

The timing of sequences of saccades in visual search

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According to the LATER model (linear approach to thresholds with ergodic rate), the latency of a single saccade in response to target appearance can be understood as a decision process, which is subject to (i) variations in the rate of (visual) information processing; and (ii) the threshold for the decision. We tested whether the LATER model can also be applied to the sequences of saccades in a multiple fixation search, during which latencies of second and subsequent saccades are typically shorter than that of the initial saccade. We found that the distributions of the reciprocal latencies for later saccades, unlike those of the first saccade, are highly asymmetrical, much like a gamma distribution. This suggests that the normal distribution of the rate r , which the LATER model assumes, is not appropriate to describe the rate distributions of subsequent saccades in a scanning sequence. By contrast, the gamma distribution is also appropriate to describe the distribution of reciprocal latencies for the first saccade. The change of the gamma distribution parameters as a function of the ordinal number of the saccade suggests a lowering of the threshold for second and later saccades, as well as a reduction in the number of target elements analysed.

Keywords: saccadic latency; visual search; latency distribution; saccadic threshold

1. TIMING CONTROL OF SEQUENCES OF SACCADES IN VISUAL SEARCH

One usually finds a face in a crowd or a book on a shelf by looking for it. This search elicits a scanning pattern of saccadic eye movements, alternating with fixation periods during which the eyes remain relatively still. The fixation period serves to analyse the foveal target (possibly terminating the search process) while the preparation of the next saccade is running concurrently (on the basis of non-foveal information). Fixation times have been shown to vary as a function of task (e.g. reading, visual search, scene perception, music reading, or typing; see the review in Rayner (1998)) and task difficulty (Hooge & Erkelens 1996, 1998; Zelinsky & Sheinberg 1997). Furthermore, the latency of the initial saccade in a series has been found to be longer than that of subsequent saccades (Hooge & Erkelens 1996; Hooge *et al.* 1999) and latencies as brief as 10–100 ms have been reported for second saccades (McPeck *et al.* 2000), which suggests that the second saccade may have been programmed concurrently with the first saccade. The dependency of the latency of the first saccade on sequence length (Zingale & Kowler 1987) is further evidence for the continuation of the saccade program across a saccade.

The scanning pattern of saccadic eye movements in visual search can be understood as a series of decision processes; for each saccade a decision has to be made regarding when, and where, to look next in the visual scene. Different processes seem to underlie these two types of decisions (Findlay & Walker 1999; Glimcher 2001). The decision, where to look, appears to be based on the saliency of the items in the visual field (e.g. Itti &

Koch 2000), whereas the timing of saccade initiation seems to be dependent on the suppression of activity in the fixation zone of the superior colliculus (SC; Munoz & Wurtz 1993*a,b*). Various attempts have been made to model the duration and variability of *single* saccadic latencies based on decision processes (Carpenter & Williams 1995; Reddi & Carpenter 2000), but can these types of models also be applied to a sequence of saccadic latencies, when concurrent processing of saccades occurs? The authors attempt to attain more insight into the temporal aspects of sequences of saccades in visual search and try to explain these in terms of serial and parallel decision processes.

Reddi & Carpenter (2000) introduced the LATER model (linear approach to thresholds with ergodic rate), which postulates that, upon presentation of a stimulus, a decision signal rises linearly from an initial level S_0 (which depends on prior knowledge) at a rate r (that depends on stimulus processing and which is assumed to be normally distributed). When S reaches the threshold level S_t (which depends on the eagerness to respond), the saccade is triggered (figure 1*a*). This model implies that the reciprocal latency of a saccade should follow a normal distribution, which is scaled by the threshold level. Changes in either the mean of the rate distribution, or the threshold level, each predict specific shifts in the cumulative distribution of reciprocal saccadic latencies when plotted on a probit scale (figure 1*b*; Reddi & Carpenter 2000).

Carpenter and colleagues (Carpenter & Williams 1995; Reddi & Carpenter 2000) showed, in line with the LATER model, that altered expectations (modifying S_0) and urgency instructions (modifying S_t) have equivalent scaling effects on the distribution of reciprocal saccadic latencies to the appearance of a cued *single* target. The model is supported by physiological recordings in both the SC and the frontal eye fields (FEF), two structures that play an important role in the generation of eye move-

