The Time Course of Stimulus Expectation in a Saccadic Decision Task

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Oswal A, Ogden M, Carpenter RH. The Time course of stimulus expectation in a saccadic decision task. J Neurophysiol 97: 2722–2730, 2007. First published January 31, 2007; doi:10.1152/jn.01238.2006. Because the time to respond to a stimulus depend markedly on expectation, measurements of reaction time can, conversely, provide information about the brain’s estimate of the probability of a stimulus. Previous studies have shown that the quantitative relationship between reaction time and static, long-term expectation or prior probability can be explained economically by the LATER model of decision reaction time. What is not known, however, is how the neural representation of expectation changes in the short term, as a result of immediate cues. Here, we manipulate the foreperiod—the delay between the start of a trial and the appearance of the stimulus—to see how saccadic latency, and thus expectation, varies with different delays. It appears that LATER can provide a quantitative explanation of this relationship, in terms both of average latencies and of their statistical distribution. We also show that expectancy appears to be subject to a process of low-pass filtering, analogous to the spatial blur that degrades visual acuity.

I N T R O D U C T I O N

Expectation—the ability to predict events in the outside world—can be regarded as almost the defining function of the brain. Yet we know relatively little about how expectation alters in response to external cues. One approach that has turned out to be quite fruitful over the last decade in terms of elucidating expectation is the study of reaction time or latency. Rather little of the time taken to respond to a stimulus is due to sensory transduction and the speed with which information is carried by nerves; rather, it represents decision time (Carpenter and Williams 1995). Reaction times in individual trials show a great deal of random variability, but with large numbers of trials, precise data can be gathered about the underlying statistical distribution, from which the parameters of the underlying decision process can be estimated. Saccades—the eye movements made to foveate a visual target—have been much used for this purpose, as with modern computer-based equipment they can be measured rapidly and noninvasively. Both with saccades and other responses, latency distributions are skewed, with a long tail toward longer reaction times; but under a wide range of conditions the reciprocal of latency is usually found to be Gaussian.

This observation led to the LATER (Linear Approach to Threshold with Ergodic Rate) model of decision making, in which a decision signal \( S \), representing the log probability of a hypothesis (such as the existence of a particular target) rises linearly from a starting level \( S_0 \) representing prior probability until it reaches a criterion or threshold level \( S_T \), at which a response is initiated (Carpenter and Williams 1995). The distribution is explained by supposing that the rate of rise \( r \) varies randomly between trials with a Gaussian or normal distribution, with mean \( \mu \) and variance \( \sigma^2 \) (Carpenter 1999); since the latency is given by \( (S_0 - S_T)/r \), it follows that the reciprocal of latency is also a Gaussian. To aid visualization it is useful to convert this Gaussian into a straight line (Fig. 1) by plotting cumulative latency distributions on a probit scale as a function of reciprocal latency. The slope of the resulting reciprobit plot is equal to \( 1/\sigma \), whereas the intercept with the horizontal 50% axis gives the median latency.

This empirically derived model is strengthened by its mathematical interpretation as an ideal Bayesian decision maker (Bayes 1763). Behavioral studies have confirmed that altering such factors as urgency, information rate, or expectation generates changes to both average latencies and, more demandingly, their statistical distribution, that are predicted by changes of the underlying parameters \( \mu \), \( S_0 \), or \( S_T \). Manipulating either prior probability or the criterion level alters the median latency in a manner compatible with a swiveling of the reciprobit plot about the fixed intercept \( I \) (Fig. 1) of the distribution with the \( t = \infty \) axis (Carpenter and Williams 1995; Reddi and Carpenter 2000). In contrast, changing \( \mu \) by modifying the information rate generates a parallel shift of the plot, without change of slope (Reddi et al. 2003).

A consequence of LATER is that there is a direct (actually logarithmic) relationship between prior probability and average latency, so that measurements of latency provide a tool by which the brain’s representation of prior probability or expectation can be probed. Previous work concentrated mainly on “static” or long-term expectation. A particularly clear example is a conventional saccadic step task, in which, after a warning cue, a visual target jumps suddenly either to the left or to the right and subjects must follow it with their eyes. Normally, one would arrange for the target to jump randomly to left or right with 50% probability, but it is an easy matter to arrange for it to jump more often in one direction than the other—for instance, 95% of the time to the left and 5% to the right. This change in probability is soon reflected in changes in the latencies in the two directions, becoming faster to the left and slower to the right, settling down asymptotically with latencies that are a logarithmic function of the probabilities on each side (Carpenter and Williams 1995).

