Control of sensorimotor variability by consequences.

Laurent Madelain¹, Lucie Champrenaut¹ and Alan Chauvin¹

1. Laboratoire Ureca, UFR de Psychologie, Université Ch. De Gaulle Lille III,
Villeneuve d'Ascq 59653, France

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To whom correspondence should be addressed:
Laurent Madelain
Laboratoire URECA
UFR de Psychologie
Université Lille III
Domaine du Pont de Bois
B.P. 149
59653 Villeneuve d'Ascq Cedex
France
Email: laurent.madelain@univ-lille3.fr
Fax: (+33) (0)3 2041 6324

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ABSTRACT

Studies of reaction time distributions provide a useful quantitative approach to understand decision processes at the neural level and at the behavioral level. A strong relationship between the spread of latencies and the median is generally accepted even though there has been no attempt to disentangle experimentally these two parameters. Here we test the ability to independently control the median and the variability in reaction times. Reaction times were measured in human subjects instructed to make a discrimination between a target and a distractor in a 2AFC task. In a first experiment, saccadic latencies were measured. In a second experiment, we used manual response reaction times. Subjects were trained to produce four different reaction time distributions. A reinforcing feedback was given depending on both the variability and the median of the latency distributions. When low variability was reinforced the standard deviation of reaction time distributions were reduced by a factor of two and when high variability was reinforced, the standard deviation returned to baseline level. Our procedure independently affected the spread and the median of the distribution patterns. By fitting the latency distributions using the Reddi and Carpenter LATER model, we found that these effects could be simulated by changing the distribution of the noise affecting the decision process. Our results demonstrate that learned contingencies can affect reaction time variability and support the view that the so-called noise level in decision processes can undergo long-term changes.
1. INTRODUCTION

Saccades are voluntary eye movements used to acquire the retinal image of an object on the fovea, the high-acuity region of the retina. Saccadic reaction time is usually short and the appearance of a target in the visual field typically elicits saccades with a latency averaging 200 ms. However, it appears that this figure is surprisingly long when compared to the neural delays associated with visual and motor processing (Reddi and Carpenter 2000). In fact, a cascade of events takes place between a visual event and a motor response, a functional description of which usually includes three stages: visual processing, response selection and motor processing (Glimcher 2003; Schall 2001). Because of this, the study of saccadic latency provides a useful quantitative tool for studying how the brain makes decisions.

A number of studies have demonstrated that low-level (i.e. visual) and high-level factors influence the average time it takes to respond to a visual stimulus. For instance, visual factors such as eccentricity (Kalesnykas and Hallett 1994), stimulus arrangement (Fischer and Ramsperger 1984; Kingstone and Klein 1993; Saslow 1967), luminance or contrast (Carpenter 2004a) have been shown to greatly affect saccade latencies. Other higher-level factors such as attention (Crawford and Muller 1992; Hoffman and Subramaniam 1995; Kowler et al. 1995; Madelain et al. 2005; Shepherd et al. 1986), expectation (Anderson and Carpenter 2006; Carpenter 2004a; Carpenter and Williams 1995) or urgency (Montagnini and Chelazzi 2005) can control saccadic reaction-time as well.
Interestingly, saccade latencies also change on a trial to trial basis, even though the procedure remains unchanged. This observation has been reported in a number of studies: over a series of trials, latency varies unpredictably over a wide range, resulting in typically skewed distributions. At a neural level, it has also been reported that responses of single neurons vary from trial to trial (Schall and Bichot 1998; Thompson et al. 1996). Moreover, most models of decision making, such as the LATER model (Carpenter and Williams 1995; Reddi and Carpenter 2000) or the diffusion model (Smith and Ratcliff 2004) are based on the hypothesis that some random noise must be incorporated into the model in order to account for reaction time distributions. It has been proposed that noisy decision processes reflect an evolutionary strategy allowing an adaptive randomization of behavior (Carpenter 1999): small variations in a number of competing processes might produce large unpredictable variations in choice of response. The nature of the process underlying this variability is unknown but is assumed to result either from some dedicated mechanisms of gratuitous randomization (Carpenter and Reddi 2001) or noisy accumulation of information (Ratcliff 2001). An important feature of these models is that they imply a mechanical relation between the mean and the variance of the distribution: changing one single parameter in these models affects both the mean and variance of the latency distributions. This relationship is also found in empirical psychometric studies, and it has recently been proposed that there is a linear relationship between the mean and variance of reaction time distributions (Wagenmakers and Brown 2007; Wagenmakers et al. 2005). Such a relation
might be of importance to allow for a better mathematical description of reaction
time distributions as well as for theoretical considerations.

