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Relating neural activity and drift diffusion models

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Abstract

The drift diffusion model predicts that variability in response time (RT) is primarily due to the time required for evidence to stochastically accumulate to a response boundary. Total RT depends on both the *quality* of perceptual processing output (the mean rate of accumulation), and also the *duration* of perceptual processing (the delay from stimulus to start of accumulation). The activity of movement neurons in the frontal eye field (FEF) is associated with a stochastic accumulation; these cells initiate a saccade when activity reaches a fixed threshold. During saccade visual search, the onset of movement neuron activity correlates with RT, and increases when search is more difficult. This suggests that the duration of perceptual processing was increased. We simulated trajectories using various forms of the drift diffusion model and measured the onset with the same analyses used to detect the onset of neurophysiological activity. We found that varying the rate of accumulation resulted in large changes in the measured onset of model trajectories even when the start of the accumulation was fixed. These results show that a correlation between the onset of neural activity and RT alone is not sufficient to conclude that changes in RT were due to changes in the duration, but not quality, of perceptual processing.

Keywords: response time models; frontal eye field; eye movements.

Neural and Mental Chronometry

One hallmark approach of cognitive psychology is decomposing response time (RT) into distinguishable stages of processing (Meyer, Osman, Irwin, & Yantis, 1988) Consider an organism confronted with a stimulus relevant to two or more potential actions. Determining the relevance of object features to potential responses first requires a perceptual stage of processing. Perceptual output is interpreted by a response preparation stage which determines whether and when a response is made.

Neurophysiological data recorded from sensorimotor structures in the primate brain have been used to test competing hypotheses about the flow of information between perceptual processing and response preparation. Different populations of neurons in the frontal eye field (FEF) and superior colliculus (SC) reflect visual information about object relevance versus explicit decisions about where and when to move the eyes. *Visual neurons* respond to a visual stimulus in their response field (Thompson, Hanes, Bichot, & Schall, 1996). Visual neuron activity evolves over time to select the location of a task-relevant object. *Movement neurons* increase their activity

before a saccade; the movement is executed when activity reaches a fixed threshold (Hanes & Schall, 1996). Neurophysiological (Lee, Helms, Augustine, & Hall, 1997) and modeling (Purcell, Heitz, Cohen, Logan, Schall, & Palmeri, 2007) work suggest a functional connection between visual and movement neurons in FEF and SC.

Visual and movement neurons represent distinct perceptual and motor processes. During saccade visual search, the time when visual neurons select a target from among distractors is modulated by changes in target-distractor similarity, but not response interference (Sato, Murthy, Thompson, & Schall, 2001). This time may indicate the conclusion of perceptual processing. A recent study asked whether movement neuron activity could be used to identify the start of response preparation (Woodman, Kang, Thompson, & Schall, 2008). They found that varying target-distractor similarity or set size modified the onset of movement neuron activity (when activity began increasing above baseline). The onset of movement neuron activity also correlated with RT within difficulty conditions, but the growth rate did not. These results suggest that both systematic and random variability in RT is due to delays in the start of response preparation.

Movement neuron activity has been interpreted in terms of stochastic accumulator models. These models assume that perceptual evidence is integrated over time until it reaches a response boundary (Boucher et al, 2007). Evidence accumulation is preceded by perceptual processing time, T_{er} (Figure 1). The output of perceptual processing is the drift rate, v, which is the average rate of accumulation. Typically, these models predict that changing the difficulty of a perceptual discrimination should primarily affect the *quality* of the information (the drift rate), but not the *duration* of perceptual processing (T_{er}). If the onset of movement neuron activity corresponds to T_{er}, then this suggests that variability in RT is due to variability in the duration of perceptual processing. This contradicts a key assumption of the stochastic accumulator framework: manipulating the difficulty of a perceptual decision should primarily influence the drift rate.

