What are the neural origins of choice variability?

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Abstract

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 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 examines responses in orbitofrontal cortex (OFC) whilst monkeys choose between quantities of two different fruit juices[5]. He begins by elegantly demonstrating that three 'classes' of neuron, which he described previously[7], are truly distinct. Activity within each class reflects different task-related variables: the identity of juice chosen

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('*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 DLPFC and striatal neurons examined by Maoz and colleagues[6]. In this experiment, monkeys select between a small proximate reward and a large delayed reward. During the decision, some neurons ('*choice*' neurons) reflect upcoming leftward or rightward choices, having controlled for effects of value[8]. These are similar to '*chosen juice*' neurons, in that they correspond to the eventual *output* of a decision: the monkey's eventual response. 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 demonstrates two key features of OFC '*chosen juice*' neurons' activity[5]. First, during the decision, they show a greater effect of chosen juice on easy decisions than difficult ones (figure 1c(i)). Second, before the decision is presented – that is, before the animal even knows what options are available – their activity is predictive of the forthcoming choice, in particular on decisions where options are close in value (figure 1c(ii)). Such prescient neurons are also found in DLPFC and striatum by Maoz et al.[6]. Different groups of cells either predict whether the monkey will make a left or right action (figure 1e(i)) or choose the large or small reward in the 1.5-second period prior to trial onset[6]. Similarly to [6], both classes of neuron are more predictive on trials where options are particularly close in value (figure 1e(ii)).

Such prescience may not come as a surprise to determinists. But 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 favoring one alternative over another prior to 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, as they found prescient activity was not selective to their '*choice*' neurons[6].

A further component of such a decision network are *non-selective* neurons, which collectively mediate competition between the selective output neurons[3](figure 1b). Full predictions of non-selective neurons' activity 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]. These predictions might therefore 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 now shows their activity is also greater on trials where values are particularly close: having controlled for chosen value, they show more activity when *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 network's choices. 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 each neuron's recorded activity, 'encoded' variables emerge as necessary consequences of network dynamics in mediating competition.

Acknowledgments

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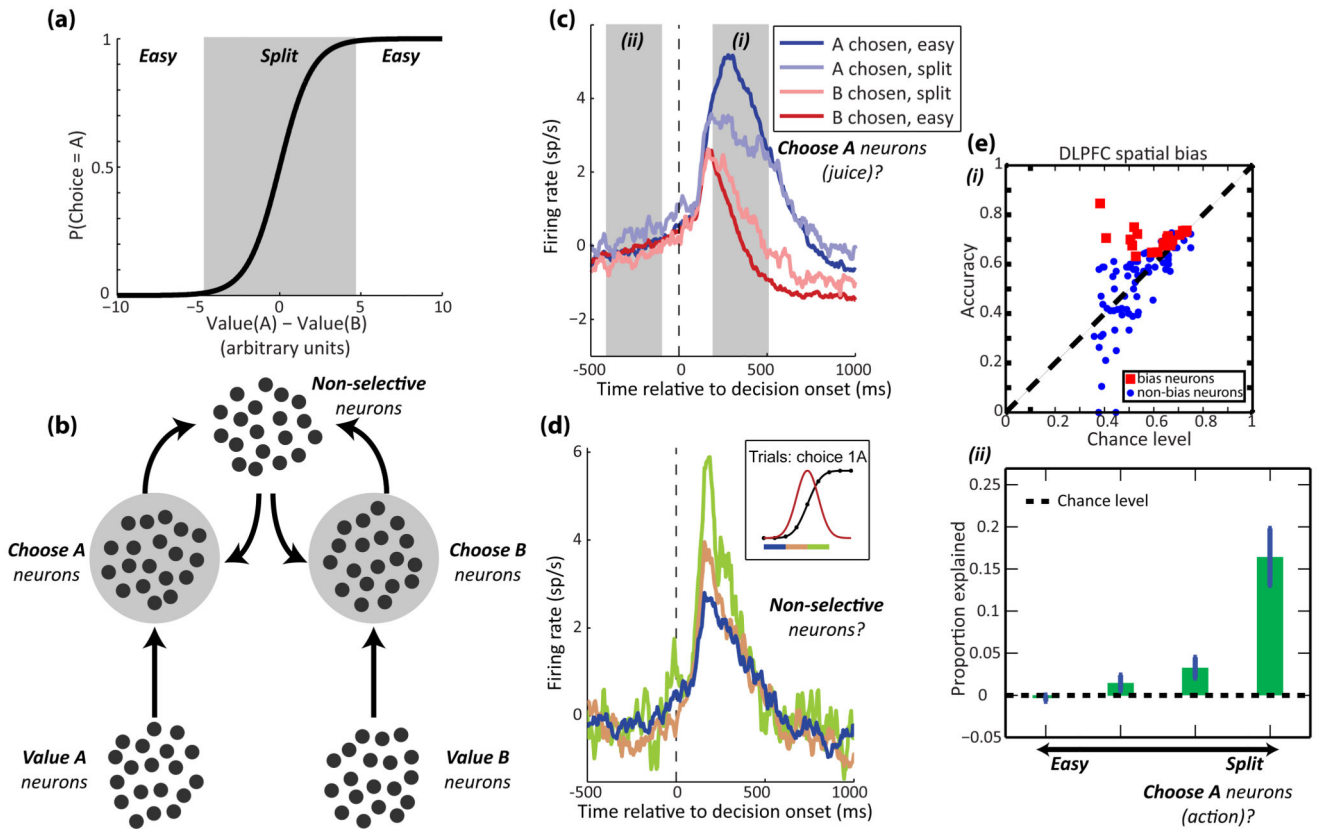
Figure 1. Trialwise variability in neural activity in the context of a winner-take-all network.
(a) When decisions are 'easy', choices are near-deterministic, but in the shaded area ('split') they become a probabilistic function of option value difference. **(b)** Schematic of winner-take-all decision network[3]. Choice (output) neurons possess stronger recurrent excitation, denoted by shaded area. **(c)**(i) Orbitofrontal cortex (OFC) 'chosen juice' neurons reflect trial difficulty[5]. After decision onset, neurons discriminate more between (choose A) and (choose B) trials on easier decisions. (ii) Prescient (pre-offer) discriminatory activity is only seen on difficult ('split') decisions. **(d)** After decision onset, OFC 'chosen value' neurons show greatest activity on split decisions, even though chosen value is held constant[5]. **(e)**(i) Dorsolateral prefrontal cortex (DLPFC) neurons show activity predictive of the animal's forthcoming action prior to decision onset[6]. Red squares denote neurons with predictive power significantly above chance. (ii) As in [5], these neurons are more predictive in split trials than easy trials. Parts **(c)-(e)** adapted from [5] and [6].