

# Neural correlates of decision processes: neural and mental chronometry

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Recent studies aim to explain the duration and variability of behavioral reaction time in terms of neural processes. The time taken to make choices is occupied by at least two processes. Neurons in sensorimotor structures accumulate evidence that leads to alternative categorizations, while other neurons within these structures prepare and initiate overt responses. These distinct stages of stimulus encoding and response preparation support variable but flexible behavior.

## Addresses

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## Abbreviations

**FEF** frontal eye field  
**LIP** lateral intraparietal area  
**MT** middle temporal  
**ROC** receiver operating characteristic curves  
**RT** reaction time  
**SC** superior colliculus  
**VIP** ventral intraparietal area

## Introduction

The neural correlates of decision making have been reviewed so often [1–4,5,6] that one might review the reviews. Instead, I focus here on new studies that relate neural processes to reaction time (RT). An enduring problem in psychology is that of explaining the duration and variability of response times [7]. However, most behavioral studies conducted with monkeys treat RT as an experimental confound to be avoided by imposing arbitrary delays in tasks in an attempt to separate the sensory-evoked from the movement-related modulation of discharge rate. Often this procedure is used without recognizing that insertion of the delay invokes additional processes of anticipation and readiness [8] that result in neural modulation [9]. In spite of the pivotal role of RT in theories of cognition, neurophysiological studies aimed at explaining the duration and variability of RT have only recently been conducted [10].

## Accumulation of evidence

### Lateral intraparietal area

A recent study by Roitman and Shadlen [11] extends a well-known line of research on the neural basis of visual discrimination. Monkeys discriminated the net direction of motion of a field of moving dots, with variable amounts of random noise, by shifting their gaze to one of two targets. Performance on this task is based on the representation of the motion stimulus in the middle temporal (MT) area [12]. However, the signals in MT are not sufficient to produce the saccade by which the discrimination is reported. To understand this transformation, activity has been recorded in sensorimotor parts of the brain that are innervated by MT, such as the superior colliculus (SC) [13], the lateral intraparietal area (LIP) [14] and the dorsolateral prefrontal cortex including the frontal eye field (FEF) [15]. The recent study by Roitman and Shadlen [11] permitted monkeys to report the direction of motion as quickly as they could. When most of the dots moved in the same direction, the monkeys produced a high fraction of correct responses with short response times. When a small fraction of dots moved coherently, the monkeys required more time and made more errors. The evolution of activity in the LIP was related to the quality of the stimulus and the time of the saccade. If the motion of the dots signaled a saccade to the target in the receptive field, the average activation of LIP neurons increased gradually following appearance of the motion stimulus. The increase was more rapid in trials with stronger motion and shorter response times. In response to a given stimulus, variability in response time was correlated with the variability in the rate of growth of an average of activity of LIP neurons. The results are interpreted in a framework that supposes that the activity of neurons in LIP (and by extension SC and FEF) corresponds to the accumulation of the difference in responses between pools of motion-sensitive neurons in area MT that represent the alternative directions of motion, which is an optimal quantity for decision making [4].

### Middle temporal and ventral intraparietal areas

A study by Cook and Maunsell [16] examined the responses of neurons in area MT and in the ventral intraparietal area (VIP) of monkeys while they detected the brief appearance of coherent motion in one of two fields of random motion. The VIP area is adjacent to LIP, and is involved at the same functional level as LIP. The monkeys' operant response was to release the lever as quickly as possible. A stronger motion signal resulted in more rapid growth of activation in MT and VIP, and in shorter RTs. The timing and pattern of activation in MT

and VIP were different; responses in MT were earlier and more phasic, whereas those in VIP were later and increased more gradually. When the activity from MT or VIP was averaged, consistent relationships were discovered between the timing of the responses to both the coherent motion and the RT. First, the latency of the initial response in the MT area was synchronized more with stimulus presentation than with the response, but the latency of the initial response in area VIP was aligned with RT. Second, the time at which the response to the coherent motion reached a certain discharge rate predicted the RT if a constant residual time of 260 msec was added for the MT responses and 200 msec was added for the VIP responses. In contrast to these timing relationships, the magnitude of activity of neurons in MT and VIP in the RT period was poorly related to the choices the monkeys made. These results contrast with those of earlier work on the MT area [12]. Further work is needed to examine whether this is related to differences in the task, stimulus or analysis.

