

NEURAL MECHANISMS OF BOTTOM-UP SELECTION DURING VISUAL SEARCH

Kirk G. Thompson

Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD, USA

Abstract- Models of attention and saccade target selection propose that within the brain there is a topographic map of visual salience that selects, through a winner-take-all mechanism, locations for further processing. The results of a series of recent experiments in monkeys performing pop-out visual search tasks suggest that the frontal eye field (FEF) functions as a map of visual salience. FEF is located at the interface of sensory and motor processing and participates in the transformation of visual information into a command to move the eyes. Visually responsive neurons in FEF identify conspicuous objects in a search array regardless of the feature that renders conspicuousness. Furthermore, selection occurs at a constant interval following search array presentation and is dissociated from saccade production. The finding of a visual salience map in FEF validates models of visual selection and can serve to guide future empirical and theoretical investigations.

Keywords - vision, saccade, salience map, attention, decision.

I. INTRODUCTION

Vision is a dynamic process. It is dependent on rapid eye movements called saccades that redirect the fovea, the high acuity region of the retina, onto informative elements in the visual scene. Before each saccade our eyes remain stable for about 200 milliseconds while visual processing takes place. During this period of fixation, our brains must decide what object to look at next and then prepare and execute the saccade.

Gaze is often directed to conspicuous objects that stand out from the background. Visual conspicuousness occurs when an object has a unique feature (e.g. color, luminance, orientation, motion, size) that sets it apart from the rest of the image. The term “pop-out” is often used to describe this capturing of attention through a bottom-up selection process. Bottom-up refers to the automatic allocation of attention based exclusively on the properties of the image. In contrast, top-down refers to selection based on cognitive factors such as the goals and knowledge of the viewer (reviewed in [1]).

In 1985 Koch and Ullman introduced the idea of a salience map to accomplish visual selection [2]. A salience map is an explicit two-dimensional map that encodes the salience of objects in the visual environment. Salience can be derived from both bottom-up and top-down factors. A winner-take-all competition within this map gives rise to a single location that corresponds to the most salient object that can, but need not necessarily, be the target for the next eye movement (reviewed in [3]). Most models of visual search have incorporated the idea of a salience map within the brain to guide covert attention [4], [5], [6], [7], and overt gaze shifts [8], [9], [10].

The spatial pattern of activity across the salience map must be able to localize the most salient object regardless of what

feature or combination of features is responsible for its salience. Thus, the neural substrate of the salience map cannot itself be sensitive to specific visual features; otherwise activation could be attributed to the specific feature rather than overall salience. In the models mentioned above, specific features of the image are encoded in parallel at lower levels of the system within multiple feature maps. These feature maps then converge onto one map of visual salience.

Does such a salience map actually exist in the brain? Recent work has pointed to brain structures within the visuomotor system that may encode visual salience. Among these are the pulvinar [11], the posterior parietal cortex (PP) [12], [13], [14], the superior colliculus [9], [15], and the frontal eye field (FEF) [16], [17] (Fig. 1). This review will focus on evidence from the frontal eye field.

II. FRONTAL EYE FIELD

The frontal eye field (FEF) is ideally positioned to contain a map of visual salience for the purpose of guiding eye movements (Fig. 1). FEF receives topographically organized converging inputs from multiple extrastriate visual cortical areas [18]. Roughly half of FEF neurons have visual responses [19], [20], [21]. The output of FEF is from a population of neurons, called movement neurons, that are located in layer 5 and discharge specifically before and during eye movements [20], [22]. FEF movement neurons send an eye movement command to the superior colliculus [23] and parts of the neural circuit in the brainstem that generates saccades [24].

