The urgency to look: Prompt saccades to the benefit of perception

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Abstract

Researchers have shown that the promptness to initiate a saccade is modulated by countless factors pertaining to the visual context and the task. However, experiments on saccadic eye movements are usually designed in such a way that oculomotor performance is dissociated from the natural role of saccades, namely that of making crucial perceptual information rapidly available for high-resolution, foveal analysis. Here, we demonstrate that the requirement to perform a difficult perceptual judgment at the saccade landing location can reduce saccadic latency (by >15%) and increase saccadic peak velocity. Importantly, the effect cannot be explained in terms of arousal, as latency changes are specific to the location where the perceptual judgement is required. These results indicate that mechanisms for voluntary saccade initiation are under the powerful indirect control of perceptual goals.
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1. Introduction

The sudden appearance of a stimulus somewhere in the peripheral visual field typically elicits a reflex-like saccade, whose latency can be as short as ∼100 ms (Fischer & Rampsberger, 1984; Guitton, 1991). However, most saccades toward a visual target have a much longer latency, averaging around 200 ms (Carpenter, 1988). The difference between the two figures above most likely represents the footprint of an elaborate decision process exerting control over the low-level visuo-motor reflex (Carpenter, 1988; Glimcher, 2003). For instance, many real life situations require that a choice be made regarding which particular stimulus, among many others, is worth looking at next (Chelazzi, Duncan, Miller, & Desimone, 1998; Schall & Thompson, 1999). To this aim, prior to any saccade, visual (bottom-up) information from the whole scene has to be integrated with cognitive (top-down) influences to select the eye-movement that will maximise the input rate of task relevant visual information (Schall & Thompson, 1999). Saccadic eye movements thus seem to be logically coupled to perception in two ways: they are constrained by low-resolution sensory sampling of the peripheral visual field, supporting detection and selection of the future saccade target, and they are motivated by high-resolution perceptual goals, namely the fine analysis of the object brought onto the fovea.

Work in human and non-human primates has demonstrated that latencies of stimulus-elicited saccades can be affected by many factors pertaining to both the perceptual and the cognitive context (Findlay & Gilchrist, 2003). These include the temporal relationship between onset of the saccade target and offset of the fixation point (e.g., see the so-called gap effect; Fischer & Rampsberger, 1984), the presence and location of distractors in addition to the target itself (Walker, Deubel, Schneider, & Findlay, 1997), the differential probability with which the target is presented at various visual field locations (Basso & Wurtz, 1998; Carpenter & Williams,

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1995; Dorris & Munoz, 1998), the sequential effects due to prior trial history (Fecteau & Munoz, 2003), the presence of anticipatory attentional cues (Kowler, Anderson, Dosher, & Blaser, 1995) and, finally, the specific rule to convert a given target location in the appropriate saccade behaviour (e.g., in antisaccade tasks; Hallett & Adams, 1980; or Go-Nogo tasks; Jüttner & Wolf, 1992). Moreover, recent behavioural experiments in monkeys have shown that when saccades to various locations are differentially rewarded, their latencies are correspondingly modulated, such that movements to the highly rewarded targets will be initiated more promptly (Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Watanabe, Lauwereyns, & Hikosaka, 2003a).

Experiments reported here explored the possibility that the decision to initiate a saccade may be sped up by the need to perform a difficult perceptual judgment at the saccade landing location under strong time pressure—what we refer to as an effect of '*perceptual urgency*'. Specifically, unlike previous studies, our experimental paradigm incorporated the natural motivation associated to executing a saccade, namely that the "saccadic goal" indeed be a relevant "goal" for perceptual analysis and behavioural control.

2. Methods

2.1. Stimuli and apparatus

Eye movements were recorded from human volunteers by means of a head-mounted video camera system for eye tracking (infrared video-based binocular eye-tracking system Eyelink I, SMI; sampling rate 250 Hz). The spatial resolution of the system was <0.02° of visual angle. Data were stored for offline analysis and in particular for the detection and characterization of saccades.

Stimuli were presented on a computer monitor (15″, refresh rate 75 Hz) placed in front of the subjects at 57 cm distance. All visual stimuli were well above detection threshold and were presented against a homogeneous grey background (luminance 9 cd/m^2). The saccade target was a blue square (0.6° × 0.6°) and had a lower luminance than the background and a (negative) Weber contrast of −30% with respect to it. The target was presented either to the left or right of the centre, at 11° of eccentricity, simultaneously with offset of the fixation point.

2.2. Subjects

Thirteen subjects (8 females; age 20–25 years) took part in the main experiment (D-task, or Experiment 1, see below) and six of them also participated to the 'biased D-task' (or Experiment 3). Four more subjects (3 females) were tested in the Staircase D-task (or Experiment 2). Experiments were approved by the Local Ethical Committee. Subjects gave their undersigned informed consent prior to the experiments and they received a monetary recompense for participation (9 euros per hour).

2.3. Experimental design: Manipulation of perceptual urgency

2.3.1. Experiment 1, D-task

In a preliminary session (Control condition), subjects were administered a standard, step saccade task to measure median saccadic latency, ML, and duration, MD, for each individual observer (Fig. 1A, within the blue contour). Subjects were simply asked to perform a saccade to the peripheral target as quickly and as accurately as they could, after its onset. Both the timing and the location of the target onset were randomised from trial to trial, so that no advanced preparation for a particular saccade would be advantageous.