Despite these strong theoretical predictions, to our knowledge there has
been no systematic attempt to study the ability to control variability in saccadic
latencies and to test experimentally for a possible dissociation between the mean
– or median – and the variability of reaction time distributions by changing one
parameter while keeping the other constant. In this paper we investigate the
effects of reinforcement contingencies on latency variability in the saccadic
system. Specifically, our experimental paradigm was designed to manipulate
independently the median and variability of reaction time distributions. We also
test for the possibility of extending our procedure to manual responses to
ascertain that the control of variability is not specific to the saccadic system.
2. METHODS

Four human subjects (21-36 years of age, two females and two males) participated in the experiment. One subject (CP) was naïve as to the experimental conditions and hypotheses, and three of the subjects were authors of the study. All experimental procedures were reviewed and approved by the Institutional Review Board and each subject gave informed consent.

The target and distractor stimuli consisted of luminance-defined Gaussian patches (sd = 0.93 deg) embedded in background noise (white uniform noise, luminance = 31 ± 23 cd/m²), the target stimulus being brighter than the mask (Fig. 1). The target and distractor stimuli were located to the right and left of a fixation point at an eccentricity of 9.22 deg.

The background noise was different on each trial so that subjects never saw the same image twice during the experiments. Prior to the experimental sessions, we obtained psychometric functions for each subject to determine the luminance value of the target stimulus that yielded approximately 90% correct responses (maximum luminance = 21.16, 21.16 and 20.85 cd/m² respectively for subject LC, LM and AC), and the luminance of the distractor was identical for all subjects (maximum luminance = 16.06 cd/m²). We used a two alternative forced choice procedure and subjects were instructed to make a saccade to the brighter luminance patch (the target stimulus).

Each trial started with a fixation period of 500 to 1000 ms during which a fixation cross superimposed on a patch of random noise was displayed at the
center of the screen (Fig. 1). The target and distractor stimuli then appeared simultaneously and were displayed for 1500 ms. The target stimulus was either placed at the right or left location in a pseudo-random fashion. A fixation cross was then displayed at the center of the monitor. Experimental sessions consisted of 200 trials; each subject performed two sessions on the same day. Prior to the first session subjects performed at least 200 training trials in which they were asked to saccade to the brightest stimulus as fast as they could.

2.1 Experiment One: Saccade latencies

The first experiment studied the ability to manipulate independently the median and standard deviation in saccade latencies distributions. Saccade latencies were computed online.

Subjects received feedback at the end of each trial depending on their choice and the latency of the saccade. If the gaze landed on the target (correct choice) and the latency remained within a set of temporal criteria, the trial was successful and an auditory tone was delivered at the end of the trial, i.e. 1500 ms after the stimulus onset (Fig. 1). If the choice was correct but the latency was too short or too long, a grey square (lighter or darker than the background, respectively) was displayed at the center of the monitor. If the eye landed on the distractor, no feedback was given. When 3 out of 5 consecutive trials were successful including the 5th one auditory feedback (a synthetic voice saying “bravo”) was delivered indicating that the subject won one point. Subjects were instructed to win as many points as they could.
To compute the upper and lower limits of the temporal criteria we used a variation of a percentile procedure (Machado 1989) that allows the criteria to change from trial to trial with respect to the latencies collected on the previous trials (Fig. 2). For each experimental condition and each subject a target median latency and a probability of reward were used: the target median latency was set with respect to a baseline performance (Fig. 2A) and the probability of reward was either 0.35 (low variability) or 0.8 (high variability). Based on the cumulative latency distribution computed over the last 50 correct trials, the lower limit was defined as the lower observed latency less than the target median latency that was within the rewarded probability range. Similarly, the upper limit was defined as the upper observed latency following the target median latency by half of the probability (Fig. 2B and C). The lower limit was automatically set to 0 (see Fig 2D) when the minimum of the last 50 correct trials was too high and the upper limit was set to 1000 when the maximum was too low. For the first 50 correct trials, the limits were computed based on the previous session, allowing across sessions changes.

This procedure had two advantages. First, it guaranteed that the probability that reaction time fell within the limits was approximately constant for all sessions within an experimental condition. Second, it encouraged the subject to respond with a median latency close to the fixed point. Because the temporal criteria changed from trial to trial based on the actual performance of the subject, maximizing the local rate of successful trials resulted in constraining the temporal criteria around the target median latency (Fig 2E).
Each subject was tested in five experimental conditions defined by a target median latency and a probability of reward: baseline, baseline median – low variability (B-LV), baseline median – high variability (B-HV), fast median – low variability (F-LV), slow median – low variability (S-LV). In the first condition (baseline), no feedback was delivered in order to establish baseline performance. Each subject performed 5 sessions (1000 trials) of these baseline trials. In a second condition (B-LV), the target median latency was the median of the baseline distribution and the probability was 0.35. These values were chosen to encourage subjects to respond with a median latency similar to the baseline one but with lower variability. In a third condition (B-HV), the target median latency remained unchanged and the probability was set to 0.8. To further encourage subjects to increase the variability of the latency distribution while keeping the median constant, the probability of receiving feedback on a successful trial was 1 minus the frequency of the latency over the last 50 correct trials. For instance, if the frequency of the binned latency X was 0.4 on the last 50 correct trials, the subjects received a feedback with a probability of 0.6 when making saccades with binned latency X, even though the latency fell within the temporal criteria. This forced subjects to vary their reaction time in order to maximize the probability of receiving a feedback. In the last two conditions (F-LV and S-LV) the probability was set to 0.35 and the fixed points corresponded to the latencies at which the frequency reached 0.2 and 0.8 in the cumulative baseline distributions respectively (Fig. 2A). In each of these experimental conditions, the limits were adjusted on a trial to trial basis (Fig. 2E). An experimental condition was
completed when both the median and standard deviation remained mostly unchanged for the 5 previous sessions (1000 trials). One subject (CP) performed the same conditions but in a different order (baseline, B-LV, S-LV, F-LV and B-HV).

