Continuous processing in macaque frontal cortex during visual search

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Abstract

A central issue in mental chronometry is whether information is transferred between processing stages such as stimulus evaluation and response preparation in a continuous or discrete manner. We tested whether partial information about a stimulus influences the response stage by recording the activity of movement-related neurons in the frontal eye field of macaque monkeys performing a conjunction visual search and a feature visual search with a singleton distractor. While movement-related neurons were activated maximally when the target of the search array was in their movement field, they were also activated for distractors even though a saccade was successfully made to the target outside the movement field. Most importantly, the level of activation depended on the properties of the distractor, with greater activation for distractors that shared a target feature or were the target during the previous session during conjunction search, and for the singleton distractor during feature search. These results support the model of continuous information processing and argue against a strictly discrete model. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

Measurements of reaction time have played a major role in the development of theories about the cognitive processes that underlie sensation, perception, memory, and action (e.g. [20]). Inferences about information processing from the time needed to perform particular tasks, however, rely explicitly or implicitly on a theory about the temporal relations among the various cognitive processes required to perform those tasks (e.g. stimulus recognition, response preparation and initiation). Thus, not surprisingly, a central issue in mental chronometry has been the nature of transmission of information between stages of the processing system (for reviews, see [9,15,16]). Is the transmission of information between stages accomplished in a discrete or a continuous manner?

Discrete information-processing models assume that one process must finish before a subsequent process can begin, so different processes operate in a strictly sequential manner. Such discrete transmission of information between stages has been assumed by the subtraction method [10] and the additive factor method [34,35], among others.

The assumption that cognitive operations follow one another in strict temporal succession has been criticized though, leading to the development of continuous information-processing models in which a process can transmit partial output before it is completely finished (e.g. [11,14,41]). Miller [17] has suggested that an exclusive distinction between discrete and continuous models may be an oversimplification, and that it is possible to construct intermediate models by varying the 'grain' size of information that is transmitted. Whereas discrete transmission would be in a single chunk, continuous transmission would be in an infinite number of small grains. From this perspective, the discrete-continuous issue can be recast in terms of whether transmission is

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ever anything less than fully discrete so that the critical question concerns whether there is a transfer of partial information about a stimulus to the response system before that stimulus has been completely evaluated.

Recently, psychophysiological studies using event-related potentials have addressed the discrete-continuous debate (for review, see [7–9]). In general, these studies have relied on the P300 potential as a marker for the end of the evaluation process, and the lateralized readiness potential (LRP) as a marker for response preparation and production. The results of these studies have suggested that whether partial information is used may depend on its utility in producing a fast and accurate response.

A series of studies of single neuron activity in primary motor cortex (M1) by Miller, Riehle, Requin and colleagues have found evidence supporting continuous information processing. In an early study, Miller et al. [18] recorded neural activity in M1 of one monkey performing a wrist flexion/extension, go/nogo task. In this task, one stimulus was assigned to a wrist flexion response, and another to a wrist extension response. When a nogo signal was presented, instructing the monkeys to withhold wrist movements, directionally-selective neurons responded with weaker versions of the response patterns to the same visual stimuli when a response was required, suggesting that neurons received partial perceptual information in favor of that movement. Requin and Riehle [22] showed similar results using a left/right, go/nogo task, and obtained additional evidence for continuous transfer of information using a stimulus-response compatibility task in which monkeys aligned a pointer with visual targets on the left or right of a starting position. In the spatially-compatible trials, they had to point at the stimulus location, whereas in the spatially-incompatible trials, they had to point at the target located in the opposite side. Results of this experiment provided evidence of transmission of information in the incompatible trials about the congruent, but incorrect response, before the incongruent, but correct response was programmed. A subsequent study by Riehle et al. [23] extended these findings using a stimulus-incompatibility task, describing neurons in M1 sensitive to the stimulus-response mapping rule, with a large functional and temporal overlap between this population of neurons, and populations sensitive to the stimulus or response side.

In electrophysiological studies described above, the continuous-discrete question was addressed in the motor cortex using tasks in which the response to particular stimuli changed between conditions. We have used a new and different approach to address the same question in the visuomotor system by recording single neuron activity in the frontal eye field (FEF) of macaque monkeys performing two conceptually different visual search tasks commonly employed in human behavioral studies [39,40,42].

FEF, located on the rostral bank of the arcuate sulcus in the frontal cortex, plays a key role in transforming the outcome of visual selection into a command to move the eyes (for review, see [26,28]). Consistent with this role, FEF has both visual and motor characteristics. Roughly, half of the neurons in FEF have visual responses [4,19,25], mediated by massive converging input from extrastriate visual areas of both the dorsal (or 'where') and ventral (or 'what') streams [1,30]. In previous studies we have shown that visual responses of FEF neurons do not distinguish the target from distractors during either popout [27,29] or conjunction visual search [2]. However, the activity of visually-responsive FEF neurons evolves to discriminate the target as reflected by a relative suppression of distractor-evoked activity. Furthermore, this selection process is dissociated from saccade production as we have shown that the time at which these neurons discriminate target from distractors does not predict the variability of saccadic reaction times [38], and that this selection does not depend on saccade production or programming [37].