What can the onset of movement neuron activity tell us about the transmission of information from perceptual processing (visual neurons) to response preparation (movement neurons)? It seems intuitive that variations in the drift rate must lead to variations in the rate of stochastic growth and not the time when activity begins increasing. However, the onset of neurophysiological activity cannot be

Table 1: Diffusion model parameters.

		v	s	η	T_{er} (s)	a	z	s_t (s)	s_z
Ratcliff et al (2003):	**Easy**	1.250	0.100	0.491	0.202	0.054	0.033	0.051	0.006
	Hard	0.440	0.100	0.491	0.202	0.054	0.033	0.051	0.006
Monkey F:	**Easy**	0.470	0.100	0.000	**0.127**	0.067	0.033	**0.000**	0.000
	Hard	0.125	0.100	0.000	**0.127**	0.067	0.033	**0.000**	0.000

'read out' as the T_{er} parameter can; rather, it must be measured. Information growth is stochastic, so the measured onset may not correspond to the start of the accumulation.

The aim of this work was to determine whether a correlation between the onset of activity and RT necessarily indicates a change in the duration of perceptual processing. We measured the onset of activity in both FEF movement neurons and simulated diffusion model trajectories using the same analyses. We show that a diffusion model may predict correlations between the onset of activity and RT although the start of the accumulation is fixed. We conclude that correlations between the onset of neural activity and RT are consistent with both changes in the duration of perceptual processing (T_{er}) and changes in the quality of perceptual output (drift rate).
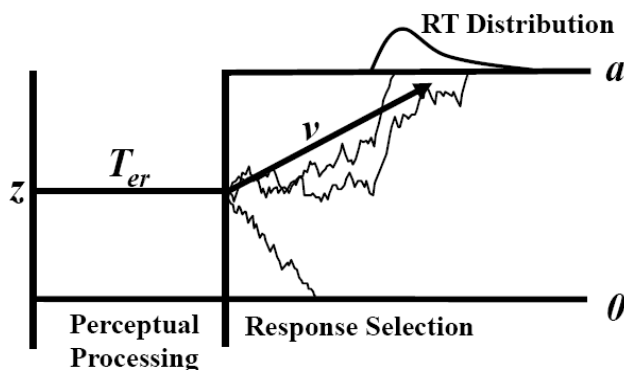

Figure 1. Diffusion model illustration.

Simulations 1:
What Can Cause Variability in Onset?

The drift diffusion model describes a mechanism in which stochastic samples of evidence accumulate toward one of two response boundaries (Ratcliff, 1978; Figure 1). The first boundary that is reached determines the response that is made and the time it takes to reach that boundary determines RT. The model also assumes some time for perceptual processes that precede the decision. Perceptual processing time varies across trials according to a uniform distribution with a mean, T_{er}, and range, s_t. Typically, T_{er} also includes time required for subsequent motor processes, but we will be modeling FEF movement neurons and can

assume a short and relatively invariable motor delay (Scudder, Kaneko, & Fuchs, 2002).

The output of perceptual processing is the drift rate, v, which is the mean rate of accumulation. Drift rate varies systematically across stimulus conditions; a higher drift rate indicates stronger evidence for a particular decision. Evidence is noisy and intratrial variability in the accumulation is distributed normally with a mean of 0 and a standard deviation, s, which can be set to 0.1 without loss of generality. Evidence begins accumulating from a starting point, z, and a decision is made when it reaches either the upper boundary, a, or the lower boundary at 0. The complete version of the drift diffusion model assumes across trial variability in the drift rate and starting point (Ratcliff & Rouder, 1998). Drift rate varies across trials according to a normal distribution with a standard deviation of η. Starting point varies according to a uniform distribution with range s_z.

Ratcliff and colleagues (2003) fitted the diffusion model to data obtained from non-human primates performing a two-alternative forced choice discrimination task. Macaque monkeys were trained to make a saccade to one of two targets positioned to the left and right of a fixation point. Each saccade target was associated with two possible categorizations of a centrally presented stimulus. The probability that an animal would be rewarded for making a saccade to the left target increased with the distance between the stimulus and the fixation point (maximum 10°). The probability of reward for a saccade to the right target varied inversely with the distance between the stimulus and fixation (minimum 2°). Both response probabilities and response time distributions for correct and error trials were fitted with the full drift diffusion model using standard techniques. Only the drift rate was free to vary between stimulus conditions (for a total of 6 free drift rates) and all other parameters were held constant across conditions. We used these parameters to begin exploring the conditions under which the diffusion model predicted a correlation between onset of accumulation and RT.