2.2 Experiment Two: Manual reaction time

The second experiment was similar to the first except that manual responses were used. Subjects were asked to press a left or right button depending on whether they saw the target stimulus on the left or on the right side of the screen. Manual reaction times were computed online by measuring the time between the stimulus and the response onset. The same five experimental conditions were used (baseline, B-LV, B-HV, F-LV, S-LV). The cumulative distributions of reaction time in the baseline condition were used to determine the target median latencies for the other 4 conditions. This experiment was conducted two months after the end of the first experiment. Only three subjects (LC, LM and AC) performed this second experiment.

2.3 Data acquisition and analysis

Stimuli were generated on a Power Mac G4 using the Psychophysics Toolbox extensions for Matlab (Brainard 1997; Pelli 1997), and displayed on a video monitor (Iiyama HM204DT, 100Hz) at a viewing distance of 60 cm. To minimize measurement errors, the subject’s head movements were restrained using a head and chin rest so that the eyes in central position were directed toward the center of the screen. Presentation of stimuli, and acquisition, display,
and storage of responses were controlled by a second computer using the LabView Real-Time software package (National Instruments®). Trigger signals from the visual display computer to the LabView computer allowed us to synchronize data collection to stimulus presentation with 1-ms resolution. Eye movements were measured continuously with an infrared video-based eye tracking system (ISCAN Inc., RK-726) at 240 Hz. Before each session, we calibrated the eye tracker by having subjects repeatedly fixate a set of seven horizontal locations to generate a linear function for converting raw eye tracker values to horizontal eye position.

For on-line saccade detection, an algorithm was used to filter and analyze the velocity signal and saccades were identified by applying a fixed set of amplitude criteria values to the velocity signal at the end of each trial. The algorithm automatically detected the onset of the first saccade within 1000 ms after the target onset and the gaze landing position was determined by taking the median position over 100 ms, 50 ms after the saccade onset. This landing position was then used to determine whether the subject chose the target or the distractor stimulus. To avoid anticipatory responses, trials in which the latency was shorter than 100 ms were discarded. Manual responses were detected online by monitoring changes in the buttons status with a 1ms resolution.

For off-line analysis, an interactive analysis program was used to filter, display, and analyze the data. Horizontal eye velocities were obtained by differentiating the eye position signal using a finite impulse response (FIR) filter (-3dB at 54 Hz). Eye acceleration was then obtained by applying the same FIR
filter to the velocity signals. Saccades were detected by applying a set of velocity and acceleration criteria.

We measured only the first saccade within 1000 ms after the target onset, and we computed latencies with respect to the target onset. We omitted trials in which the saccade was opposite in direction to the probe stimulus (incorrect responses) or had a latency shorter than 100 ms (anticipatory responses, less than 0.2% of the trials). Saccades were measured in the last 5 sessions (1000 trials) of each condition.
3. RESULTS

3.1 Learned changes in variability of saccade latencies

As illustrated by the distributions plotted on Figure 3 for a single subject (AC), the latency distribution in the baseline condition was broader than in the low variability conditions (B-LV, F-LV and S-LV). Figure 3A shows the latency distribution for a single subject (AC) in the second condition (B-LV) superimposed to the baseline distribution. It can be seen that, although the median latencies are similar (464 and 476 ms, respectively, in the baseline and B-LV conditions), the dispersion of the saccade latencies was greatly reduced by our procedure. In particular, the frequencies in the high and low tails of the distribution were much smaller in the B-LV condition, leading to an increase in the frequencies at the center of the distribution. A similar effect was observed in the F-LV and S-LV conditions (Fig 3C and D), although the median latencies were now respectively shorter (392 ms) or longer (572 ms) than in the baseline trials. In contrast, the distribution in the high variability condition was very similar to the baseline one (Fig. 3B) with identical medians (464 ms).

These changes in the distributions were similar for the other subjects. To estimate the changes in the medians we computed bootstrap percentile intervals (p<0.05) using Martinez & Martinez (2002) Matlab toolbox (Fig. 4A). These revealed that the medians from the F-LV and S-LV conditions were systematically faster (by 69 ms on average) and slower (by 89 ms on average)
than the baseline ones. For the B-HV condition, all the medians fall within the percentile intervals. For the B-LV condition, two were faster (by 12 ms and 16 ms respectively for subjects LM and CP) while one was slower (12 ms for subject AC).