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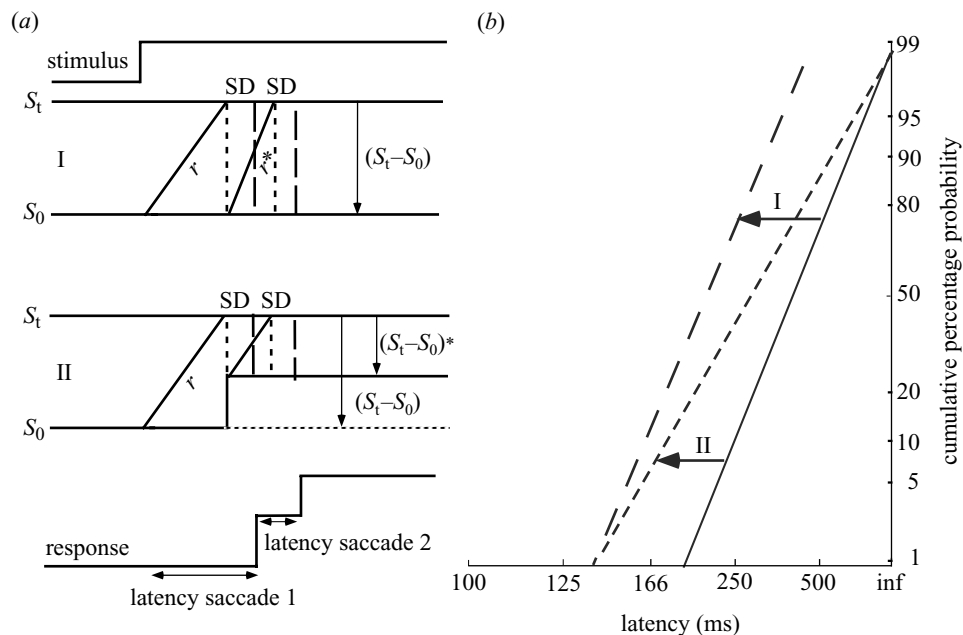


Figure 1. (a) An adaptation of the LATER model (Reddi & Carpenter 2000) to account for multiple saccades. When a stimulus is presented, a decision signal S rises linearly from an initial level S_0 at a rate r . That rate is assumed to be Gaussian distributed in the LATER model. Once S reaches the threshold level S_t , the first saccade is initiated and executed after a dead time (SD) of *ca.* 70 ms. The exact onset of the rise of the decision signal for the second saccade (S^*) is unclear. It may start as soon as the decision signal for the first saccade begins to rise, resulting in an interval of concurrent processing. Alternatively, it may start when the threshold for the first saccade is reached, i.e. at the onset of SD. Shorter latencies for the second saccade may occur when the rate of rise of the decision signal for the second saccade (r^*) is higher than that for the first saccade (I), or when the threshold level to be reached ($(S_t - S_0)^*$) is lowered (II). (b) A change in the mean rate of rise r , without a change in threshold, predicts a parallel shift of the cumulative reciprocal latencies on a probit scale (I), whereas a pure lowering of the threshold rise ($S_t - S_0$) predicts a change in the slope of the curve (II).

ments. It has been found that the activity of visuomotor neurons in the FEF rises linearly upon presentation of a target stimulus and that this rate of rise shows variability from trial to trial (Hanes & Schall 1996). Once the activity reaches a threshold, a saccade is generated. A physiological correlate for varying baseline levels of build-up neuron activity has been observed in the SC (Dorris & Munoz 1998). Changes in the mean rate of rise with the amount of information provided have also been demonstrated (e.g. Kim & Shadlen 1999). Furthermore, the LATER model has been successful in predicting saccadic behaviour in a countermanding paradigm (Hanes & Carpenter 1999). More recently, the model has been extended to the latencies of single saccades to a *choice* of (two) targets, to simulate the competing stimuli encountered in the real world (Leach & Carpenter 2001), providing more evidence that LATER can successfully describe the latencies of single saccades in a wide range of conditions. However, when looking for an object in the real world, targets are hardly ever captured by a single saccade. Therefore, it would be useful to test whether the model can also be applied to more than one saccade.

The application of the LATER model to sequences of saccades is not straightforward. The first complication arises from the notion of the saccadic dead time: the period before the onset of a saccade during which the saccade can no longer be inhibited or altered. It is known that saccade initiation typically occurs after 30 ms upon SC stimulation (Robinson 1972; Sparks *et al.* 2000). Based on behavioural data, however, the saccadic dead time is estimated to be slightly longer. Hooge *et al.* (1996)

required subjects to follow an object (a 'C') that jumped between the corners of a square. Occasionally, the 'C' changed into an 'O', after which the subjects had to stop tracking the object. By varying the 'jump' frequency of the object, the authors were able to determine the time-period during which an intended saccade could not be inhibited. This resulted in an estimated dead time of *ca.* 70 ms. By implication, processing rates are related to the reciprocal of saccade intervals diminished by 70 ms. This estimate exceeds the lag between SC activation and saccade initiation, which may imply that the SC is downstream of the point where the decision to cancel or alter saccades is taken.

Another complication is that the onset of the processing of information for the second, and later, saccades is not self-evident. In a search task for the heading direction in visual flow (Hooge *et al.* 1999), it was found that the saccade endpoint error diminished over time very similarly, whether one or two saccades were made during the interval from stimulus onset. However, the error reduction during the second interval was much higher. This suggests that visual processing for the second saccade was initiated during the fixation interval that precedes the first saccade. Given these notions of a saccadic dead time and a potential interval of concurrent processing, the question arises of whether slow first and fast later saccades during search follow the same distribution of reciprocal latencies while only the threshold level differs. Alternatively, both the processing rate distribution and the threshold may differ for subsequent saccades in a search task.

