Research Article

The Effect of Visual Search Efficiency on Response Preparation

Neurophysiological Evidence for Discrete Flow

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ABSTRACT—*Most models assume that response time (RT) comprises the time required for 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, a finding consistent with prolonged perceptual processing during less efficient search. We now report that the buildup of saccadic movement-related activity in FEF is delayed in inefficient visual search. 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 hypothesis that information is transmitted discretely between perceptual and response stages of processing during visual search.*

Since response time (RT) was first measured, it 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, 2001). However, the stage conception of RT remains controversial (e.g., Luce, 1986). One point of disagreement concerns how information flows between processing stages (see Fig. 1a). 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 (e.g., Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992) methods. Although continuous-flow models are favored by some researchers, many of the findings consistent with such models can be accounted for by a discrete-flow model that asynchronously transmits separate features (like color and shape) from the perceptual stage to the response-preparation stage (Miller, 1982, 1988; Roberts & Sternberg, 1993). A critical problem researchers face in evaluating these hypotheses is how to reliably measure the termination of one stage and the beginning of a subsequent stage with sufficient temporal resolution among populations of neurons that plausibly instantiate the required functions (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 appear to perform perceptual processing and response preparation (for a review, see Schall, 2004). One population of neurons in the frontal eye field (FEF), posterior parietal cortex, and superior colliculus discriminates target objects in visual search arrays (e.g., McPeek & Keller, 2002; Schall & Hanes, 1993; Thomas &

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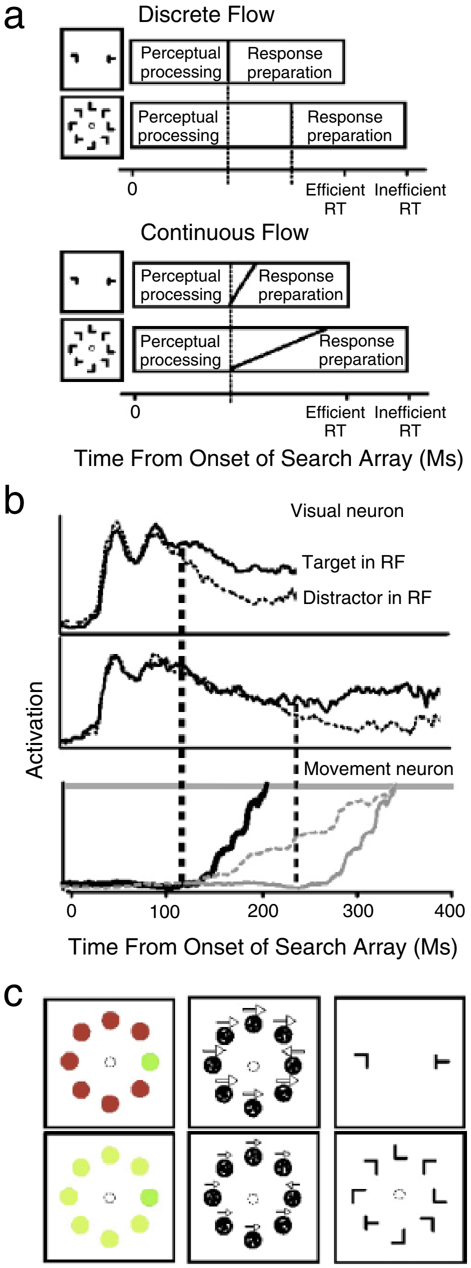

Fig. 1. Predictions of discrete versus continuous flow. The illustration in (a) shows the relative timing of perceptual processing and response preparation in efficient search (a two-object array) and inefficient search (an eight-object array). According to discrete-flow models, response preparation does not begin until perceptual processing is finished, and therefore is delayed in inefficient search. According to continuous-flow models, response preparation can begin gradually as soon as any perceptual information is available, and therefore begins at the same time in efficient and inefficient search, but proceeds more gradually in inefficient search. Thus, the dashed line indicates when response preparation begins in both conditions, and the diagonal lines indicate differences in the rate of this preparation. RT = response time. The top two graphs in (b) show the response of a visual neuron in the frontal eye field when the search target (solid line) or distractor (dotted line) appears in the neuron's receptive field (RF); the upper graph illustrates the pattern of activation on trials with short RTs, and the lower graph illustrates the pattern of activation on trials with long RTs. The thick dashed vertical line indicates when the visual neuron discriminated the target from a distractor when search was easy, and the thin dashed vertical line indicates when the visual cell selected the target in the hard search trials. The bottom graph in (b) illustrates hypothesized patterns of activity of movement-related neurons in the frontal eye field. Saccades are initiated when the activity reaches a threshold (horizontal gray line). The solid black line indicates movement-related activity in the case of efficient search. When RTs are longer and search is more inefficient, the continuous-flow hypothesis predicts that movement-related activity begins as soon as any information about target location is available (dashed gray line), whereas the discrete-flow hypothesis predicts that movement-related activity begins only after the target is selected by visual neurons (solid gray line). The illustrations in (c) are examples of the search arrays used in (from left to right) the color and motion feature-search tasks and the spatial-configuration search task. Examples of displays in the efficient-search condition are in the top row, and examples of displays in the inefficient-search condition are shown in the bottom row. In (c), the size of the arrows represents motion coherence, with smaller arrows indicating lower motion coherence. An example of the intermediate set size (4) is not shown.

