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The effect of visual search efficiency on response preparation: Neurophysiological evidence for discrete flow

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Abstract

Many models assume that response time (RT) consists of successive processing stages, but they disagree about whether information is transmitted continuously or discretely between stages. We tested these alternative hypotheses by measuring when movement-related activity began in the frontal eye field (FEF) of macaque monkeys performing visual search. Previous work showed that RT was longer when visual neurons in FEF took longer to select the target, consistent with prolonged perceptual processing during less efficient search. We now report that the buildup of saccadic movement-related activity in FEF is delayed when visual search is more demanding. Variability in the delay of movement-related activity accounted for the difference in RT between search conditions and for the variability of RT within conditions. These findings provide neurophysiological support for the discrete transmission of information between perceptual and response stages or processing during visual search.

Since first measured, the time taken to respond to a stimulus has been hypothesized to be a composite of the times taken to complete a series of different computations at different processing stages (Donders, 1868/1969; Meyer, Osman, Irwin, & Yantis, 1988). This premise has been substantiated by demonstrations that different manipulations influence distinct subprocesses (Sternberg, 1969; Sternberg, 2001). However, the stage conception of response time (RT) remains controversial (e.g., Luce, 1986). One point of disagreement concerns how information flows between processing stages (Figure 1). According to discrete-flow models, a later stage (e.g., response selection) cannot begin until a prior stage (e.g., perception) is completed. According to continuous-flow models, a subsequent stage can begin before a prior stage has completed processing.

Predictions of discrete- and continuous-flow models have been examined using behavioral (e.g., Eriksen & Schultz, 1979; Pashler, 1984), modeling (McClelland, 1979), and electrophysiological methods (e.g., Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992). Although favored by some, many of the findings consistent with continuous-flow models can be

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accounted for by a discrete model that asynchronously transmits separate features (like color and shape) from the perceptual stage to the stage of response preparation (Miller, 1988; Miller, 1982; Roberts & Sternberg, 1993). A critical limitation in evaluating these hypotheses is the reliable measurement of the termination of one stage and the beginning of a subsequent stage using measures with sufficient temporal and functional resolution (e.g., Gratton et al., 1988; Miller & Hackley, 1992; Osman et al., 1992).

Neurophysiological data from sensorimotor structures can distinguish between these models with unprecedented resolution because different subpopulations of neurons perform perceptual processing and response preparation (reviewed by Schall, 2004). One population of neurons in the FEF, posterior parietal cortex, and superior colliculus discriminate target objects in visual search arrays (e.g., McPeck & Keller, 2002; Schall & Hanes, 1993; Thomas & Pare, 2007). These neurons produce an initially indiscriminant volley of activity that subsequently evolves to signal that the target or a distractor is in its receptive field. These neurons distinguish the target from distractors later when search response time (RT) is longer because of greater similarity of the target and distractors but not when RT is longer because of response competition (Sato, Murthy, Thompson, & Schall, 2001; Thompson, Hanes, Bichot, & Schall, 1996). Therefore, the time at which these neurons signal target location marks the conclusion of perceptual analysis.

A different population of neurons in FEF and superior colliculus instantiate response preparation; the activity of these neurons increases gradually before a saccade into the neuron's movement field so that saccades are initiated when the discharge rate reaches a threshold (Hanes & Schall, 1996). If saccades are prepared but not executed, the movement-related activity, but not the visual activity, is modulated in a manner sufficient to control gaze (Hanes, Patterson, & Schall, 1998). Thus, models of information flow can be tested by measuring the duration of perceptual processing through the activity of visual neurons and the beginning and duration of response preparation through the activity of movement-related neurons (Schall, 2004) (Figure 1B).

