Research Focus

Neural computations of decision utility

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How are decision alternatives represented in the primate brain? A recent study by Sugrue *et al.* sought to answer this question by integrating behavioral, computational and physiological methods in examining the choice patterns of monkeys placed in a dynamic foraging environment. They observed specific encoding of the relative value of alternatives by neurons in the parietal cortex, providing an important starting point for researchers interested in how value and probability are combined in the brain to arrive at decision outcomes.

Good decision-making is a prime example of intelligent behavior. We admire wise judges, effective business executives, clever investors, skillful physicians, triumphant generals, winning coaches, and thoughtful acquaintances who make good decisions and get what they want. In our own lives, we spend considerable effort in making personal decisions, some of which are fundamental to survival and the propagation of our genes, such as choosing mates, deciding where to live and selecting food. Innovative new research, such as recent work conducted by Sugrue, Corrado and Newsome [1] is making real progress in gaining insight into the neural processes that underlie these decisions and choices.

Traditional models of decision-making

We think of a decision 'occurring' when a person (or any organism) has an unfulfilled need and takes an action to achieve the goal of satisfying that need. A good decision is one that chooses the best available course of action in the face of uncertainty about what consequences will occur after the action is taken. For many years, psychologists and economists (and before them philosophers and mathematicians) have attempted to model decision-making processes theoretically. The focus of scientific research on decision-making has been on situations in which alternative courses of action for the decision-maker are presented in a 'choice set', with the decision-maker required to choose one alternative. The primary activity for the decision-maker is to evaluate each possible alternative and to choose the one most likely to achieve the desired goals. The dominant theoretical framework, Subjective Expected Utility Theory (SEUT), posits two fundamental characteristics of an alternative, which must be combined before reaching a decision, namely (i) the 'value' of the alternative, and (ii) the probability that this value will be attained. Formal decision theories, such as SEUT, propose that the value of each alternative is

weighted by its attendant probability, and the option with the highest probability-weighted values (or 'utility') is then chosen. The simple SEUT model provides a good first approximation of human (and much non-human) decision behavior [2,3].

In recent years, there has been a concerted effort by neuroscientists to begin to examine the question of how we make decisions in neural terms, and the data produced by this effort are beginning to play valuable roles in both constraining and validating traditional models of decision-making. Studies in the nascent field of neuroeconomics [4] are using methods such as single-unit recordings and fMRI to understand better the neural basis of decision-making and to locate brain regions that might exhibit neural activity correlated with the calculations prescribed by SEUT, that is, the weighting of the value of outcomes by their likelihood of occurrence (see [5] for a recent overview).

Representation of utility in the brain

The recent study by Sugrue *et al.* [1] makes a substantial contribution to this burgeoning field. Their method placed two rhesus monkeys in an experimental setting akin to a natural environment, requiring the animals to 'forage' through this environment to seek out rewards (drops of juice). The monkeys were presented with two possible colored targets, red or green; on each trial, they were free to choose either of these targets. The choice was made via an eye saccade to the favored target. The probability of juice being available at each target was subject to change at fixed points throughout the experimental session. The monkeys therefore had to update their internal representations of the value of each of the targets dynamically to maximize their reward in this task. The results demonstrated that they did so spectacularly well. Both monkeys in the task exhibited classic 'matching behavior' [6], that is, matching the ratio of their choices to the ratio of rewards of the two targets. Furthermore, the monkeys altered their choice behavior very quickly as the reward rates of the two targets changed, despite the fact that these changes were unsignaled.

Sugrue *et al.* formalized this matching behavior with a simple local matching law. This departs from the traditional matching law by introducing a decay function whereby more distant rewards play a diminished role in updating the utility of a given target. Essentially, the model predicted that the probability of selecting a given target was a function of how often that target had provided a reward in the (recent) past, as compared with total successes across targets (see Box 1). This local

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Box 1. The local matching law and decision-making

Interestingly, the simple local matching law used by Sugrue *et al.* bears a striking resemblance to many models used in more traditional, behavioral studies of decision-making. Such studies have suggested ratio models of this nature as a useful predictor of decision behavior. There is a general consensus that the integration of subjective probabilities or strengths of beliefs follows a ratio rule, usually attributed to Luce's Choice Axiom [21]. 'Support Theory' is the best-known example of this ratio of primitive strengths approach [22]. Support Theory proposes that the judged likelihood of any hypothesis is given by the support for that hypothesis compared with the support for the alternative(s). For example, Koehler [23] applied Support Theory to predictions of the outcomes of 20 National Basketball Association games. Participants made independent assessments of the strength of each of the teams, and then judged the results of various games. Koehler found that by using these strength assessments as support values, and hence as inputs to the simple ratio model, the participants' outcome probability judgments could be predicted extremely well. Similar results have been reported by other researchers [24,25].

matching law proved an excellent predictor of the monkeys' choices, but more importantly, allowed a direct metric as to how the monkeys valued the target at any given point in time. On every trial it was therefore possible to compute the probability that the monkey would select either the red or the green target – in essence providing a window into the utility of each option.