Method

Ratcliff et al. (2003) assumed several different drift rates for the stimulus conditions. To simplify matters, we only used the best-fitting drift rate parameters from two stimulus conditions, an easy condition (>8° separation, strong evidence for a leftward saccade) and a hard condition (6°

separation, weak evidence for a leftward saccade). We were particularly interested in contrasting two variations of the diffusion model; a version that explicitly allowed variability in perceptual processing time ($s_t > 0$; the version that was originally fit) and a modified version that assumed no variability in perceptual processing time ($s_t = 0$).

We simulated trajectories for the two variations of the diffusion model using a random-walk approximation (with step size $\tau = 0.001$) (see Ratcliff & Tuerlinckx, 2002). T_{er} was appended to the beginning of each trajectory as a constant equal to the starting point for that trial (as pictured in Figure 1). As is the case with actual neurophysiological data, we analyzed the trajectory as if T_{er} was not known; rather, the onset (when activity first began increasing) needed to be estimated using a sliding window algorithm. If either model predicts a positive correlation between the measured onset of activity and RT, then we will have evidence that this is a viable model of FEF movement neuron activity. If *only* the model that assumes $s_t > 0$ predicts a correlation with RT, then we will have evidence that the onset of model activation coincides with the conclusion of perceptual processing time

The onset of activity for each simulated trajectory was calculated using the same backward sliding window algorithm that has been used to analyze neural data (Woodman et al., 2008). The window (t +/- 50 time-steps) was started at RT and moved backwards in single time-step increments. At each increment, a Spearman correlation coefficient was calculated. The onset was defined as the time point when the correlation remained nonsignificant for 100 time steps. Only correct trials in which the process terminated at the positive boundary were analyzed, but this onset analysis could easily be extended to error trials by reversing the sign of the trajectory.

For each simulated trial, we generated a diffusion model trajectory and predicted RT. We simulated 100 trials to mirror the average number of trials observed in a typical neurophysiological experiment. Trials were sorted by predicted RT and divided into deciles. The first and last deciles were dropped to minimize the influence of outliers on correlations. An onset was calculated for the last trial within each group, which mimicked the analysis of actual neurophysiology as will be explained shortly. The Pearson correlation coefficient was calculated between the onset of activity and RT for the remaining trajectories. We repeated this process 100 times and calculated the mean correlation and the percentage of significant correlations across those 100 samples ($\alpha = 0.05$). To contrast the predicted onset across difficulty condition, we calculated the mean onset time across deciles and samples for the easy and hard conditions.

Results and Discussion

The parameters from Ratcliff et al. (2003) that we used for the simulations are listed in the top row of Table 1. The first set of simulations used this full set of parameters as given.

There was strong positive correlation between the onset of activity and RT for the vast majority of sampled simulated trials using both the easy ($\bar{r} = 0.854$, 93.0% had $p < 0.05$) and hard ($\bar{r} = 0.862$, 90.0% had $p < 0.05$) conditions.

This result is not surprising. The mean perceptual processing time ($T_{er} = 0.202$ s) accounted for the bulk of the total RT for both conditions ($\overline{RT}_{easy} = 0.222$ s; $\overline{RT}_{hard} = 0.241$ s). More importantly, variability in perceptual processing time was relatively large ($s_t = 0.051$ s). Since T_{er} determines when the accumulation can begin, that variability directly affects the onset of activity. Variability is large, so the onset is highly likely to correlate with RT. For now, the association of measured onset with the end of perceptual processing seems justified.

