Manipulating saccadic decision-rate distributions in visual search

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The Gaussian shape of reciprocal latency distributions typically found in single saccade tasks supports the idea of a race-to-threshold process underlying the decision when to saccade (R. H. Carpenter & M. L. Williams, 1995). However, second and later saccades in a visual search task revealed decision-rate (=reciprocal latency) distributions that were skewed Gamma-like (E. M. Van Loon, I. T. Hooge, & A. V. Van den Berg, 2002). Here we consider a related family of Beta-prime distributions that follows from strong competition with a signal to stop the sequence, and is described by two parameters: a fixate and saccade threshold. In three saccadic search experiments, we tried to manipulate the two thresholds independently, thereby expecting change in shape and mean of the reciprocal latency distribution. Interestingly, rate distributions for later saccades were significantly better fit by Beta-prime than by Gamma functions. Increases in the distribution's skew were found with higher display density, but only for second and later saccades. First saccade rate distributions were not altered by the expected target location or by visual information presented prior to the search, but making pre-search saccades did influence both thresholds. The mean rate remained a stereotyped function of ordinal position in the saccade sequence. Our results support strong competition between two decision signals underlying the timing of saccades.

Keywords: saccades, eye movements, latency, decision model, timing

Introduction

To maintain a high-resolution representation of the world around us, our brain needs to balance its time spent fixating and making saccades. A different environment or observer action may call for another optimal balance. In visual search, fixation duration is found to be determined by the difficulty of the foveal task (Hooge & Erkelens, 1998; Jacobs, 1986). In reading experiments it has been found that the fixation duration is influenced immediately by the foveated stimulus (Rayner & Pollatsek, 1981), but in search tasks, fixation durations are found to be influenced by the accumulated history of preceding fixations (Hooge & Erkelens, 1998; Vaughan & Graefe, 1977). Also, a priori expectations about the stimulus are found to affect fixation duration (Carpenter & Williams, 1995; Kowler, Martins, & Pavel, 1984; Viviani, 1990). Thus, various visual and nonvisual cognitive factors are found to influence the timing of saccades. How does the brain control this balance?

The timing of saccades is believed to be processed largely independent of where a saccade is planned (for an overview, see Findlay & Walker, 1999). During fixation, the foveal target is analyzed, the peripheral stimulus is sampled, and a new saccade prepared (Viviani, 1990). Fixation duration, the time between saccades, is typically in the or-

der of 200 to 800 ms. The estimated time for perceptual processing is estimated to be 100 ms (Salthouse, Ellis, Diener, & Somberg, 1981) up to 400 ms in heading tasks (Hooge, Beintema, & van den Berg, 1999). Motor preparation takes about 100-150 ms (Becker & Jurgens, 1979). Considerable variation in fixation duration is found that cannot simply be accounted for by these perceptual and motor times.

The probabilistic nature of the latency of a single saccade in response to target appearance has been explained to result from a stochastic element in a rise-to-threshold decision when to saccade (Carpenter & Williams, 1995). The idea is that the sensory decision signal to make a saccade accumulates in time at a certain rate, and that the latency follows from the time it takes the neural signal to reach threshold. Conversely, the reciprocal latency gives the decision-rate (s^{-1}) at which the neural signal rises from baseline until threshold. Whereas latencies are typically skewed in their distribution, their reciprocal values are distributed normally (Carpenter & Williams, 1995), fitting the idea of a stochastic decision-rate underlying the timing of saccades.

Race-to-threshold models are supported by findings in frontal eye fields (FEF) and the superior colliculus (SC) (Dorris, Pare, & Munoz, 1997; Munoz & Wurtz, 1995), brain structures involved in the planning and execution of

eye movements. Preceding a saccade, visuomotor neurons in FEF will show a rise in activity at a rate that varies from trial to trial (Hanes & Schall, 1996). Importantly, the execution of the eye movement is not locked to the onset of the target stimulus, but to the time at which a threshold is reached (Thompson, Hanes, Bichot, & Schall, 1996). Also, in perceptual decision processes, a direct correlation between neuronal activity near threshold and reaction times has been found (Ditterich, Mazurek, & Shadlen, 2002). They showed that micro-stimulation in MT affected reaction time in a motion direction task. Reaction times decreased in response to the preferred motion of a neuron nearby when motion in its null direction was shown.

Recently, distributions of reciprocal latencies were analyzed in a two-dimensional search study in which multiple saccades were made (Van Loon, Hooge, & Van den Berg, 2002). Van Loon et al. found that the rates for the first saccade are Gaussian distributed, as was found before in single saccade studies (Carpenter & Williams, 1995; Reddi & Carpenter, 2000). However, analyzing subsequent fixation durations between saccades, Van Loon et al. found that the rate distributions of second and later saccades were typically skewed Gamma-like, having more tail at higher rates. Even with a latency correction for concurrent processing that could already start before the first saccade, the rate distributions of second saccades still deviated from Gaussian (Van Loon et al., 2002). Then what might underlie the skew in later saccades?

In contrast to single saccadic reaction tasks, multiple-fixation search not only requires a decision when to make a saccade, but also a decision to stop the sequence. This notion, and the finding of Beta-like skewed decision-rate distributions for later saccades inspired Van den Berg and Van Loon (in press) to postulate a decision model where two signals race toward their own threshold, but not independently. Each bit of incoming sensory information either contributes to an incremental step toward the threshold 's' to make a saccade, or to an incremental step toward the threshold 'f' to maintain fixated, thus terminating the saccade sequence. Importantly, each decision bit cannot contribute to both races at the same time, hence forming a strong form of competition between the decision to make a saccade or to maintain fixation. Now, the chance p of an incremental step toward the saccade threshold s over the chance of incremental step toward the fixation threshold f is $r = p/q$. Note, $q = 1-p$ because of our assumption of strong competition, so that $r = p/(1-p)$. The ratio r we associate with the observable decision-rate in our experiments. The ratio r has a probabilistic nature that is described by the probability function Beta-prime:

$$\beta_{s,f,\tau}(r) = b^{-1}(s,f) \frac{(r\tau)^{s-1}}{(1+r\tau)^{s+f}} \ .$$

Here the Beta function $b(s,f)$ is used as normalization factor, and the parameters s and f are the thresholds for sac-

cade initiation and maintaining fixation. Note, the observable decision-rate has the dimension [s^{-1}], whereas the ratio r is dimensionless. Therefore, we need to include a third fit parameter τ [s] to scale the decision-rate distribution along the time axis, but this parameter turns out be close to 1 (Van den Berg & Van Loon, in press, and see Methods).

The above dual race model assumes a strong form of competition. In that, it is essentially different from dual race models that have been proposed to explain saccadic reaction times in countermanding tasks (e.g., Hanes & Carpenter, 1999) where the execution of a single saccade is to be cancelled if a stop signal is presented. The dual race models assume that an explicit "go" and "stop" signal each race to threshold independently, the stop signal canceling the saccade if it reaches threshold earlier.

In single saccade reaction tasks, evidence for the existence of a decision threshold when to make a saccade has been found by urging subjects to be quick or accurate (Carpenter & Williams, 1995; Reddi & Carpenter, 2000). Those manipulations altered the decision-rate distributions, consistently with a change in initial start value and threshold, respectively. Here we seek evidence for the proposed strong form of competition in first and later saccades, by an attempt to manipulate the two thresholds independently. To this end, we varied (1) the density of the display, (2) the expected target location, and (3) the visual information and saccadic activity preceding the start of search. We discuss the results in terms of the two thresholds that regulate the degree of competition between a signal to saccade and a signal to keep fixating.