Paré, 2007). These neurons produce an initially indiscriminant volley of activity that subsequently evolves to signal that the target or a distractor is in their receptive fields (see Fig. 1b). These neurons distinguish the target from distractors at a later time when search RT is longer because of greater similarity of the target and distractors but not when RT is longer because of greater response competition (Sato, Murthy, Thompson, & Schall, 2001; Thompson, Hanes, Bichot, & Schall, 1996). Therefore, the time at which these neurons signal target location plausibly marks the conclusion of perceptual analysis.

A different population of neurons in FEF and superior colliculus instantiates response preparation; the activity of a neuron in this population increases gradually before a saccade into the neuron's movement field, and a saccade is initiated when the discharge rate reaches a threshold (see Fig. 1b: Hanes & Schall, 1996). If saccades are prepared but not executed, the movement-related activity is modulated in a manner sufficient to control gaze, whereas the activity of visual neurons does not determine whether and when a saccade will be made (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 by measuring the beginning and duration of response preparation through the activity of movement-related neurons (Schall, 2004; see Fig. 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 by manipulating the visual similarity among the search stimuli (in color space or motion coherence) or the number of distractors in the search array (see Fig. 1c). These stimulus manipulations provide large variability in RT 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 than in 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 relative to efficient search (see the large difference in onset of activity between the black and gray solid lines in the bottom graph of Fig. 1b).

METHOD

Four macaque monkeys (*Macaca radiata* and *Macaca mulatta*) participated in color and motion feature-search tasks, and a 5th participated in a search task in which the target was defined by the spatial configuration of line segments (rotated *T* among rotated *L*s, and vice versa). All procedures were approved by the Vanderbilt Institutional Animal Care and Use Committee.

Stimuli and Procedures

The surgical and training procedures we used have been described previously (Schall, Hanes, Thompson, & King, 1995). Through juice-reinforced operant conditioning, the 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/m^2) was used to map movement fields of the neurons and to determine whether each neuron exhibited saccadic movement-related activity.

Stimuli appeared on a black background (< 0.1 cd/m^2) with a white fixation point (46.9 cd/m^2, $0.2^\circ \times 0.2^\circ$). The target was randomly placed in a location at the optimal eccentricity for the neuron whose activity was being recorded in a given session. During color and motion search, seven evenly spaced, identical distractors were presented along with the target; for inefficient search, difficulty was increased by presenting distractors that were closer to the target in color space or that were degraded in motion strength (Fig. 1c; see Sato et al., 2001, for specific stimulus parameters). During spatial-configuration search, the target was a *T* among *L* distractors, or vice versa; difficulty was varied by manipulating set size (one, three, or seven distractors), and the orientation of the distractors was randomly determined on each trial (upright or rotated by $+90^\circ$, $+180^\circ$, or $+270^\circ$; across sessions, the orientation of the target was rotated). Stimuli were scaled according to the cortical magnification factor (from 0.6° at 6° eccentricity to 1° at 10° eccentricity in color search; from 1.5° at 6° eccentricity to 2.5° at 10° eccentricity in motion and spatial-configuration search). Search difficulty was manipulated through target-distractor feature similarity or set size, with different levels of difficulty randomly interleaved across trials. The color, direction of motion, and form (*T* or *L*) of the target rotated across days.

Each trial began with 600 to 1,000 ms of fixation, after which the search array was presented. Reward was withheld if a saccade was made to any location other than the target's location. On 10 to 35% of trials, no target was presented (catch trials), and the monkeys were rewarded for maintaining fixation for at least 750 ms after the search array appeared. For each neuron recorded, we collected data from at least 75 trials in conditions of both efficient and inefficient search.