In a second session (D-task condition), a new component was added to the original task, whose purpose was to increase motivation and urgency to redirect gaze to the target. Immediately after completion of the saccade, subjects were required to perform a two-alternative forced-choice letter discrimination at the saccade goal location (Fig. 1A, within the red contour). The letter to discriminate was a white capital letter E or F (with font size of 14 or 18 for different subjects; the size difference did not produce any appreciable difference in performance and will not be discussed), and had a luminance of about 60 cd/m^2 and a Weber contrast of about +500% relative to the background. The letter, which could not be discriminated with peripheral vision, appeared after a critical delay, T^*, from saccade target onset and was removed after ∼13 ms (one refresh period). The 'perceptual urgency' condition was tailored for each subject individually, by setting $T^* = ML + MD$. The time taken to program and execute the saccadic eye movement was thus the central limiting factor to achieve a good level of letter discrimination performance. In practice, since saccades of a given amplitude have approximately constant duration (Becker, 1989), around MD, saccadic latency was presumably the main determinant of letter discrimination accuracy. Latencies longer than ML would in fact bring the fovea onto the letter location at a time when the letter is no longer available, therefore preventing an accurate perceptual judgement. Note that the nature of the saccade target and its time of onset, as well as the immediate visual context, were exactly the same between the Control and the D-task conditions, excluding that the oculomotor behaviour would be affected by any confounding difference across tasks.
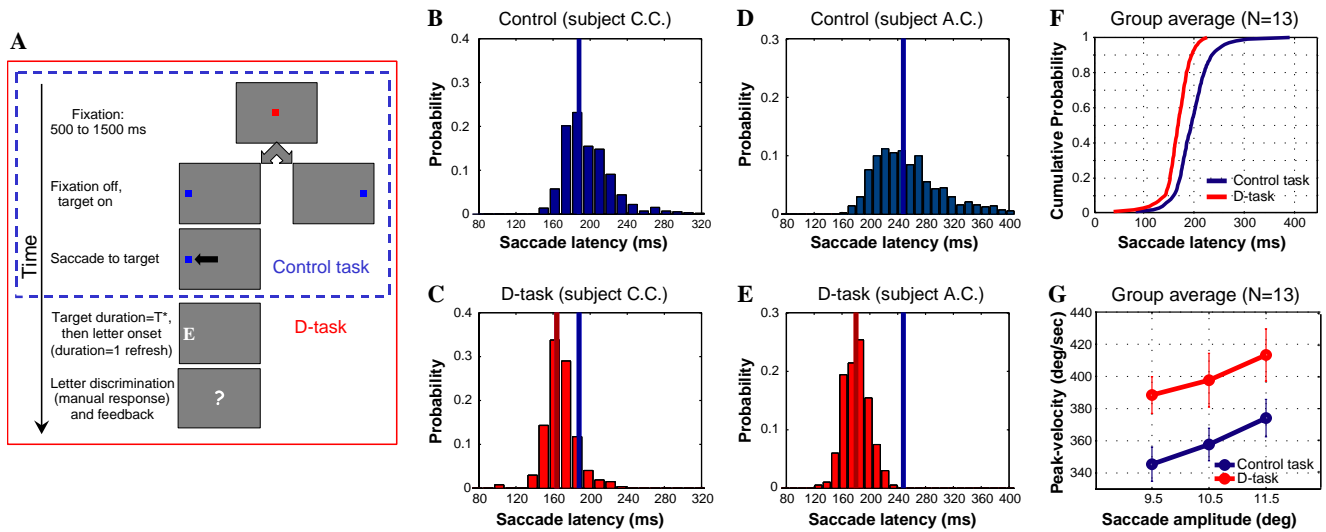
Fig. 1. The effects of perceptual urgency on saccadic latency and peak velocity. (A) We compared eye movements generated in a standard stimulus-elicited saccade task (Control task, schematically described within the blue dashed contour) with those generated when the observer is under time pressure to perform a speeded letter discrimination task at the location of the saccade goal (D-task red solid contour). The saccadic latency distribution histograms for two example observers are shown both in the Control (B and D), and the D-task (C and E). The blue vertical line in (B–E) represents the median latency (ML) computed in the Control condition, whereas the red vertical line in (C and E) represents the median latency in the D-task condition. (F) Group average cumulative distribution of saccadic latencies in the Control (blue) and D-task (red) condition. A *vincentization* procedure (Ratcliff, 1979) was applied to homogeneously sample the latency distribution from different subjects. (G) Mean saccadic peak velocity computed for three 1-deg-wide amplitude bins and averaged across subjects, in the Control and D-task conditions.

2.3.2. Experiment 2, staircase D-task

In the staircase experiment, after an initial session of the Control task (600 trials), subjects ($N = 4$) were to perform in a single session of the D-task in which the critical letter onset delay, T^*, was reduced or kept constant depending on the discrimination performance evaluated over discrete blocks of 40 trials each. Specifically, T^* was reduced by around 13 ms (one refresh of the monitor) if performance over the previous 40-trials block was at least 75% correct. The session was terminated after a minimum of four 40-trials blocks in which the average performance remained below 75% correct, but it was prolonged if performance, even though below threshold, showed a consistent trend for improvement across consecutive trial-blocks.

2.3.3. Experiment 3, biased D-task

Six of the 13 subjects from Experiment 1 were also tested with a slightly modified version of the D-task, the biased D-task (Fig. 3A). On one side of fixation (e.g., the left), the letter to be discriminated was presented, after time T^* from target onset, only in a fraction, p_D, of the total trials. In the remaining fraction, $1-p_D$, randomly interleaved with the previous trials, the saccade target remained visible for 800 ms, replicating the original Control task, and no letter was presented. We let p_D vary across blocks and take one of the following values: 0, 0.25, 0.75, and 1. Importantly, on the opposite side (e.g., the right), the letter to be discriminated was presented with the complementary probability, $1-p_D$, so that the

overall number of discrimination trials (and therefore the overall difficulty of the task) was held constant across blocks.

2.4. Data analysis

A minimum of 600 trials in the Control task and 200 trials in the D-task (unbiased condition) were collected from each of the 13 subjects (in two 1-h daily sessions). The initial 200 trials of the first session (Control-task) were considered as practice and were excluded from the analysis of saccadic latency and peak-velocity. Instead, only 20 trials were excluded from the initial part of the second, D-task, session, since by the start of this session subjects were already familiar with the basic task and experimental apparatus. In the biased D-task a minimum of 1500 trials (including all probability conditions) were collected during four daily sessions.

Saccades were automatically detected in the data file as those eye movements with velocity greater than 30 deg/s or acceleration greater than 800 deg/s^2. As a general rule, trials presenting eye-blink artefacts in the eye position record in close proximity to the saccade were discarded, and so were those trials with saccadic eye movements preceding target onset or with latencies <80 ms (anticipatory saccades) or, finally, with saccades in the wrong direction.

