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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].

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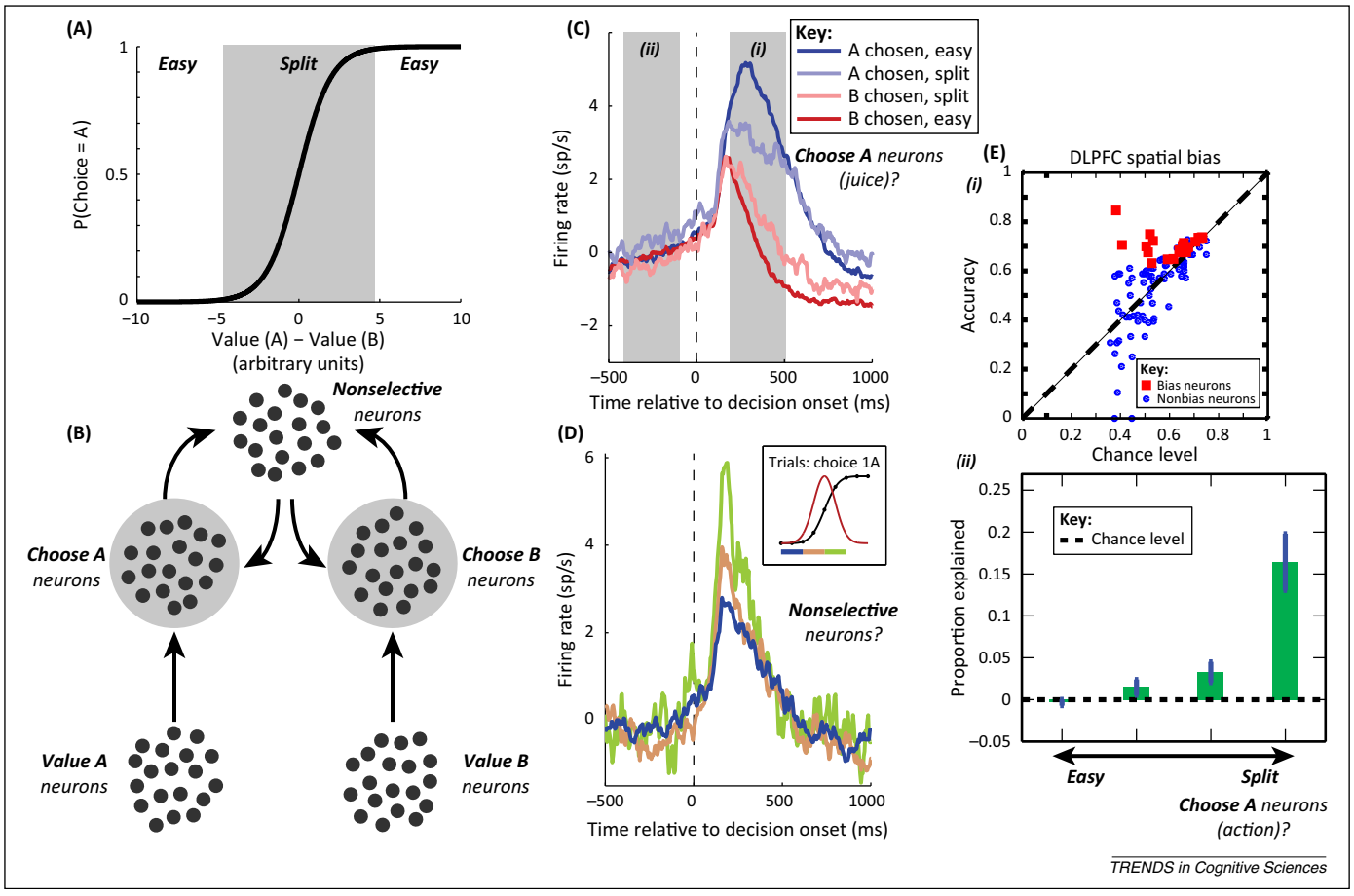