The universally accepted motor function of FEF is mediated by layer 5 movement-related neurons that exhibit little or no sensory response to stimulus presentation but are active specifically before and during saccades [4,13], and project to the superior colliculus [33], as well as parts of the brainstem saccade-generating circuit [32]. In fact, FEF is defined as the region of frontal cortex from which saccades are elicited with currents of less than 50 μA [5]. Furthermore, unlike visually-responsive neurons, characteristics of the activity of movement-related neurons account for the variability observed in reaction times as described by Hanes and Schall [13].

We have previously investigated saccade target selection in FEF during a visual search in which monkeys shifted gaze to a target defined by the conjunction of color and shape [2]. We found that the activity of many visually-responsive neurons not only discriminated target from distractors, but also discriminated among the distractors based on their visual similarity to the target and based on the history of target properties used across sessions. To the extent that movement-related neurons in FEF represent a processing stage closer to saccade production, discrete and continuous processing models make different predictions regarding the activity of these neurons.

A strictly discrete processing scheme would predict that while visually-responsive neurons participate in discriminating target from distractors, only the final outcome of the discrimination (i.e. target location) would be conveyed to the movement-related neurons. Thus, movement-related neurons would only activate for the saccade that is produced based on the outcome of processing in the visual selection stage. On the other

hand, a continuous processing scheme would predict that information about the likelihood that each stimulus, including distractors, is the target of the search influences the activation of the movement-related neurons. Thus, evidence that movement-related neurons are modulated by similarity and priming would support a continuous processing model. Note that this approach does not rely on attributing differential behavioral responses to stimuli across conditions. The task is always to find and shift gaze to the defined target. Instead, we use differences in the visual properties and behavioral significance of the various distractors to determine whether information about these distractors is reflected in the motor preparation and execution stage.

The nature of information transmission between stages was also tested in a modified popout visual search which, unlike conjunction search that relies entirely on a memory representation of the target, is based on conspicuousness. In this task, monkeys searched for the stimulus with the oddball shape. However, we changed the behavioral significance of one of the distractors by changing its color. Studies with human subjects have shown that despite being irrelevant to the task, the color singleton attracts attention (e.g. [36]). We took advantage of this fact and investigated whether movement-related neurons are modulated by the conspicuousness of the distractors. Finding that movement-related neurons are modulated by distractor properties would show that these neurons receive information about more than just the final outcome of visual selection (i.e. target location), and thus would support a continuous processing model.

2. Methods

2.1. Subjects and physiological procedures

Data were collected from one *Macaca mulatta* and one *M. radiata*, weighing 9 and 7 kg, respectively. The animals were cared for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. The surgical procedures have been described previously [29].

2.2. Stimuli and apparatus

The experiments were under the control of two personal computers which presented the stimuli, recorded action potentials and eye movements sampled at 1 kHz and 250 Hz, respectively, and delivered the juice reward. Monkeys were seated in an enclosed chair within a magnetic field to monitor eye position with a scleral search coil. Stimuli were presented on a video monitor

(70 Hz non-interlace, 800×600 resolution) viewed binocularly at a distance of 57 cm in a dark room. For all the tasks, the background was uniform dark gray (CIE, $x = 205$, $y = 234$) with a luminance of 0.1 cd/m². The fixation spot was a white (30 cd/m²) square subtending 0.1°. In the conjunction visual search task, the stimuli were either red (CIE, $x = 621$, $y = 345$) or green (CIE, $x = 279$, $y = 615$) matched for luminance (2.3 cd/m²), and could be either crosses or outline circles. In the feature visual search task with a singleton distractor, stimuli were also either red (CIE, $x = 623$, $y = 339$) or green (CIE, $x = 277$, $y = 611$) matched for luminance (5.8 cd/m²), and could be either filled circles or squares.

2.3. Behavioral procedure

Each conjunction search trial began with the presentation of a central fixation spot. Monkeys were required to fixate the central spot to within 0.5°. After an interval of fixation (~ 500 ms), the search array was presented. The target stimulus was a combination of one of two colors (red or green) and one of two shapes (cross or circle) and was presented among three or five distractors. In the four-stimulus configuration (Fig. 1A), the target was presented along with a distractor that had the target color but not the same shape ('same-color' distractor), another distractor that had the target shape but not the target color ('same-shape' distractor), and a distractor that had neither the target color nor the target shape ('opposite' distractor). In the six-stimulus display, there was an additional same-color
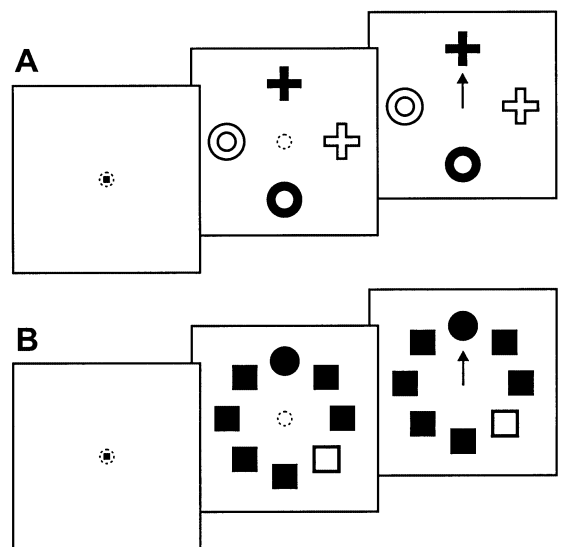