The same approach to analyse saccadic latency data can

be used to investigate the underlying causes for the observed differences in saccadic latencies among search tasks of various difficulty, in other words, to unravel whether this variation is due to different rate distributions and/or different threshold levels. Therefore, sequences of saccades were analysed from two different search tasks that were employed in a study investigating the differences in visual search strategies in moving and stationary radial patterns (described in Van Loon *et al.* 2002). The first search task corresponded to the detection of moving objects in sparse environments during simulated self-motion. It consisted of finding a target element with a deviating direction of motion in the expanding pattern of moving dots in a simulated self-motion display. The second search task was a matched static version of the first task, in which the display consisted of a radial pattern of lines and the target element was a line with a deviating orientation in relation to the rest of the pattern.

Our analysis shows that systematic changes occur in the threshold and the rate distribution, suggesting that activity related to a saccade to a second or later goal is started during the preceding fixation interval.

2. MATERIAL AND METHODS

Four subjects (the three authors EL, AB and IH and one naive subject, MC) with a mean age of 32.8 yr (s.d. \pm 7.8) participated. All subjects were experienced in wearing scleral coils for eye-movement recording.

(a) Visual stimuli

Displays were generated by an Apple G3 computer and comprised a pattern of radial motion or lines (figure 2). Stimuli were back-projected by a Sony VPH 1270 QM projection television (frame rate, 75 Hz; display rate, 47 Hz) on a translucent screen (distance, 2.0 m; 63° horizontally \times 47° vertically; 1024×768 pixels) in a completely darkened room. To prevent head movements, a bite board was used. Subjects looked binocularly. In the motion-direction task, a perspective projection of a moving box filled with dots was presented. The simulated box (simulated size $h \times w \times d$: $10.14 \times 13.51 \times 19.00$ m) contained 120 red dots. On average, $39 (\pm 7)$ dots were visible on the screen. Each dot had a diameter of 0.2° and did not scale with simulated distance. The distance between the observer and the front of the simulated box was 7 m at stimulus onset. To simulate observer motion, all dots were displaced within the box at a speed of 8 ms^{-1} . This resulted in a radial pattern of projected motion on the screen. Its centre corresponded to the direction of simulated observer motion. This simulated heading direction was randomly varied (the centre of the radial pattern was at a random position in an area of $30 \times 30^\circ$ around the fixation point).

Viewing time was 1.5 s. In order to prevent the target element from disappearing from the screen before the end of this viewing period, a 362 ms motion was repeatedly shown during these 1.5 s. Thus, each dot moved along a linear trajectory away from the centre for 362 ms and was subsequently stepped back to its starting position. This occurred for more than four cycles, until the motion stopped. The resets of different dots' positions were asynchronous. The elements in the static display were matched with those in the radial-motion display, in that line length was equal to dot trajectory length. Target elements were presented at random locations concentric with the fixation point at eccen-

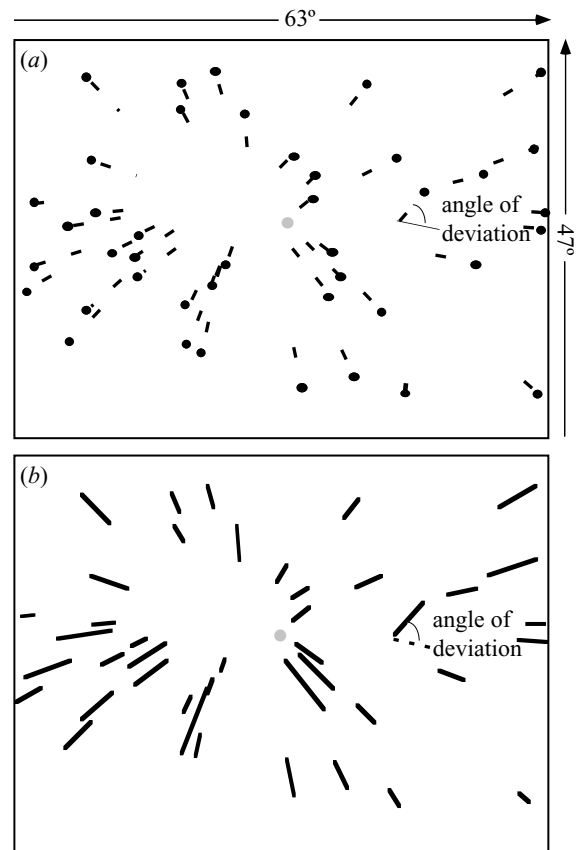


Figure 2. The displays for the (a) motion direction and (b) line orientation search tasks. In reality, red elements were projected onto a black screen. The stimulus elements are not drawn to scale.

tricties of 2, 6, 10, 14, 18 and 22° . To match the difficulty of the task in each display for each eccentricity and for each subject, individual threshold levels (as determined in a psychophysical pilot study) were taken as the amount of deviation in orientation/motion direction of the target. The threshold levels were the angles of deviation in the orientation/motion direction relative to the rest of the radial pattern (see figure 2) that were required in order to detect the target in 75% of the cases using a two-alternative forced choice procedure.