Data Analysis

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

Our analyses focused on four characteristics of the activity of movement-related neurons that could contribute to the observed RT effects. Systematic adjustment of RTs could have been due to changes in (a) baseline firing rate, (b) the onset of movement-related activity, (c) the threshold activation necessary to initiate saccades, or (d) the rate of growth of activation to the threshold.

To measure the time at which movement-related activity began, 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 postsynaptic potential (growth = 1 ms, decay = 20 ms). Trials were sorted by RT into groups of at least 10 trials. For each RT group, the onset of movement-related activity was calculated as the first time point that met the following criteria: (a) the SDF no longer decreased significantly according to a Spearman correlation ($\alpha = .05$) over a time window ranging from -20 ms to $+20$ ms, (b) the spike density at that time was less than the SDF during the 20 ms preceding saccade onset, and (c) 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 through 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 the 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) than in the inefficient-search condition (245.5 ms; 50.05-ms difference), $F(1, 39) = 87.02$, $p < .0001$. Saccades were also significantly more accurate during the efficient-search condition (94.8% correct) than during the inefficient-search condition (79.5% correct), $F(1, 39) = 149.16$, $p < .0001$.

Figures 2a through 2e show the activity of a representative neuron during efficient and inefficient search. The beginning of activation of this neuron increased systematically and significantly with RT in both efficient and inefficient feature search, *p*s $< .05$ (Fig. 2c). Saccades were initiated when the discharge rate reached a threshold that did not vary with condition ($p > .30$; Fig. 2e). Baseline activity and the rate of growth of the movement-related activity did not vary significantly as a function of RT (*p*s $> .20$, Figs. 2b and 2d).

The sample of neurons recorded during the feature-search tasks consistently showed that RT was related to the variation in the beginning of movement-related activation, but not to baseline activity, threshold activation, or rate of growth. Figures 2f through 2i show for each neuron the mean difference between efficient and inefficient search for each measure of neural activity as a function of the mean difference in RT between inefficient and efficient search. Across neurons, baseline firing rate did not vary significantly between the efficient-search (14.2 spikes/s) and the inefficient-search (14.4 spikes/s) conditions, $F < 1.0$ (Fig. 2f). Similarly, the threshold for initiating a saccade did not differ between the efficient-search (64.4 spikes/s) and inefficient-search (62.7 spikes/s) trials, $F < 1.0$ (Fig. 2i). The rate of growth of movement activity did not differ significantly between efficient search (0.40 spikes/s/ms) and inefficient search (0.52 spikes/s/ms; Fig. 2h); although this effect approached significance, $F(1, 39) < 3.8$, $p = .06$, it should be noted that this difference was in the direction opposite of that predicted by continuous-flow models and was driven largely by 3 of the 40 neurons from 2 monkeys. When these 3 neurons were excluded from the analyses, the same pattern of results was found for the other neural measures, and the difference between the rates of growth in the two search conditions was essentially eliminated (0.42 spikes/s/ms for efficient search and 0.49 spikes/s/ms for inefficient search).

However, there was a clear relation between the time of the beginning of movement-related activity and RT (Fig. 2g). The average beginning of movement-related activation across the 40 neurons was significantly earlier during efficient search (83.7 ms) than during inefficient search (133.8 ms), $F(1, 39) = 36.48$, $p < .0001$. Notably, the difference in onset time of movement-related activity between the conditions (50.1 ms) corresponded quantitatively to the RT difference between the search conditions (50.05 ms). The strong correlation between these measures, $r^2 = .846$, $t(38) = 14.47$, $p < .001$, indicates that the difference in onset time between efficient and inefficient search strongly predicts the observed RT difference. Moreover, the difference in onset time between efficient and inefficient feature search was significant for each of the 4 monkeys, *p*s $< .05$. 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 levels of search efficiency arise from variation in the beginning of movement-related activity.