Fig. 1. Schematic representation of visual search tasks. The monkeys' task was to shift gaze to a target defined by a conjunction of shape and color (A) or a target defined as the shape singleton while ignoring the task-irrelevant color singleton (B). Dotted circles represent the monkey's current point of fixation; the arrow represents the saccade to the target. Stimuli are not drawn to scale.

distractor and an additional same-shape distractor. With these choices, both displays were balanced for the number of stimuli containing any given color or shape. The stimuli, spaced evenly on the circumference of an imaginary circle around fixation, were placed such that one stimulus always fell in the center of the neuron's response field. Monkeys were rewarded for making a single saccade to the target within 2 s of search array presentation. The target did not change within a daily recording session and was chosen pseudo-randomly across experimental sessions with the requirement that the same color/shape combination was not used in two consecutive sessions. Monkeys were instructed what the target would be for a given session during a block of detection trials in which monkeys were rewarded for making a saccade to the target presented alone.

The procedure for feature search trials was the same as that for conjunction search trials except for the stimuli used in the search. The target, defined as the shape singleton, was presented along with seven distractors that were all circles when the target was a square, and all squares when the target was a circle. During trials with a singleton distractor, all but one of the distractors were of the target color (Fig. 1B). We refer to the distractor that differed from all stimuli in color as the 'singleton distractor', and to the other distractors as the 'non-salient distractors'. The target shape and color were selected randomly on each trial. In order to investigate the effects of the task-irrelevant singleton distractor, blocks of feature search with a singleton distractor alternated with blocks of regular feature search in which there was no color singleton. Within each block of search with a singleton distractor, all possible combinations of target and singleton distractor locations were presented without replacement on errors. The number of search trials without a singleton distractor were matched to that of search trials with a singleton distractor.

We also used a memory-guided saccade task that was used to classify neurons (see below). Each memory-guided saccade task began with the presentation of a central fixation spot. After an interval of fixation, a single target stimulus was presented briefly (50–100 ms). Monkeys were rewarded for maintaining fixation at the central spot for another 500–1000 ms after which time a change of color of the fixation spot instructed the monkeys to make a single saccade to the remembered location of the target. Once the saccade was made, the target reappeared to provide feedback and a target for the monkeys to fixate.

2.4. Spike density function and time of target discrimination

The spike density function was generated by convolving action potentials with a function that resembled a postsynaptic potential [38]. The time at which target discrimination started was determined as follows. First, we derived the spike density functions for all correct trials in which the target fell in a neuron's response field and those in which distractors fell in the response field. The difference between these two spike density functions reflected the discrimination process. The time at which the difference function crossed a baseline difference (determined from activity measured before stimulus presentation) was selected as the time of target discrimination only if the difference function continued to grow past the baseline difference plus 3.5 S.D.s of the baseline difference, and if it did not drop below that level for at least 50 ms.

2.5. Neuronal classification

Neurons were classified as visually-responsive or movement-related based on standard criteria described in previous reports [4,13,25]. Briefly, visually-responsive neurons exhibit strong responses associated with stimulus presentation; the average latency of such responses is around 60–70 ms with latencies as early as 35–40 ms [31,38]. In contrast, movement-related neurons have little or no response to visual stimuli, but very strong activity before both visually-guided and memory-guided saccades.

3. Results

3.1. Conjunction search

We have described behavioral performance during conjunction search in previous reports [2,3]. Here, we present our analyses of the activity of movement-related neurons in FEF. We recorded from 65 neurons in 52 sessions, of which 21 were classified as movement-related. This fraction of movement-related neurons is comparable to, if not somewhat greater than the fraction observed in previous comprehensive mapping studies [4,25]. The center of the movement field of these neurons had eccentricities ranging from 4° to 12°, with an average eccentricity of 7.8° (S.E.M. = 0.4°).

The target color or shape remained the same with respect to the previous session during recordings from 15 neurons, and changed in both color and shape during recordings from six neurons; the average delay between the session in which these neurons were recorded and the previous session was 1.5 days. Because our previous studies with this conjunction search did not reveal a significant difference between color and shape information, we combined activity associated with distractors that shared a target feature (e.g. color or shape), and refer to this combination as 'similar distractors' in relation to the target. However, to inves-

tigate the effect of priming on movement-related activity, when the target remained the same color or shape from the previous session, we refer to a similar distractor that was the target during the previous session as a 'primed similar distractor', and the other similar distractor as the 'unprimed similar distractor'.