The statistical analysis of latency distributions constitutes a major component of this study and will be extensively outlined in Section 3.

3. Results

3.1. Experiment 1

3.1.1. Effects of perceptual urgency: Reduction of saccadic latency

The first experiment assessed the extent to which saccadic performance may be affected by a manipulation of perceptual urgency. To this aim, we compared saccadic latency between an initial session of the Control condition and a subsequent session of the D-task condition, only the latter urging participants to perform prompt saccades to the benefit of perception (see Section 2). The urgency manipulation exerted quite a dramatic influence on saccadic reaction time (SRT) distribution in all subjects, with shorter latencies in the D-task than in the Control condition (see Figs. 1B–E for two example subjects, and Fig. 1F for the group average). For all subjects but one, a 2-sample Kolmogorov–Smirnov test revealed a significant difference between the latency distribution in the Control and the D-task condition ($p < 0.05$). For the remaining subject the effect was only marginally significant. Across subjects, mean latency ranged between 159 and 249 ms in the Control condition, and between 147 and 186 ms in the D-task condition, with an average latency reduction of 32.4 ms (or 15.6%; highly significant: 1-way ANOVA, $p < 0.005$). The latency variance did also greatly decrease, by at least 30% in each individual. These effects were obtained with an average letter-onset delay, T^*, of 210 ms.

The experimentally elicited shift of the SRT distribution toward shorter latencies occurred in a step-wise fashion from the very onset of the D-task, with virtually no adaptation delay, excluding a practice effect between the first (Control) and the second (D-task) experimental session. Owing to the robust latency reduction, subjects attained very high levels of performance in letter discrimination (92% on average across subjects), relative to the theoretical value predicted on the basis of the Control SRT distribution (i.e., 75%, if one assumes no discrimination error following saccades landing onto the letter location prior to letter onset). Importantly, across participants, nearly half of the total letter discrimination errors (48.6%) occurred in association with the 25% of the total trials with the longest saccadic latencies, whereas only 22.6, 12.0, and 16.9% of the total letter discrimination errors occurred in association with the remaining three quartiles of the total trials (from second longest to shortest, in terms of saccadic latencies).

For 2 out of 13 subjects, a short session (200 trials) of the Control task was repeated at the end of the D-task. Remarkably, the urgency effect on saccadic latency turned out to be reversible: the SRT distribution obtained during this repeated Control session was statistically indistinguishable (2-sample Kolmogorov–Smirnov test, $p > 0.1$) from the distribution obtained during the initial Control session. This result strengthens the notion that the latency reduction elicited by the perceptual urgency manipulation was not due to a mere practice effect.

The proportion of saccades with latencies in the range 80–120 ms (sometimes referred to as express saccades; Fischer & Rampsberger, 1984) was overall very low, averaging 1.5% across subjects in the Control condition and 3.7% in the D-task, a non-significant difference. In general, the decrease of saccadic latency in the D-task condition did not correspond to the emergence of a new population of saccades observable in the profile of the SRT distribution. One exception to this was represented by subject G.R., whose saccadic latencies underwent a particularly dramatic decrease during the D-task, giving rise in this condition to a distinct express-like peak accounting for about 10% of the data. For one additional subject (A.C.) a distinct express-like peak was present in both the Control and D-task condition, but it was enhanced in the urgency condition—comprising almost 15% of the total saccades.

The fraction of direction errors increased from slightly above 1% in the Control condition to slightly below 10% in the D-task condition. However, as will be further specified later, we do not believe that a strategic speed-accuracy trade-off be the main determinant of the perceptual urgency effect. For instance, for those subjects who were tested with a longer session of the D-task (like in the case of the biased D-task; see below) the fraction of direction errors was rapidly reduced, and it did not differ from the Control condition after an initial, transitory phase.

3.1.2. Effects of perceptual urgency: Increase of saccadic peak velocity

We next asked whether our urgency manipulation might affect other saccadic parameters, such as peak velocity, which is commonly assumed to be constant for a given saccadic amplitude (Becker, 1989). Given the nature of the paradigm, saccadic amplitudes spanned a small range around 11° (target eccentricity), both in the Control and the D-task condition (although for some subjects the fraction of hypometric saccades was greater in the latter), making our data inadequate to explore the complete *main-sequence* relationship (Bahill, Clark, & Stark, 1975) of peak-velocity as a function of amplitude. Fig. 1G plots mean peak-velocity, averaged across subjects, for three 1-deg amplitude bins around target distance. A two-way ANOVA with the factors amplitude bin and task revealed only a significant main effect of task ($p < 0.005$): Mean saccadic peak velocities were higher in the D-task than in the Control task. The percent increase in peak-velocity ranged from 2 to 30% across subjects (two subjects showed no increase or a non-significant decrease), and the group average effect amounted to ∼10%, corresponding to an increase of 35 deg/s. Increases in saccadic peak-velocity during the D-task relative to the Control task were not

due to an increase in saccadic amplitude during the D-task, as the main-sequence relationship (Bahill et al., 1975) would predict. On the contrary, a significant reduction of saccadic gain (by between 15 and 25%) was observed in 6 of the 13 participants, while changes in gain were negligible in the remaining participants.

As one might predict given the observed increase in saccadic peak velocity, saccadic duration underwent a slight reduction in the D-task condition relative to the Control condition. Across participants, average saccadic duration was 58.9 ms in the Control task, and 54.1 ms in the D-task, and this was a significant difference ($p = 0.5$). One should note, however, that across subjects this reduction in saccadic duration amounted to only about 15% of the reduction in saccadic latency.