We evaluated competing information-transmission hypotheses by measuring the beginning of movement-related activity in the FEF of macaques performing visual search. The difficulty of perceptual processing was varied through manipulations of the visual similarity between the search stimuli (in color space or motion coherence) or the number of distractors in the search array (Figure 1C). These stimulus manipulations provide large RT variability between conditions (Duncan & Humphreys, 1989; Wolfe, 1998). Figure 1B illustrates how the pattern of activity of movement-related neurons can distinguish between continuous and discrete flow. The continuous flow hypothesis predicts that movement-related activity begins as soon as any information about target location is available, so the rate of growth to the trigger threshold should be more gradual in inefficient as compared to efficient search. The discrete flow hypothesis predicts that movement-related activity begins only after the target is selected by visual neurons and so should be systematically delayed during inefficient as compared to efficient search.

Method

Four macaque monkeys (*Macaca radiata* and *M. mulatta*) participated in the color and motion search tasks and a fifth participated in the spatial configuration search task. All procedures were approved by the Vanderbilt Institutional Animal Care and Use Committee.

Stimuli & Procedures

Surgical and training procedures have been described (Schall, Hanes, Thompson, & King, 1995). Using juice-reinforced operant conditioning, monkeys were trained to produce one saccade to foveate a target in a visual search array. A memory-guided saccade task with a single stimulus (gray, 8.3 cd/m²) was used to map the receptive field and to determine whether each neuron exhibited saccadic movement-related activity.

Stimuli appeared on a black background (<0.1 cd/m²) with a white fixation point (46.9 cd/m², 0.2° × 0.2°). The target was randomly placed in a location at the optimal eccentricity for the recorded neuron. During color and motion search, difficulty was manipulated by presenting seven, evenly spaced, identical distractors that were closer to the target in color space or degraded in motion strength (Figure 1C, see Sato et al., 2001 for specific stimulus parameters). During search for T or L targets, difficulty was varied by manipulating set size (1, 3, and 7 distractors) and the orientation of the distractors was randomized on each trial (either upright, +90°, +180°, +270°). Stimuli were scaled according to the cortical magnification factor (0.6° at 6° eccentricity to 1° at 10° eccentricity in color search; 1.5° at 6° eccentricity to 2.5° at 10° eccentricity in motion and T and L search). Search conditions were randomly interleaved across trials. Target color, direction of motion, and form (T or L, possibly rotated) changed across days.

After 600–1000 ms of fixation, the search array was presented. Reward was withheld if a saccade was made to any location other than the target. On 10–35% of trials, no target was presented (catch trials) and the monkey was rewarded for maintaining fixation for at least 750 ms after the search array appeared. For each neuron recorded at least 75 trials of each condition were performed.

Data Analysis

Data acquisition and analysis procedures have been described (Thompson et al., 1996; Sato et al., 2001). Error trials were excluded. Neurons were classified as movement related if they exhibited a ramp-up of activity during the memory guided saccade task immediate preceding saccades (Bruce & Goldberg, 1985).

Our analyses focused on four characteristics of the activity of movement-related neurons that could contribute to the observed RT effects. Shorter RTs could have been due to differences in 1) baseline-firing rate, 2) the beginning of movement-related activity, 3) the threshold activation at which saccades were initiated and 4) the rate of growth of activation to the threshold.

To measure the time at which of movement-related activity began in relation to RT we used a sliding-window algorithm that worked backward from the initiation of the saccade to

determine when movement activity began increasing. Spike-density functions (SDFs) were calculated using a filter with an impulse-response function shaped like a post-synaptic potential (growth = 1 ms, decay = 20 ms). Trials were sorted by RT into groups of at least 10 trials. For each RT group, the beginning of movement-related activity was calculated as the first time point that met these criteria: (1) the SDF no longer decreased significantly according to a Spearman correlation ($\alpha=0.05$) over a time window ranging from -20 ms to +20 ms, (2) the spike density at that time was less than the SDF during the 20 ms preceding saccade onset, and (3) the correlation remained nonsignificant for 20 ms as the center of the window continued to move backward from the saccade.