Spatial-Configuration Search

To test the generality of these findings, we trained a 5th monkey to perform visual search for a target composed of two line segments (a rotated *T* among randomly rotated *L*s, and vice versa) embedded in search arrays with one, three, or seven distractor objects. Search for targets defined by a spatial configuration of identical line segments results in search slopes of 20 to 30 ms/

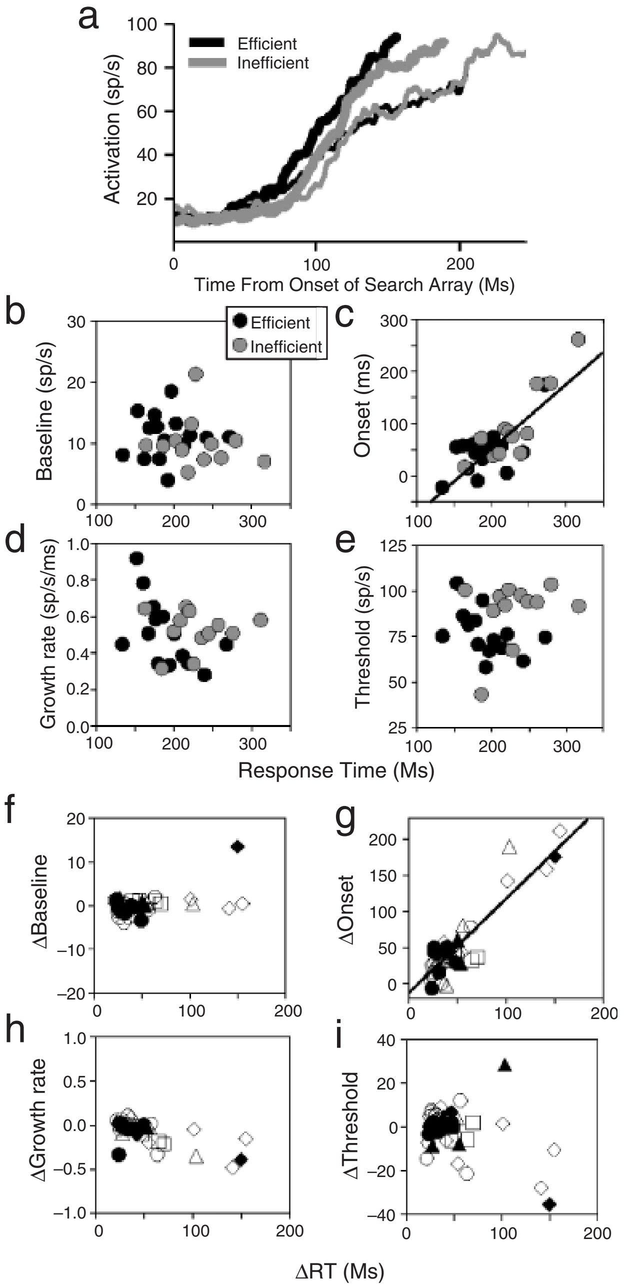

Fig. 2. Neurophysiological results for a representative neuron (a–e) and the population of neurons tested (f–i) during color and motion search. The graph in (a) presents average spike-density functions (SDFs; sp/s = spikes per second) for a representative neuron for efficient and inefficient search on trials with the fastest half (thick lines) and slowest half (thin lines) of response times (RTs). The four graphs below show (b) baseline activity, (c) onset time, (d) growth rate of activation, and (e) threshold activation from the same neuron as a function of RT and search condition (efficient vs. inefficient). Trials were grouped by RT, and each data point represents the results for a different RT group. The four graphs at the bottom show differences in neural measures between efficient and inefficient search as a function of difference in RT between inefficient and efficient search, for the entire sample of neurons. The neural measures are (f) baseline activity, (g) onset time, (h) growth rate of activation, and (i) threshold activation. Different symbols distinguish data from different monkeys (circles, squares, triangles, and diamonds for the 4 monkeys, respectively) and neuron types (open symbols: visual-movement neurons; filled symbols: pure-movement neurons). Linear regression lines are drawn for the two cases in which the neural measure varied significantly with RT.

item with human observers (Wolfe, 1998). In the present study, task performance during recordings from 18 movement-related neurons showed similar decreases in RT with set size, and this effect was significant (set size 2: 216.7 ms, set size 4: 246.1 ms, set size 8: 303.5 ms), $F(2, 34) = 39.37, p < .0001$. This variation of RT was not due to a speed-accuracy trade-off; accuracy decreased significantly with set size (set size 2: 93.7%, set size 4: 89.0%, set size 8: 87.3%), $F(2, 34) = 10.34, p < .001$.

TABLE 1

Number of Neurons for Which Each Neural Measure Varied Significantly, as a Function of Task and Condition

	Color and motion search		Spatial-configuration search		
Neural measure	Efficient	Inefficient	Set size 2	Set size 4	Set size 8
Baseline	7/40	5/40	0/18	1/18	0/18
Onset 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. This table presents results of within-condition analyses of data from trials grouped by response time (RT). Each fraction indicates the number of neurons (out of 40 during color or motion search and out of 18 during spatial-configuration search) for which the measure of neural activity varied significantly across RT groups (linear regression, *p*s < .05).