(b) Data collection

Horizontal and vertical movements of the left eye were measured with an induction coil mounted in a scleral annulus in an a.c. magnetic field (Robinson (1994); Skalar eye position meter 3020, Delft, The Netherlands). Signals were sampled at 500 Hz with a National Instruments 16-bit PCI-MIO-XE50 analogue-to-digital converter and fed through a low-pass analogue filter with a cut-off frequency of 62 Hz. Data were stored and analysed offline. A computer program determined saccade onset and offset using a velocity threshold ($20.0^\circ \text{ s}^{-1}$) and a criterion of a minimum fixation duration of 30 ms, to prevent the incorrect identification of very short saccadic latencies as an artefact of the procedure. Visual inspection of the records confirmed that this optimized saccade detection. Each subject performed 360 trials in both search tasks. To increase the number of saccades for our analysis, additional datasets were collected in the line-orientation search task for subjects AB (1849 trials), EL (2150 trials) and MC (1964 trials).

(c) Task

Before the start of each trial, the subject was required to fixate a 0.3° dot in the centre of the screen. Upon presentation of the display, the subject was to find and fixate the target element that deviated from the rest of the expanding pattern.

(d) Data analysis

A MATHEMATICA program (Wolfram) used the Marquardt–Levenberg method to find the best-fitting normal distribution fits (mean, μ ; s.d., σ) for both the uncorrected and corrected (for saccadic dead time and an interval of concurrent processing) first and second saccade data. A constant value of 70 ms was taken for the saccadic dead time.

To analyse the possible effect of concurrent preparation of two saccades during a search, a concurrent processing interval was introduced by extending the observed fixation interval before the saccade. That extension thus reaches into the interval prior to the previous saccade. It was varied from 50 to 550 ms in steps of 50 ms.

The cut-off points for inclusion in the analysis were determined by visual inspection of the frequency plots of the reciprocal latencies, by estimating the boundary of the symmetrical portion of the curves (see figure 3*a,b*). A cut-off point of 200 ms was used for the first saccades and one of 100 ms for the second saccades. Based on the estimated parameters, the μ/σ ratios for both the first and second saccade were calculated. A similar procedure was followed to carry out fits with the gamma distribution (see below).

3. RESULTS**(a) Search performance, number of saccades and saccadic latency**

Search performance averaged across subjects was better for the static than for the motion display, but an ANOVA showed no significant difference between the performance of the two tasks ($F(1,3) = 3.47$, $p = 0.16$). In the line-orientation task, on average 55% ($\pm 7\%$) of the targets were found and 40% ($\pm 5\%$) of the targets were found in the motion-direction task.¹ On average, 3.5 (± 0.4) saccades were made in the line-orientation task and 2.0 (± 0.1) in the motion-direction task. For each dataset, this resulted, on average, in 329 second and 223 third saccades for analysis in the line-orientation task and 207 second and 67 third saccades in the motion-direction task. Saccadic latencies were shorter in the line-orientation task than in the motion-direction task and longer for the initial saccade than for the second and third saccades. The mean latencies of the first three saccades, averaged across subjects, were 398 (± 59), 245 (± 29) and 270 (± 15) ms in the line-orientation task and 650 (± 109), 378 (± 58) and 307 (± 55) ms in the motion-direction task, respectively.

(b) Effect of saccade number and search task

The raw distributions of the uncorrected reciprocal latencies of the first and second saccades are shown in figure 3*a,b*, respectively (the distributions of the third saccades are not shown here, but they are similar to the distributions of the second saccades). When plotting the same two distributions on a probit scale (figure 3*c*), a difference was found in the slope for the initial and second saccade, suggesting a difference in the threshold level S_t . The change in slope is observed for both the motion-direction

and line-orientation search tasks. However, the two tasks can be distinguished by a parallel shift of the curves for the respective saccades, corresponding to a difference in the mean processing rate r of *ca.* 1.5 s^{-1} .

(c) Further analyses of the curves

To find out whether there is solely a difference in threshold level between the first and subsequent saccades, we performed a more critical test. If the Gaussian rate distribution does not change, scaling by a change in threshold will maintain the ratio of the mean and the standard deviation of the distribution. The rate distributions of figure 3*c* did not maintain constant μ/σ ratios across subsequent saccades. These distributions, however, did not take into account a potential interval of concurrent processing prior to the initial saccade. Note that if one alters the latency by a fixed amount of concurrent processing, both μ and σ of a distribution will change. Therefore, we investigated whether there exists an interval of concurrent processing that results in an invariant ratio of μ/σ for the first and the second saccades (see figure 4). This was found to be the case for most datasets, varying from an interval of 250–400 ms in the line-orientation task to 400–550 ms in the motion-direction task. In only one case was it impossible to find an invariant ratio of μ/σ for the first and the second saccades (subject AV in the line-orientation task).

However, despite invariant μ/σ ratios, the reciprocal distributions failed to obtain the same shape when the latencies were extended with the interval of concurrent processing that resulted in equal μ/σ ratios (as shown in figure 4). Kolmogorov–Smirnov statistics confirmed that, with the inclusion of this concurrent processing interval, four out of the eight datasets of reciprocal latencies of second saccades could not be described by a Gaussian distribution ($p < 0.05$). This suggests that the difference in the rate distributions for the initial and subsequent saccades cannot solely be explained by the saccadic dead time and concurrent processing prior to the initial saccade and a change in $(S_t - S_0)$. It indicates that the rate distribution itself is not invariant across saccades. As can be seen in figure 3, the distribution of the second saccades is much more skewed than that of the first saccades and deviates from the linear probit curve (figure 3*c*). In the case of the first saccades, the reciprocal latencies follow a straight line, corresponding to a normal distribution, with a small sub-population of fast responses (e.g. in subjects EL and MC for the line-orientation task), which presumably correspond to ‘express saccades’ (Fisher *et al.* 1993; Sommer 1997). For the first saccade, this sub-population is easily distinguished in the data for exclusion from statistical analysis. However, when looking at the curves for the second saccades, this is less straightforward. Firstly, it is difficult to determine where the ‘tail’ should be cut off (see figure 3) and secondly, the upper part of the curves is not perfectly linear, suggesting that the processing rate r does not vary in a Gaussian manner for low rates, either.