The activity of one representative movement-related FEF neuron during conjunction search trials in which the initial saccade was directed to the target is shown in Fig. 2. Consistent with its classification, this neuron does not respond to the brief presentation of the target in its response field during the memory-guided saccade task, but responds strongly before a saccade is generated to the remembered location of the target when it was flashed in the response field (Fig. 2A). Accordingly, during conjunction search, in contrast to the activity of visually-responsive FEF neurons [2], this neuron does not exhibit an early non-selective visual response that does not discriminate target from distractors (Fig. 2B). Instead, this neuron exhibits strong, almost immediately selective movement-related activity that grows steadily until the saccade is generated to the target in its movement field. However, the activity of this neuron was clearly not determined solely by the impending saccade; this neuron was also activated when distractors were in its movement field but no saccade was ultimately generated to that location. Most importantly, similar to our previous observation with visually-responsive neurons, the activation in relation to distractors in the movement field depended on the properties of the distractor, with more activation elicited by distractors similar to the target, and relatively more activation for the primed similar distractor.

The average of the normalized activity of the 15 movement-related FEF neurons recorded when the target during the previous session was a similar distractor is shown in Fig. 3A during conjunction search trials in which the initial saccade was directed to the target (i.e. correct trials). The response of this population of neurons is consistent with the observations made regarding the response characteristics and modulation of the neuron shown in Fig. 2. To quantify the effect of distractor properties on movement-related activity, for each neuron we calculated pairwise differences between the average neural activity associated with the different distractor types. Because of the variable firing rates across the population of neurons, the pairwise differences were normalized by dividing by the average of the activity for all three distractor types. Because of differences in the numbers of each distractor type in four- and six-item displays, and because saccade latency increases slightly with set size [3], all analyses were conducted separately for the two set sizes. However, there were no significant differences in the pattern of neural modulation between the two set sizes, so the data were combined for this report. The analysis was conducted

in two 30 ms intervals, one starting at the time at which a neuron discriminated the target from distractors, and the other ending 10 ms before saccade initiation. These two intervals of analysis were largely independent, with an average overlap of only 4.5 ms across the 15 neurons analyzed.

The results of this analysis, shown in Fig. 3B, confirmed the above observations on the modulation of movement-related neurons in FEF. The mean normalized difference between the activity associated with an unprimed similar distractor and the opposite distractor was significantly positive in both the post-selection (mean $= 0.35$, $t_{26} = 5.37$, $P < 0.001$) and the pre-saccade (mean $= 0.29$, $t_{26} = 5.34$, $P < 0.001$) intervals, reflecting the influence of distractor similarity to the target on the activity of movement-related neurons in FEF. Furthermore, the mean normalized difference between the activity associated with a primed similar distractor and an unprimed similar distractor was also significantly positive in both the post-selection (mean $= 0.22$, $t_{26} = 2.50$, $P < 0.05$) and the pre-saccade (mean $= 0.15$, $t_{26} = 2.69$, $P < 0.05$) intervals, reflecting the effect of priming on the activity of these neurons. Although these two effects appear somewhat reduced in the pre-saccade interval as compared to the post-selection interval, the difference was not significant ($P > 0.05$).

We have found that movement neurons are modulated according to the properties of distractors in their movement field, even though a saccade was generated to the target outside the boundaries of their movement field. Before casting these results in terms of a dichotomy between discrete and continuous processing however, we considered potential differences in gaze behavior that may explain our findings.