Baseline activity was measured as the average of the SDF from -200 ms until the search array appeared. We measured threshold activation as the average of the SDF in the interval 10–20 ms before saccade initiation (Hanes & Schall, 1996). Growth rate was measured by subtracting the threshold-activity level from the onset-activity level and dividing by the time interval between onset and the response. The same pattern of results was found when the growth rate was measured by fitting a regression line to the SDF for each RT group. Fifty-eight movement-related neurons recorded from 5 monkeys had sufficient data for these analyses (40 neurons recorded during feature search and 18 neurons during spatial-configuration search).

RESULTS

Color and motion feature search

Mean RT across all motion and color feature-search trials was significantly faster in the efficient search condition (195.4 ms) compared to the inefficient condition (245.5 ms), a 50.05 ms difference, $F(1,39) = 87.02$, $p < 0.0001$. Saccades were also significantly more accurate during the efficient search task (94.8% correct) than during inefficient search (79.5% correct), $F(1,39) = 149.16$, $p < 0.0001$.

Figure 2 shows the activity of a representative neuron during efficient and inefficient search and grouped by RT within each condition. The beginning of activation of this neuron increased systematically and significantly with RT in both the efficient and inefficient feature search conditions, $ps < 0.05$ (Figure 2C). Saccades were initiated when the discharge rate reached a threshold that did not vary with condition ($p > 0.30$, Figure 2E). Baseline activity and the rate of growth of the movement-related activity also did not vary significantly as a function of RT ($ps > 0.20$, Figure 2B and 2D).

The relationship of RT to the variation in the beginning of movement-related activation but not to baseline, threshold, or rate of growth was observed consistently among the sample of neurons recorded during the feature-search tasks. Figures 2F–I show for each neuron the mean difference of each measure of neural activity as a function of the mean difference in RT between inefficient and efficient search conditions. Across neurons, baseline-firing rate did not vary significantly between the efficient search (14.2 spike/sec) and the inefficient (14.4 sp/s) search conditions, $F < 1.0$ (Figure 2F). Similarly, the threshold for initiating a saccade did not differ between efficient (64.4 sp/s) and inefficient (62.7 sp/s) search trials, $F < 1.0$ (Figure 2I). The rate of growth of movement activity did not differ significantly

between efficient (0.40 sp/s/ms) and inefficient search (0.52 sp/s/ms) (Figure 2H); although this effect approached significance, $F(1,39) < 3.8$, $p = 0.06$, it should be noted that this difference is in the direction opposite that predicted by continuous-flow models and was driven largely by 3 of the 40 neurons from two monkeys. When these three neurons are excluded from the analyses the same pattern of results was found across the other neural measures while the difference between the rates of growth in the two search conditions was essentially eliminated (0.42 sp/s/ms for efficient search and 0.49 sp/s/ms for inefficient search).

However, a clear relationship was observed between the time of the beginning of movement-related activity and RT (Figure 2G). The average beginning of movement-related activation across the 40 neurons was significantly earlier during efficient (83.7 ms) compared to inefficient (133.8 ms) search, $F(1,39) = 36.48$, $p < 0.0001$. Notably, the difference between beginning times of movement-related activity between search conditions (50.1 ms) corresponded quantitatively to the RT difference between search conditions (50.05 ms). The strong correlation between these measures ($r^2 = 0.846$, $t_{38} = 14.47$, $p < 0.001$) indicates that the difference of beginning times between efficient and inefficient search strongly predicts the observed RT difference. Moreover, the effect of beginning time between conditions was significant across neurons for each of the four monkeys tested in the feature-search tasks, $ps < 0.05$. Table 1 shows results of further within-condition analyses.

To summarize, the data indicate that random variation of RT within search conditions and systematic adjustments of RT across search efficiency arise from variation in the beginning of movement-related activity.

Spatial configuration search

To test the generality of these findings, a fifth monkey was trained to perform visual search for a target composed of two line segments (e.g., a rotated T among randomly rotated Ls, and vice versa) embedded in search arrays with 2, 4 or 8 objects. Search for targets defined by a spatial configuration of identical line segments results in search slopes of 20–30 ms/item with human observers (Wolfe, 1998). Task performance during recordings from 18 movement-related neurons showed similar decreases in RT with set size. Mean RT differed significantly across set size 2 (216.7 ms), 4 (246.1 ms), and 8 (303.5 ms), $F(2,34) = 39.37$, $p < 0.0001$. This variation of RT was not due to speed-accuracy tradeoff; accuracy decreased significantly with set size (set size 2 – 93.7%, 4 – 89.0%, 8 – 87.3%, $F(2,34) = 10.34$, $p < 0.001$).