The next set of simulations eliminated all variability in T_{er}. While there was now only a weak correlation between the measured onset and RT for the easy condition ($\bar{r} = 0.118$, 5.0% had $p < 0.05$), the average correlation between the measured RT and predicted response time for the hard condition was fairly strong ($\bar{r} = 0.703$, 73.0% had $p < 0.05$). Furthermore, the mean onset time was 16 ms longer for the hard condition than the easy condition, although there was no difference in T_{er} time across conditions. These results suggest that the onset time may not necessarily mark the conclusion of perceptual processing and the start of response preparation.

Simulations 2:
Comparing Neural and Simulated Onsets

The first set of simulations showed that the diffusion model predicts a modest correlation between onset and RT even when there was no variability in the perceptual processing stage preceding the response selection stage. However, those analyses were limited in several respects. We did not have access to the neural data from the Ratcliff et al. (2003) study, so we cannot be certain that the movement neurons actually showed an onset shift in each condition. Furthermore, we removed variability in perceptual processing by forcing T_{er} and s_t to zero, but we cannot know if this model actually fits the behavior. So it may be an implausible representation of the true accumulation process. The next set of simulations addressed these issues.

Again, our primary goal was to see if onset would vary with RT when variability in perceptual processing was fixed within and across conditions. We analyzed behavioral and neurophysiological data from a subset of the data reported in Woodman et al. (2008). Data were collected from a Macaque monkey (Monkey F) that performed a saccade visual search task. The animal was trained to make a single saccade to an odd-ball target among seven distractors arranged equidistant from fixation in a circular array. The target was defined by color and difficulty was manipulated by varying the similarity between the target and distractors.

Table 2: Onset predictions from simulations 1 and 2.

	Easy Discrimination			Hard Discrimination		
	Mean r	%Sig	Mean onset	Mean r	%Sig	Mean onset
Variable T_{er}:						
Ratcliff et al (2003):	0.854	93.0%	0.208	0.862	90.0%	0.225
Constant T_{er}:						
Ratcliff et al (2003):	0.118	5.0%	0.007	0.703	73.0%	0.023
Monkey F:	0.852	92.0%	0.171	0.934	99.0%	0.220

The easy search condition used a red target among green distractors and the hard condition used a yellow-green target among green distractors. RT was defined as the time when the animal's eyes left fixation. During the search, neural activity was recorded from FEF. Recorded cells were classified as movement neurons if they showed an increase in activity prior to a saccade to their response field (Bruce & Goldberg, 1985). A total of 36 cells showed movement-related activity. Trials were classified as correct if a single saccade was made to the target. Only correct trials in which the target was inside the movement field of the cell were analyzed.

Method

For each movement neuron, we determined the onset of activity for groups of trials and assessed the relationship between onset and RT. Each trial produced a neural spike train that was aligned on the appearance of the stimulus array. For each neuron, correct trials were sorted by RT. Trials were binned into groups of ten and a single spike density function was generated that represented the average neural activity over time (Sato et al, 2001). The same algorithm that was used to define the onset of model activity in the first set of simulations was used to identify the onset of neural activity. The size of the window for neural data was ±25 ms to reflect the time-scale of the neural activity. The correlation between measured onset for each RT bin and the mean RT of that bin was determined for every neuron. We computed the mean correlation and the percentage of significant correlations ($\alpha = 0.05$) across cells to compare with model predictions.

Behavioral data were fitted using a simplified version of the diffusion model. The EZ diffusion model assumes that drift rate, residual time, and boundary separation are the only model parameters and have no variability across trials (Wagenmakers, van der Maas, & Grasman, 2007) The starting point of the diffusion process is fixed at the mid-point of the response boundaries and does not vary (i.e., $z = a/2$). Specifically, we used the *EZ2* method to fit easy and hard conditions simultaneously (Grassman, Wagenmakers, & Van der Maas, 2009). Since easy and hard conditions were interleaved within recording sessions, we assumed that only drift rate, v, varied across conditions. Once these parameters were defined, we simulated the diffusion model trajectories using the same procedure described in the first set of simulations. Measures of onset and the relationship between onset of activity and RT were also quantified using the same methodology.

