Trends in Cognitive Sciences

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Spotlight

Neurons That Update Representations of the Future

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A recent article shows that the brain automatically estimates the probabilities of possible future actions before it has even received all the information necessary to decide what to do next.

'The future depends on what we do in the present', as Gandhi said. Each action we take defines and constrains our possible future. This is true for political action, but also for everyday movements. If we are running and our leg is fully stretched, whatever we do next, the set of possible motions is constrained: they need to involve a flexion of the knee. An efficient prediction system should take this into account dynamically. It should continuously update a representation of the possible future actions before they happen, along with the associated uncertainty. Do brains do this? Glaser *et al*. [1] present evidence that indeed they do.

Predicting the future is often thought to be what brains have evolved to do. An efficient way to make predictions involving uncertainty is to represent knowledge with probability distributions and to acquire new knowledge by following the rules of probabilistic inference. It has thus become popular to think that the brain performs (an approximation of) probabilistic (a.k.a. 'Bayesian') reasoning. This idea has already had a profound impact in cognitive science and is consistent with a large body of work in human and animal behaviour [2,3].

However, the details of this hypothesis are unclear. In particular, there remains a large gap between the behavioural studies supporting the Bayesian hypothesis and uncovering the underlying neural substrate. Is the brain truly representing probability distributions? Where would those distributions live? How would they be represented? How flexibly are those representations updated, in particular when they should be dynamically changing? Glaser *et al*. [1] shed light on such issues.

In their experiment, three monkeys were trained to reach for four targets on each trial, one after the other, using their hand. On each trial, the position of the next target was conditioned on the current hand position: targets were more likely to appear approximately opposite the current hand position, with a slight clockwise bias. Additionally, the farther the hand position was from the centre of the workspace, the more likely the upcoming target was to be in the opposite direction. The authors first measured whether monkeys learned these probability distributions by looking at their behavioural performance. They found that indeed their initial reaches were biased by expectations about the target and their uncertainty.

The monkeys were implanted with electrode arrays in the primary motor cortex (M1) and dorsal premotor cortex (PMd). Neurons in the PMd are known to be active during the preparation for the reach and also during the reach itself. They are broadly tuned, responding best to one direction of reach. Glaser and colleagues find that a small population of PMd neurons, which they call 'potential response' (PR) neurons, are modulated before target presentation, based on the anticipated possible target locations. Moreover, the preferred directions of these neurons were distributed approximately in proportion to how likely upcoming movement directions were. The authors also could decode the movement that the PR neural population was planning in the 100 ms before target presentation. They find that the planned reaches decoded before target onset were usually approximately to the position opposite to the current hand position. This representation contained information about the uncertainty of the future positions, supporting the idea that it is really a probability distribution that is represented on single reaches, across the population of neurons. Such representation was not found in M1.

This line of work is important as it helps bridge the gap between neural representations and probabilistic computations. It also raises a number of questions. If PMd neurons represent the probability distribution of upcoming possible reaches, is this encoded as a continuous function or as samples of this distribution? At a theoretical level, there has been a longstanding debate about whether the brain uses probabilistic population codes (PPCs) [2] versus sampling codes, where only a few hypotheses would be represented with frequencies proportional to their probabilities, either across time or across the population of neurons [3,4]. At present Glaser *et al*.'s data seem compatible with both explanations. In theory, PPCs and sampling make different predictions, particularly about how the representation of uncertainty depends on the number of neurons involved in representation or how it would evolve in time. However, teasing them apart is proving difficult [5]. By recording more neurons, systematically decoding the neural activity using different codes, and comparing the predictions to behavioural performance, extensions of this study could possibly start answering such questions.

Other questions could be asked as well. How and where is this 'prior' distribution about likely future motion directions integrated with the information provided when the target appears (the 'likelihood') and 'read out' to lead to the actual decision? This would address how Bayes' rule is implemented, a question that has started to be investigated in various other domains [6]. Of particular importance will be to understand the nature of the necessary approximations used in these computations and how they can explain suboptimal behaviour [7].

This work might also pave the way to new neural theories of how the brain can build complex representations on fast timescales in more cognitive domains. Similar problems exist in speech processing; for example, where, when hearing streams of words, our brain needs to represent the syntactic and semantic structure of the sentence on the fly, anticipating future words. Cognitive flexibility may also be related to how fluidly the brain can represent likely future actions, contexts, or thoughts.

Ultimately, looking at individual differences in the flexibility of this representation could have implications in the clinical domain. It is often thought that mental disorder, in particular autism and schizophrenia, could be described as a failure mode of the predictive system [8,9], related either to the brain using wrong or incompletely learned beliefs or to failures in how neural networks implement approximate 'Bayesian' computations [10]. The neural substrate underlying this prediction system and the factors involved in its fluidity or its possible impairments, as well as the precise nature of the 'code', are still largely to be discovered.

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