Figures 3a through 3e show that the pattern of activity of a representative neuron during the performance of this task was identical to that obtained during the color and motion search tasks. Figures 3f through 3i show the population-level data, with each data point representing a different neuron and different symbols indicating different neuron types. As in the feature-search tasks, saccades were generated when movement-related activity reached a fixed threshold that did not vary across set size (set size 2: 38.5 spikes/s, set size 4: 38.4 spikes/s, set size 8: 38.4 spikes/s), $F < 1.0$ (see Fig. 3i). Baseline activity did not differ significantly across set sizes (set size 2: 10.7 spikes/s, set size 4: 11.0 spikes/s, set size 8: 10.9 spikes/s), $F < 1.0$ (see Fig. 3f). The rate of growth of activity, shown in Figure 3h, varied slightly but significantly with set size, $F(2, 34) = 4.56, p < .05$ (set size 2: 0.27 spikes/s/ms, set size 4: 0.25 spikes/s/ms, set size 8: 0.23 spikes/s/ms), but this effect was due to the activity of two neurons (see Table 1). Only the variation in the onset time of the movement activity accounted for the variability in saccade latency (see Fig. 3g). For the vast majority of neurons, the variability of RT across set size was related to changes in the beginning of movement activity (Table 1). This was most evident at the larger set sizes, for which the variability of RT was greatest. Across the neuron sample, delayed onset of the buildup of movement-related activity accounted for the increase in RT across set sizes. Specifically, mean onset time increased significantly across set sizes 2 ($M = 105.9$ ms), 4 ($M = 137.6$ ms), and 8 ($M = 201.7$ ms), $F(2, 34) = 49.82, p < .0001$. Moreover, the mean differences in onset time of movement activity between set sizes 2 and 4 (31.7 ms) and between set sizes 4 and 8 (64.0 ms) corresponded closely to the mean differences in RT between set sizes 2 and 4 (29.4 ms) and between set sizes 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, nonoverlapping 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 in resolving 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 in studies measuring event-related potentials during discrimination tasks requiring manual responses (e.g., Smulders, Kok, Kenemans, & Bashore, 1995).

We tested competing hypotheses derived from discrete- and continuous-flow architectures by using 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). 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 are consistent with discrete flow between the perceptual and response stages. When stimulus manipulations made search more difficult, movement-related activity began after a delay that was precisely equal to the difference in RT between the 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 postperceptual 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 task with easily perceived targets is due to variability in the postperceptual 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 paradigms like the stop-signal task and the PRP paradigm likely tax response processes differently than do set-size and target-distractor-similarity manipulations in visual search, which overload perceptual attention mechanisms.