3.2. Experiment 2

3.2.1. Limits of the perceptual urgency effects

To explore the maximum extent to which perceptual urgency can reduce saccadic latency, in Experiment 2 we tested four additional subjects with a *staircase* version of the D-task, whereby the time pressure to perform the letter discrimination was gradually increased over time (see Section 2). Figs. 2A and B illustrate (respectively, for one example subject and for the group average) that, following a large latency reduction obtained during the initial phase (trial 1-to-100) of the staircase experiment, relative to the Control task, no reliable reduction could be further elicited by means of the staircase procedure (Kolmogorov–Smirnov test for the equality of two sample distributions, $p > 0.1$ for all subjects). In this experiment, due to the increased time pressure, the overall fraction of letter discrimination errors was larger than in the original D-task (approaching chance level in the final portion—last 160 trials—of the staircase). Accuracy was high only on those trials in which a saccade was initiated with a latency shorter than the critical value $ML = (T^* - MD)$ and the line of gaze was close enough (within ~1°) to the letter location at the time of letter onset. When either condition was not satisfied, accuracy dropped to near chance level (Fig. 2C). Although not unexpected, the error pattern shown in Fig. 2C provides nice evidence that the rationale for this study was well grounded.

3.3. Experiment 3

3.3.1. A selective effect of perceptual urgency, not just an increase in arousal

To rule out the possibility that our results were the consequence of a generic increase in alertness or arousal due to the additional requirement of the letter discrimination task, in Experiment 3 we tested 6 of the 13 subjects from Experiment 1 with a slightly modified version of the D-task. In the biased D-task (see Section

2 and Fig. 3A) the probability p_D of having to perform the speeded letter discrimination was modulated on each side separately. By means of this manipulation, the perceptual urgency effect on SRT distribution was replicated in a side specific fashion, and its magnitude was a monotonic function of p_D, the latency being shorter the larger p_D, i.e., as more discrimination trials were presented on a given side. Figs. 3B and C show the cumulative latency distribution as a function of p_D for two example subjects, while Fig. 3D shows the same data for the group average. The pair-wise difference between latency distributions with $p_D = 0$, 0.25 and 0.75 was significant in all subjects (1-tail Kolmogorov–Smirnov test, $p < 0.01$), whereas the difference between latency distributions with $p_D = 1$ and 0.75 reached significance in only 2 out of 6 subjects. Interestingly, we observed no significant difference between latency distributions in the extreme conditions of the biased D-task ($p_D = 1$ and $p_D = 0$, respectively) and in the matching, spatially symmetric conditions of the previous tasks (the original D-task and the Control task, respectively). The latter result suggests that the effect obtained with the urgency manipulation is not constrained by a limited-resource mechanism, nor is it due to a side-specific motor bias, since the same level of latency reduction could be achieved in the symmetric D-task condition of Experiment 1 and in the biased D-task condition ($p_D = 1$) of Experiment 3.