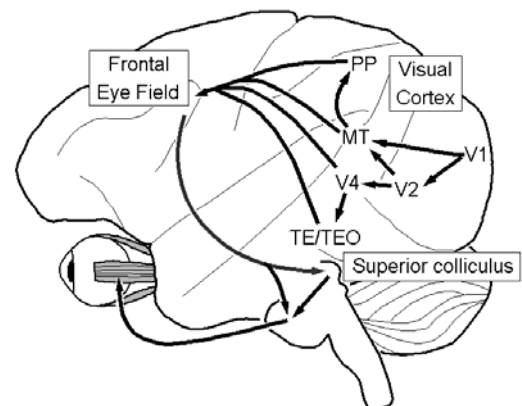


Fig. 1. Simplified schematic of anatomical connections within the visuomotor system of the monkey. Visual information from multiple visual cortical areas converges onto the frontal eye field. The frontal eye field sends an eye movement command to the superior colliculus and brainstem saccade generator, which sends a motor signal through the cranial nerves to the eye muscles.

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Neurons in FEF have spatially defined response fields and FEF is topographically organized. The ventrolateral part of FEF represents central regions of visual space and electrical stimulation of this region evokes short amplitude saccades. The dorsolateral part of FEF represents peripheral regions of visual space and electrical stimulation of this region evokes larger amplitude saccades [20], [25].

The visual cortex is organized into functionally specialized areas that contain neurons that are broadly tuned to one or a few feature dimensions [26], [27]. The processing in these areas corresponds conceptually to the feature maps in models of visual search [2]-[9]. As a result of the extensive convergence from extrastriate visual cortex, the visually responsive neurons in FEF do not exhibit selectivity for stimulus features [28], [29], but instead exhibit activation that represents visual salience. The remainder of this paper will review recent work that supports this view.

III. SACCADIC TARGET SELECTION

A. Target selection during visual search

The visual search paradigm has been used extensively to investigate visual selection and attention [4], [30]. In a visual search task, multiple stimuli are presented, and from among them a target is discriminated. To investigate how the brain

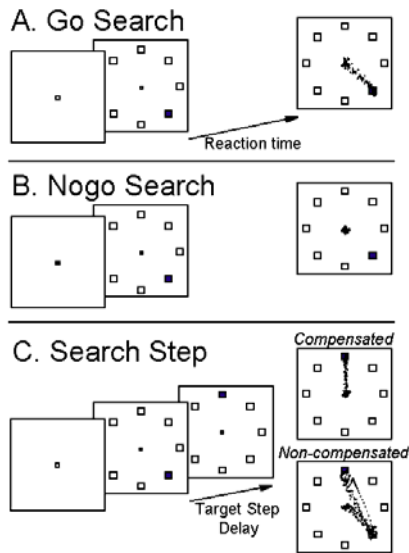


Fig. 2. Visual search tasks. Three different pop out search tasks were used. The tasks were run in separate blocks of trials. Monkeys began each trial by fixating the central spot. The sequence of each task is shown on the left. Eye position traces are shown on the right indicating the monkey's behavior during each task. Target location was randomized from trial to trial. **A.** Go search task. A search array appeared and the monkey was rewarded for making a saccade to the oddball. **B.** Nogo search task. Monkeys were rewarded for maintaining fixation on the central spot for the entire trial. Monkeys did not indicate location of target in this task. **C.** Search-step task. Most trials were the same as in go search (A). On the remaining trials the target swapped positions with a distractor after a short delay called the target step delay and monkeys were rewarded for shifting gaze to the new target. On search-step trials monkeys either compensated for the target step or failed to compensate. Noncompensated saccades were typically followed by a second corrective saccade.

selects targets for visually guided saccades, recordings of neural activity were made in the FEF of monkeys trained to shift gaze to an oddball target stimulus among identical distractor stimuli (e.g. red target among green distractors) (Fig. 2). This task is an example of pop-out search, and therefore is controlled by a bottom-up selection process.