Methods

Saccadic eye movements were measured while subjects searched for a line target that differed in orientation from lines arranged in a radial pattern. The tasks and stimuli were similar to those used by Van Loon et al. (2002).

Stimuli

Stimuli were viewed monocularly, with the left eye placed 30 cm in front of a 19" FD Trinitron CRT (1024 by 768 pixels, refresh rate 75 Hz). The brightness and contrast of the monitor were set to 35%, and the room was completely darkened.

Each trial lasted 3 s, and started with 1-s presentation of a central fixation marker (0.25-deg yellow square), followed by a search display. The search display consisted of thin (0.2 deg) red lines on a black background. The lines were drawn according to the trajectories of points over time when simulating 1-m observer translation through a homogenous cloud of points that extends 1 to 21 m in front of the observer. Thus, line length on average increased for lines further away from the radiant (mean 1.6±1 deg). Each trial, a new pattern of lines was presented with its radiant

randomly placed within 15 deg from the screen center. We used low (Lo), middle (Mi), and high (Hi) stimulus densities, corresponding to respectively 15±3, 58±7, and 233±14 visible lines on a 63-by-47-deg screen (see Figure 1).

The target was either peripheral or foveal. A peripheral target had a random position on a circle, concentric with the center of screen, with an eccentricity randomly chosen from 6, 12, or 18 deg. A foveal target was presented at the center of the screen. The target was a single line that deviated in line orientation from that expected by the radial pattern of lines. The angle of deviation was chosen between 25 and 40 deg, based on pilot studies aimed at maintaining a constant level of difficulty for the three stimulus densities. As for the pattern lines, the target's length scaled with its distance to the pattern's radiant. Given the trial-by-trial variation in the radiant's position, the mean target line length was 1.6 deg for a central target and 2.5 deg for a target at 18-deg eccentricity.

Task

Subjects were instructed to fixate the central fixation marker before starting a new trial by button press. As soon as the search display came on, subjects were to saccade as quickly as possible to the target and keep fixating the target until the end of the trial.

Subjects

All subjects (the authors JB, EL, and AB, and three naive subjects) had normal vision or corrected-to-normal vision. Subject AC and AR had no prior experience with search tasks. Four subjects (AB, AC, JB, and EP) participated in the first experiment, and five (AB, AR, JB, EL, and EP) in the other two experiments.

Eye movement recording

During the trials, the orientation of the left eye (i.e., eye position) was monitored by an infrared camera (SMI EyeLink I, 250 Hz), mounted on the subject's bite board. In Experiment III, saccades were detected on-line using a 20 deg/s minimum eye velocity criterion to trigger the switch of the display on a saccade.

The raw eye position data, supplied by the Eyelink PC, were stored and analyzed off-line. Eye positions recorded during fixation of five targets (8-deg apart, arranged in a cross) preceding each session were used to correct for possible linear scale or shear in the raw data. Mean eye position recorded during each 1-s fixation interval preceding the line stimulus was used to correct for possible drift between trials.

Saccades were detected using a 20 deg/s eye velocity threshold (see also van der Steen & Bruno, 1995). Small saccades that could not be distinguished from noise were removed afterward by a minimal saccade amplitude criterion of 1 deg, a minimal duration between saccades of 30 ms, and by disregarding saccade intervals during which
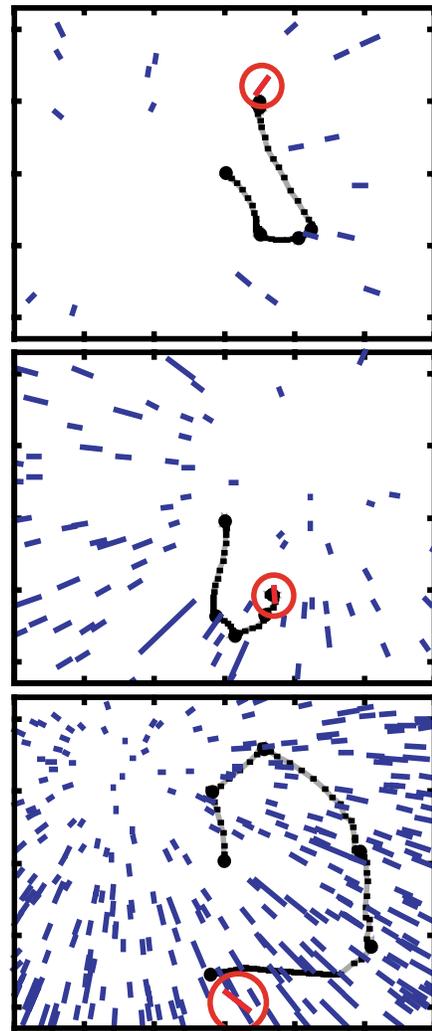

Figure 1. Example line stimuli from Experiment I for the three densities. The target line (red) is encircled for clarity. Superimposed are eye traces (gray line) and fixations (solid dots). Data from subject AB.

the variance in eye velocity did not exceed the variance during noisy adjacent fixation intervals by a factor of 9. Subjects performed at least 480 trials for each condition to allow fits to the distribution of inverse latencies.

Data analysis

Search performance was quantified by the fraction of successful trials. Trials were defined successful when the last fixation was within 3 deg from the target line.

The decision-rates were computed from the reciprocal latencies. The saccade decision must be reached before the so-called saccadic deadtime, a period at the end of fixation during which the saccade can no longer be cancelled. To correct for this, we defined the latency of the first saccade as the time between target appearance and saccade onset, minus an estimate of the saccadic deadtime (70 ms after Hooge & Erkelens (1996)). Additionally, we assume that

processing of a subsequent saccade starts concurrently at the time the decision for the previous saccade had been reached. With the corrections for concurrent processing and saccadic deadtime canceling each other, we defined the latency for second and later saccades as the entire intersaccadic interval.

Frequency distributions of the decision-rates up to 15 [s]$^{-1}$ (i.e., fixation durations > 67 ms), grouped into bins of 0.35 [s]$^{-1}$, were fitted using Marquardt-Levenberg's nonlinear fit procedure programmed in Mathematica (Wolfram). A minimum of 50 saccades was required for a fit. Fit results were checked for stable solutions by varying the starting values.

As goodness-of-fit measure we calculated the Kolmogorov-Smirnov statistic (the maximal difference between the measured and the fitted cumulative distribution multiplied by the square of the number of data). Its probability follows the K-S distribution. Values less than 0.05 indicate that the fit and the data are significantly different.