To estimate the dispersions we computed the standard deviation for each set of data and the bootstrap percentile intervals (p<0.05) for the baseline standard deviations. Figure 4B shows that the standard deviation was significantly reduced in the low variability conditions when compared to the baseline condition for all subjects. On average, the standard deviation in the baseline condition was almost twice as large as in the low variability conditions (99 vs. 54, 45 and 57 ms in the B-LV, F-LV and S-LV respectively). In the high variability condition the standard deviations (105 ms on average) were significantly higher for subjects LM and CP (by 18 ms and 9 ms respectively) while it was lower in one other subject (subject LC by 5 ms) compared to the baseline.

To illustrate the distinctness of the distributions, we show cumulative frequency distributions for each condition for each subject (Fig. 4C, D and E). In general, the slopes were steeper in the low variability distributions, reflecting the lower dispersions, while the curves for the baseline and B-HV distributions were almost perfectly superimposed. It can be seen that our procedure also affected the median latencies (the point at which the cumulative frequency equals 0.5). In the baseline, B-LV and B-HV conditions, the median latency remained almost unchanged (with a 7 ms average absolute difference). In the F-LV conditions, the median latency was slightly shorter than the point at which the cumulative
frequency reached 0.2 in the baseline distributions (by 8 ms on average) and in
the S-LV it was slightly shorter than the point at which the cumulative frequency
reached 0.8 in the baseline distributions (by 9 ms on average).

Overall, our procedure was able to constrain the latency distributions: the
dispersions were smaller in the low variability conditions and larger in the
baseline and high variability conditions and the median latencies were close to
the chosen target median latencies. One could postulate that these variations in
latencies were correlated with changes in the accuracy of the task, following a
classical speed-accuracy tradeoff law. However, the percent correct remained
mostly unchanged during the experiment. On average, the proportions of correct
responses were 84.4 %, 88.1 %, 87.8 %, 87.6% and 90.9% in the baseline, B-
LV, B-HV, F-LV and S-LV conditions, respectively. It is therefore not surprising
that the correlation coefficients between median latencies and percent correct
(0.35, p=0.12) and between standard deviations and percent correct (-0.35,
p=0.13) were low. Interestingly, we did not observe any significant change in the
peak velocities of saccades.

The number of trials necessary to achieve learning revealed large inter-
conditions differences. On average, 4800 trials were necessary to complete the
B-LV condition, 1900 trials were collected in the B-HV condition, 1250 in the F-LV
condition, and 2950 trials in the S-LV condition.

3.2 Learned changes in variability of manual reaction times

In the second experiment, the changes in the distributions were similar to the
ones in the first experiment. Figure 5A shows the medians as well as the
bootstrap percentile intervals (p<0.05) for the three subjects. These revealed that the medians from the F-LV and S-LV conditions were systematically faster (by 65 ms on average) and slower (by 87 ms on average) than the baseline ones. For the B-LV condition, all the medians fall within the percentile intervals. For the B-HV condition one median was slower (by 10 ms for subject LC).

To estimate the dispersions we computed the standard deviation for each set of data and the bootstrap percentile intervals (p<0.05) for the baseline standard deviations. Figure 5B shows that the standard deviation was significantly reduced in the low variability conditions when compared to the baseline condition for all subjects. On average, the standard deviation in the baseline condition was almost twice as large as in the low variability conditions (102 vs. 50 and 56 ms in the B-LV, F-LV and S-LV respectively). In the high variability condition the standard deviations (117 ms on average) were significantly higher for subjects LC and LM (by 32 ms and 15 ms respectively) compared to the baseline.

In the cumulative frequency distributions (Fig. 5C, D and E) the slopes were steeper in the low variability distributions than in the baseline distributions, reflecting the lower dispersions, while the curves for the B-HV distributions were slightly shallower. Our procedure also affected the median latencies: In the baseline, B-LV and B-HV conditions, the median latency remained almost unchanged (with a 4 ms average difference). In the F-LV conditions, the median latency was similar to the point at which the cumulative frequency reached 0.2 in the baseline distributions (± 1 ms on average) and in the S-LV it was slightly
shorter than the point at which the cumulative frequency reached 0.8 in the baseline distributions (by 3 ms on average).

The proportions of correct responses were in general high (92.8% on average). The correlation between accuracies and median latencies (0.5, p=0.057) and between standard deviation and percent correct (-0.09, p=0.75) were not significant.

Again, the number of trials necessary to achieve learning revealed large inter-condition differences. On average, 3200, 1133, 1333 and 3333 trials were necessary to complete the B-LV, B-HV, F-LV and S-LV conditions respectively.

