What are the neural origins of choice variability?

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Two recent studies examine neural activity predictive of upcoming choices during value-guided choice. Their results may be cast in light of a competitive winner-take-all decision network. This viewpoint places certain decision variables not as features of the environment to be encoded, but as emergent properties of network activity.

Economists deride inconsistency. Nobel Laureate Paul Samuelson once quipped to Congress, ‘…if Parliament asked six economists for an opinion they always got seven answers. Two from John Maynard Keynes.’ Variability of opinion is similarly troublesome in many classical economic models of choice. Such models predicate rational behaviour on deterministically selecting the most valuable alternative. However, human choices are known to be a probabilistic function of value (Figure 1A). In light of this, the question arises: what are the neural origins of choice variability?

When making economic decisions, neural activity in several brain regions reflects values of choice alternatives [1]. Less clear is the mechanism by which comparison of alternatives occurs, but one proposal is that it parallels mechanisms underlying perceptual choice [2]. One physiologically realistic ‘winner-take-all’ network model of perceptual choice [3] makes predictions of bulk neural activity during economic decisions [4], as well as predictions of single neuron responses (Figure 1B). However, the latter have rarely been tested directly. Here, the trial-to-trial choice variability, so perilous in economic modelling, can become a blessing. One can isolate neurons with differential activity contingent upon the subject’s upcoming choice, even though the options presented are identical. In doing so, one studies the mechanisms by which decisions are realised. This approach was adopted in two recent studies of economic choice, investigating single-unit activity in prefrontal cortex [5,6] and striatum [6].

Padoa-Schioppa examined responses in orbitofrontal cortex (OFC) while monkeys chose between quantities of two different fruit juices [5]. He began by elegantly demonstrating that three ‘classes’ of neuron, which he described previously [7], are truly distinct. Activity within each class reflected different task-related variables: the identity of juice chosen (‘chosen juice’); the quantity of one particular juice offered (‘offer value’); or the value of the chosen option, irrespective of identity (‘chosen value’).

Closely related variables have also been previously isolated [8] in the dorsolateral prefrontal cortex (DLPFC) and striatal neurons examined by Maoz and colleagues [6]. In this experiment, monkeys selected between a small proximate reward and a large delayed reward. During the decision, some neurons (‘choice’ neurons) reflected upcoming leftward or rightward choices, having controlled for effects of value [8]. These are similar to the ‘chosen juice’ neurons, in that they correspond to the eventual output of a decision: the eventual response of the monkey. However, they differ in that their activity reflects the selected action rather than the selected juice.

What happens to these ‘decision output’ neurons as the choice unfolds? Padoa-Schioppa demonstrated two key features of the activity of OFC ‘chosen juice’ neurons [5]. First, during the decision, they showed a greater effect of chosen juice on easy decisions than on difficult ones (Figure 1Ci). Second, before the decision was presented (that is, before the animal even knew which options were available) their activity was predictive of the forthcoming choice, in particular on decisions where options were close in value (Figure 1Cii). Such prescient neurons were also found in DLPFC and striatum by Maoz et al. [6]. Different groups of cells either predicted whether the monkey would make a left or right action (Figure 1Ei) or choose the large or small reward in the 1.5-s period before trial onset [6]. Similarly to [5], both classes of neuron were more predictive on trials where options were particularly close in value (Figure 1Eii).

Such prescience may not come as a surprise to determinists. However, it can also be considered in the framework of neural competition, such as the winner-take-all network model in Figure 1B [3–6]. Consider if the output neurons in the network (either in juice reference frame in OFC, or action reference frame in DLPFC) have, through noise, more activity favouring one alternative over another before the decision. This may then bias the network to select this alternative in the presence of weakly discriminatory value inputs, when values are close. By contrast, when values are further apart, the inputs override any predictive bias in the network, and drive the network to select the most valuable option. There are two possible schemes by which this might emerge. Bias may be intrinsic within the network, or separate ‘bias neurons’ may be connected to output cells. Padoa-Schioppa’s findings appear to support the former [5]. Maoz et al. argue explicitly for the latter, because they found prescient activity was not selective to their ‘choice’ neurons [6].
A further component of such a decision network is the pool of nonselective neurons, which collectively mediate competition between the selective output neurons [3] (Figure 1B). Full predictions of the activity of nonselective neurons have not yet been detailed. However, they underlie the majority of bulk neural activity in the network, and this reflects a combination of chosen and unchosen values on each trial [4]. Therefore, these predictions might be related to ‘chosen value’ neurons described by Padoa-Schioppa (Figure 1D). Such cells are defined as principally reflecting chosen value in a stepwise regression [7]. Importantly, Padoa-Schioppa has now shown that their activity is also greater on trials where values are particularly close: having controlled for chosen value, they show more activity when the unchosen value is greater [5] (Figure 1D). Put another way, their activity is greatest when competition between options is greatest.

Finally, consider the inputs to such a decision network. These may correspond to ‘offer value’ neurons in OFC. One might again expect variability in such neurons to bias the choices of the network. Surprisingly, however, this was not what was found [5]. The activity of such neurons did not discriminate between trials where different juices were chosen, either preceding or during the trial. Recent theoretical work may offer an explanation here: a single neuron may not be predictive of choice if its noise is decorrelated from other, similarly selective neurons [9]. Such correlations might be expected of output choice neurons, with strong recurrent connections in the decision network [3], but not necessarily of value-coding inputs.

Together, these two studies may reflect a movement away from straightforward considerations of what decision variables neurons ‘encode’ during choice [10]. The critical point is that correlates of some variables (such as chosen value) might never need to be ‘decoded’ directly. Instead, by considering mechanisms influencing choice that give rise to the recorded activity of each neuron, ‘encoded’ variables emerge as necessary consequences of network dynamics in mediating competition.

Acknowledgements
This work was supported by the Wellcome Trust (Sir Henry Wellcome Fellowship 098830/Z/12/Z). I thank Tim Behrens for many garrulous yet fruitful discussions on ideas within this article, and Pip Hobby for comments on the manuscript.

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