Gauss, Gamma, and Beta-prime fits compared

The binned decision-rate distributions were parameterized by fitting them with the Beta-prime function. As comparison, the data were fitted with the Gauss and Gamma function as well. Figure 2 shows individual data, with fits for the first saccade up to the fourth. Because differences between fits are most pronounced at the tails of the distribution, we plotted the cumulative probability on a probit scale. In such format, a pure Gaussian rate distribution is a straight line that reaches $p = .5$ at the mean rate. Indeed, for each subject, the first saccade data resemble a straight line, but the p(K-S) values (see insets) indicate that the first saccade distribution cannot be distinguished from a Beta-prime or Gamma distribution either. For second and later saccades, the Gaussian function does not fit the data very well, as the plotted data seems to curve, and fast rates (i.e., short latencies) occur
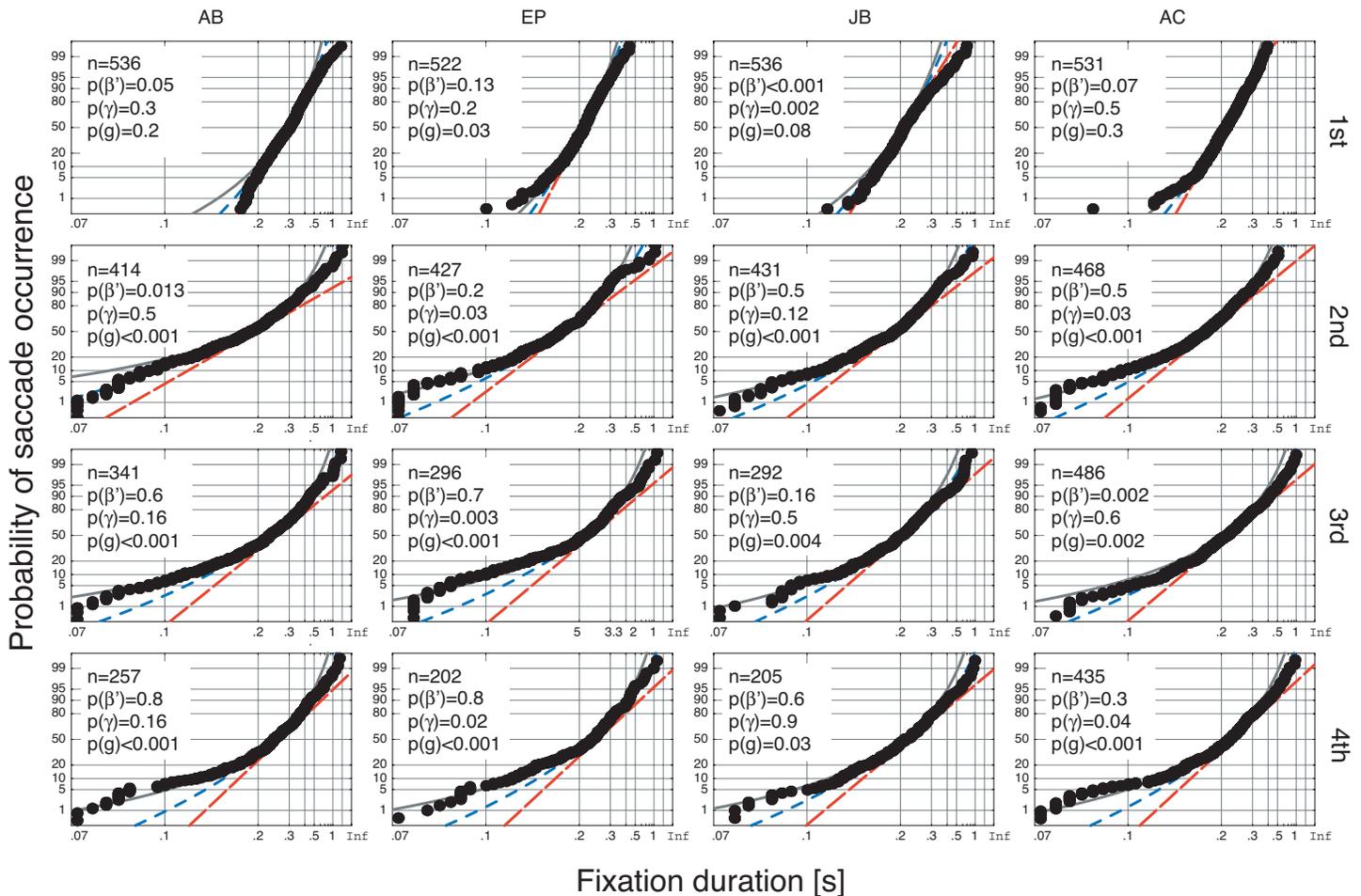

Figure 2. Decision-rate distributions and fits for Experiment I, middle density condition (Mi). Graphs are given for each subject (left to right), for first up to fourth saccade (top to bottom). In each graph, probability of saccade occurrence is plotted cumulatively on probit scale as a function of decreasing decision-rate. The upper axis indicates corresponding fixation durations. Solid dots represent raw data. Lines indicate fits by Gaussian (blue dashes), Gamma (red dashes), and Beta-prime (gray solid) functions. Inset of each graph shows the number of saccades (*n*) and the goodness of each fit (*p* values based on the Kolmogorov-Smirnov statistic).

more frequently than predicted by a Gaussian distribution. The Gamma function has larger tails, but the Beta-prime function seems best at fitting the data, giving slightly higher *p* values (e.g., fourth saccades).

Figure 3 compares the goodness of fit for the Beta-prime, Gamma, and Gauss function in Experiment I-III. Plotted as function of saccade number is the fraction of fits that satisfies our criterium of a good fit [i.e., *p*(K-S) > 0.05]. The fraction varies considerably across experiments and saccade number. Generally, for first saccades, the fraction of good fits for Gauss, Gamma, and Beta-prime functions is about equal, none of the fractions being consistently greater or smaller over the three experiments. In contrast, for second and later saccades, the fraction of successful Gauss fits is consistently smaller than that for the Gamma
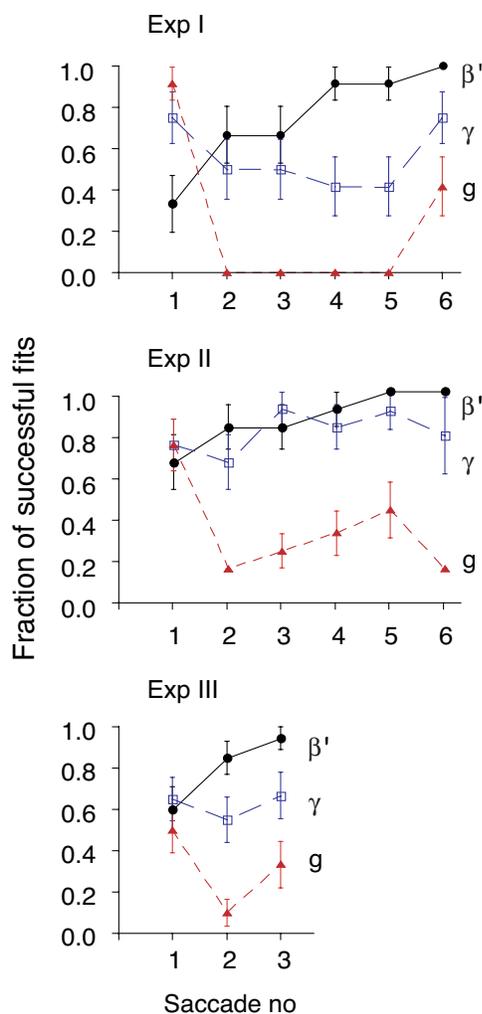
function. This confirms the earlier findings by Van Loon et al. (2002). Furthermore, for second and later saccades, the fraction of successful fits for the Beta-prime function was consistently higher than that for the Gamma function in two out of three experiments.

Although *p*(K-S) is a measure of goodness of fit that is corrected for sample size, we observed that *p*(K-S) values could still decrease when adding more samples. This observation may implicate that the beta-prime model still does not fully capture all aspects of saccade timing in visual search. Most importantly, it means that goodness-of-fit comparisons should be restricted to equally sized data. In that light, the increased fraction of successful fits with higher ordinal saccade number (Figure 3, Experiment I) might also be attributed to the reduced number of saccades (insets, Figure 2). However, we can validly compare the relative goodness of each fit per data set. For later saccade data, Beta-prime fitted better than Gamma in 77% of all fits, the goodness of fits *p*(K-S) being significantly different (p_{140} < .001 in a two-sided paired *t* test). For first saccade data, *p*(K-S) values were not significantly different between Beta-prime and Gauss (p_{41} < .44, paired *t* test). Overall, the Beta-prime seems best suited for describing the rate data. For this reason, in the following we look only at the Beta-prime parameters.