However, in such an experiment there is another kind of expectation at work, operating over a shorter timescale, and related to the structure of a single trial. In a reaction time task, a trial typically begins with some kind of warning cue, followed after a delay by the stimulus: this delay is the foreperiod. Clearly the subject’s expectation that the target will move is considerably higher after the cue than before; furthermore, it is...
well known that if the foreperiod is constant, latencies become much shorter and there is an increased tendency to anticipate, resulting in errors (Luce 1986). For this reason, experimenters normally make the foreperiod randomly variable from trial to trial, so that the target is not expected at a particular time: in general, the more variable the foreperiod, the slower the reaction time (Bevan et al. 1965).

Typically the foreperiod consists of a fixed portion $F_0$ and a portion $F_R$ of random duration: $F_0$ is intended to minimize any immediate interference from the cue and ensure that the subject is ready to respond to the stimulus. The simplest kind of randomization, used routinely by nearly all experimenters, is for the distribution of $F_R$ to be rectangular; that is, that the probability that $F_R$ lies between $t$ and $(t + \delta)$ is given by $S(t)$, where $S(t)$ is a constant $\alpha = \delta/T$ and $T$ is the maximum possible value of $F_R$. However, although $S$ is constant, the subject’s expectation throughout the foreperiod is not (Bertelson 1966; Elthon and Lawrence 1955; Requin et al. 1973; Thomas 1967). It is clear that as time goes on, and $t$ approaches $T$, expectation—the probability of the target appearing in the next $\delta$ given that it has not done so already—will increase; when $t = T - \delta$ the subject can be absolutely certain that it will appear in the next $\delta$. [This assumes there are no catch trials, that is, trials in which the target is not presented at all. If the proportion of such trials is $q$, then $S = \alpha/(1 - q)$ and the expectation just before the end of the foreperiod is $l/(1 - q)$ rather than $l$.] It is clear that the subject’s expectation $E(t)$ that the target will appear in the next period $\delta$ is given, for $\delta > (T - t)$, by $\delta/(T - t)$, and will rise hyperbolically throughout $F_R$ (Fig. 2).

From the experimenter’s perspective, this can be an undesirable state of affairs because it means that a component of the variability of the RT is due to the timing of the stimulus rather than to variability within the decision mechanism itself. What is needed is a “nonaging” foreperiod (Nickerson and Burnham 1969): that is, one for which it is $E(t)$ rather than $S(t)$ that is constant, so that the stimulus is always equally unexpected. To see how this can be achieved, we need to begin with the relation between $S$ and $E$ in the more general case, when $S$ may be varying, $E(t)$, which may be termed the hazard function (Luce 1986), is given by the objective probability of the stimulus appearing in the next period $\delta$ as a fraction of the remaining total objective probability

$$E(t) = \frac{S(t)\delta}{\int_s^t S(u)du} \quad (1)$$

Thus to achieve a nonaging foreperiod, so that $E(t)$ is constant, equal say to $\beta$, for all $t$ we must have

$$k\int_0^\infty S(u)du = S(t) \quad (2)$$

where $k = \beta/\delta$, and for which the solution is $S(t) = ke^{-kt}$, giving $\int_0^\infty S(u)du = 1$, as required.

Foreperiod effects on response times have been quite widely studied by psychologists in an attempt to probe the underlying cognitive phenomena (Buckholtz and Ruggins 1978; Karlin 1966; Niemi and Näätänen 1981; Polzella et al. 1989). Most of these studies have used foreperiods with constant $E(t)$ and, although they have often led to plausible qualitative descriptions, what seem to be lacking are the kinds of precise quantitative explanations that can be directly related to underlying processes of decision making. The LATER model makes a clear quantitative prediction about what should happen for both short-term as well as long-term changes in expectation. Increasing expectation should increase the starting level $S_0$, resulting in a reduction of median latency. An additional and more exacting prediction is that the change in $S_0$ should result in alterations of the slope of the reciprobit plot, such that it swivels about a fixed infinite-time intercept $I$ (Fig. 1). Conversely, measurements of reaction time distributions allow the experimenter to estimate how $E(t)$, which can be thought of as the probability of the stimulus, is translated into alterations in $S_0$, in a sense the probability response, and this is what we set out to do in this study. A second, more pragmatic, aim is to determine the extent to which measures of reaction time variability are in practice contaminated if—as is usually the case—foreperiods are aging rather than nonaging.
coordinates \( x = 0.6256, y = 0.3409 \), luminance = 24.6 cd m\(^{-2}\) that could appear with equal probability either 5° to the left or right of the third, central black central fixation spot (luminance = 0.00), which remained on throughout the experiment, thus preventing its offset from providing a cue. Participants were seated 1 m away from the monitor (which subtended 16.4° vertically and 21.8° horizontally), with their heads supported by a chin rest. The screen had a white background of uniform luminance 28.8 cd m\(^{-2}\) and ambient lighting was arranged to be slightly less than this.