3.4. Saccade latency and models of decision making: A computational analysis

Reddi and Carpenter (2000, 2003) have carried out an elegant series of experiments to assess the influence of urgency on saccadic latencies in human observers. In their paradigm, the urgency condition was simply instantiated by verbally instructing subjects before the start of the experiment to trade accuracy in favour of speed (thus allowing for more saccade direction errors). Similar to our results, the authors found that the urgency condition elicited a robust latency reduction relative to a non-urged condition (emphasising direction accuracy instead of speed). According to Carpenter and colleagues (1988; Carpenter and Williams, 1995), a simple theoretical model, called LATER and schematically described in Fig. 4, is capable of explaining the basic statistical features of SRT distributions. Specifically, Reddi and Carpenter (2000, 2003) found that the LATER model could account for the effects of urgency on SRT distributions in their study, under the hypothesis that increasing urgency lowers the threshold level at which a growing decision signal will trigger a saccade. Figs. 5A and B show with simulated data the types of change, relative to an arbitrary baseline, predicted by the LATER model when the critical threshold level is lowered and when the mean rate of rise of the decision
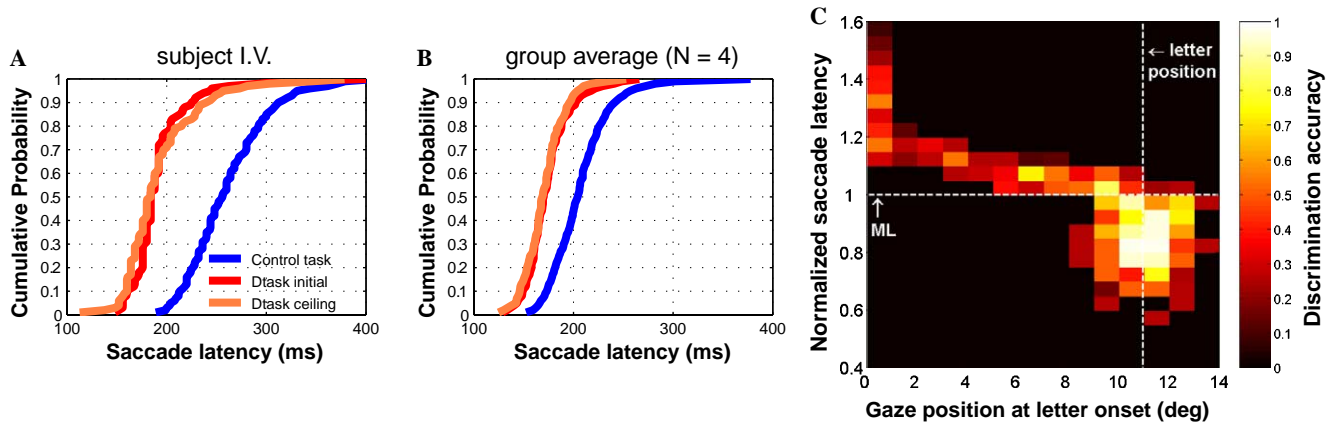
Fig. 2. Immediate onset of the perceptual urgency effect and pattern of letter discrimination errors. Cumulative distribution of saccadic latencies for one example observer (A) and for the group average (B). Following the large and abrupt left-shift of the SRT distribution obtained during the initial session of the D-task (red curve), relative to the Control task (blue curve), only a weak, non-significant reduction of saccadic latencies could be obtained by means of the staircase procedure. The curve in orange depicts the latency distribution for the final part (160 trials) of the session using the staircase procedure, during which letter discrimination performance was at or near chance level. (C) The plot illustrates the group-average ($N = 4$) accuracy in letter discrimination during the staircase experiment. Accuracy is colour-coded for each pair of values of gaze position at letter onset and saccadic latency (normalised with respect to the critical value $ML = (T^* - MD)$). As expected, performance was near optimal only on trials in which a saccade was initiated with a latency shorter than the critical value $ML = (T^* - MD)$ and gaze position was very close to the letter location at letter onset.
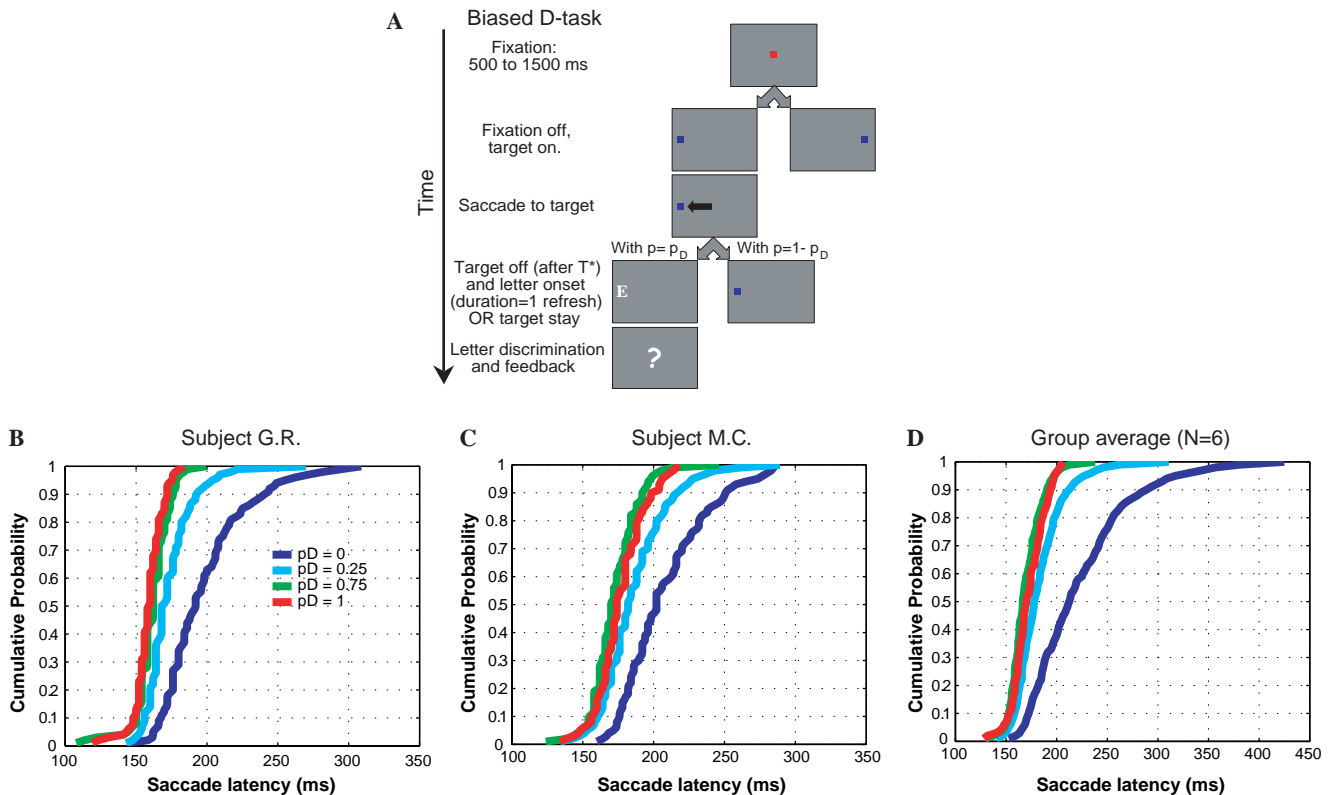

Fig. 3. The effects of a lateral bias in perceptual urgency (biased D-task). (A) Schematic illustration of the biased D-task. The probability with which the discrimination letter is presented at the saccade goal location is changed in a complementary fashion on the two sides of fixation by changing the parameter p_D across blocks. The cumulative distribution of saccadic latencies is shown for four different values of p_D, both for two example subjects (B and C) and for the group-average (D).

signal increases, respectively. The effects of the urgency manipulation obtained by Reddi and Carpenter were consistent with the "swivel" effect represented in