Initially, saccade target selection in FEF was investigated using a go search task (Fig. 2A) [28], [31]. It was found that most FEF visually responsive neurons responded initially indiscriminately to the target or the distractor of the search array in their receptive field. However, before saccades were generated, a discrimination process took place by which most visually responsive neurons ultimately signaled the location of the oddball stimulus (Fig. 3A). Thus, the activity of FEF visual neurons does not represent specific features of objects, but rather reflects the evolution of the visual selection or saccade preparation processes.

B. Timecourse of target selection

Having found that it was possible to observe saccade target selection in the activity of FEF visual neurons, an analysis was carried out to determine when the selection was accomplished and the time of target discrimination was related to when the saccade was made [32]. It was found that FEF visual neurons

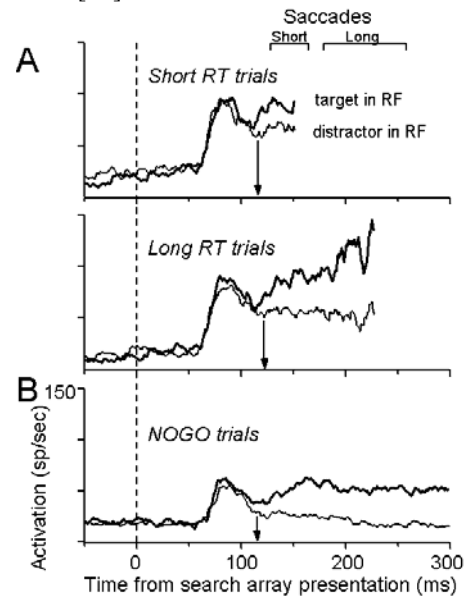


Fig. 3. Visual selection of a conspicuous target. The neural activity of a single FEF visual neuron is shown following presentation of a pop-out search array during (A) GO search and (B) NOGO search. Each plot shows the activation when the oddball stimulus appeared in the receptive field (RF) (thick line) and when distractors appeared in the receptive field (thin line). The trials are aligned on the time of search array presentation. **A.** The time course of activation during a block of GO search trials. The activation during subsets of trials in which reaction times (RT) were short or long are shown separately. The plots of neural activity end at the mean reaction time for each group. The ranges of reaction times for the short and long trials are indicated across the top. **B.** The time course of activity during a block of NOGO trials. The times of target discrimination (solid arrows) were approximately the same in all three subsets of trials showing dissociation between the visual selection of a stimulus in FEF and the production of saccades (modified from [15]).

discriminate the target from a distractor in a pop-out search array at a fairly constant interval after search array presentation (Fig. 3A). In other words the time at which the target of the saccade was identified did not predict when the eyes moved. This finding suggests that the target selection process in FEF is more closely linked to visual processing than to saccade production.

III. DISSOCIATION OF VISUAL SELECTION FROM SACCADDES

A. Visual selection without saccades

To examine further the dissociation of visual selection in FEF from saccade production, Thompson et al. [33] tested the hypothesis that the selection observed in FEF does not require saccade planning and execution. FEF activity was recorded while monkeys were instructed to maintain fixation during presentation of the pop-out search array (Fig. 2B). Although no saccade was made to the oddball, FEF neurons still discriminated the oddball from distractors at the same time and to the same degree as when a gaze shift was produced (Fig. 3B). Thus, the visual selection observed in FEF identifies potential targets for saccades, but does not require the generation of saccades.

B. Visual selection with competing saccade targets

The nogo search experiment [33] showed that the visual selection process in FEF is not dependent on the production of a saccade. However, because monkeys had been trained to make saccades to the target, it could be argued that the observed selection reflected some kind of latent saccade programming. The search step task (Fig. 2C) was designed to test this possibility and to ultimately determine if the selective activity in FEF reflects perceptual or motor processes [34].