**Data collection**

Horizontal eye movements were recorded using a binocular infrared oculometer (Ober Consulting, Poznan, Poland) (Ober et al. 2003), consisting of dual differential infrared reflectance transducers comparing reflectance from the medial sclera and pupil of each eye. It had a bandwidth of 250 Hz, symmetrically linear to 7% within ±30°, and a noise level equivalent to 10 min arc. The output voltage was sampled at 100 Hz, synchronized to the display frames. The PC-based saccadic analysis system SPIC (Carpenter 1994) was used to detect saccades in real time and record their latencies in 10-ms intervals, control stimulus presentation, and display and store eye movement data for subsequent analysis. The traces were inspected after experimental runs so that erroneous saccades caused by blinks, head movements, or other artifacts and those with latencies <50 ms were withheld from further analysis.

**Behavioral tasks**

In all tasks, subjects were instructed to fixate the central dot until a target appeared in the periphery, toward which a saccade had to be made as quickly as possible. At the end of every response gaze was to be shifted back to the central fixation dot, in preparation for the next trial. The detection of a saccade was signaled, after a delay of 50 ms, by the stimulus disappearing and by a tone; together these acted as warning signals signifying the start of a new trial. Subjects performed saccades in blocks of 200 trials, separated by breaks as required so that the data for any one protocol were completed in a single session.

We used three different protocols, each with a different kind of variable foreperiod \( F_R \), after the fixed period \( F_0 \), which was 700 ms under all conditions. Blocks of trials for each of the paradigms were interleaved. All subjects undertook all protocols and large numbers of saccades (typically several thousand per protocol) were performed by each subject, ensuring that their distributions were stable and not subject to further statistical change.

**PROTOCOL 1: NONAGING FOREPERIOD (NF).** Here the probability of stimulus appearance at each 10 ms interval after the fixed initial foreperiod \( F_0 \) of 700 ms decreased exponentially, to generate a nonaging foreperiod (see INTRODUCTION) with a mean value of 1,000 ms. To avoid occasional very long waits, \( F_R \) was curtailed at 2,300 ms by programming SPIC to select a different random value, using the same algorithm, if the initially chosen value exceeded 2,300 ms. In this and the following tasks, random numbers were generated by a congruence method (Abramowitz and Stegun 1965) with a cycle length of over \( 10^7 \).

**PROTOCOL 2: AGING FOREPERIOD (AF).** Here the random foreperiod \( F_R \) was of maximum duration \( T = 1,000 \) ms and the stimulus could appear with equal probability at intervals of \( 6 = 10 \) ms. As explained in the INTRODUCTION, during \( F_R \) the expectation \( E(t) \) will then rise hyperbolically with the lapse of time.

**PROTOCOL 3: FIXED FOREPERIOD (FF).** Here we used a fixed foreperiod, \( E(t) \) then approximating to a delta function. In the majority of trials (88%) the target appeared after a fixed foreperiod of 700 ms. To probe the time pattern of subjective expectation \( E'(t) \) generated by this delta function, in a small number of probe trials (10%) SPIC selected...
a foreperiod at random from six different times, positioned symmetrically around 700 ms: 370, 440, 510, 890, 960, and 1,030 ms. To discourage anticipatory responses, a further 2% of trials were catch trials, in which a warning signal was presented without a subsequent stimulus.

Data analysis

Latency distributions under specific experimental conditions were displayed and analyzed within SPIC. We used the Kolmogorov–Smirnov (K-S) one-sample test (Kolmogorov 1941) to determine the agreement between observed distributions and theoretical distributions predicted by LATER. The same criterion was also used to calculate a line of best fit for the main part of the distribution, ignoring the fast population, and from this the median latency, slope, and intercept of the line with the infinite time axis could be estimated. The K-S two-sample test allowed us to compare observed distributions with one another, by testing the hypothesis that both could have come from the same distribution (Kolmogorov 1941). We used a log-likelihood test to determine whether successive reciprobit distributions could be modeled more accurately by a parallel shift or by swiveling about the intercept \( I \) on the infinite time axis, calculating maximum likelihood for a set of data under the constraints of a common slope (for shift) or a common intercept (for swivel). An advantage of using log-likelihood measures is that their values may be summed across participants to give an overall likelihood in favor of swivel as opposed to shift or vice versa. In the third (fixed foreperiod) experiment, for each subject separately a least-squares fit of a Gaussian distribution was fitted to the observed mean promptness (i.e., reciprocal latency) for each of the probes, using Origin (OriginLab, Northampton, MA).