Parameters of the Beta-prime distribution

Fitting the decision-rate distributions with the Beta-prime function, we found the third free parameter τ to be close to 1 for each experimental condition, ordinal number in the saccade sequence, and subject (τ = 1.05 s ± 0.06 *SD* over all fits). When fitting with a fixed parameter (τ = 1 s) *p* values turned out to be somewhat higher (25%). Including a third scale parameter also resulted in lower fit quality for the Gauss and Gamma function, so we assume this is a general effect of overfitting, by an enhanced chance of finding a local minimum in the residuals. Using a fixed scale factor τ = 1 affected the Beta-prime parameters only marginally, resulting in about 10% smaller ($s+f$) values and 3% smaller ratios $s/(f–1)$. Therefore, effectively, the rate distributions can be well described by a Beta-prime function that takes only two free parameters s and f. All reported fit parameters and goodness of fit have been obtained using this constant τ of 1 s.

With the Beta-prime parameters s and f, we associate the threshold for saccade initiation and hold fixation, respectively. In our results, however, we will report the ratio $s/(f–1)$ and the sum ($s+f$) instead, because these terms more directly describe the shape of the Beta-prime distribution. Mathematically, the ratio of the thresholds $s/(f - 1)$ equals the mean of the Beta-prime distribution, thus a higher ratio implies a higher mean rate (i.e., shorter latencies). Furthermore, the sum of the thresholds ($s+f$) reflects the asymmetry in the distribution [i.e., a lower sum

Figure 3. Fraction of fits with *p*(K-S) > .05 for Experiments I-III as function of ordinal position in the saccade sequence. Fractions and their *SE* for Experiment I, II, and III are based on 12, 10, and 20 fits, respectively. For Experiment II, only fits of trials with eccentric targets have been selected.

of thresholds ($s+f$) will broaden the Beta-prime distribution and skew it toward shorter rates, i.e, longer latencies]. These relations will be explained below.

The observed decision-rate distribution is based on the reciprocal latencies of decisions where the saccade threshold was reached earlier than the fixation threshold (for obvious reasons we cannot measure the latency of successful withheld saccades). Fits to the decision-rate distributions show that the saccade threshold s is always larger (about 4 times) than the fixation threshold f. This means that for a saccade to occur, the chance p of an incremental step toward the saccade threshold must be proportionally (about four times) larger than the chance q for a step toward the fixation threshold. Because we identify the ratio p/q with our observed decision-rate r, the latter must on average be proportional (about a factor four) with the ratio of decision thresholds.

The second relation can be understood when considering what would happen if the saccade threshold is lowered, while keeping a constant ratio of thresholds $s/(f–1)$ (i.e., mean decision-rate). Lowering both thresholds will bring the decision in favor of a saccade more under the influence of spontaneous activity. Thus, the rate distribution will broaden. Moreover, this broadening will be asymmetrical about the mean decision-rate. Given that the fixation threshold is 4 times lower than the saccade threshold, a proportional lowering of fixation and saccade thresholds will increase the chance of reaching the fixation threshold more than the chance of reaching saccade threshold. To keep the mean decision-rate constant, relatively many fast decision-rates will need to occur, hence the tendency for the Beta-prime distribution to have more tail at higher rates when the threshold sum is lowered.

Experiment I: Stimulus density

The number of elements in the search stimulus has been found to influence the timing of saccades (for an overview, see Moffit, 1980). Also, adding remote distractors has been found to increase fixation durations (Walker, Deubel, Schneider, & Findlay, 1997). These changes might reflect general changes in the decision-rate thresholds. To manipulate the decision-rate distributions for first and later saccades, we varied the display density.

Procedure

Search displays were presented at three different densities (Lo, Mi, and Hi). Each density (Figure 1) was presented in a block of 180 trials, the order of the blocks balanced across subjects and sessions. The subjects completed three sessions (three densities per session). The fixation dot remained visible during the presentation of the search display.

Results

To investigate whether the manipulations affected aspects of saccadic search other than the decision-rates, we first computed the mean number of saccades and the performance for each subject, condition, and target eccentricity. Figure 4 shows the fraction of successful search trials as a function of experimental condition, split by subject. Generally, we observed large individual differences. Despite these differences, we found consistent effects of the experimental manipulations in Experiment I. The mean performance across the four subjects and three target eccentricities clearly improved with higher density ($F_{2,33}$ = 13, $p < .001$). We also found that the average number of saccades per trial (4.4, 3.9, and 3.7 saccades for Lo, Mi, and Hi, respectively) decreased significantly with denser displays ($F_{2,6474}$ = 300, $p < .001$ in an ANOVA across subjects and target eccentricities).
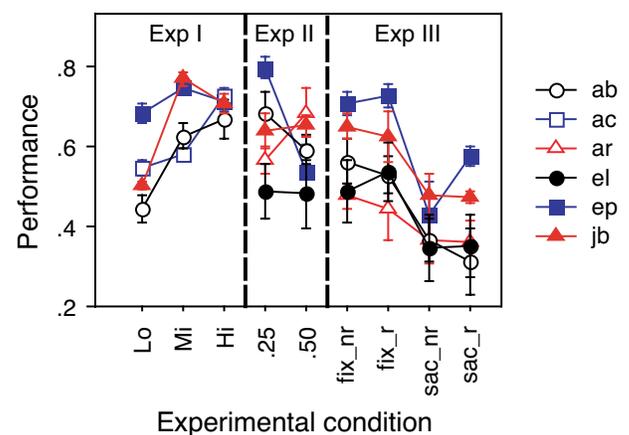

Figure 4. Fraction of successful search trials, in which the last fixation was on the target, as function of experimental condition, split by subject for Experiments I-III. Values represent average fractions (±*SE*) for data pooled across target eccentricities.

To quantify the rate distributions for each condition and subject, we analyzed the saccade and fixation thresholds s and f that follow from the Beta-prime fits. To compare the variability over individuals and experiments, we plotted the sum ($s+f$) and the ratio $s/(f–1)$ of the thresholds for the different experiments, split by subject, for first or later saccades (Figure 9a-9d). Generally, considerable differences were found between individuals, but individual data showed consistent levels over time.

The results for the density experiment, averaged over subjects, are shown in Figure 5 as function of ordinal position in the saccade sequence. We found that second up to sixth saccades have more skewed rate distributions than first saccades, as reflected by a lower sum of thresholds s and f (Figure 5a). This general skew in rate distributions for later saccades confirms earlier observations by Van Loon et al. (2002), but extends them to longer sequences (Van Loon et al. analysis was confined to the first four saccades

in a sequence). As follows from Figure 5, the ratio of thresholds (or mean rate) for first saccades was markedly lower than for later saccades. Interestingly, second saccades had clearly increased rates compared to the other saccades.

Regarding the influence of density, for first saccades, neither the sum nor ratio of the thresholds was influenced by density (Figure 5). For second and later saccades, the mean rate also did not vary with density. However, the sum of thresholds for second and later saccades did show an effect, increasing significantly with higher density ($F_{2,57}$ = 6.5, p = .003 in an ANOVA with data pooled over the four subjects and saccade 2 up to 6).

Discussion

For later saccades (ordinal position > 1) the sum of thresholds increases. This means that the symmetry in the decision-rate distribution significantly increased with denser search displays. No such effect was found for the first saccade. The former, but not the latter finding, fits well with the suggestion by Van Loon et al. (2002) why rate distributions for later saccades would be skewed. Gamma distributions arise when independent stochastic poisson distributions are summed, and will approach the symmetric Gaussian given enough independent contributions. Van Loon et al. speculated that each line element might act as a potential target and add a stochastic component to the saccade decision-rate signal. If after the first saccade, a smaller part of the stimulus is analyzed, with a reduced number of stimulus elements than for the first saccade, the skew should increase. Our results support this speculation, because we found that the skew for later saccades increased when stimulus density decreased.