Figure 1. Trialwise variability in neural activity in the context of a winner-take-all network. **(A)** When decisions are 'easy', choices are near deterministic, but in the shaded area ('split') they become a probabilistic function of option value difference. **(B)** Schematic of winner-take-all decision network [3]. Choice (output) neurons have stronger recurrent excitation, denoted by the shaded area. **(C)** Orbitofrontal cortex (OFC) '*chosen juice*' neurons reflect trial difficulty [5]. (i) 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 the chosen value is held constant [5]. **(E)** (i) Dorsolateral prefrontal cortex (DLPFC) neurons show activity predictive of the forthcoming action of the animal before 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 in easy trials. Adapted from [5,6] (C–E).

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.

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Color synesthesia improves color but impairs motion perception

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A recent study showed that color synesthetes have increased color sensitivity but impaired motion perception. This is exciting because little research has examined how synesthesia affects basic perceptual processes outside the context of synesthetic experiences. The results suggest that synesthesia broadly impacts perception with greater neural implications than previously considered.

In a recent paper, Banissy and colleagues [1] examined whether color synesthesia influences basic feature-level perception in the absence of inducing stimuli. They found that synesthetes who experience color as their evoked sensation (concurrent) are better at discriminating color than non-synesthetes. Interestingly, this improved color perception comes at the expense of impaired motion perception: synesthetes have elevated motion coherence thresholds compared with non-synesthetes. By independently investigating the three dimensions of color, Banissy and colleagues provide a strong replication of their previous finding of enhanced hue perception in color synesthetes and extend it to saturation and luminance [2]. The novel result is that synesthetes have impaired motion perception. These findings are interesting because much extant research on synesthesia has focused on validating the phenomenon, investigating its origins, or examining how synesthetic experiences interact with other perceptual and cognitive functions [3]. By contrast, few studies have examined how mechanisms underlying synesthesia may influence basic perceptual processes [1], let alone those unrelated to the synesthesia.

To measure basic color perception, Banissy and colleagues tested groups of color synesthetes and non-synesthete controls on a visual-search task in which targets and distracters differed along a single color dimension in each trial: hue, saturation, or luminance (Figure 1A). Similar to their past findings [2], the color synesthetes were able to discriminate colors of different hue as well as saturation and luminance better than the non-synesthete controls (Figure 1B). This group difference was not due to a generalized task advantage because the synesthetes did not differ from controls when discriminating line orientation. Surprisingly, when judging the global direction of motion in random-dot kinematograms (Figure 1C), the synesthetes had elevated motion-coherence thresholds (i.e., reduced performance) compared with the neurotypicals (Figure 1D).

One common model posits that synesthetic experiences arise due to increased connectivity between cortical regions that process the inducing and concurrent features [4]. For example, it has been argued that grapheme–color synesthesia arises due to excess connectivity between regions of the brain that subserve form and color processing. For color synesthesia, it is not unreasonable to conclude that such excess connectivity could lead to finer-scale color representations [2]. However, this idea does not explain why color synesthetes would have impaired motion perception, which is largely mediated by cortical regions distinct from those that process either form or color. Research applying transcranial magnetic stimulation in neurotypicals suggests that brain regions involved in motion and color processing (i.e., hMT+ and hV4, respectively) can mutually inhibit one another [5]. Banissy and colleagues reason that the impaired motion perception observed in the color synesthetes may be an indirect consequence of a synesthesia-induced bias toward color in the interaction between color and motion processes [1]. A similar argument was used to explain the authors' recent finding that form- and color-processing areas (i.e., hV4) in the brains of color synesthetes had increased gray-matter volume compared with non-synesthetes. Moreover, an area central to motion perception (i.e., hMT+) had decreased gray-matter volume compared with non-synesthetes [6]. We find it entertaining that the

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