3.3 Assessing changes in latency variability using the LATER model

To examine whether the shapes of the latency distributions might explain the changes in saccade programming we used the LATER model (Reddi and Carpenter 2000). This simple model assumes that response latencies are a function of the time it takes for a monotonically rising decision signal to reach a threshold value (Fig 6 top panels). The decision signal depends on the rate of information accumulation and the threshold represents the urgency. The rate of rise changes on a trial by trial basis following a Gaussian distribution. When the distributions of latencies are plotted on a reciprobib graph (i.e., plotting the cumulative probability on a probit scale as a function of the reciprocal of latency) a straight line results (Fig 6 intermediate panels). According to this model, changes to the saccade trigger mechanism alter the reciprobib plots in distinctive ways (Fig 6, top panels). Changes in the threshold (θ) with no change in the rate of rise alter the slope, such that the line pivots about the infinite-time intercept.
Changes in the rate of rise ($\mu$) of the decision signal with no change in the threshold result in a parallel shift of the line. A third possibility, not usually included in discussions of the LATER model (but see Madelain et al. 2005) is that increasing the variability of the rate of rise (the standard deviation of the rate variable, $\sigma$) decreases the slope and intercept of a cumulative distribution without changing its median.

We applied the LATER model to the saccade latency distributions following the fitting methods described by Reddi and Carpenter (Reddi and Carpenter 2000). Two distinct patterns emerged from the reciprobit lines (fig 6 intermediate panels). First, the distributions of latencies for the F-LV and S-LV conditions seemed to involve a swivel around the infinite-time intercept from the distribution in the B-LV condition, attributable to an increase or decrease of threshold ($\theta$). Second, the distributions of latencies for the baseline and B-HV conditions mostly involved a rotation around the median from the distribution in the B-LV suggesting that the changes in distributions were mostly a consequence of an increase of the standard deviation of the rate of rise ($\sigma$). To obtain a quantitative evaluation of these observations we contrasted the three alternative hypotheses that the distributions in the baseline, B-HV, F-LV and S-LV might be obtain from the B-LV distribution either through a swivel around the infinite-time intercept, a parallel shift, or a rotation around the median. We first computed the best fits compatible with the three hypotheses in terms of the required changes in the model and the sum of square error associated with each fit (Fig 6, bottom panels). We found that the SSE was systematically smaller for the rotate model
for the baseline and B-HV conditions and for the swivel model for the F-LV (except for subject CP) and S-LV conditions. This was true for both saccade and manual response latencies. This led us to compute the difference of LogLikelihood for the rotate versus swivel models. As illustrated in Figure 7 (panel A) the differences in the distributions in the B-LV condition versus the baseline and B-HV conditions were more likely to be a consequence of a change in variability than a change in threshold. On the other hand, the distributions in the F-LV and S-LV conditions were more likely to come from a change in threshold when compared to the B-LV condition. We performed the same analysis for the manual responses latencies and found similar results (Figure 7B).
4. DISCUSSION

We have shown that variability in reaction times may be manipulated through learned contingencies. The standard deviation of latency distributions were typically reduced by a factor of two in the low variability conditions both for saccadic and manual responses. Furthermore, our data revealed that our procedure affected independently the median and the variability: in each experiments three conditions produced similar medians (i.e. the baseline, B-LV and B-HV conditions) while three conditions produced similar variability (B-LV, F-LV and S-LV conditions). Interestingly, our learning procedure involved long-term modifications, allowing us to progressively shape the distributions by adapting the upper and lower limits of the temporal criteria used to modulate the consequences of the subjects’ responses: there was a cumulative change in the involved decision processes so that variability progressively decreased in the low-variability conditions.

We will first discuss the possible effects of the reinforcement contingencies on variability, then we will discuss what these results say about decision process models, and finally, what are the implications of the ability to voluntary control the variability of reaction times.

4.1 Effects of the reinforcement contingencies

Recent experiments in monkeys have shown that latencies were shorter when making a saccade to a rewarded location than to non-rewarded locations
(Ikeda and Hikosaka 2003; Takikawa et al. 2002; Watanabe et al. 2003). These changes at the behavioral level were correlated with modulations at the neural level (see also (Platt and Glimcher 1999; Sugrue et al. 2004). An interpretation is that saccades are, at least partly, under the control of their consequences. In natural situations, a saccade to a particular stimulus allows an optimization of the visual perception of the target. This optimization in return acts as a reinforcer for the saccadic system, allowing subsequent adaptive responses to changes in the environment. A recent study used this observation to build a new experimental design (Montagnini and Chelazzi 2005). Subjects were asked to perform a letter discrimination that required a saccade to a peripheral stimulus displayed for a brief interval following the median saccade landing time such that saccade latency was the main determinant of the task accuracy. In other words, subjects were reinforced when making saccades with short latency by the ability to perform the perceptual task. Montagnini and Chelazzi (Montagnini and Chelazzi 2005) showed that saccade latencies in humans are reduced under these conditions of perceptual urgency. Together, these results strongly suggest that triggering a saccade is an operant behavior (i.e., a class of response controlled by environmental contingencies, (Skinner 1981).