Fig. 5A, i.e., they were compatible with a lowered threshold of saccade initiation. The same cannot be said for the latency distributions we sampled under our
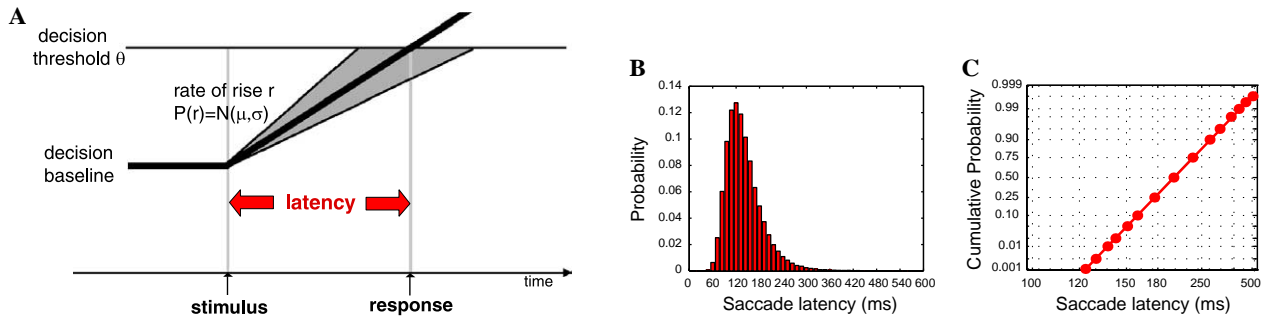
Fig. 4. The LATER model. (A) The LATER model of saccade initiation (Carpenter, 1988; Carpenter & Williams, 1995) is based on the simple idea that a *decision signal* will rise linearly (with a normally distributed rate r, $P(r) = N(\mu, \sigma)$) from a baseline value to a fixed threshold θ. The model can readily reproduce the typical skewed distribution of saccadic reaction time (SRT), shown in (B). (C) In the model, the inverse of saccadic latency is proportional to the rate r, thus it must follow a normal distribution as well. Therefore, if one plots the cumulative SRT distribution as a function of the inverse latency (reversed, so that latency still increases to the right), and one also applies an appropriate nonlinear transformation to the *y*-axis (leading to the so-called *recinorm–probit* plot), data will be represented by a straight line. Note that this representation tends to magnify the short- and long-latency tails of the distribution.
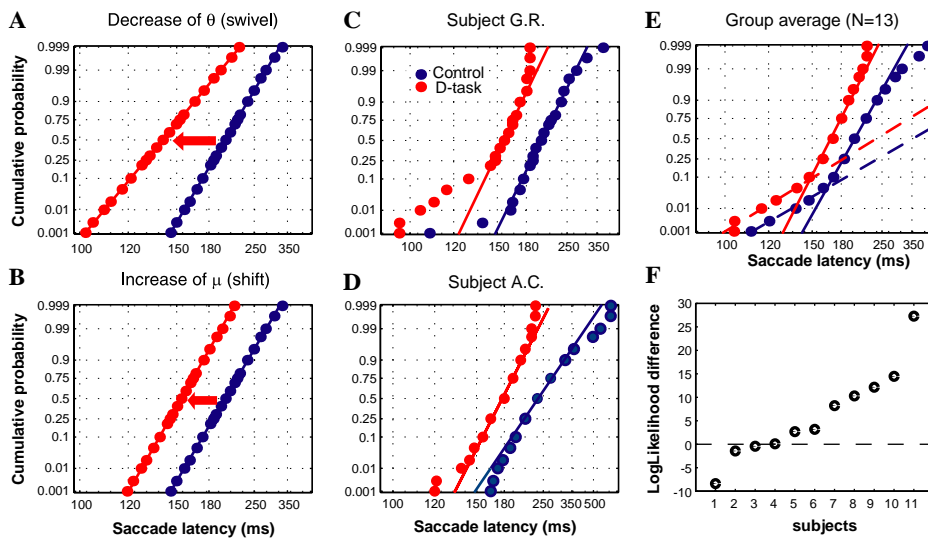

Fig. 5. Accounting for the urgency effect in relation to the LATER model. (A and B) Changing either one or the other of the two main parameters in the model (the threshold θ or the mean rate μ) produces a characteristic change in the distribution (red points), respectively, a swivel with a fixed common origin at latency = ∞ (simulated data in A), or a parallel shift (simulated data in B) of the latency distribution, relative to a baseline condition (blue points). Experimental SRT distributions (and best-fits) in the Control task (blue points) and in the D-task condition (red points) are plotted according to the recinorm–probit representation for two example subjects (C and D), and for the group-average (E). Data in (C–E) seem to be better explained by the shift than the swivel hypothesis. In (E), we have also plotted (dashed curves) the LATER best fit for the short-latency tail of the distributions, to underscore the fact that a small fraction of the data (<10%) follows a distinct probability distribution (express-like saccades). (F) Difference of LogLikelihood (ΔLL) for the shift versus swivel models fitted to the data to account for the change in SRT distribution between the Control and the D-task condition, plotted for each of 11 subjects.

urgency condition, as shown in Figs. 5C and D for two example observers and in Fig. 5E for the group average (only data from 11 out of 13 subjects are pooled to obtain the plot in Fig. 5E—see below).

To obtain a quantitative (statistical) evaluation of the latter observation concerning the effects of perceptual urgency on saccadic latencies, we performed a similar analysis of latency distributions to the one presented by Reddi and Carpenter (2003). For 11 out of 13 subjects run in Experiment 1, a Kolmogorov–Smirnov one-sample test (*p* > 0.1) supported the hypothesis that

the distribution of saccadic latencies was satisfactorily represented by the LATER model, both in the Control and the D-task condition. The short-latency tail of the distribution was excluded from the analysis (Reddi & Carpenter, 2000) when it was apparent that it represented a distinct subpopulation of saccadic latencies, i.e., with a distinct slope in the norm-probit plot (see, for example, the short-latency tail of group-average SRT distributions in Fig. 5E). Although the latency range for this subpopulation is somewhat larger than the range typically associated with express saccades, it is conceiv-

able that this subpopulation may correspond to express-like saccades. For each subject and condition, the fraction of excluded data were never greater than 10%. An even smaller ($<5\%$) fraction of trials had to be excluded at the opposite, long-latency tail of the distribution for the same reason (with the exception of one subject, S.M., for whom the longest 15% of SRT data clearly deviated from the LATER fit). Interestingly, deviations from the LATER predictions of the rightmost tail of the latency distribution happened to show an opposite trend in the Control and in the D-task (see Figs. 5C–E), representing exceedingly long and exceedingly short latency saccades, respectively, with respect to the model fit.

For each of the 11 selected subjects we contrasted the two alternative hypotheses that the SRT distribution in the D-task might be obtained from the Control distribution through a change in slope (swivel) of the linear function fitting the data in the recinorm–probit plot or through a simple parallel shift of the same function. By means of a constrained optimisation procedure (MATLAB, Optimisation Toolbox), we first computed the best fits compatible with the two contrasted hypotheses in terms of the required changes in the model parameters. Finally, we computed the difference of Log-Likelihood (ΔLL) for the shift versus swivel models. As illustrated in Fig. 5F, for 8 out of 11 subjects the difference was positive and the overall sum of the differences

across all 11 subjects was 68.3, a highly reliable difference (the average value across all 11 subjects, 6.2, was significantly greater than zero, $p < 0.02$), supporting the notion that, contrary to the results obtained by Reddi and Carpenter, our perceptual urgency manipulation exerts its effects by virtue of an increase of the mean rate of rise (μ) of the decision signal (shift of the distribution), rather than by a reduction of the criterion (θ).