The first alternative explanation involves micro-saccades during the period of fixation when stimuli are present, before the saccade to the target has been generated. It is conceivable that the neuronal modulation of movement neurons we observed is due to differences in the monkeys' tendency to make micro-saccades to distractors in their movement field related to their properties (i.e. similarity to the target and matching the target of the previous session). Although given the size of the fixation window and the eccentricity of the movement field of neurons we analyzed we do not expect such potential differences in fixation behavior to significantly affect the activity of these neurons, we nevertheless tested this possibility empirically. However, because our eye monitoring system did not allow us to reliably detect micro-saccades, we examined this potential confound by calculating the distance between the distractor in the movement field and the average position of the eye in the fixation window during the interval spanning from stimulus presentation to saccade initiation. If indeed monkeys had an increased tendency to make micro-saccades towards a distractor in the
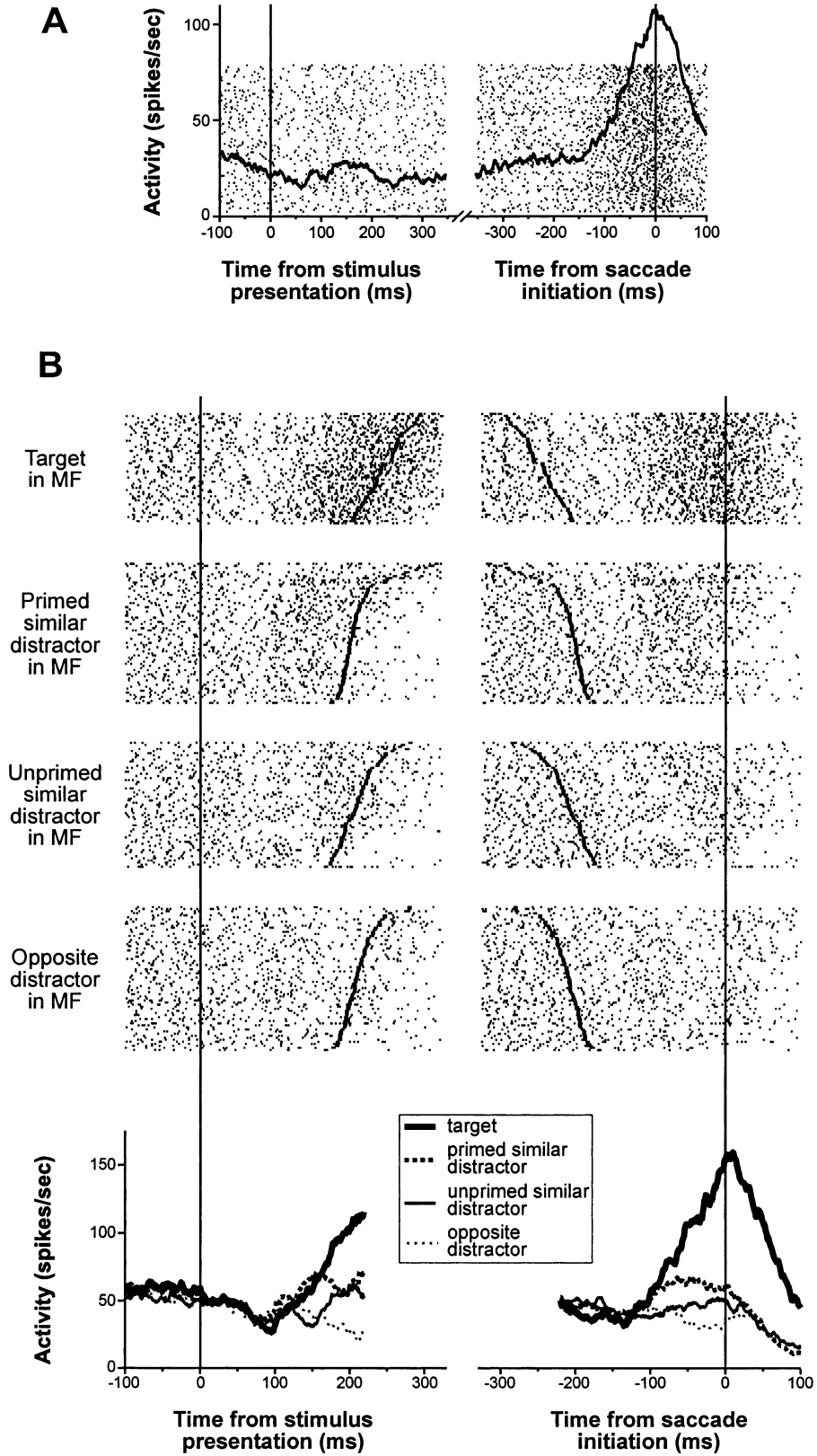
Fig. 2. (*Caption on next page*)

movement field of the neuron when that distractor was similar to the target or when it was the target of the previous session, the average distance from fixation to

that stimulus should be on average smaller than when the opposite distractor was in the movement field. Using the same distractor categories as in the above

analysis (i.e. primed similar, unprimed similar, or opposite distractor), we found no evidence for a tendency of monkeys to make micro-saccades to a distractor in the movement field as a function of the properties of that distractor (ANOVA: $F(2, 87) < 1$, $P > 0.05$).

The second alternative explanation involves the curvature of saccades made to the target outside the movement field. If the activity related to distractors in the movement field played a role in the trajectory of the saccade generated to the target, saccades to a target position near the movement field should exhibit greater curvature towards the movement field when the distractor in it was similar to the target or it was the target of the previous session than when that distractor shared no features with the target. To quantify the magnitude of the curvature of saccades, we used a measure adapted from the 'maximum deviation from desired trajectory' measure described by Quaia et al. [21]. For the purpose of our study, we defined 'desired trajectory' as the straight line between the fixation point of the monkey and the target position. We then found the maximum amount of deviation from this trajectory during the saccadic eye movement. We conducted this analysis only for target positions that were within 90° of the movement field position occupied by a distractor; deviations towards the movement field were arbitrarily assigned positive values, while deviations away from the movement field were assigned negative values. There was no significant difference in the degree of curvature of saccades as a function of the properties of the distractor in the movement field (ANOVA: $F(2, 87) = 1.14$, $P > 0.05$).