In the search-step task most trials were identical to go search, but on about a third of the trials the target unexpectedly switched places with a distractor. The monkey's task was to shift gaze to the new target location to receive a juice reward. The timing of the target step was adjusted so that the monkeys were able to compensate for the target step on about half the trials. On the remaining trials the monkeys did not compensate for the target switch and initially looked at the original target location and were not rewarded. The question to be answered was: Does the selective activation reflect the location of the pop-out target or does the selective activation predict the monkey's impending eye movement? The answer is that the selection reflects the visual stimulus, not the monkey's behavior.

Figure 4 shows the typical results. The early phase of the response during search-step trials was identical to the response elicited by a distractor during go search trials; the early nonselective visual activity was followed by suppression. This is because the stimulus conditions were identical prior to the target step. The activation grew markedly following the target step. Furthermore, the growth of activity on trials in which monkeys compensated with a saccade to the final target located

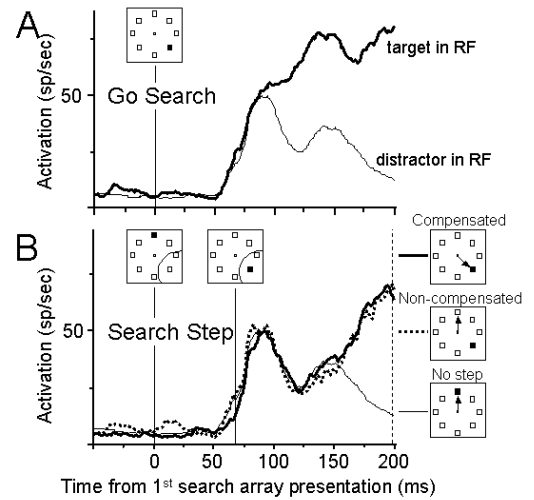


Fig. 4. Frontal eye field visual neuron. **A.** Activation when the target (filled) or distractors (open) fell in the receptive field. Following the initial 100 msec of activation that did not discriminate target from distractor, the activity was modulated strongly. The response to the distractor was suppressed, and the response to the target grew. **B.** Averaged activity on compensated (thick black) and non-compensated (dotted) target-step trials when the distractor in the receptive field unexpectedly became the target compared with activity on no-step trials when distractors remained in the receptive field (thin black). In both compensated and noncompensated trials the neuron responded equally strongly to the unexpected appearance of the target in the receptive field. The fact that the activity before the mean noncompensated saccadic reaction time (vertical dashed line) was indistinguishable for the search-step trials with opposing saccade directions means that the activity of this neuron could not be involved in saccade production. Only presaccadic spikes were used in constructing the response.

in the receptive field was identical to the growth of activity on trials in which monkeys failed to compensate and produced a saccade to the original target located outside the receptive field. In other words, the activity of this neuron represented accurately the new location of the target regardless of whether compensated or noncompensated saccades were produced. This is strong evidence that this selection process is distinct from immediate saccade production.

These findings suggest that FEF may play a role in covert orienting of visual attention as well as overt saccade generation. This conclusion is supported by psychophysical studies showing that attention is allocated automatically to the pop-out oddball in a search array [35] and by recent brain imaging studies showing that a region including FEF in human frontal cortex is activated in association with both attention and saccade tasks [36], [37].

IV. CONCLUSION

Models of visual attention and saccade target selection posit the existence of a map of visual salience in the brain that specifies locations for further processing based on the properties of the image. The stage of processing represented by the salience map is distinct from motor preparation processes because it may or may not lead to an overt orienting response

such as a saccade. The characteristics of the visual selection observed in the population of FEF visually responsive neurons are consistent with it being a salience map. FEF visual neurons exhibit a selective response for conspicuous stimuli at a time that is linked to the presentation of the visual stimulus. Also, visual selection occurs regardless eye movement behavior. It seems clear that a functional salience map exists in FEF, and further work will determine how this map may be distributed across other visuomotor areas such as the posterior parietal cortex and the superior colliculus. Nevertheless, the idea of a salience map appears to be a physiologically sound theoretical construct that will be useful in guiding future theoretical and empirical investigations.

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