We took a closer look at the second saccades in order to see whether it was possible to distinguish a subset that is responsible for the nonlinear lower part of the curve. There may be a class of second saccades that behaves differently, for example corrective saccades. However, an investigation of the characteristics of the faster (latency less than 120 ms) saccades did not reveal any distinctions

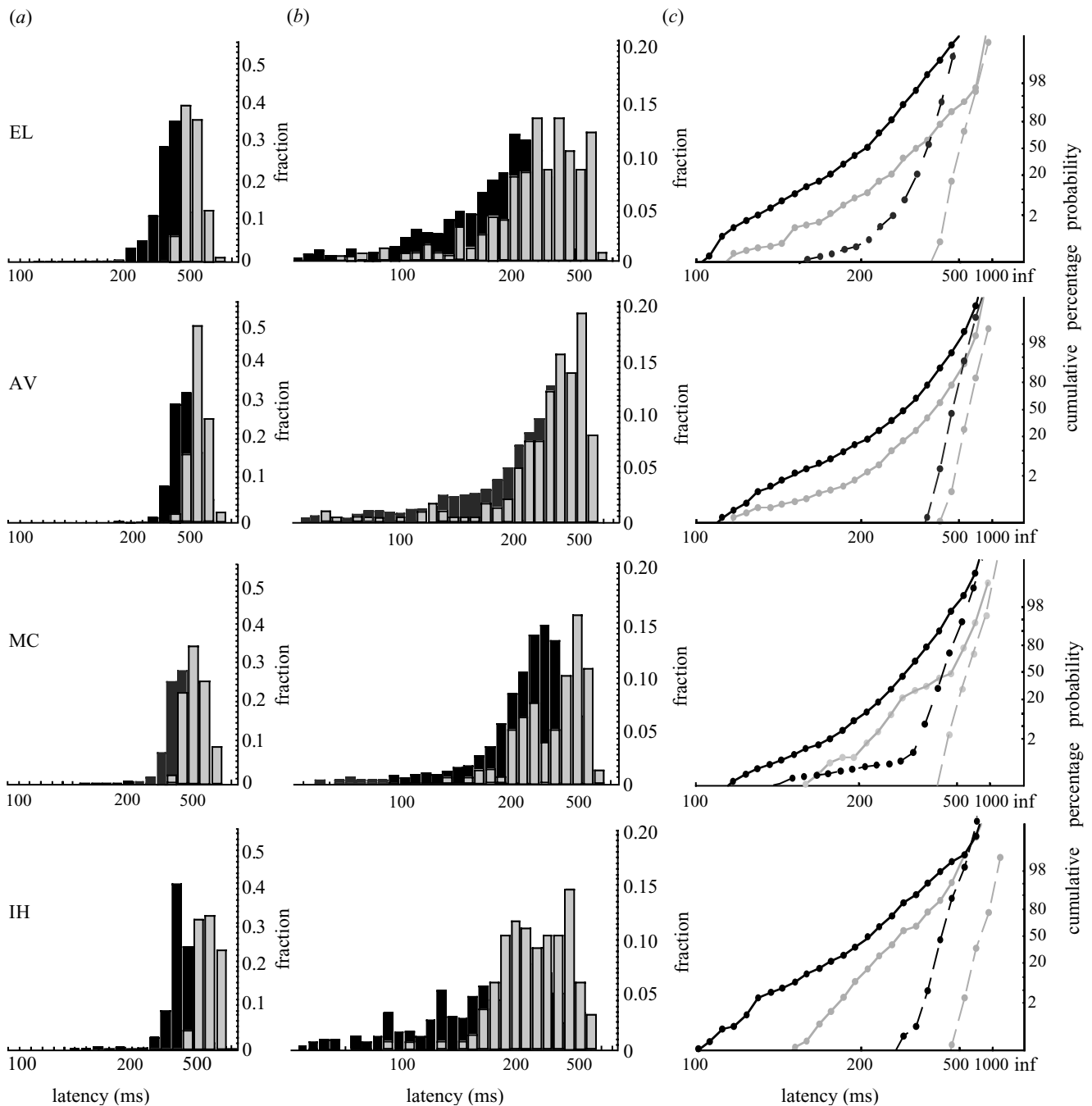


Figure 3. Raw distributions of the reciprocal latencies in the two search tasks for the (a) first and (b) second saccades, respectively. The line-orientation task is represented by black bars and the motion-direction task is represented by grey bars. (c) Reciprobbit plot for the first (dashed lines) and second (solid lines) saccades in both the line-orientation and motion-direction search tasks. Subjects' initials are shown on the left.

in terms of amplitude, first/second saccade amplitude ratio, or direction. Therefore, we concluded that the normal distribution of the rate r , which the LATER model assumes, may not be appropriate for the rate distributions of the subsequent saccades in a scanning sequence. There is another, more fundamental reason why the assumption of a normally distributed processing rate in the LATER model has its shortcomings. The normal distribution, by definition, ranges from $-\infty$ to ∞ , whereas in reality negative processing rates do not exist (this is also why the percentage cumulative frequency does not reach 100 in the LATER model).