#### Selection for pursuit and saccades

In an image with many moving objects, a selection process must guide pursuit [17]. Several studies have explored the properties of this selection process and its relation to saccade target selection. If two potential targets for pursuit move simultaneously, then before a commitment to pursue one of the targets, the eyes move according to the vector average of the motion of the two targets [18,19]. Selection of a stimulus for pursuit can be dictated by selection of that stimulus for a saccadic gaze shift [20]. The pursuit of the selected stimulus is accurate immediately after the saccade is completed. Given the 50-100ms afferent delay of the visual system, this means that the velocity of the stimulus that is to be pursued must have been represented accurately before the saccade was initiated. Evoking a saccade by electrical stimulation of the FEF or the SC to one of two targets moving in different directions causes an immediate selection of that stimulus for the guidance of pursuit [21]. This finding suggests that the neural structures that are responsible for producing saccades can influence directly and immediately the representation of visual motion that guides pursuit eye movements.

#### Superior colliculus

A study by Krauzlis and Dill [22] related the activity of neurons in the SC to the time of initiation of either pursuit or saccadic eye movements to one of two stimuli, distinguished by their color. The initial response of the SC did not distinguish between the two stimuli, but this was followed by suppression of the response to the non-target and increase of the response to the target, which preceded both saccades and pursuit. Curiously, the difference in activity between representing the target and the non-target was less for pursuit than for saccades, and fewer cells selected the target for pursuit. This study also sought

to predict which eye movements were initiated from the activity of the neurons, and the time at which they were initiated. The authors performed an analysis in which average responses were constructed from random samples of all of the trials from all of the neurons. The difference in the amount of neural activity that represented the target and the non-target was quantified with receiver operating characteristic (ROC) curves, which were constructed from the two distributions of sampled activation as a function of time. (An ROC curve quantifies the degree of overlap of the two distributions of neural activity. Complete overlap yields a value of 0.5, and complete separation, a value of 1.0. The ROC has been a popular and effective measure of the difference of neural activity in two conditions.) This analysis is derived from earlier studies of the activity of neurons in the FEF recorded during a visual search [23,24]. Krauzlis and Dill supposed that movements were initiated when the ROC values reached a certain criterion, and arrived at that criterion by working backwards from the observed RT distributions. The criterion ROC value was 0.55 for pursuit and 0.68 for saccades.

The conclusions of this study seem compatible with the observations and conclusions of the studies just reviewed. However, on closer inspection certain aspects are difficult to reconcile for several reasons. The first issue is an assumption shared with the previous studies, that the neurons sampled are homogeneous. However, numerous studies have described a clear heterogeneity of neurons in sensorimotor structures. For example, a recent study of SC in monkeys performing pop-out visual search found that neurons with combined visual and movement-related activity (visuomovement neurons) discriminated the target from distractors but phasic and tonic visual neurons did not [25]. Also, the relationship between the time of target discrimination and RT varied across neuron types. Certain visuomovement neurons selected the target after an interval that did not vary with saccade latency. Other visuomovement burst and prelude neurons and movement neurons with no visual response discriminated the target at a time synchronized on saccade initiation. The second issue concerns the functional implication of the analysis. The most explicit model of the decision process in tasks such as this holds that the discharge rate of neurons in SC, LIP and FEF corresponds directly to the accumulating difference of the activity of the visual neurons representing the alternatives [4]. If so, then deriving an ROC from the activity of the SC neurons amounts to a difference of a difference. This may be legitimate, but then which neurons accumulate the difference of SC activity? The third issue concerns the meaning of the ROC measurement. Prior studies of area MT equated the ROC values derived from the difference in neural activity representing the alternatives directly to the percent of correct behavioral responses [12]. That is, an ROC value of 0.75 corresponded to 75% correct

choices. Now, the data analyzed by Krauzlis and Dill were all correct trials, so what sense can be made of an ROC of 0.55–0.68 corresponding to 100% correct performance? If the ROC derived from SC activity is not equivalent to percent correct, then either the neurons are not really playing a critical role in guiding the choice, or the analysis is flawed. The fourth issue concerns the incompatibility of this scheme with earlier demonstrations that saccades are initiated when the absolute, not relative, firing rate of saccade-related neurons in SC and FEF reaches a threshold [10,26].

### Computational theories

Stepping back, the key insight about decision-making afforded by this line of research is that alternatives that are more difficult to distinguish result in a longer period of less-differentiated neural activity and a longer RT. That is, RT is only as quick as neural activity allows. This general interpretation is attractive because the form of neural activity observed in these sensorimotor association areas corresponds to the general form of sequential sampling models, known as random walk or diffusion. In these models, a single accumulator represents the relative evidence for two alternative stimuli [27]. According to these models, errors arise from noise in the representation of the stimuli [28]. Also, in this architecture, diffusion that favors one choice constitutes disfavor for the alternative, which should prohibit any inclination to produce the non-selected response. However, partial activation of the non-selected response has been observed [29]. The alternative to a diffusion of the difference between choices is a race among accumulators representing each option [30–32]. The formula that describes the outcome of such models is at the heart of biased choice theory [33], which is the historical and conceptual counterpart to signal detection theory. Biased choice theory attributes the unpredictability of the response to the decision process rather than to the stimulus representation. Both signal detection theory and biased choice theory provide quantitative descriptors of discriminative ability and response criteria. These theories are mathematically equivalent under reasonable assumptions, so it should not be surprising that race and diffusion models can account for common sets of data [34] or that intermediate models are conceivable [35].