Figures 3A–E show that the pattern of activity of a representative neuron is identical to that obtained during the color and motion search tasks. As in the feature search tasks, saccades were generated when movement-related activity reached a fixed threshold that did not vary across search array set size (set size 2, mean = 38.5 sp/s; set size 4, 38.4 sp/s; set size 8, 38.4 sp/s), $F < 1.0$. Baseline activity did not differ significantly across set sizes (set size 2, mean = 10.7 sp/s; set size 4, 11.0 sp/s; set size 8, 10.9 sp/s), $F < 1.0$. The rate of growth of activity varied slightly but significantly with set size, $F(2,34) = 4.56$, $p < 0.05$ (set size 2, mean = 0.27 sp/s/ms; set size 4, 0.25 sp/s/ms; set size 8, 0.23 sp/s/ms), but this effect was due to the activity of two neurons (see Table 1). Only the variation in the beginning time of the

movement activity accounted for the variability in saccade latency. For the vast majority of neurons, the variability of RT grouped trials within conditions was related to movement-activity beginning (Table 1). This was most evident at the larger set sizes in which the variability of RT was greatest, thus, affording the largest behavioral effect with which to pull out a significant regression. Across the neuron sample, delayed beginning of growth of movement-related activity accounted for the increase in RT across set sizes. Specifically, mean beginning time increased significantly across set size 2 (mean = 105.9 ms), 4 (mean = 137.6 ms), and 8 (mean = 201.7 ms), $F(2,34) = 49.82$, $p < 0.0001$. Moreover, the mean differences between movement activity beginning time between set size 2 and 4 (31.7 ms) and between set size 4 and 8 (64.0 ms) correspond closely to the mean differences of RT between set size 2 and 4 (29.4 ms) and between set size 4 and 8 (57.5 ms).

Discussion

This study addresses a question as old as experimental psychology (Donders, 1868/1969). Is RT composed of the durations of distinct, non-overlapping stages of processing? This question has remained undecided because of a lack of direct measures of the start and finish times of intermediate stages (e.g. Woodworth, 1938). Measuring the activity of single neurons in monkeys performing cognitively demanding RT tasks provides new leverage on this classic problem. The activity of specific neurons in sensorimotor structures provides measures of the beginning and duration of visual selection and response preparation during visual search tasks requiring eye-movement responses (Bruce & Goldberg, 1985; Hanes & Schall, 1996; Sato et al., 2001; Thompson et al., 1996). Similar logic has been employed successfully measuring event-related potentials during discrimination tasks requiring manual responses (e.g., Smulders et al., 1995).

We tested the competing hypotheses given by discrete- and continuous-flow architectures during visual search tasks that demanded fast, accurate saccades to maximize reward. Previously reported analyses of visually responsive neurons recorded in FEF during the performance of these tasks showed that when visual selection of the target by the neurons took longer, RT was slower (Sato et al., 2001). Given this, discrete-flow models predict that movement-related activity in FEF should begin only after the location of the target is selected by visual neurons. In contrast, continuous-flow architectures predict that movement-related activity will begin as soon as any visual information is available. Our results were consistent with discrete flow between the perceptual and response stages. When stimulus manipulation made search more difficult, movement-related activity began after a delay that was precisely equal to the difference in RT between search conditions. That is, the slower the search RT, the greater the delay in saccade preparation. Moreover, RT variability within each condition was best explained by variability in the beginning of movement-related activity.