(d) A different approach

A distribution that has several properties that make it a suitable alternative to describe rate distributions is the gamma (Γ) distribution². In contrast to the normal distribution, it is defined for positive values only. It is characterized by two parameters, a shape parameter ' k ' (symmetry increases for higher k) and a scale parameter λ (for given k , the distribution's mean is proportional to λ). Moreover, if two identically Γ -distributed variables are added, their sum is again Γ -distributed with shape parameter $2 \cdot k$ and scale parameter λ . If n independent, identically Γ -distributed processes contribute to the decision to

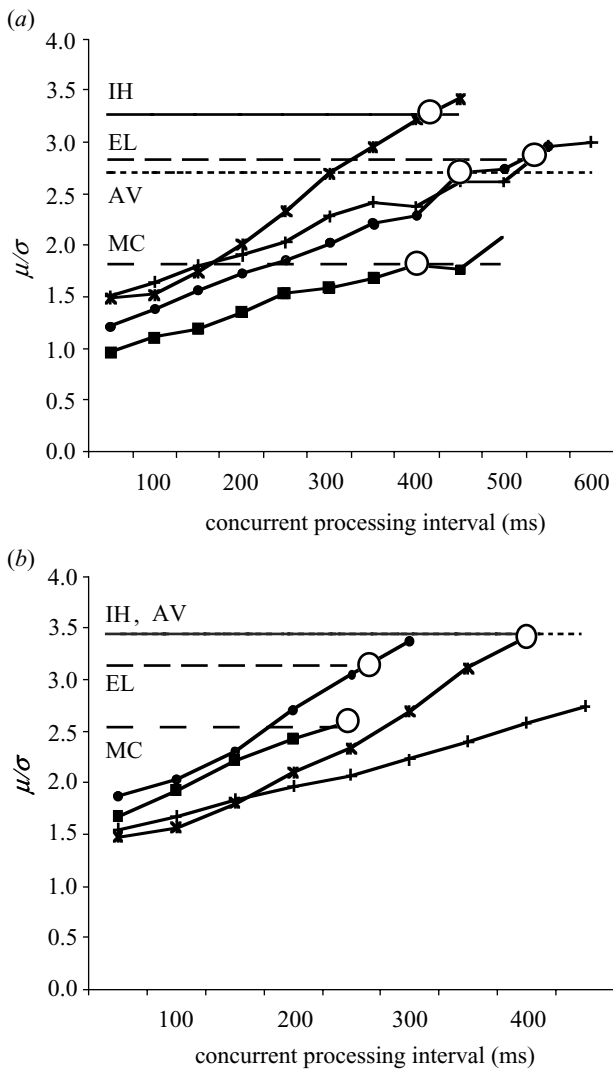


Figure 4. The μ/σ ratios for the (a) motion-direction task and (b) line-orientation task of the second saccade as a function of the length of an added interval of concurrent processing. White circles denote the interval for which the μ/σ ratio of the second saccade is equal to that of the first saccade. The extent of the horizontal lines indicates the maximum concurrent processing interval for each subject (i.e. the mean time from stimulus onset to the first saccade minus the dead time). The vertical location of the horizontal line indicates the μ/σ ratio of the first saccade for each subject.

make a saccade, one expects a gamma distribution for the reciprocal saccadic intervals with shape parameter $k' = k*n$: the distribution will become more symmetrical for increasing n . The gamma distribution therefore has the additional advantage that it describes both symmetrical and skewed distributions.

We follow the logic of the LATER model, in that the reciprocal saccadic latencies reveal the rate divided by the threshold rise ($S_t - S_0$) for saccade initiation. The scaling of the rates by the threshold means that a gamma fit to the inverse latency provides a scale parameter $\lambda' = \lambda/(S_t - S_0)$, which is inversely proportional to the threshold. An increase in the common distribution's scale parameter (λ) will scale up the distributions of all saccades in a sequence. Variations in λ between saccades within a sequence will reveal changes in threshold ($S_t - S_0$). Thus, by fitting