Our data revealed that consequences might act on the median as well as on the variability of saccadic reaction times. In other words, the median and variability are operant dimensions, i.e., response attributes influenced by reinforcers. Our experimental procedure was based on the assumption that, given a baseline repertoire of latencies, one may modify the probability of
emission of a subclass of latencies by controlling the relationship between a range of latencies and the reinforcer. In the Low-variability conditions this range of latencies was restrained in order to increase the probability of a narrow subclass, while in the High-variability condition the range was maintained large. This results in the modifications plotted in Figure 3. To put the matter in terms of selectionist formulation, in the B-LV condition, extreme values were selected against from the population of latencies (Figure 3A), whereas in the F-LV and S-LV conditions (Figures 3C and 3D) fast or slow subclasses were selected respectively. This is analogous to stabilizing selection (Fig 3A) and directional selection (Figures 3C and 3D), two concepts used in population genetics to account for changes in populations. We are confident that contingencies are responsible for these changes, instead of simple repetition of the task, because variability was set back to its baseline level in the B-HV condition.

It is interesting to point out that our procedure was successful because subjects maximized the local probability of reward. To make that point clearer, we will discuss the B-LV condition more precisely. The probability of reinforcement was set to 0.35 and the actual upper and lower limits of the temporal criteria were first computed based on the baseline distribution. Therefore, subjects could have obtain 35% of reinforced trials by maintaining this overall distribution at its baseline level. However, maximizing the local probability of reinforcement resulted in local changes in the distributions that, in return, resulted in reducing the range of reinforced latencies. This is apparent in Figure 2E. In other words, subjects could have obtained the exact same global
proportion of successful trials without changing the variability of the latencies distributions, but they did not. However, a point was given only when 3 out of 5 consecutive trials were successful, an incentive to maximize the local probability of success. We think that without this incentive we might have failed to show reductions in variability.

It should be pointed out that inducing these changes in variability required a large number of trials, about 10000 on average for each subject in each experiment. Although we did not explicitly measure the difficulty of learning, the number of trials necessary to achieve learning might reveal inter-conditions differences. Interestingly B-LV and S-LV conditions systematically required about three times as many trials as the B-HV and F-LV conditions for subjects AC and LM. This implies that it is somehow easier to increase variability than to decrease it unless the median reaction time is reduced as well. The latter observation is in conformity with a number of experiments indicating that the mean and variability in reaction time are usually tightly linked (Wagenmakers and Brown 2007). Interestingly, the average number of trials in the first condition was smaller in the second experiment than in the first one (3200 and 5200 respectively). This might indicate a transfer of the learned changes, despite the fact that two months elapsed between the two experiments. However, our experiments were not designed to test for this facilitation and further studies are necessary to explore this possibility.
4.2 Decision models

Visual processing, response selection and motor processing are the three stages associated with a reaction time (Glimcher 2003; Schall 2001). Although each of these stages might contribute to variability in latencies, we think that our procedure mostly affected the response selection – or decision process. First, the visual stimulus was constant all through the experiments for a given subject, preventing from major changes in visual processing. The effects of perceptual learning were probably limited because subjects were trained to respond to the stimulus prior the first session. Moreover, perceptual learning should always result in faster and less variable latencies. Second, it is commonly accepted that the motor processing stage’s contribution to latencies variability is only limited (Hanes and Schall 1996). This is why we now focus on decision models.

A class of reaction time models assumes that motor responses are triggered when an internal decision signal reaches a threshold value (Reddi and Carpenter 2000; Smith and Ratcliff 2004). By applying Carpenter’s LATER model to our reaction time data we found different patterns of changes associated with changes in latency distributions. Although previous studies using this model have generally identified only changes in threshold or changes in the mean rate of decision signal (but see (Kurata and Aizawa 2004; Madelain et al. 2005; Montagnini and Chelazzi 2005) our data suggest that our procedure might affect either both factors or the variability of rate. As we pointed out elsewhere (Madelain et al. 2005) the LATER model does not fully disentangle the effects in changes in these three factors. In fact, any change in the reciprobit plot attributed
to a single parameter (e.g., the threshold) could also be attributed to a
combination of modifications in the other two parameters (e.g., rate and
variability of the decision signal). This could be viewed as a weakness of the model
but classical interpretations using the LATER model are usually based on the
assumption that each of these parameters is related to a particular property of
the situation. This allows predicting specific changes in the distributions when
manipulating one of these properties. The rate of rise is related to the time it
takes to accumulate information, while the initial level reflects prior expectation.
The threshold corresponds to a significance level in a statistical test: given a
particular case what probability of making the wrong decision does the system
accept? It should be pointed out that the threshold and initial level induce similar
changes. In our experiments, the rate of rise and the initial level probably
remained unchanged because the distractor and target stimuli remained constant
as well as the probability of target location. Therefore, we propose that only the
threshold and variability of rate of rise were affected by our manipulations. In fact,
the distributions in the B-LV, F-LV and S-LV conditions were compatible with
swiveling around about a common infinite-time intercept, which indicates a
change in threshold. In other words, it might be that when manipulating the
medians while maintaining the variability approximately constant, urgency was
mostly affected. The distributions in the baseline, B-LV and B-HV conditions were
compatible with a rotation around the median, which indicates a change in
variability. Therefore, directly manipulating the variability of the distributions is
best explained by a change in the variability of the rate of rise.
To our knowledge, only two papers have explored the possibility of altering the variability of the rate of rise in isolation (Madelain et al. 2005; Montagnini and Chelazzi 2005). However, this is the first direct evidence that in some specific manipulation this parameter must be included to properly use the LATER model. This maybe problematic in that the reciprobit plot allows only two parameters, the slope and infinite-time intercept. Traditional use of the LATER model assumes that two parameters are at play, the threshold (or the initial level of the rate of rise that is functionally equivalent but has a different conceptual meaning) and the average rate of rise, to capture the changes in the reciprobit plot, each fitting parameter finding its equivalent in the model. However, we now show that a third parameter (the variability of the rate of rise) must be taken into account when the experimental manipulation imposes a particular variability on the distributions.