The average of the normalized activity of the 6 movement-related FEF neurons recorded when the target changed in both color and shape from the previous session is shown in Fig. 4A during correctly performed conjunction search trials. The quantification of the neural modulation in this condition is shown in Fig. 4B. The two intervals of analysis overlapped on average by 4.8 ms across these six neurons. The mean normalized difference between the activity associated with a similar distractor and the opposite distractor was still significantly positive in the post-selection interval (mean = 0.30, $t_{11} = 3.79$, $P < 0.01$), but not in the pre-saccade interval (mean = 0.05, $t_{11} = 0.86$), reflecting the late relative increase of the activation of the opposite distractor due to priming. Furthermore, there was no evidence that fixation behavior ($t_{11} = 1.64$, $P > 0.05$) or the curvature of saccades to the target ($t_{11} = 1.71$, $P > 0.05$) was affected by the properties of the distractor in the movement field.

3.2. Feature search with singleton distractor

As expected from findings with human observers [36], the presence of the singleton distractor affected the performance of the monkeys during feature search. As compared with feature search without a singleton distractor, monkeys took significantly longer to initiate a saccade to the target (258.5 versus 250.4 ms; $t_{11} = 2.36$, $P < 0.05$) and made significantly more errors (33.0% versus 28.9%; $t_{11} = 4.15$, $P < 0.01$). The largest effect was, however, observed in the pattern of errors monkeys made during feature search with a singleton distractor. After accounting for the difference in the number of the two distractor types, errant saccades were about three times more likely to land on the singleton distractor than on one of the distractors that shared the target color (74.6% versus 25.4%; $t_{11} = 8.77$, $P < 0.001$).

We recorded from 23 neurons in 12 sessions while monkeys performed a feature search with a singleton distractor; of these neurons, 12 were classified as movement-related. The center of the movement field of these neurons had eccentricities ranging from 6° to 12°, with an average eccentricity of 9.7° (S.E.M. = 0.6°). The average of the normalized activity of these movement-related neurons during correctly performed trials is shown in Fig. 5A. Similar to the movement-related neurons described above, these neurons had no visual response and only exhibited selective movement-related activity. As expected, these neurons were maximally activated for saccades to the target in their movement

Fig. 2. Activity of one movement-related FEF neuron during the memory-guided saccade and the conjunction visual search tasks. (A) Activity of the neuron during the memory-guided saccade task when the target was flashed in its movement field aligned on stimulus presentation at time zero (left) and on saccade initiation at time zero (right). Each dot indicates the time of an action potential relative to the event of alignment; each row represents neural activity recorded in one trial. The average spike density function is shown overlaid on the raster plot. (B) Activity of the same neuron during conjunction search trials when the target (top rasters), the primed similar distractor (upper middle rasters), the unprimed similar distractor (lower middle rasters), and the opposite distractor (bottom rasters) was in its movement field (MF). Activity in the left column is shown relative to the presentation of the conjunction search array, and in the right relative to the initiation of the saccade to the target. Horizontal tick marks in the raster plots of the left column indicate the time of saccade initiation and those of the right column indicate the time of stimulus presentation; trials were sorted by increasing saccade latency. The average spike density functions derived from the raster plots are superimposed in the bottom plot for the activity of the neuron when the target (thick solid line), the primed similar distractor (thick dotted), the unprimed similar distractor (thin solid), and the opposite distractor (thin dotted) fell in its movement field. All arrangements of both the four- and the six-element conjunction search arrays were combined. Only spikes that occurred before saccade initiation were used in the calculation of the spike densities aligned on stimulus presentation.
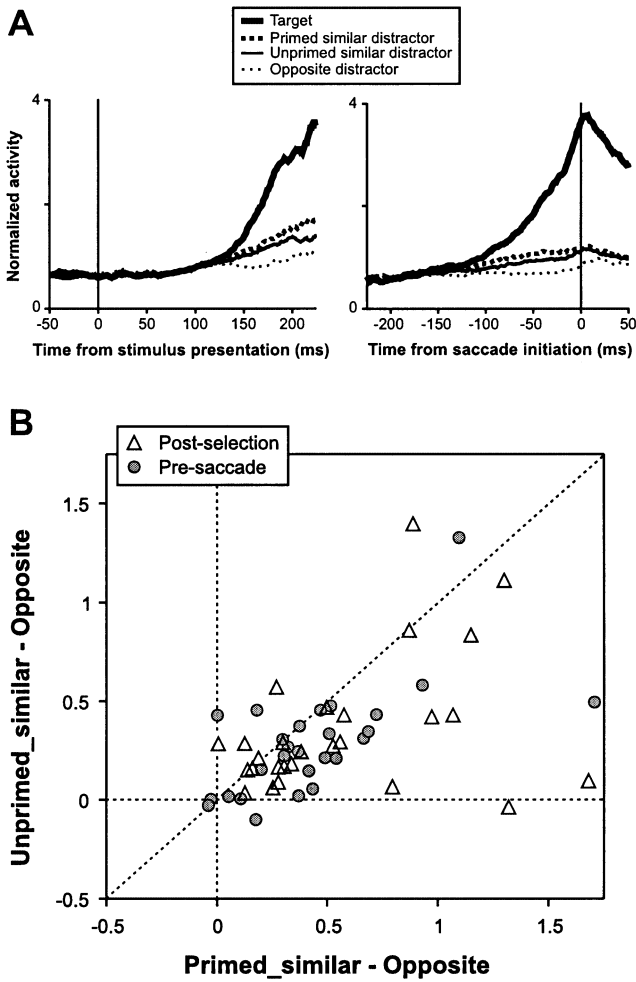
Fig. 3. Activity of a population of FEF movement-related neurons during conjunction search when the distractor that was target during the previous session shared a feature with the current target. (A) Average normalized spike density functions aligned on stimulus presentation (left) and saccade initiation to the target (right) at time zero as a function of the type of conjunction stimulus in the movement field. Spike densities were normalized by dividing them by the average activation across all stimulus types during the time interval from stimulus presentation to saccade production. All arrangements of both the four- and the six-element arrays were combined. Only spikes that occurred before saccade initiation were used in the calculation of the spike densities aligned on stimulus presentation, which are plotted only up to the mean saccade latency. (B) The normalized difference between the activity associated with the unprimed similar distractor and that associated with the opposite distractor is plotted as a function of the normalized difference between the activity associated with the primed similar distractor and that associated with the opposite distractor for each neuron and for each set size in both the post-selection (triangles) and the pre-saccade (gray-filled circles) intervals.