Finally, we checked whether the LATER parameters change across conditions revealed a particular pattern when confronted to the shift and swivel hypotheses. Of the three fundamental parameters μ, σ, and θ defined in the LATER model (see Fig. 4 and its caption), experimental SRT distributions allow to directly estimate the value of two independent parameters which are function of them: $M = \mu/\theta$ and $S = \sigma/\theta$. The LATER model makes distinct predictions concerning the way in which S and M/S should change in the case of an increase of μ (shift hypothesis) or a decrease of θ (swivel hypothesis). We subdivided the 11 subjects into two groups depending on whether the ΔLL value was positive or negative. The upper panels of Fig. 6 illustrate the average results for subjects ($N = 8$) with positive ΔLL values, while the lower panels illustrate the average results for subjects ($N = 3$) with negative ΔLL values. Moreover, solid lines in each plot join the group-average parameter values in the Control and D-task conditions, whereas the dashed
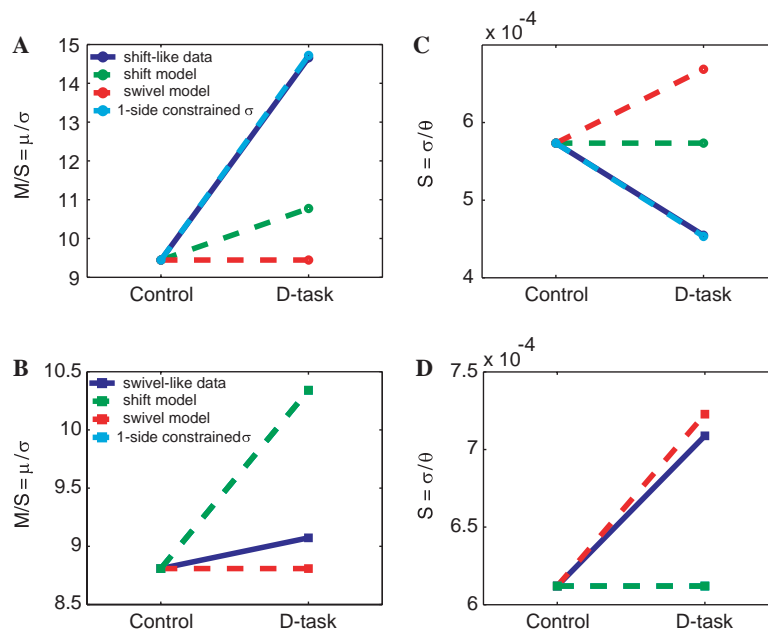

Fig. 6. Model parameter changes associated to the urgency effect. The predictions of the LATER model concerning the change of parameters $M/S = \mu/\sigma$ (A and B) and $S = \sigma/\theta$ (C and D) associated with a shift (green dashed curves) or a swivel (red dashed curves) of the distribution are compared with the experimental estimates of the same quantities in the two conditions (solid blue line). The upper panels (A and C) illustrate the average results for subjects ($N = 8$) with positive ΔLL values, while the lower panels (B and D) illustrate the average results for subjects ($N = 3$) with negative ΔLL values. When σ is allowed to decrease (*1-side constrained σ* model, dashed cyan curve), the parameter change for the group of subjects illustrated in (A and C) (shift-like data) is perfectly fitted, while no improvement is obtained in fitting swivel-like data illustrated in (B and D). The cyan line is almost exactly superimposed onto the experimental data in (A and C) while it is perfectly superimposed (thus not distinguishable) onto the green curve representing the shift-hypothesis in (B and D).

lines represent (for a given Control mean value) the group-average parameter-change predicted to occur in the D-task condition by the shift (green) and the swivel (red) hypothesis, respectively. The cyan dashed line illustrates the best-fit parameters change for a third model, in which weaker constraints are imposed (see below). For both model parameters (M/S and S, shown in the left and right panels, respectively), the "behaviour" of the three subjects with negative ΔLL (swivel-like data) turned out to be very close to the swivel model prediction. In contrast, although the shift model could predict the "behaviour" of the majority ($N = 8$) of the subjects with positive ΔLL better than the swivel model (upper panels, shift-like data), actual data from these subjects were not well accounted for by either model alone. It seems that the simple shift hypothesis is inadequate in fully describing the effects of our urgency manipulation. A possible reason may be that the hypothesis does not incorporate a reduction in the variance of the decision signal (σ^2), as supported by the observation that the parameter change of shift-like data were fitted with much greater success by a model in which σ was only 1-side constrained (cyan line), i.e., it was allowed to remain constant or to decrease. Importantly, the partial release of the constraint on the σ parameter did not improve the goodness of fit with respect to the original shift-model for the three subjects whose "behaviour" was best fitted by the swivel model (for this reason the cyan line in Fig. 6B and D is completely hidden by the green line). This suggests that the fitting improvement obtained with this third model for the eight subjects with positive ΔLL (shift-like data) is not simply due to a weaker constraint but it rather reflects a true functional mechanism affecting saccadic latency.

4. Discussion

With the present study, we have demonstrated that saccadic latencies are strongly affected, namely reduced, by a form of perceptual urgency. This influence on saccadic latency may be particularly relevant ecologically, given that saccades are normally executed to rapidly acquire an object of interest for privileged, foveal processing, and sometimes the object is available only fleetingly. It is important to underscore that the Control and D-task conditions were identical with respect to all spatial and temporal characteristics of the saccade task itself, which is different from the experimental manipulations typically leading to a change in saccadic latency (see Section 1). Our findings thus reveal an indirect influence on oculomotor mechanisms, exerted by the urgency to re-orient gaze toward a location that is relevant for a subsequent act of perception.

In addition to a reduction of saccadic latency, we also observed a relatively modest yet reliable increase in saccadic peak velocity. This is quite remarkable, as it shows that our urgency manipulation had an impact on the encoding of 'low-level' kinematic parameters of saccades, traditionally thought to be rather impermeable to behavioural manipulations.