Although the variability in RT during these visual search tasks is accounted for by perceptual processing requirements (e.g., Sato et al., 2001), other paradigms tax other stages of processing and, therefore, other mechanisms. For example, the variation of RT in the psychological refractory period (PRP) paradigm, in which two targets demand speeded responses, is accounted for by post-perceptual response selection mechanisms (Luck, 1998)

and not the perceptual mechanisms taxed during visual search (Pashler, 1991). Similarly, the findings of Hanes and Schall (1996) indicate that RT variability in a stop-signal tasks with easily perceived targets, is due to variability in the post-perceptual response process carried out by FEF movement neurons. The most plausible conclusion from these diverse studies is that different task manipulations overload different limited-capacity mechanisms at different stages of processing (Luck & Vecera, 2002; Sigman & Dehaene, 2006; Sternberg, 2001). The isolated targets presented in RT tasks like countermanding and the PRP paradigm likely tax response processes unlike set size and target-distractor similarity manipulations in visual search which overload perceptual attention mechanisms.

The present findings are consistent with the hypothesis of discrete-information transmission of the output of perceptual processing to the response preparation stage. Such a conclusion requires careful consideration of the relationship between the present findings and evidence that has been used to argue for continuous-flow models. A number of event-related potential studies have measured the lateralized readiness potential (LRP) as an index of response preparation in subjects performing manual go/no-go tasks with target stimuli composed of two features, one easy to perceive that indicated response hand (e.g., S for left hand, T for right), and one more difficult to perceive which indicated whether the response should be withheld (e.g., smaller for go and larger for no-go) (e.g., Miller & Hackley, 1992; Osman et al., 1992). These studies found LRP activation beginning before perceptual processing of all of the features of the stimulus was completed. However, particular features of these studies may limit the generality of their conclusions. For example, Ilan and Miller (1998) emphasized that these ERP studies required observers to process stimuli that were defined by a conjunction of visual features with one far easier to perceive than the other. Given the possibility that different visual features can be encoded at different rates, such demonstrations of continuous information transmission from encoding to response preparation could be attributed to independent encoding of different visual features that can each transmit discretely to a common response-preparation stage. This hypothesis has been elaborated as the *asynchronous discrete coding* model (Miller, 1988; Miller, 1982).

The asynchronous discrete coding model provides a parsimonious account of other results from single-unit recording studies that were interpreted as consistent with continuous flow. For example, Bichot et al. (2001) required monkeys to shift gaze to a target defined by color and shape and found subthreshold movement-related activity in the FEF when the stimulus in the movement field shared a feature with the target. Likewise, results from the skeletomotor system using conjunction stimuli were interpreted as continuous flow between perceptual and movement-related neurons (Miller, Riehle, & Requin, 1992; Riehle, Requin, & Kornblum, 1997). Thus, using targets defined by multiple stimulus features, single-unit studies have obtained data consistent with either the continuous-flow hypothesis or the asynchronous discrete coding hypotheses. In contrast, another single-unit study that monitored activity in the primary somatosensory and motor cortex of macaque monkeys detecting tactile stimulation on different digits obtained data entirely consistent with discrete flow (Mouret & Hasbroucq, 2000)¹.

¹Mouret and Hasbroucq (2000) used a single monkey so the generality of their findings could not be assessed.

Although we favor the asynchronous-discrete coding account of the difference between the present and previous findings (i.e., Bichot et al. 2001), we acknowledge several boundary conditions in drawing our conclusions. First, the absence of catch trials in the previous conjunction search experiment meant that a movement was necessary for reward on every trial. Accordingly, speed may have been stressed more than accuracy. Given the possibility of control over how information is transmitted, configuring the visual-motor system for continuous transmission would afford greater speed at the cost of accuracy. Evidence consistent with top-down control of information flow exists from electrophysiological studies (Gratton, Coles, & Donchin, 1992; Low & Miller, 1999) and behavioral paradigms (e.g., McElree & Carrasco, 1999). In fact, speed-accuracy adjustments may occur through strategic slowing of response processes (e.g., Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Thus, it is possible that the present task context discouraged the use of partial perceptual information to prepare the saccades, unlike the task used by Bichot et al. (2001). Future research will test whether reconfiguration is possible between discrete-flow and continuous-flow states of the system based on task demands. Second, although we found evidence for the discrete transmission of information across the perception-action boundary, it is possible that information might flow continuously between other intermediate stages of processing (Sternberg, 1969). Finally, it is possible that localizing search targets with saccades might not occur based on partial information while manual responses could be guided by partial output.