Other decision models, for instance the diffusion model (Smith and Ratcliff 2004) or the leaky competing accumulator model (Usher and McClelland 2001), also assume that a reaction time results from the projection on the time axis of the intercept of a decision signal reaching a threshold level. Variability in the drift, which represents the encoded stimulus information, generates variability in the reaction time distribution: a Gaussian process (the drift variability) generates asymmetrical distributions. Here the drift rate varies randomly from trial to trial for any given stimulus, because of random variations in the efficiency of visual transduction and encoding. The inclusion of drift variance in the model serves two functions. On the one hand, it allows the model to predict that correct responses will be made, on average, more rapidly than errors. On the other
hand, it limits the speed-accuracy tradeoff and ensures that observers cannot attain arbitrarily high levels of accuracy (Smith and Ratcliff 2004). In this class of models, variability is used because it generates errors and variable reaction times. Assuming variability reflects some perceptual noise requires a fixed standard deviation of the drift variability in the model for a given experimental condition. This implies that variability grows with the mean reaction time due to the geometry of the decision process (Wagenmakers and Brown 2007; Wagenmakers et al. 2005). However, our data show a clear independence between the mean and variance even though the stimuli, probability of target location, and urgency remained constant. This implies that these models must also account for changes in variability without changing the drift and threshold. Again, the drift variability must be adaptable independently of the drift, the initial level, and the threshold.

4.3 **Significance of reaction time variability**

A number of studies explored the possibility of controlling variability of behavior. For instance, (Blough 1966) rewarded pigeons for pecking a response key if the time between consecutive pecks had occurred less frequently in the recent past. The results were such that the distributions of inter response time were close to those of a random model, unlike the stereotyped baseline distributions. Similarly, when animals received a reinforcer for generating sequences of left or right responses, provided that such sequences had not occurred during the most recent trials, they produced high degrees of variability (Page and Neuringer 1985; Shimp 1967). On the other hand it has been reported
that reinforcing a class of responses reduces variability (see (Boulanger et al. 1987) for a review). Taken together, these results indicate that one effect of reinforcement is to reduce variability unless reinforcement is contingent to response variation itself (see (Neuringer 2002) for a review).

Montagnini and Chelazzi (Montagnini and Chelazzi 2005) observed a diminution of variability when rewarding eye movements and our data suggest that variability in reaction times might be manipulated by controlling its relationship with environmental contingencies, a pattern of results compatible with previous work on variability in behavior. Interestingly, this implies that, to some extent, the baseline level of variability in our experiment also reflects environmental constraints, even though we did not explicitly manipulate them. Because baseline variability was higher than in the Low-variability conditions one could postulate that these constraints were not very strong: a high level of variability might just reflect that all latencies are equally adapted to the context. This view departs from Carpenter’s proposition that variability reflects some sort of purposeful internal randomization (Carpenter 1999). An alternative could very well be, for instance, that the saccadic system does not always allocate all its resources to produce particular latencies because the point in time at which the gaze lands on the target is simply not relevant. However, when the situation imposes a particular range of reaction time, the system might allocate a less variable amount of resources to control the latencies. Of course this does not imply that the system is totally free of random noise, and in fact it seems
impossible to completely eliminate the variability, but it appears that postulating a deliberate randomization of reaction times is not necessary.

That variability is related to particular environmental constraints is at the root of selectionist theories. The ability to select a particular class of responses is constrained by the range of variations. Whatever increases variability might contribute to the appearance of new responses (Neuringer 2002) and it is not surprising that the relationship between the level of variability and the ability to learn new responses has been experimentally demonstrated (Grunow and Neuringer 2002). These ideas have also been proposed in relation to the LATER model: randomness in timing might result in randomness of choice, allowing unpredictable or exploratory behaviors (Carpenter 2004b). Therefore, the functional significance of the ability to control variability of reaction time might extend beyond noise reduction and reflect adaptive abilities of living organisms.
Reference list


Captions

Figure 1 : Methods. Temporal sequence of a trial for experiment 1 and 2. The brightness difference between the target (right) and distractor (left) stimuli have been enhanced for better legibility.