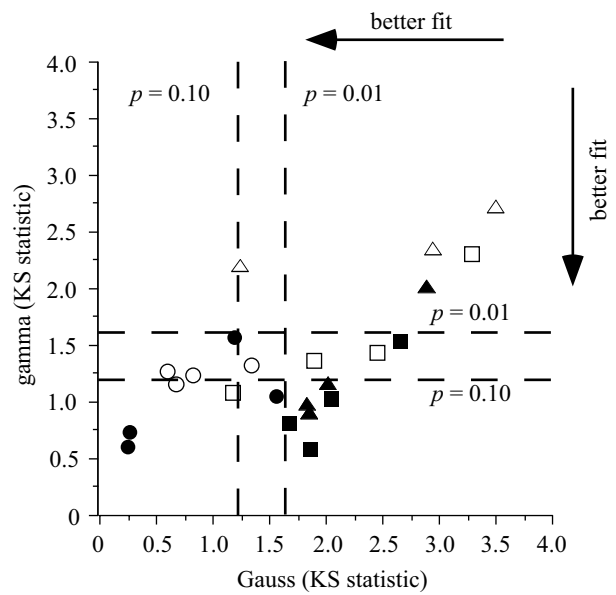


Figure 5. KS statistics for the first (circles), second (squares), and third (triangles) saccade in both the motion-direction (open symbols) and the line-orientation (filled symbols) task. Horizontal and vertical lines denote the value of the test statistic that corresponds with a probability of 0.01 and 0.10 that the distribution is drawn from either a Gaussian or a gamma distribution, respectively. Each data point represents one distribution.

gamma distributions to inverse latencies (corrected for the dead time), we seek regularities in the shape and scale parameters across saccades. This may inform us about changes in threshold and the number of decision processes that contribute to saccade initiation during saccadic scanning.

(e) *Gamma fit parameters*

Kolmogorov-Smirnov tests of the individual distributions for each saccade in the two tasks confirmed that the asymmetric inverse latency distributions of second (and third) saccades are more like a gamma distribution than a Gaussian distribution. Whereas the inverse latency distributions of the first saccades could be fit by a Gaussian as well as a gamma distribution, those of second saccades were shown to be significantly different from the Gaussian distribution, but not from the gamma distribution (see figure 5). Due to the small number of saccades available for analysis, the fits for the third saccades are less good using either of the distributions.

Results of the gamma fits show that, in both search tasks, the shape parameter k' of the distribution is much higher for the initial saccade than for subsequent saccades (figure 6). The shape parameter k' is, in most cases, about twice as high in the line-orientation task as in the motion-direction task. The scale parameter λ' , however, is low for the first saccade, rises about fourfold (i.e. threshold decreases fourfold) for the second saccade and gradually decreases again for the third and fourth saccade. Thus, the threshold is not constant in a scanning sequence but is highest for the initial saccade and lower for subsequent saccades. These systematic changes in the scale parameter λ' occur for either type of search display, suggesting that the reduction in threshold rise for subsequent saccades in

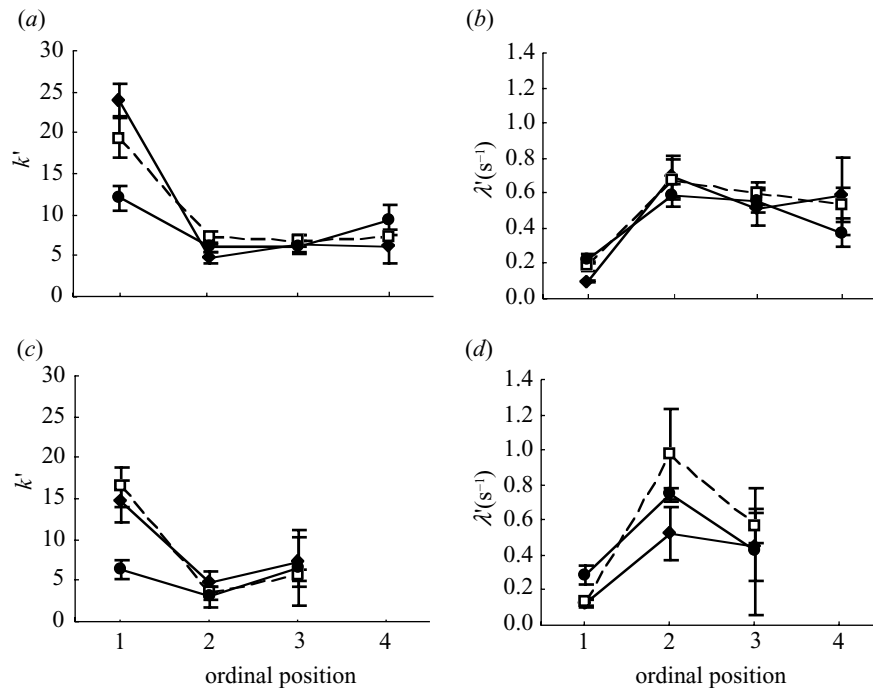


Figure 6. Estimated values for the parameters k' and λ' , based on gamma fits to the reciprocal latency data of subsequent saccades in the (a) line-orientation task and (b) motion-direction task for subjects AB (filled diamonds), EL (open squares) and MC (filled circles). Error bars denote 95% confidence intervals for the parameter estimates.

a sequence is inherent to the saccadic system and independent of the mean processing rate of the stimulus display.