Despite certain limitations of interpretation, the present findings demonstrate that activation of a population of neurons instantiating response preparation begins later when search RT is longer, consistent with the discrete-flow hypothesis. This also verifies a key assumption of the additive-factors method by showing that the manipulation of a factor that selectively influences the duration of the perceptual stage changes the beginning but not the duration of the subsequent stage of response preparation. Although these results cannot rule out every form of continuous or cascaded information transmission, they at least force such models to mimic discrete transmission during search tasks like those used here.

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Figure 1.

Predictions of discrete versus continuous flow. (A) According to discrete flow, response preparation does not begin until perceptual processing is finished and so is delayed in inefficient (e.g., 8 object array) as compared to efficient (e.g., 2 object array) search. According to continuous flow, response preparation can begin gradually as soon as any perceptual information is available and so begins at the same time but proceeds more gradually in inefficient as compared to efficient search. (B) Top panels show response of a visual neuron in FEF when the search target (solid) or distractor (dotted) appears in the receptive field (RF) on trials with short (top) and long RTs (middle). RT was delayed when

the neuron selected the target later. Bottom panels illustrate hypothesized patterns of activity of movement-related neurons. Saccades are initiated when the activity reaches a threshold (horizontal gray). The continuous flow hypothesis predicts that movement-related activity begins as soon as any information about target location is available (dashed gray). The discrete flow hypothesis predicts that movement-related activity begins only after the target is selected by visual neurons (solid gray). (C) Search arrays for color, motion direction, and spatial configuration targets.

Figure 2.

Neurophysiological test of discrete versus continuous flow for representative neuron (A–E) and population (F–I) during color and motion search. (A) Average SDFs for efficient (black) and inefficient (gray) search for the fastest (thick) and slowest (thin) half of RTs. (B) Baseline activity plotted as a function of RT-grouped trials for efficient (black) and inefficient (gray) search. Similar plots of onset time (C), growth rate (D), and threshold activation (E) from the example neuron. Differences in baseline activity (F), beginning time (G), growth rate (H), and threshold activation (I) as a function of difference in RT between inefficient and efficient search trials. Data distinguished for different monkeys (F, circles; L,

squares; M, triangles; O, diamonds) and neuron types (visual-movement neurons, empty; pure-movement neurons, filled). Linear regression lines are drawn when the neural measure varied significantly with RT.

Figure 3.

Neurophysiological test of discrete versus continuous flow for representative neuron (A–E) and population (F–I) during spatial configuration search. (A) Average SDFs for set size 2 (thick black), 4 (thick gray) and 8 (thin black). Baseline activity (B), beginning time (C), growth rate (D), and threshold activation (E) plotted as a function of RT for set sizes 2 (black), 4 (gray), and 8 (open). For sample, differences in baseline activity (F), beginning time (G), growth rate (H), and threshold activation (I) as a function of difference in RT between set sizes 8 and 2. Data distinguished for neuron type (visual-movement neurons, empty; pure-movement neurons, filled).

Table 1

Within-condition analyses for each cell.

	Color & Motion		Spatial Configuration		
	Efficient	Inefficient	Set Size 2	Set Size 4	Set Size 8
Baseline	7/40	5/40	0/18	1/18	0/18
Beginning Time	22/40	26/40	9/18	14/18	17/18
Growth Rate	8/40	3/40	3/18	2/18	3/18
Threshold	13/40	5/40	2/18	2/18	2/18

Note. Results of the within-condition analyses for the different neural measures as a function of RT grouped trials. Fraction indicates how many neurons out of 40 during color or motion search and 18 during spatial configuration search had each measure of neural activity vary significantly across RT groups (linear regression, $ps < 0.05$).