We found no significant changes in mean rate [i.e., threshold ratio $s/(f–1)$] for either first or later saccades when density increased. This lack of a decreased mean rate seems to contrast with reports of longer fixation duration when the number of stimulus elements per fixation increases (i.e., Mackworth, 1976; Moffitt, 1980) or when the number of distractors increases (Walker et al., 1997). However, our stimulus may have been different in that the line elements do not merely act as distractors but also help to locate the target line. Thus, a possible effect of more distractors may have been balanced by an increased target saliency.

If the search required a serial analysis of each element, the performance should drop with each four-fold increase of the number of line elements (see Figure 4, Experiment I). Because performance did not decrease, the search must have been facilitated by other factors. Probably, the increased overlap with neighboring lines with higher density made the target line more visible or pop-out. Also, increased density may have helped to recognize the pattern of lines against which to compare the target line.

Whereas we find no effect on the mean rate, we do find an increased performance and reduced number of saccades with higher density. This joint result is consistent
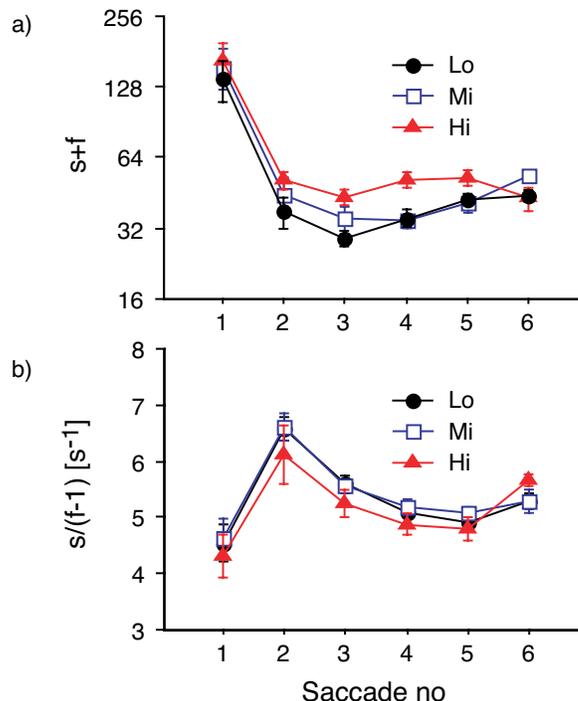

Figure 5. Beta-prime parameters for Experiment I as function of ordinal position in the saccade sequence, split by density condition. Values represent averages (±*SE*) over subjects. a. Sum of thresholds. b. Ratio of thresholds (i.e., mean rate).

with a proposal by Hooge and Erkelens (1999) that it is only the foveal task, not the peripheral task, that determines the fixation duration, whereas the peripheral task may influence the number of saccades. In our case, a facilitated peripheral task (more pop-out as hinted by the better performance) would make it more likely that the next saccade occurs in the appropriate direction, hence explaining the reduced number of saccades.

The decreased mean rate (i.e., increased latency) of the first saccade is also commonly observed (e.g., van Loon et al., 2003). Novel, however, is that the second saccade has a significantly faster rate or shorter latency than subsequent saccades. A possible explanation may be that the second saccade has been planned while the first was still underway (McPeek, Skavenski, & Nakayama, 2000).

Despite the effect of density, rate distributions for second and later saccades were still far more skewed than for first saccades. In the next two experiments, we investigated whether we could also manipulate the skew of the rate distribution for the first saccade.

Experiment II: Foveal target probability

The decision-rate distribution for first saccades so far seems indiscernible from a Gaussian distribution as predicted by single-threshold models (Reddi & Carpenter,

2000). This would suggest that the timing of the first saccade does not involve a competition. In the foregoing experiments, the target never appeared at the screen center so that subjects never expected to hold fixation. Could this low expectation of foveal targets explain the steady Gaussian shape of rate distribution found for first saccades?

Here we sought to increase the competition between fixation and saccade signals in the first saccade by including foveal targets. Specifically, we asked whether increased expectation of a foveal target leads to a more skewed rate distribution for first saccades.

Procedure

We used the middle stimulus density condition of Experiment I. As the search display came on, the fixation dot was replaced by a line that was either part of the radial pattern, or was the target with a deviating orientation. In a first block, foveal targets were presented in a quarter of the trials ($p = .25$). The probability for a target at 6, 12, and 18-deg eccentricity thus was 25% each. In a second block, foveal targets were presented in half of the trials ($p = .5$). In that case, the probability of a target at eccentricities 6, 12, or 18 deg was 16.7% each. A block was completed in sessions of 240 trials to obtain a minimum of 480 trials per subject.

Results

Trials with eccentric targets showed no significant effect of foveal target probability on the mean performance across five subjects ($F_{1,28} = 1.0$, $p = .3$) (see Figure 4). Also, the mean sequence length was constant (3.5 saccades) in both conditions ($F_{2,4300} = 3.0$, $p = .4$). The potential appearance of a foveal target did have an effect. The performance with 50% foveal targets was significantly lower than the middle density condition of Experiment I ($F_{1,16} = 10$, $p = .006$ across three subjects). Remarkably, when the target was presented centrally, subjects often did make a saccade sequence (in 92 and 83% of the trials with 25 and 50% foveal targets, respectively, averaged over subjects). The sequence length in that case clearly decreased with higher foveal target probability (3.7 and 2.8 saccades, respectively). For these central targets, the performance was 0.7 and did not change significantly with higher foveal target probability ($F_{1,8} = 1.3$, $p = .3$).

We first analyzed the rate distribution based on trials with eccentric targets only. Across subjects no systematic effect of foveal target probability was observed on the threshold sum or ratio (Figure 6a and 6b, eccentric targets), neither for first nor later saccades. For centrally presented targets, the rate distribution for first saccades (that were erroneously initiated) revealed a sum of thresholds that was somewhat lower than for eccentric targets, but the difference was not significant ($p = .09$; two-tailed t test). Also, compared to Experiment I (Mi density condition, three subjects) no significant difference was found between the sum or ratio of thresholds, neither for first saccades

nor for later saccades ($F_{2,6} = 0.17$, $p = .8$ and $p = .6$, respectively) nor for later saccades ($F_{2,38} = 0.6$, $p = .5$ and $p = .9$, respectively).

Discussion

Performance was not affected by manipulation of the probability of a target at foveal and peripheral locations. Subjects reported they often could not withhold a saccade even if they noticed that the target had appeared at the fixation point. Perhaps, the presence of a fixation point immediately before target appearance may have masked the detection of the foveal target somewhat. But, higher probability of target appearance at the screen center did raise the subject's success to withhold the saccade by about 10% and also reduced the mean sequence length for central target trials with about one saccade. Therefore, subjects had ample information to alter their expectancy of target probability at the center and eccentric. Despite all this, no consistent effects were found on the shape of rate-distributions (sum of thresholds) or mean rate (i.e., ratio of thresholds) of first or later saccades.