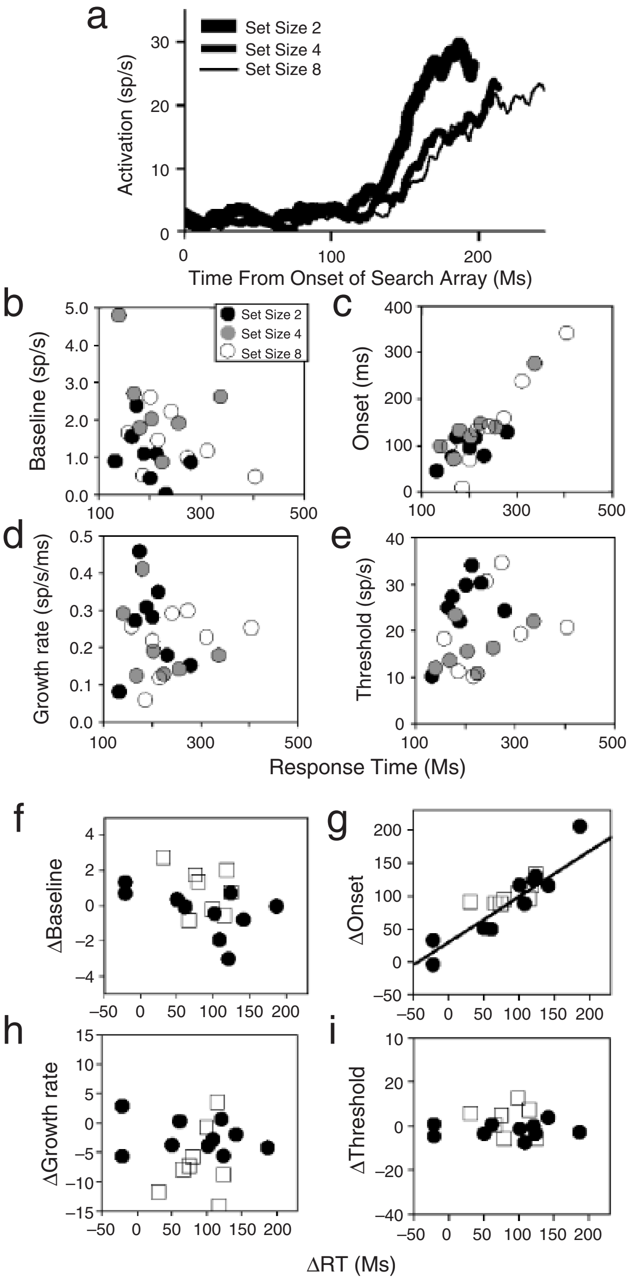

Fig. 3. Neurophysiological results for a representative neuron (a–e) and the population of neurons tested (f–i) during spatial-configuration search. The graph in (a) presents average spike-density functions (SDFs; sp/s = spikes per second) for a representative neuron for the three set sizes. The four graphs below show (b) baseline activity, (c) onset time, (d) growth rate of activation, and (e) threshold activation from the same neuron plotted as a function of response time (RT) and set size. The four graphs at the bottom show differences in neural measures between set sizes 8 and 2 as a function of difference in RT between set sizes 8 and 2, for the entire sample of neurons. The neural measures are (f) baseline activity, (g) onset time, (h) growth rate of activation, and (i) threshold activation. Each data point represents a different neuron, and different symbols distinguish data from different neuron types (open squares: visual-movement neurons; filled circles: pure-movement neurons). A regression line is drawn for the neural measure that varied significantly with RT.

The present findings are consistent with the hypothesis that the output of perceptual processing is transmitted discretely to the response-preparation stage. Such a conclusion requires careful consideration of the relation between the present findings and evidence that has been used to argue for continuous-flow models. A number of event-related potential studies 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 that was easy to perceive and indicated the response hand (e.g., “S” for the left hand, “T” for the right hand), and one that was more difficult to perceive and indicated whether the response should be withheld (e.g., smaller stimulus for *go* and larger stimulus for *no-go*; e.g., Miller & Hackley, 1992; Osman et al., 1992). These studies found that LRP activation began before perceptual processing of all 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 studies required observers to process stimuli that were defined by a conjunction of visual features, one of which was 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 be transmitted discretely to a common response-preparation stage. This hypothesis has been elaborated as the *asynchronous discrete-coding* model (Miller, 1982, 1988).

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, Rao, and Schall (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. This subthreshold movement-related activity could have been due to partial preparation of the eye-movement response because the item in the movement field matched one of the features of the target object. Likewise, results from studies of the skeletomotor system using conjunction stimuli were interpreted as reflecting continuous flow between perceptual and movement-related neurons, although it is possible that these effects were due to one of the features of a nontarget matching the searched-for target (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 hypothesis. 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]

Although we propose that the asynchronous discrete-coding hypothesis accounts for the difference between the present and previous findings, we acknowledge several boundary conditions in drawing these conclusions from our data. First, the absence of catch trials in the conjunction-search experiment of Bichot et al. (2001) meant that a movement was necessary for reward on every trial. Accordingly, speed may have been emphasized more than accuracy. Configuring the visual-motor system for continuous transmission would afford greater speed at the cost of accuracy, and evidence consistent with top-down control of information flow has been obtained in 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 and his colleagues. Future research will need to test whether the system can be reconfigured between discrete-flow and continuous-flow states to accommodate task demands. Second, although we found evidence for the discrete transmission of information across the perception-action boundary, it is possible that information flows continuously between other intermediate stages of processing (Sternberg, 1969). Finally, it is possible that saccades localizing search targets might not be prepared on the basis of partial information, whereas 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, a finding consistent with the discrete-flow hypothesis. Our results also verify a key assumption of the additive-factors method by showing that manipulating a factor that selectively influences the duration of the perceptual stage changes the beginning but not the duration of the subsequent response-preparation stage. Although these results cannot rule out every form of continuous or cascaded information transmission, they at least force models based on such transmission to mimic discrete transmission during search tasks like those used in the present study.

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[1] Mouret and Hasbroucq tested a single monkey, so the generality of their findings could not be assessed.

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