field. However, the movement neurons were also activated when distractors fell in their movement field and monkeys shifted gaze to the target outside their movement field. The level of the activation associated with distractors depended on the properties of the distractors, being greater for the color-singleton distractor than for the other non-salient distractors.

The quantification of the distractor-specific modulation of movement-related activity in FEF during the feature search task is shown in Fig. 5B during the same post-selection and pre-saccade intervals used in the analysis of neural data during conjunction search. These two intervals of analysis were largely independent, with an average overlap of only 3.8 ms across the 12 neurons analyzed. The average normalized difference between the activation associated with the singleton distractor and the activation associated with the other non-salient distractors was significantly positive in both the post-selection (mean $= 0.36$; $t_{11} = 5.15$, $P < 0.001$) and the pre-saccade (mean $= 0.33$; $t_{11} = 3.14$, $P < 0.01$) intervals. The magnitude of this modulation was not significantly different between the two intervals of analysis ($t_{11} = 0.35$).

As with the conjunction search data, we inspected whether the differential responses to distractors in the movement field could be explained by differences in
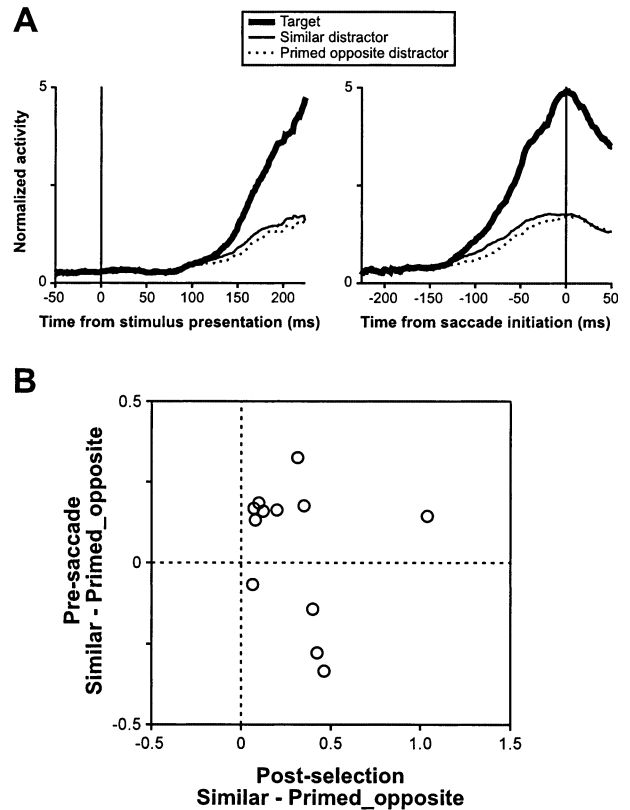