The parsimonious (and probably oversimplified) LATER model (Carpenter, 1988; Carpenter & Williams, 1995) has proven quite successful in describing a consistent portion of saccadic reaction time data in the present experiments. In particular, with reference to the central notion of the model that a decision signal must grow to a threshold level to initiate a saccade, the urgency effects reported here seem to stem from a steeper rise of the decision signal, in combination with a reduction of its variability. The results obtained with simulation of the experimental data, illustrated in Fig. 6, indicate that for the majority of subjects actual data collected in the D-task condition could be fitted with much greater success if, in addition to a steeper rise of the decision signal, variance was allowed to decrease relative to the Control condition. Reddi and Carpenter (2000, 2003) have previously explored the effects of urgency on saccadic latencies. However, while in their work urgency was simply instantiated by an instruction to the subjects to emphasize speed at the expense of accuracy, the paradigm developed here imposed a critical time constraint for executing the saccade by means of the required letter discrimination, and no explicit instruction was given to the subjects regarding the saccade task (in particular none encouraging to trade accuracy for speed). These differences between our paradigm and that of Reddi and Carpenter may help explain the observation that, while the effects obtained in their study could be accounted for in terms of a lowered threshold for saccade initiation, the effects reported here seem to be compatible with an increase in the rate of rise of the saccade decision signal, together with a decrease of its variability. Future experiments may help clarify this possibility by directly comparing the consequences of the type of urgency manipulation employed by Reddi and Carpenter with those of our own perceptual urgency manipulation. In relation to this point, it is also interesting to consider the results of a previous study exploring the spatio-temporal distribution of visual selective attention during oculomotor smooth pursuit (van Donkelaar & Drew, 2002). The authors found that the change of the distribution of manual reaction times for target detection at an attended vs. non-attended location was consistent with a shift of the recinorm–probit curve, analogous to the effects on saccadic latency produced by our perceptual urgency manipulation. Furthermore, the authors suggested that the likely neurophysiological correlate of the observed shift of the distribution could be the enhancement of neural responses in posterior

visual cortex when selective attention was aligned with the target visual stimulus. This aspect is elaborated below.

Our data also seem to imply that the reduction of reaction time variability, in turn due to a reduced variability in the rate of growth of the decision signal (i.e., a lower value of the parameter σ in the LATER model), might be an efficient strategy, in combination with an overall decrease of the mean latency, to maximally improve performance in a speeded task. It has been speculated (Carpenter, 1999) that the large spread of latency distributions, rather than pure biophysical noise, might be the footprint of an evolutionary strategy favouring adaptive randomisation of behaviour. It is noteworthy that at least part of such variability seems to be susceptible of modulation (specifically reduction) through top-down task-dependent control mechanisms like the ones engaged in our perceptual urgency paradigm.

Our results bear strong similarity with the reported effects of motivational factors on saccadic control in monkeys, which have been well characterized both at the behavioural and neural level (Glimcher, 2003; Ikeda & Hikosaka, 2003; Platt & Glimcher, 1999; Sugrue, Corrado, & Newsome, 2004; Takikawa et al., 2002; Watanabe et al., 2003a, Watanabe, Lauwereyns, & Hikosaka, 2003b). It has been shown that saccadic latencies in macaques are reduced in relation to rewarded versus non- or less-rewarded target locations. Interestingly, location-specific manipulations of reward schedule and expectation can also increase peak velocity of saccades, besides reducing their latency (Takikawa et al., 2002; Watanabe et al., 2003a), which is again similar to the increased saccadic peak velocity obtained with our paradigm. Whether or not our results are functionally equivalent to the aforementioned reward-related effects remains an open issue. Although it is conceivable that proficient performance in letter discrimination (and the resulting positive feedback that we delivered to our subjects) may act as a form of location-specific reinforcement for human observers, it is also possible that a perceptual gain at the saccadic goal location engages other mechanisms from those underlying reward-driven learning.

Neural activity in saccade-related brain areas of the macaque, such as LIP (Platt & Glimcher, 1999; Sugrue et al., 2004) and the basal ganglia (Watanabe et al., 2003b), is enhanced in advance of a saccadic eye movement when a reward is expected. Moreover, in a recent study, Ikeda and Hikosaka (2003) have recorded single-cell activity from the deep layers of the monkey's superior colliculus during a memory-guided saccade task with an asymmetric reward schedule. Interestingly, they have found two types of reward-related modulations in this structure: some neurons showed increased anticipatory (or baseline) activity when reward was expected following a saccade to the neuron's movement field, while other neurons showed enhanced gain of activation after onset of the saccade target stimulus inside the movement field. The authors conjectured that the first type of modulation might be determined by inputs from the basal ganglia, while the enhanced gain could result from cortical input, notably from fronto-parietal regions. It is tempting to speculate that saccade-related activity in the superior colliculus could represent, or at least contribute to, the neural correlate of the LATER decision signal. In particular, the increase in activation gain reported by Ikeda and Hikosaka (2003) would be consistent with the notion, supported by the LATER model-fit of our own data (shift effect), that motivational factors might boost oculomotor responses, leading to a steeper rise of the saccadic decision signal. On the other hand, the finding of an anticipatory increase of baseline activity would be consistent with the notion of a lowered threshold for saccade initiation, given that SRT data do not allow one to distinguish an increase of signal baseline from a reduction of threshold level. At any rate, based on a consistent bulk of electrophysiological evidence, we conjecture that the effects of perceptual urgency revealed in the present study may be mediated by the same structures involved in the reward-related modulation of saccade initiation, including the superior colliculus, the basal ganglia and parietal area LIP. In this regard, it would be particularly interesting to know whether the reduction of saccadic latency in monkeys as a result of reward schedule is accounted for by changes in the rate of rise of the saccadic decision signal or in the threshold level at which a saccade is initiated, or in both. Unfortunately, to the best of our knowledge, this type of analysis is yet to be performed.

Finally, the observation that saccadic latencies are considerably shortened under conditions of perceptual urgency poses a serious methodological *caveat* for experimental research in vision. It is traditionally believed that presenting a visual stimulus in the periphery of the visual field for 200 ms or so will effectively prevent foveation of the stimulus, given the notion that latency of voluntary saccades is rarely shorter than 200 ms. Contrary to this common belief, we show here that foveation of a visual target can occur well within this short stretch of time, particularly when demanded by perceptual needs.

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