Assessing this utility measure allowed the researchers to investigate whether particular neurons were representing the utility signal for each target. Based on previous work by their group and others [7–11], they targeted the lateral intraparietal (LIP) area of the posterior parietal cortex, an area that appears to be involved in guiding saccadic eye movements. After recording directly from neurons in this area, the researchers indeed found that LIP neurons parametrically encoded the respective utilities of the two target colors on a trial-by-trial basis, strongly suggesting that a utility-like measure operates in the brain.

Deciding where to go now

Other researchers are also now seeking to examine this type of choice behavior in animals [12], and there has in recent years been a vast increase in the number of functional neuroimaging studies concerned with understanding the brain basis of decision-making in humans, examining people in a wide variety of decision-making contexts – as they make decisions about which gambles to choose [13], as they play economic games [14–16], and even as they choose which member of the opposite sex they might want to take to lunch [17].

The Sugrue *et al.* study suggests some interesting paths for future research to follow. In addition to the interesting empirical results produced by this study, one important contribution is that it is concerned with directly examining 'free' choice. Previous studies in this area have also tracked neuronal activity as it related to determinants of decision choice, but those studies typically examined conditioned or instructed behavior. The monkeys in the Sugrue *et al.* research were free to decide in any way they

wished, and examining this type of decision behavior would seem to offer the best insight into understanding the processes and computations underlying real-life decision-making.

A fundamental question raised by the study concerns the nature of the neural utility measure. As the authors point out, although neurons in the lateral intraparietal area underlie some measure of utility, it seems likely that the integration of probability and value information is carried out elsewhere in the brain. This raises the obvious question of where in the brain these values are computed. It would be especially important if distinct neural systems were identified that independently reflect both the value and the probability of the options under consideration. Although the Sugrue *et al.* paper manipulated the probability that a given target contained the reward, the reward *amount* itself was fixed across the experiment. Therefore, it would be interesting to systematically manipulate both the probability and amount of the reward that could be obtained. Work of this nature (e.g. [10]) might help to elucidate the underlying characteristics of the utility measure, and provide support for the classical model of SEUT. In addition to investigating brain areas that compute and respond to utilities, researchers are also attempting to discover *how* these utility values are encoded. There is some evidence that the mesancephalic dopamine system might play an important role in this [18]. Computational models of neural activity in prediction, decision and consumption have also been proposed by several researchers [19,20].

How does someone trade-off monetary value, immediate sensory gratification and prospects for good health when choosing a vacation or a meal? If a person or an animal is to decide between such difficult-to-compare options a common valuation system is essential. This capacity to make sensible trade-offs by representing incommensurate and uncertain consequences in a common cognitive metric is one of the central skills underlying effective decision-making. There is accumulating evidence that the brain does perform utility calculations like those prescribed by Subjective Expected Utility Theory, and neuroscientific methods offer a rich new source for those seeking to understand the neural basis of decisions and choices.

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The puzzle of working memory for sign language

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Why is immediate-serial-recall (short-term memory) span consistently shorter for sign language than it is for speech? A new study by Boutla *et al.* shows that neither the length of signs, nor the formational similarity of signed digits, can account for the difference. Their results suggest instead that the answer lies in differences between the auditory and visual systems. At the same time, however, their results show that sign language and spoken language yield equivalent processing spans, suggesting that reliance on immediate-serial-recall measures in clinical and educational testing is misplaced.

One might expect that working memory for sign language would parallel working memory for visual-spatial materials, rather than for speech. Instead, the evidence indicates that working memory for speech and sign are strikingly similar (for reviews see [1,2]). For both language types, information is maintained in a phonological rather than a semantic code, and both speakers and signers use an articulatory mechanism to rehearse subvocally or submanually [2]. For sign language, phonological coding is based on manual rather than oral features (e.g. hand configuration, place of articulation on the body, movement, and hand/arm orientation) [3].

Despite these intriguing parallels, storage capacity has been found to differ significantly for speech and sign, with speakers consistently exhibiting a longer span than signers. The recent study by Boutla, Supalla, Newport and Bavelier [4] attempts to identify the factors that explain this discrepancy. One possible explanation is that – at least when a standard digit-span task is used – the visually similar number signs in American Sign Language (ASL) give rise to a phonological similarity effect and thus poorer memory for signers. However, the difference in span is not just limited to digits. Another frequently proposed explanation builds on the fact that signs take longer to articulate on average than words do [5]. On this theory, the longer articulation time creates the equivalent of a word-length effect, thus reducing span [6]. A third possibility is that deaf people simply have a smaller short term memory capacity than hearing people, and thus the difference is unrelated to language modality.

The persistence of the span difference
The study by Boutla *et al.* [4] shows that none of these explanations is sufficient. The sign stimuli in their

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Available online 28 October 2004