Fig. 4. Activity of a population of FEF movement-related neurons during conjunction search when the distractor that was the target during the previous session shared neither feature with the current target. (A) Conventions as in Fig. 3. (B) The normalized difference between the activity associated with a similar distractor and that associated with the primed opposite distractor during the pre-saccade interval is plotted as a function of the normalized difference between the activity associated with a similar distractor and that associated with the primed opposite distractor during the post-selection interval for each neuron and for each set size.
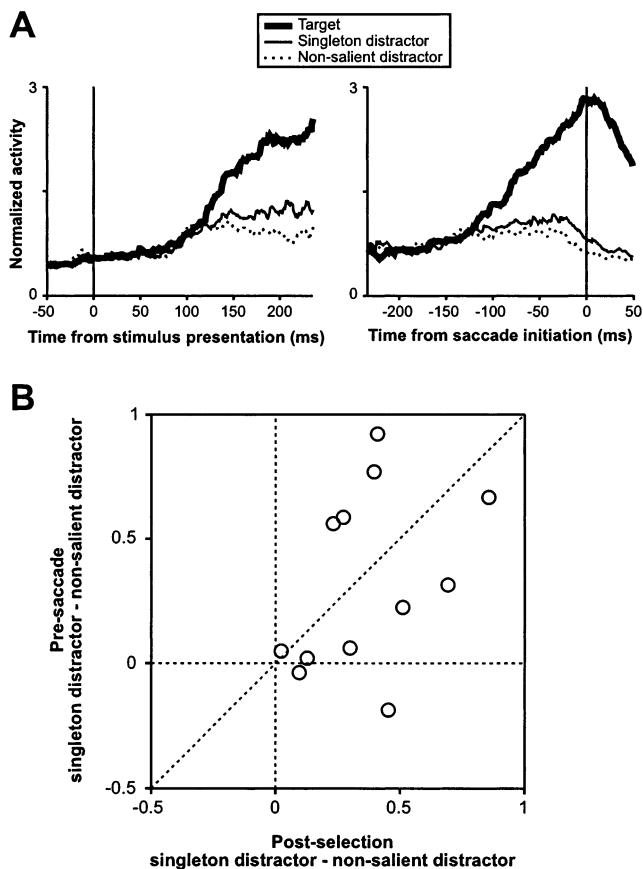
A

B

Fig. 5. Activity of a population of FEF movement-related neurons during a shape feature search with a singleton distractor. (A) Conventions as in Fig. 3. (B) The normalized difference between the activity associated with the color singleton distractor and that associated with the non-salient distractors in the pre-saccade interval is shown as a function of the same measure in the post-selection interval.

monkeys' fixation behavior while stimuli were present. Again, there was no significant difference in monkeys' tendency to make micro-saccades to a distractor in the movement field as a function of the properties of that distractor ($t_{11} = 0.30$, $P > 0.05$). We did not find it necessary to investigate whether the curvature of saccades to the target was affected by the properties of the distractor in the movement field since only target positions that were in the opposite hemifield of the movement field were used in the analysis of distractor-related modulation.

4. Discussion

In this study, we have shown in two conceptually different visual search tasks that the activity of movement-related FEF neurons is modulated by more than just whether a saccade is made into the movement field. In both tasks, although activation was maximal when the search target was in the movement field and the saccade was made to this location, activation was also

observed when the saccade was made to the search target outside the movement field and only distractors were in the movement field. Furthermore, in both tasks the activation associated with a distractor in the movement field depended on the properties of the distractor, ruling out the possibility that the observed activation can be accounted for by the possibility, however unlikely, of the target falling within the boundaries of the movement field. During conjunction search, movement-related activation was greater for distractors that were similar to the target and for distractors that were the search target during the previous session. During shape feature search with a color singleton distractor, activation was greater for the singleton distractor in the movement field than for the other non-salient distractors in the movement field. Moreover, these results cannot be explained by the relative location of the target with respect to the movement field because, on average across trials, it was not significantly different for each of the different distractor types in the movement field.

These results clearly show that partial information about stimuli is relayed to the movement preparation stage rather than just the final outcome of the visual selection process or the target location. Thus, these findings are not consistent with strictly discrete transfer of information between stages of processing represented in FEF. However, these data do not allow us to determine the 'grain' size [17] of the information transferred between the visual selection stage and the response stage. Furthermore, evidence suggests that the nature of the transfer may depend on speed–accuracy trade-offs with transmission more continuous if speed is favored over accuracy, and more discrete if accuracy is favored over speed [9]. This is not surprising because the accumulation of partial information about the target and distractors can be used to prepare the response earlier, while running the risk of responding inaccurately. On the other hand, if transfer of information takes place only when the visual selection stage has completely evaluated the stimuli, accuracy would increase at the expense of reaction time. In our task, monkeys received a juice reward in every correct trial. It is conceivable that if we had penalized our monkeys more severely for incorrect responses (for example by giving them a juice reward only if they performed correctly a certain number of trials consecutively) thereby emphasizing accuracy over speed, less or no information about distractors would have been observed in the response stage, and the information about the target would have started to accumulate at a later time when the selection stage fully resolved its location.

In conclusion, these data show that partial information about stimuli can be used by the response stage during visual search. This finding may be related to the more general finding that information processing across

visual and visual-association structures of the brain may be operating more simultaneously than once thought [6,31] through a complex web of both feedforward and feedback connections [12,24].

Acknowledgements

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