### Distinguishing accumulation of evidence from response preparation

None of the studies or models mentioned above are explicit about how a measure of evidence reaching a criterion is translated into a motor command, and all suppose a fixed residual time to initiate the movement. However, numerous other observations indicate that a post-perceptual stage of response preparation contributes to the delay and variability of RT. First, movements are only produced by muscle contractions initiated by particular circuits in the brainstem or spinal cord. Key

elements of such circuits are not influenced by cognitive factors [36]. Thus, when approaching the final common pathway, neural activity is only involved in producing movements and has nothing to do with the context in which those movements are expressed.

Second, a series of studies has investigated how the time of target selection during visual search by neurons in the FEF relates to RT [23,37\*]. If the target was easily discriminated from distractors, the time taken for most, but not all, visually responsive neurons to represent its location in the array was relatively constant. If discrimination of the target was difficult, the time taken for neural activity in the FEF to represent the location of the target was longer. This difference was not seen during efficient search when saccade latency was delayed because of response conflict. When visual discrimination was more difficult, the increase in time taken to locate targets among similar distractors was accompanied by an increase in the variability of the selection time across trials. Consequently, the variability in the visual selection time accounted for some, but not all, of the variability in saccade latency. This happens because the production of an accurate saccade cannot proceed until the target is located. Variability in response preparation accounts for the remaining delay and variability of RT.

Third, a large body of work on scanning eye movements has demonstrated the dissociation between target selection and saccade initiation [38]. A controlled experiment was performed by Murthy *et al.* [39\*] to investigate whether selection of the singleton in a search array by FEF neurons could be dissociated from production of the saccade. In rare random trials, the target of the search array changed location. In some of these trials, the monkeys shifted their gaze to the original target location. Even when the monkeys' gaze shifted away from the pop-out singleton, visual neurons in the FEF represented the current location of the target. Complementary results have been obtained in the SC [40]. Thus, neurons in the FEF and the SC can represent the location of a visual target even though gaze is shifted elsewhere. If an explicit representation of the sensory evidence obliges the corresponding movement, then saccades directed away from the singleton should be impossible.

Fourth, if eye movements were produced directly by a sufficient accumulation of evidence, then how could movements that are not mapped directly onto a stimulus be produced? Such a system could not produce anti-saccades; however, presaccadic activity distinct from visual activity that is sufficient to produce antisaccades has been observed [41]. The influence of stimulus-response mapping was explored in a recent study using electrical stimulation of the FEF to probe the evolution of a perceptual choice [42\*]. The direction of an eye movement evoked from the FEF was influenced by the

direction of another eye movement that the monkeys would make to signal the direction of motion in a random dot display. The magnitude of the deviation was proportional to the strength of the motion signal and the duration of the motion presentation. When an anti-saccade response was required, the deviation was in the opposite direction (observed in a single monkey). However, when monkeys reported the direction of motion by shifting their gaze to different colored spots appearing at random locations, the deviation was absent. This study provides compelling evidence for the dissociation of the accumulation of evidence from production of a response.

Thus, current findings are compatible with the general view that RT is occupied by formally distinct stages of processing [43]. Determining the relative contributions of successive stochastic processes to RT poses both technical and conceptual challenges. For example, questions remain as to whether the transformations within and the transmission between stages are continuous or discrete [44,45]. Also, it is possible that distinct stages may have different architectures. Perhaps the stimulus encoding stage conforms to models with a single diffusion process because perception is exclusive; that is, you cannot see this and that at the same time. On the other hand, a race model has been applied with considerable success to response preparation and control [46].

## Conclusions

Psychophysics and reaction time form the empirical foundation of experimental psychology. Mechanistic understanding has come from mathematical models of covert processes that replicate performance. Models can be constrained by elucidating the neural processes that realize the covert cognitive processes, but only if the tasks are performed under the conditions that gave rise to the model. Descriptions of the properties of neurons do not explain the functions performed; therefore, a computational level of description is necessary to explain function. An intellectual synergy is developing; neurophysiological data can constrain redundant models, while new models embody the interpretation of neural function. A deeper understanding of the neural basis of decision making can be expected as research proceeds nourished by neurobiology and inspired by psychology.

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