We expected an effect on the mean rate of the target probability distribution given previous reported effects of target probability on latency. Kowler et al. (1984) found that expectations based on sequential steps in prior trials played a role in anticipatory eye movements, but also saccades. He and Kowler (1989) found a small decrease in latency (10 ms) for saccades toward the location with highest
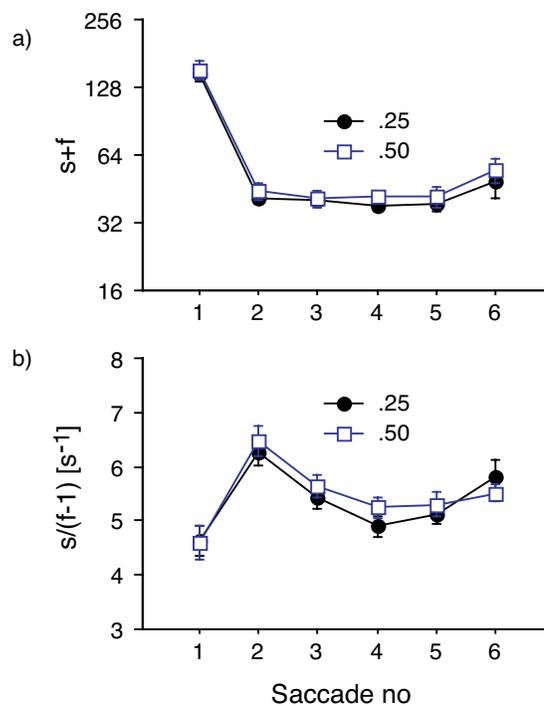

Figure 6. Beta-prime parameters for Experiment II as function of saccade number (eccentric targets only), split by foveal target probabilities conditions. Values represent averages (±*SE*) over subjects. The sum of the fixation and saccade threshold (a) and their ratio (b).

probability of target appearance. Also Carpenter & Williams ([1995](#)) found that in trials with two possible eccentric target locations, the mean fixation duration decreased for the location with highest probability. Moreover, they found that the Gaussian width of the decision-rate distribution changed in accordance with a change in start or threshold value. In those studies, however, the targets were always located eccentrically, whereas in our experiment the targets could also appear at the fixation point. Our paradigm with a competing target at the fixation point may have had more similarity with so-called countermanding tasks in which shortly following presentation of a peripheral target, a central stop signal is presented (Asrress & Carpenter, [2001](#)). In trials where a stop signal was presented, the latency was typically 10 ms or so longer than in control trials without stop signal. We, however, find no significant difference for the mean rate between central and eccentric target trials.

In [Experiment I](#), the fixation marker remained visible during the presentation of the target, whereas in [Experiment II](#), the fixation point was replaced by a line element. Generally, the removal of the fixation point prior to target presentation is expected to reduce saccadic latencies by tens of ms, as modeled by Clark ([1999](#)). However, when comparing [Experiment I](#) (Mi density) with [Experiment II](#), neither for first nor for later saccades did we find any significant changes in the reciprocal latency distribution (decision-rate threshold ratio or sum). This suggests the fixation point and line element are about equally salient.

We found no influence of probability of foveal target appearance on the timing of saccades, and no differences between central or peripheral targets. A possible difference with our study is that those studies concern tasks where only a single saccade is made. For instance, in the countermanding paradigm, the fraction of successfully withheld saccades is much higher than in our experiments. In our experiment, subjects rarely held fixation when the target was presented centrally. We do find a variation in the mean sequence length and number of saccades, suggesting subjects do take probability into account. Subjects frequently made saccades when the target appeared at the fixation point. This may be part of a certain strategy. One subject, for instance, reported to find it more difficult to judge the relative orientation for lines at the fovea, and to facilitate her judgment by making a saccade toward a more eccentric position. Other subjects reported to follow a strategy to initially saccade away from the radiant towards an area where the lines were longest and thus most visible.

Experiment III: Visual/motor history

The shape of the rate distribution of first saccades remains symmetric despite considerable changes in density or the probability of target appearance at the fovea. Why is its shape so constant and different from the rate distribution

found for all subsequent saccades? Later saccades differ from first because prior to the first saccade, no visual analysis and saccadic activity has taken place. Hence, we investigated whether the rate distribution of the first search saccade would skew as in later saccade distributions when (1) the subject has already made a saccade before the search, or (2) when the locations of the lines are visible before the saccadic search starts.

Procedure

The stimulus was similar to that in [Experiment I](#), middle density stimulus, but it was preceded by a pre-search display with the same number of lines. The pre-search display switched to the search display by having one of its lines deviate in orientation to become the target. The fixation point disappeared at the onset of the search display, like in [Experiment II](#). Motion pop-out of the target line was masked by simultaneously changing the orientations of the other lines through a 90-deg shift of the radiant in counterclockwise direction with respect to the center of the screen ([Figure 7](#)). This global change of the local line orientations also served as a cue for the subject to start searching.

The pre-search information on the scene layout (the positions of lines) was varied by having all lines refresh their positions during the switch of the radiant or not. The pre-search saccadic activity was varied by having subjects make saccades or maintain fixation during the pre-search display. The two manipulations amounted to four conditions for the pre-search period with each condition pre-
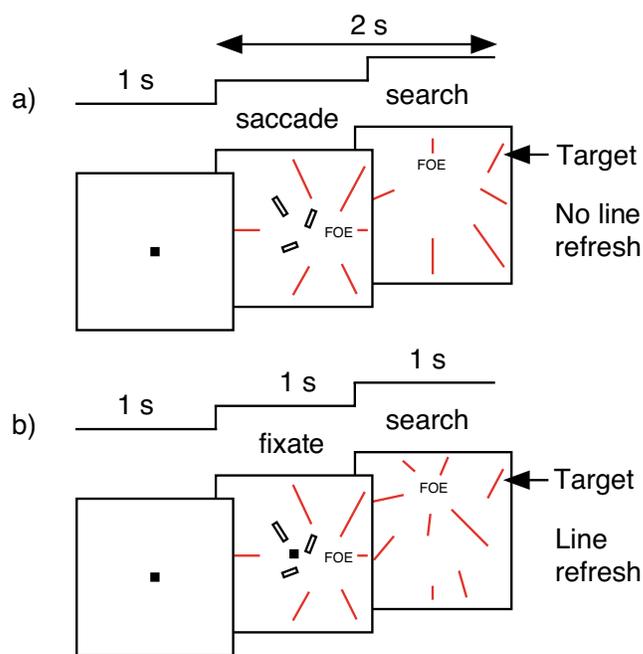

Figure 7. Two stimulus conditions from [Experiment III](#). Prior to the search display, subjects either saccade on centrally positioned lines (upper panel) or fixate a central marker (lower panel). The search display is preceded by lines with the same (upper panel) or refreshed positions (lower panel).

sented in a block of 360 trials and the order of the blocks balanced across subjects.

The switch to the search display occurred after 1-s pre-search display. In the fixation conditions, the subject had to maintain fixation during the pre-search display. In the saccade conditions during the pre-search display, the subject was to saccade at his own pace between three lines that were colored white to make them pop out. These white lines were close (within 10 deg) to the fixation point, so that at the onset of the search display the eye had not strayed far from the screen's center as in the fixation condition. In the saccade conditions, the switch to the search display was triggered on the first saccade following the end of the 1-s pre-search display. Because trial duration was fixed at 3 s, the presentation time of the search display was 1 s in the fixation conditions, and somewhat less than 1 s in the saccade conditions.

Results

We found that the execution of saccades prior to the start of search (about 2.5 on average) significantly reduced the mean performance compared to fixation conditions ($F_{1,58}$ = 29, p < .001 across five subjects (see Figure 4). Subjects reported that the saccadic task during the pre-search display hampered subsequent search more than the fixation task. No effect of refreshing the line positions was evident. Moreover, whether a line display or just a fixation point was presented prior to the search display did not significantly alter performance ($F_{2,6}$ = 1.2, p =.36, comparison of the two fixation conditions of Experiment II with the middle density condition of Experiment I across three subjects). The mean sequence length for the fixation conditions (2.2 saccades) was about a saccade shorter than in Experiments I and II, probably as a result of the reduced search time. Moreover, the sequence was significantly shorter for the saccade conditions (2.0 saccades) ($F_{1,7174}$ 0, < 001). Furthermore, a small increase in sequence length was found when refreshing lines, but only in the fixation condition.