Results and Discussion

The onset of FEF movement neuron activity correlated positively and consistently with RT for both the easy ($\bar{r} = 0.61$, 63.9% with $p<0.05$) and hard conditions ($\bar{r} = 0.74$, 75.0% with $p<0.05$). The mean onset also significantly increased across conditions (easy mean onset = 0.109 s; hard mean onset = 0.148 s; paired t = 9.21, p < 0.05). These results agree with previous reports of a larger population of neurons from the same database (Woodman et al., 2008).

The best fitting parameters for the EZ diffusion model to the behavioral data for the easy and hard search conditions are listed in Table 1. The model accounted reasonably well for the mean RT ($\overline{RT}$) and RT variance (σ^2) for both the easy ($\overline{RT}_{obs} = 0.192$ s; $\overline{RT}_{prd} = 0.194$ s; $\sigma^2_{obs} = 0.002$; $\sigma^2_{prd} = 0.002$) and hard ($\overline{RT}_{obs} = 0.236$ s; $\overline{RT}_{prd} = 0.235$ s; $\sigma^2_{obs} = 0.006$; $\sigma^2_{prd} = 0.007$) conditions. Notably, the model accounted for the data well when only drift rate (strength of perceptual evidence) was free to vary across conditions, although we did not evaluate alternative models.

When the best fitting parameters were used to simulate diffusion model trajectories, the measured onset of activity correlated positively with RT for the vast majority of sampled easy trials ($\bar{r} = 0.852$, 92.0% with $p<0.05$) as well as hard trials ($\bar{r} = 0.934$, 99.0% with $p<0.05$). The correlations were stronger than observed in the neural data, but the general observation that onset correlates with RT is clear. Importantly, there was also an increase in the mean observed onset between difficulty conditions (easy mean onset = 0.171 s; hard mean onset = 0.220 s) conditions. Thus, the model predicted a difference in onset of 0.039 s although Ter was fixed across conditions; this difference simply emerges from the stochastic buildup of activity in the diffusion model, how those trajectories vary over time, and how onset is measured. We also note that the difference between the predicted onset of activity for hard and easy conditions (0.049 s) is relatively close to the difference observed in actual movement neurons (0.038 s), even though that quantity was not explicit in any of the model fits.

To conclude, a positive correlation between onset of activity and RT within difficulty conditions and an increase in the mean onset across difficulty conditions was observed in neural activity and was also observed in a diffusion model that assumed no variability in the discrete processing stage preceding the decision-making stage. This questions the assumption that the onset of neural activity indicates the

end of perceptual processing and the start of response preparation.

Simulations 3: Parameter Exploration

The first two sets of simulations provide converging evidence that a diffusion model that assumes no variability in perceptual processing can nonetheless predict a correlation between onset of response preparation and RT and an increase in the mean onset when perceptual difficulty is increased. Following Woodman et al. (2008), this model would incorrectly attribute variability in RT to variability in perceptual processing time, when in fact there was none. This result is rather surprising since *only* the drift rate (the mean rate of accumulate) varied across conditions and T_{er} (the actual *start* of the accumulation) was equivalent in all conditions.

This final set of simulations aimed to characterize the conditions for producing a correlation between onset and RT in the diffusion model. In other words, what parameter values are likely to predict a correlation between onset and RT. For these simulations, we did not fit the diffusion model to data. Instead, we explored a range of parameter space for the diffusion model and the conditions under which there was a correlation between onset of activity and RT.

Method

Following Simulations 2, we assumed a version of the diffusion model with no parameter variability. We fixed T_{er} and explored how values of drift rate, v, and boundary, a, influenced the correlation between onset and RT. The centroid for our exploration of parameter space was the values providing the best fit to Monkey F's behavioral data from simulation set 2 (table 2, row 3). We also explored the effect of systematic variations in drift rate when the response boundary is set arbitrarily high. Simulated trajectories and the measured relationship between onset and RT were calculated as described in previous simulations.

