficient-coding model to that of a reward-based one (or any other non-information-based one, for that matter); rather, they have only compared their model to a fairly naïve

alternative. In particular, rather than considering two sources of noise (in encoding and in the decision step) like the efficient-coding model, the alternative only assumes noise over the rating scale. Thus, the better predictive performance of the authors' information-objective efficient-coding model in the rating task may be attributable rather to its two sources of noise than to its optimizing an information objective per se. To be sure, RCCP argument against an information objective is not without its problems: they do not compare the predictions of the two candidate objectives in remotely similar ways and therefore cannot be holding each to the same descriptive standard in their analysis. Indeed, they allow that encoding maximizes reward assuming an (imagined) uniform joint prior for offer values apparently without noticing that such a prior implies a linear CDF and therefore optimally linear tuning curves per the information objective; these predicted curves may or may not be equally consistent with the quasi-linear tuning curves they measure as those predicted by the reward objective, but this analysis is simply not done.

The experimental designs of RCCP and PWR also differ in the access they give the authors to the "true" stimulus values participants are choosing between (and estimating, in the case of PWR). In RCCP, the identities of the options in different choice sets are constant (only the quantity of each kind of juice is varied), but in PWR, the identities of the options are varied. As a result, whereas RCCP could determine quantitatively the subjective value of each offer in a choice set (once they computed the relative values of the juices for each monkey), PWR had to infer subjective option values from participants' subjective ratings; as PWR themselves note, the subjective ratings on which they base their analysis may be as biased as the choice behavior they are seeking to account for. Similar to the previous criticism, the subjective value signal in the brain may be too noisy or degraded as measured at the level of psychophysics to adequately distinguish between competing coding objectives.

Despite these differences, there are some important similarities between the papers. In each paper, participants were primarily motivated by the value of their choices in the choice task; in particular, in PWR, the reward they received was not in proportion to the consistency of their estimates between rating phases or the accuracy of their ratings (as compared, for example, to the "true" subjective values inferred from rating data). In principle, this suggests that a reward objective should be most task-relevant in both experiments. However, an argument could be made that an information objective is most task-relevant in the experimental phases of PWR from which data was used to fit the model, because these phases involved estimation of "true" subjective value from a noisy representation of it; as mentioned in the introduction, the expected error in such an estimation is minimized using an information objective. In this case, it becomes clear that the truth about "how subjective value [or some other value] is encoded" may be highly task-dependent; this point has recently been illustrated by Schaffner et al. (2021), who show that the "fitness" (equally, "efficiency") of a neural code is tied to the reward structure used in the experimental task (e.g., estimate v. choice accuracy, in their orientation-discrimination design). In PWR, that the same efficient coding model derived from experimental phases where the task-relevant objective is estimate accuracy predicts behavior in experimental phases where the task-relevant objective is choice accuracy suggests either that the encoding scheme learned in the rating phases has not had enough time or data to be overwritten, or that the predictions of both objectives (reward and information) are very similar.

The disagreement between RCCP and PWR highlights two key issues in the study of efficient coding models for subjective value: (1) what constitutes “efficiency” may be highly task-dependent, so blanket claims about which objective is involved in encoding a given value (e.g., “Thus the coding of offer values in OFC, while context-adapting, is not optimal in the sense of information transmission,” RCCP, p. 3) are likely overstated; and (2) there is a need for experimental designs (like that of Schaffner et al. 2021) that adequately distinguish between candidate efficient coding objectives in a given task (unlike either RCCP or PWR).

## References

- Barlow, H. B. (1961). Possible principles underlying the transformations of sensory messages. In W. A. Rosenblith (Ed.), *Sensory Communication* (pp. 216–34). The MIT Press.  
<https://doi.org/10.7551/mitpress/9780262518420.003.0013>.
- Laughlin, S. (1981). A simple coding procedure enhances a neuron's information capacity. *Zeitschrift Für Naturforschung C*, 36(9–10), 910–912. <https://doi.org/10.1515/znc-1981-9-1040>.
- Polanía, R., Woodford, M., & Ruff, C. C. (2019). Efficient coding of subjective value. *Nature Neuroscience*, 22(1), 134–142. <https://doi.org/10.1038/s41593-018-0292-0>.
- Rustichini, A., Conen, K. E., Cai, X., & Padoa-Schioppa, C. (2017). Optimal coding and neuronal adaptation in economic decisions. *Nature Communications*, 8(1), 1208. <https://doi.org/10.1038/s41467-017-01373-y>.
- Schaffner, J., Tobler, P. N., Hare, T. A., & Polania, R. (2021). Neural codes in early sensory areas maximize fitness. *bioRxiv* (2021.05.10.443388).  
<https://doi.org/10.1101/2021.05.10.443388>.