The rate distributions of the first saccade during the search task show that the refresh of line locations did not significantly influence the sum of thresholds of the first search saccade ($F_{1,16}$ = 0.34, p = .57, data pooled over saccade conditions). In contrast, making pre-search saccades significantly decreased the threshold sum for first saccades (Figure 8a, $F_{1,16}$ = 4.68, p = .046, data pooled over refresh conditions). Closer examination (Figure 9a) showed that this effect was caused by two subjects (EP and JB). The other three subjects showed no effect. Experimental conditions did not systematically influence the sum of thresholds in later saccades (Figure 8a), or the ratio of thresholds in first and later saccades (Figure 8b).

We found that saccadic displacements during pre-search altered the rate distribution of the first saccade during the search period for some subjects. How different

is the first search saccade from the first saccade to a pop-out target? For this, we looked at the rate distribution of the first pre-search saccade (Figure 9a, III*), in which case subjects had only to saccade toward one of three nearby white lines. The sum of thresholds did not differ from those of the first search saccade in Experiment I (Mi density) ($F_{1,7}$ = .21, p = .7, data from three subjects). Thus, the timing of the first saccade did not depend on the search task.

Discussion

Our results show that prior visual information on the global scene layout does not change the shape of the distribution of the first search saccade (i.e., the threshold sum is constant). Perhaps, the effect of knowing the line positions a priori was reduced by the simultaneous global orientation change in all lines, which we applied to prevent motion pop-out of the target stimulus. This would also explain the lack of an influence of refreshing position on the performance, although performance and the rate distribution of first saccades need not be directly correlated. But, Figure 9a also allows us to look at the effect of just the sudden onset of a visual display (which does not happen for later saccades) by comparing a condition with sudden onset
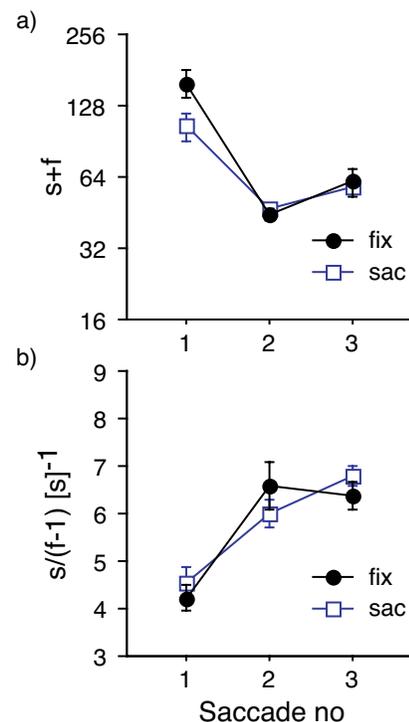

Figure 8. Beta-prime parameters for Experiment III as function of saccade number, split by the subject's task during the pre-search display (saccadic steps or fixation). Values represent the mean (±*SE*) of five subjects, pooled over lines-refresh and no-refresh conditions. The sum of the fixation and saccade threshold (a) and their ratio (b).
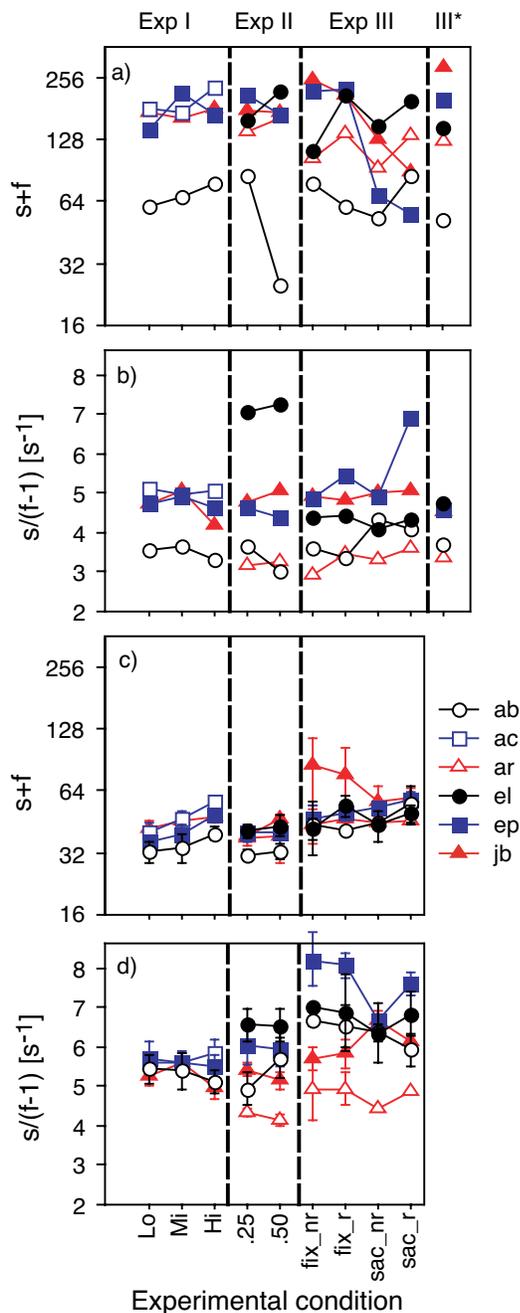
Figure 9. Threshold data from Experiments I-III as function of experimental condition, split by subject. The sum of the fixation and saccade thresholds *(s+f)* and their ratio *(s/f–1)* for the first saccade (a and b) or averaged over later saccades (c and d). An additional column (III*) in a and b shows thresholds of the first saccade of the saccade sequence preceding the search display (data pooled over lines-refresh and no-refresh conditions).

of the line display (Experiment I, Mi density) with a condition where a line display was already present (Experiment III, fixate/refresh condition). Here as well, we find no difference in the sum of thresholds ($F_{1,4}$ = 493, p = .8, data from three subjects). Thus, both findings

suggest that the prior visual history has no influence on first saccade rate distribution.

Two of five subjects showed a clear change in the decision-rate distribution (lowering of thresholds) when making saccades prior to the search. These two subjects (EP and JB) also showed highest performance for that task (see Figure 4). In general, however, we find little evidence for a correlation between the sum of thresholds and performance. For instance, a clear drop in performance is observed for all subjects when making pre-search saccades compared to pre-search fixation ($F_{1,58}$ = 29, p < .001, data from five subjects, pooled over target eccentricities and refresh conditions).

A likely explanation for this performance drop is the reduced available search time. In the saccade conditions the target appeared somewhat later than in the fixation conditions, as it was displayed at the onset of the first saccade following the 1-s pre-search. Indeed, the mean sequence length in the saccade conditions was about 0.2 saccade smaller than in the fixation conditions. Also, the first search saccade in the saccade condition may already have been programmed, in which case subjects had one saccade less to home in on the target. Indeed, the mean performance over the fixation conditions in Experiment III reveals a consistent drop in performance compared to Experiment I (Mi density, $F_{1,2five}$ = 4.7, p = .04, data from three subjects pooled over target eccentricities).

General discussion

Summary

We manipulated the stimulus density, probability of the target's appearance at the fixation point, and the visual and motor history preceding a search saccade to look for changes in the distribution of the reciprocal fixation duration (i.e., decision-rate distribution). Our main goal was to investigate whether the decision-rate distributions for all saccades that occur during visual search can be framed by a two-parameter function that has a physiological interpretation.