Results and Discussion

The response boundary, a, was varied across a range from 0.01 to 0.2 in increments of 0.01 while all other values were fixed (Figure 3a). At the lowest levels of a, there was little or no correlation between the measured onset and response time. As a increased, a greater correlation between onset and RT was observed, but eventually reaches asymptote. The reason is as follows. When the distance between boundaries is small, the diffusion process terminates rapidly with little variability in RT. Since, variability in RT is so low, significant correlations are rarely observed. When the distance between bounds is large, predicted RT may vary across a larger range. However, further increases in the distance between bounds do not influence the relationship between onset and RT. This suggests that relatively wide

decision boundaries are necessary, but not sufficient to predict a correlation between the onset of activity and RT.

We also varied the drift rate parameter, v, across a range from 0.1 to 1.5 in increments of 0.1 (Figure 2). As drift rate increases, there is a clear decrease in the percentage of significant correlations between onset and RT. Recall that drift rate dictates the mean rate of the accumulation and that variability around that mean within a trial is normally distributed with a fixed standard deviation of 0.1. The ratio of drift rate to within-trial variability -- the signal-to-noise ratio -- is a primary determinant of the shape of the predicted diffusion trajectory. When the signal-to-noise ratio is very low, variability in RT is due primarily to the accumulation of noise. As the ratio increases, the shape of the trajectory is increasingly driven by the value of drift rate. This provides one insight into the source of the correlation between onset and RT. When drift rate is low, the trajectory of the diffusion is more likely to wander around the starting point of the accumulation prior to reaching a decision bound. The neural measures of onset will capture this as a shift in onset.
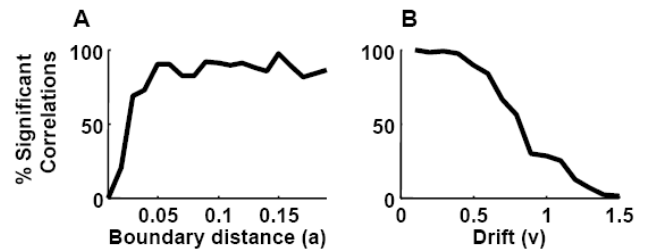

Figure 2: Systematic exploration of the effect of drift rate and boundary distance on the correlation between onset and RT.

General Discussion

A fundamental question of cognitive psychology is how information flows through sequential stages of information processing. Discriminating between competing models has been notoriously difficult using behavioral data alone. Neurophysiology promises a window on the inner workings of information processing.

Woodman et al. (2008) observed that variability in the onset of movement neuron activity is correlated with RT. This is consistent with a model in which increased perceptual processing time causes a delay in both the onset of response preparation and RT. In a series of simulations, we showed that a model with no variability in the perceptual processing stage readily produces a significant correlation between onset and RT and an increase in onset when perceptual difficulty is increased. Thus, observing this correlation is not a signature for a particular architecture of information processing. Our simulation results suggest that observed relationships between the onset of neural activity and RT alone are not sufficient to conclude whether the start of an accumulation was delayed. Rather, the results could be

explained equally well by assuming a model in which the strength of perceptual evidence was varied.

In FEF, systematic changes in the time when visual neurons select the target suggests that the duration of perceptual processing may, in fact, increase with target-distractor similarity (Sato et al., 2001). Presumably, these visual neurons serve as the perceptual input for movement neuron activity (Purcell et al., 2008). It is possible that some combination of delays in the duration and quality of perceptual processing in visual neurons contributes to the observed pattern of movement neuron activity.

This raises the issue of whether information is transmitted from perceptual processing discretely, or whether there is temporal overlap. The issue of information transmission is complex, and there are several ways in which a given stage can be considered discrete or continuous (Miller, 1988). These results cannot directly speak to the temporal relationship of the perceptual processing and response preparation because all diffusion models assumed serial stages of processing. However, by showing that variability in the quality of perceptual processing mimics shifts in the onset of activation, this work opens the door to the possibility that visual neuron activity may be input to movement neurons in a truly cascaded fashion.

More generally, these results demonstrate that applying identical analyses to both model dynamics and neurophysiological data can reveal counterintuitive predictions. In this case, one particular measure, the onset, was not adequate to draw strong conclusions. This work suggests that future efforts should focus on developing new analyses of neurophysiological data to distinguish alternative model architectures.

Acknowledgments

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