Figure 2 : Methods. (A) Single baseline cumulative frequency distribution of saccade latencies (Subject LC). The diamonds indicate the target median latencies used for the four experimental conditions (see text for explanations). (B) Upper and lower limits of the temporal criteria for a single session in the B-LV condition (subject LC). The gray dots indicate the corresponding saccade latency for each trial. (C) Computation of the upper and lower limits of the temporal criteria for a single trial. The small circles plot the cumulative frequency distribution of saccade latencies for the previous 50 trials. The diamond indicates the target median latency up and down triangles indicate the upper and lower limits respectively. (D) Same as (C) except that the lower limit is set to 0 due to the lack of short latencies in the previous 50 trials. (E) Changes of the upper and lower limits of the temporal criteria for a single subject (LC) in the saccade experiment. Vertical gray lines indicate the beginning of a session. Changes of experimental conditions are indicated in the text boxes above the graph.

Figure 3 : Frequency distribution of saccade latencies for the baseline (gray histograms) and (A) B-LV, (B) B-HV, (C) F-LV and (D) S-LV experimental condition respectively (black histograms) for a single subject (AC).
Figure 4: Saccadic latencies. (A) Median of saccadic latencies in the last five sessions of the baseline (black circles), B-LV (white circles), B-HV (white diamonds), F-LV (white up-triangles) and S-LV (white down-triangles) conditions respectively for the four subjects. The vertical black lines indicate the 95% percentile intervals. (B) Standard deviations of saccadic latencies in the last five sessions of the baseline (black circles), B-LV (white circles), B-HV (white diamonds), F-LV (white up-triangles) and S-LV (white down-triangles) conditions respectively. The vertical black lines indicate the 95% percentile intervals. (C, D, E and F) Individual cumulative frequency distributions of saccade latencies for the baseline (bold line) B-LV (circles), B-HV (diamonds), F-LV (up-triangles) and S-LV (down-triangles) conditions respectively.

Figure 5: Manual reaction times.

(A) Median of manual reaction times in the last five sessions of the baseline (black circles), B-LV (white circles), B-HV (white diamonds), F-LV (white up-triangles) and S-LV (white down-triangles) conditions respectively for the three subjects. The vertical black lines indicate the 95% percentile intervals. (B) Standard deviations of manual reaction times in the last five sessions of the baseline (black circles), B-LV (white circles), B-HV (white diamonds), F-LV (white up-triangles) and S-LV (white down-triangles) conditions. The vertical black lines indicate the 95% percentile intervals. (C, D, and E) Individual cumulative frequency distributions of manual reaction times for the baseline (bold line) B-LV
(circles), B-HV (diamonds), F-LV (up-triangles) and S-LV (down-triangles) conditions respectively.

Figure 6: The LATER model. Upper panels: Schematic illustrations of the LATER model (left) and changes in the reciprobit plots associated with each parameter (right). Intermediate panels: Reciprobit plots of the latencies for the first experiment for the baseline (gray squares) B-LV (circles), B-HV (diamonds), F-LV (up-triangles) and S-LV (down-triangles) conditions respectively. Bottom panels: histograms of the sum of square error associated with each model in the saccade (upper line) and manual responses (bottom line) experiment. The vertical axis is broken for better legibility.

Figure 7: Difference Log-likelihood for the rotate versus swivel models fitted to the data to account for changes in latency distributions with respect to the B-LV condition. (A) Saccade experiment. (B) Manual responses experiment.


Figure 5
Madelain, Champrenaut, Chauvin

A. Graph showing median latency (ms) for subjects LC, LM, and AC.
B. Graph showing standard deviation (ms) for subjects LC, LM, and AC.
C. Cumulative frequency plots for Subject LC, showing time wrt stimulus onset (ms).
D. Cumulative frequency plots for Subject LM, showing time wrt stimulus onset (ms).
E. Cumulative frequency plots for Subject AC, showing time wrt stimulus onset (ms).
Figure 6
Madelain, Champrenaut, Chauvin

Target onset
Response initiation
Threshold level
Decision signal
Latency

Cumulative probability (%)
Increased \( \theta \)
Decreased \( \mu \)
Decreased \( \sigma \)

Cumulative probability (%)

Time wrt stimulus onset (ms)

Subject LC
Subject LM
Subject AC
Subject CP

Baseline wrt B-LV
B-HV wrt B-LV
F-LV wrt B-LV
S-LV wrt B-LV

Models
Figure 7

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Time wrt stimulus onset (ms)

LogLikelihood Difference

Swivel wrt B-LV

Rotate wrt B-LV

baseline B-HV F-LV S-LV

-40

-20

0

20

40

60

Subject LC

Subject LM

Subject AC

Subject CP

Page 45 of 45