We found that for each subject, condition, and ordinal position in the saccade sequence, the decision-rate distribution is well described by a Beta-prime function. Beta-prime distributed decision-rates are predicted by a parsimonious model of reaction times based on the thresholds set for two accumulators (one for maintaining fixation, the other for initiating a saccade) that compete over a single stream of visual activity (as described elsewhere in detail [Van den Berg & Van Loon, in press] and briefly here in the Introduction). In the following, we discuss the results in terms of such thresholds.

Variation of thresholds for later saccades

In Experiment I, we found that the rate distribution of second and later saccades tended to be more symmetric with increased stimulus density, while the mean rate remained constant. In terms of a competition between fixation and saccade signals, the increased stimulus density led to higher saccade and fixation thresholds s and f, while their ratio remained constant. How might we interpret these effects in terms of a competition between fixation and saccade signals?

Saccade and fixation-related neurons differ in their retinotopic organization. Whereas saccade-related burst and build-up neurons of the SC encode the direction of a saccade by a retinotopic map, fixation cells in the SC lie in the rostral pole of the SC, corresponding to only the retinal locations around the fovea (Munoz & Wurtz, 1993). The FEF also has a retinotopic map for saccade-related neurons and physiological correlate of fixation neurons (Dias & Bruce, 1994). More visual stimulation by increased stimulus density might bring the fixation and saccade neurons closer to their threshold. Possibly, the saccadic system raises both fixation and saccade thresholds to avoid saccade initiation by noise.

Invariant thresholds for first saccades

In Experiment II, we expected that increased probability of a target at the fixation point would increase the competition between fixation and saccade signals, causing the rate distribution of the first saccade to become less Gaussian. A Gaussian-shaped rate distribution can be modeled well by a race-to-threshold model with only a single saccade threshold (Carpenter & Williams, 1995). In terms of our proposed scheme of competing signals, the fixation threshold is set so high for the first saccade that it would never be reached. But, we found that with increased probability of a foveal target, subjects still did not lower their fixation threshold for the first saccade.

We expect thresholds to influence not only the timing of saccades but also the probability toward one or the other decision. Because in Experiments I and III a saccade was always to be made, the choice for the alternative decision could not be measured. In contrast, Experiment II does allow us to look at the fraction of decisions to hold fixation when central targets were presented. It is reassuring that we find a nearly constant fraction of failed fixations (about 90%), as this is consistent with our finding of constant thresholds based on the rate distribution of first saccades.

The lack of an effect of target probability on thresholds seems to contrast with reported effects on saccade-related activities in SC. Build-up neurons typically show an early rise in activity that diminishes before the saccadic eye movement. As the likelihood of a saccade being made into its response field increases, the neuron's base-line activity rises while the saccade latency is shortened (Basso & Wurtz, 1998; Dorris & Munoz, 1998). However, in these electrophysiological studies, targets were always presented

eccentrically and only single saccades were made. Perhaps, if we had urged our subjects to make as few saccades as possible, the effect of foveal probability may have become visible.

Influence of preceding visual and saccadic activity on thresholds for first saccade

In a second attempt to influence first saccade rate distributions (Experiment III), we found that the threshold for the first search saccade was lowered after an initial saccade. A possible interpretation might be that in the fixation and/or saccade neurons some residual activity remains after the initial saccade, such that the threshold is reached earlier. Indeed, it has recently been shown that for short saccadic intervals, a second peak of activity can reside in the collicular motor map (McPeek & Keller, 2002). In this manner, pre-selection or preparatory activity may bring the second saccade closer to threshold.

However, looking at individual data, we found that making pre-search saccades lowered the thresholds to the level of later search saccade, and no intermediate levels (compare saccade conditions Figure 9a and 9c for subjects JB and EP). Munoz and Wurtz (1993) showed that during fixations between spontaneous saccades preceding the presentation of a fixation target, fixation cells are sporadically active, suggesting they might play a role only in active fixation. Our data could support a theory of disengagement of ocular fixation (Munoz & Wurtz, 1992) stating that fixation cells play no more role in the timing of saccades during search. We would like to consider an alternative view, though, on the basis of the skewed probability distributions. Once the state of fixation is released and subjects start searching, the base activity of the fixation cells is decreased and their threshold lowered. Only subtle variations in the initial fixation threshold or baseline activity can then be achieved that have not yet been measured.

Independent thresholds

Do we find evidence for two independent thresholds? From earlier work (Van Loon et al., 2002), we already knew that the mean rate (ratio of thresholds) was lower for the first saccade than for later saccades, whereas the skew (inversely proportional to sum of thresholds) was increased for later saccades. In this work, we show that the mean rate (ratio of thresholds) is not influenced by target probability, density, or visual history, but behaves very stereotyped as a function of ordinal saccade number. However, the sum of thresholds can indeed be manipulated for later saccades. Thus, at least for later saccades, we find evidence for two independent thresholds.

Alternative models

An alternative explanation for the different rate distributions for first and later saccades could be a difference in the predictability of stimulus timing. The latency of the first

saccade depends on the time of stimulus onset, a more or less unpredictable event. After the first saccade, the saccade latencies (or fixation durations to be more precise) are self-generated. One might therefore argue that the more pre-dictable stimulus timing evokes more anticipatory saccades with short latencies, hence explaining the larger tail at high rates in the distribution for second and later saccades. It is of course questionable whether the small number of short latency observations in the data allows discerning a sub-population of anticipatory responses. Such bimodal popu-lations could be modeled by two loosely coupled saccadic decision units working in parallel (see Reddi, Asrress, & Carpenter, 2003). But, such a two-stage process model would be less efficient in terms of parameters than the Beta-prime distribution, and would not allow the saccade se-quence to stop.

Alternative models that as in our Beta-prime model take two competing signals are so-called dual-race models, with stop and go signals that race toward their threshold independently (e.g., Hanes & Carpenter, 1999). We should, however, point out that these models have not been designed to describe competition for later saccades under more natural conditions of search, but only for sin-gle saccades in countermanding tasks. However, much as the independence of stop and go signals may seem attrac-tive, it seems highly unlikely that the decision to stop, based on foveal information, is made independent of peripheral information that would urge the machinery to continue making saccades. Recently, the idea that stop and go signals would rise independently has been challenged in counter-manding experiments (Ozyurt, Colonius, & Arndt, 2003). Furthermore, such models based on the superposition of two Gaussians with different shape theoretically allow nega-tive latencies to occur, and probably will not fit very short saccade latencies for very short delays between the go and stop signals (Van Loon et al., 2002).

There is physiological support for a competition be-tween saccade and fixation-related signals. The superior colliculus contains fixation cells, which, only when sup-pressed, allow a saccadic eye movement to be made toward the location encoded by the bursting saccade neuron. Fur-thermore, connections have been established, possibly ena-bling competition between colliculus and FEF. For in-stance, similarity in the time course of the gap effect found for fixation neurons in the colliculus and electrically evoked saccades in FEF suggests collicular input to FEF (Opris, Barborica, & Ferrera, 2001). But, also in FEF, physiological correlates of fixation neurons have been found (Dias & Bruce, 1994), allowing for a competition within FEF.

Conclusions

In visual search tasks, we find a uniform description of the distribution of reciprocal fixation durations for first and later saccades is best given by a Beta-prime function,

rather than by a Gamma or Gauss. This supports a strong competition process between two decision signals that is governed by two decision-rate thresholds. The distributions for second and later saccades skewed less with denser displays, which corresponds to an increase in both thresholds. The more symmetrical distribution for first saccades is less manipulable. For these, the sum of thresholds did not vary with display density or higher probability of targets at the fovea, but did lower when the first search saccade was preceded by a saccade. In all experimental conditions, the mean rate, corresponding to the ratio of thresholds remained a stereotyped function of ordinal saccade number.

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