4. DISCUSSION

The timing of saccades in a search task shows a characteristic pattern. Distributions of reciprocal latencies of second and subsequent saccades are non-Gaussian, with a relatively large fraction of high-rate visual processing compared with a Gaussian distribution. For these saccades, the gamma distribution yields much better fits to the reciprocal latencies than the Gaussian distribution. Even if one extends the latencies of second saccades with an interval of concurrent processing preceding the previous saccade, only half of the data can be described as Gaussian. Moreover, we note that μ/σ ratios are maintained (the open circles in figure 4) for concurrent processing times that are usually less than 1σ below the maximum concurrent processing time. Thus, a significant fraction of the second saccades needs concurrent processing that extends prior to stimulus onset, which in our view reduces the value of a concurrent processing hypothesis as an explanation for the changing distribution for the second saccade.

The parameters of the gamma distributions for different saccades in a series show systematic changes that are similar for different subjects and visual stimuli. The symmetrical shape of the distribution for the first saccade becomes skewed for later saccades and the scale parameter (reflecting inverse threshold) increases. One could simply take these changes as fact, but we believe it is useful to stretch our interpretation (admittedly adding speculation) of the meaning of the change of the shape parameter. A more symmetrical gamma distribution is characterized by

a high value for the shape parameter, which points to many independent stochastic contributions to the decision. What could constitute these independent contributions? Most probably, these parallel independent contributions are related to the parallel processing of the visual elements in the scene. It is plausible that the decision to generate a saccade towards a display element in the line-orientation task is based on a comparison of its orientation to the orientations of other elements from different parts of the visual field. Each comparison could partially contribute to the decision rate. Once a threshold level is reached, the saccade is initiated towards that display element (cf. the visual-saccadic decision-making model by Shadlen *et al.* 1996). If true, the first saccade was based on a greater number of such comparisons (from figure 6, one reads twice as many or more) than the later saccades. A larger number of elemental contributions will not only make the distribution more symmetrical; it will also increase the mean of the rate signal. However, because the threshold (inversely related to the scale parameter λ' ; see figure 6) is approximately four times higher for the first saccade than for later saccades, the mean latency for the first saccade (latency = threshold/rate) is nevertheless longer. The pattern of gamma distributions for different saccades in a series, then, suggests that an initial analysis of many (possibly all) elements prior to the first saccade is followed by a series of short-latency saccades in which a smaller fraction of the elements is analysed.

A similar analysis holds for the motion stimulus. The longer latencies (lower decision rates) for the motion stimulus (figure 3) are not accompanied by a consistently higher threshold parameter (i.e. lower λ' in figure 6). Also, the shape parameter (figure 6: k') is similar, or lower, than that for the line-orientation task. Thus, the data suggest that the partial decision rate delivered by each comparison

of motion directions (as an analogue to the orientation comparisons mentioned above) is smaller and/or the number of comparisons is lower for the motion task.

Physiological studies show that both the FEF and the SC are important in the generation of saccades. The SC contains a fixation zone that corresponds to foveal retinal locations (Munoz & Wurtz 1993*a,b*). Suppression of the maintained activity in this fixation zone releases a saccade. Programming of the direction, however, is dependent on the activity distribution in the rest of the retinotopic map (Munoz & Wurtz 1995*a,b*). The FEF also contain fixation-related and movement-related neurons that are involved in the interaction between gaze holding and gaze shifting (Hanes *et al.* 1998) and both types of neurons project to the SC (Sommer & Wurtz 2000). Our data could mean that the suppression of the activity of the SC fixation zone is based on activation, in part, of the map outside the fixation zone, where the extent of that part is variable across saccades in the search sequence. Secondly, distributions for second and later saccades reveal larger-scale parameters (reflecting a lower threshold). This may mean that part of the activity that is built up to terminate fixation is maintained across a saccade (a rise of S_0 in terms of the LATER model). Neurophysiological evidence for this has been reported by McPeck & Keller (2002), who found that, in monkeys, even during the execution of a saccade, neural activity related to the processing of a second goal could be concurrently maintained in the SC motor map.

In summary, we conclude that the LATER model does not seem to hold for sequences of saccades, as the distributions of the reciprocal latencies of second and subsequent saccades do not follow the assumed normal distribution. However, we note that, for some of the data, this problem could be solved by the inclusion of an interval of concurrent processing preceding the previous saccade. In either case, saccadic latencies in a sequence seem to vary because the threshold decreases, possibly because activity to program the first saccade is in part maintained for a saccade to a second, or later, goal (McPeck *et al.* 2000). We speculate that the decision signal for saccade generation is dependent on integrated activity from different parts of the visual field with rates that are each drawn from a common gamma distribution. We presume that the elementary common-rate distribution remains the same within a sequence, because the stimulus is unaltered. Yet, this common-rate distribution may vary for different stimulus displays, accounting for differences in the rate of processing (and therefore, in saccadic latencies) in different search tasks.

ENDNOTES

¹Note that the percentages of detection in the search tasks were lower than the 75% correct levels that were obtained in the psychophysical pilot study. This is presumably due to the fact that, in the pilot study, a two-alternative forced choice procedure was used, whereas programming a saccade involves a multiple-choice condition. Part of the success in the psychophysical forced choice task may result from the subject's identification of the non-target of the pair without positively identifying the alternate object as the target.

$${}^2\Gamma_{k,\lambda}(r) = \frac{1}{\Gamma(k)} \binom{r}{\lambda}^k \frac{e^{-r}}{r^\lambda}$$

where r is the rate of rise (s^{-1}).

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