Simulations

Using SPIC, we ran Monte Carlo 1,000-trial simulations of single LATER units, to predict the responses of each subject to the aging foreperiod task. We used the LATER parameters \( \mu \) and \( \sigma \) previously estimated for each subject by minimization of the Kolmogorov–Smirnov statistic. Because any early responses formed only a small proportion of the whole and have only a negligible effect on median latency, for simplicity they were ignored.

However, because our results demonstrate that expectation is subject to temporal blurring (see DISCUSSION), we convoluted the calculated hazard function \( E(t) \) with a single Gaussian function, \( G(t) \) of unit area, and a mean \( \mu \) and variance \( \sigma^2 \) estimated for each subject from the best-fit Gaussian fits in the third (fixed foreperiod) experiment. The resulting function \( E'(t) = E(t) * G(t) \) was then used as a representation of the starting level of the decision unit, to calculate the predicted distributions of latencies.

RESULTS

Nonaging foreperiod

We separated responses in the nonaging foreperiod task into four groups, corresponding to four successive ranges of foreperiods up to the maximum 1,000 ms, and the corresponding set of four reciprobit plots of saccadic latency is shown for two subjects in Fig. 3. A Kolmogorov–Smirnov test demonstrated for all four subjects that the four distributions were statistically indistinguishable \( (P > 0.1) \). Adjacent to each reciprobit is a plot demonstrating the change in mean latency as a function of foreperiod duration. ANOVA confirmed that there was no significant change in mean latency (for subjects A–F: A, \( P = 0.16; \) B, \( P = 0.09; \) C, \( P = 0.47; \) D, \( P = 0.87; \) E, \( P = 0.67; \) F, \( P = 0.59; \) \( n = 46 \)), indicating that a nonaging foreperiod has no significant effect on saccadic latencies or their distributions.

Aging foreperiod

Figure 4 shows, for two subjects, the distributions of latencies recorded in four successive time intervals of the aging foreperiod. It can be seen that—unlike for a nonaging foreperiod—there are now significant differences in the latency distributions that depend systematically on foreperiod (K-S two-sample tests; \( P < 0.05 \)). Median latencies decrease progressively with increasing foreperiod and so do the slopes of the distributions. This is as would be expected if the changes arose from an increase in prior probability or expectation, which in LATER should result in swiveling of the distribution about its intercept \( I \) with the \( t = \infty \) axis (see Fig. 1). As described in METHODS, we used a log-likelihood test to determine whether the distribution set for each subject was more compatible with swiveling about the infinite time intercept \( I \), than with a parallel shift, which would signify a change in the mean rate of rise \( \mu \). The overall likelihood favoring swivel as opposed to shift, summed across all six subjects, was 17.1 log units of support, corresponding to a conventional significance level of \( P < 0.0001 \). As with the nonaging foreperiod, mean latencies were calculated in successive 50-ms intervals to highlight the time course of any change (Fig. 4, right). It was observed that mean latencies decreased initially toward a minimum, which occurred between 750 and 825 ms, before rising again.

Fixed foreperiod

In the fixed foreperiod experiment, the target usually appeared after exactly 700 ms, but in 10% of trials it appeared at a different time, acting as a probe to estimate the degree of temporal precision of the expectation around the expected 700 ms. Figure 5 shows the mean promptness observed for each of the six probes used, for each participant. It can be seen that in each case the promptness is greatest for the expected time of appearance, and falls off as the time of the probe diverges from the expectation. These data were well fitted (no value of \( R^2 \) was <0.956) by Gaussian functions, with widths that varied from subject to subject (Fig. 5, bar chart): the mean width across all participants was 353 ± 16.5 ms (mean ± SE).

Simulations of responses during aging foreperiods

To confirm the complete model, including both calculation of \( E(t) \) and its modification \( E'(t) \) by a process of Gaussian blur, we performed Monte Carlo simulations, using the best-fit values of \( \mu \) and \( \sigma \) from each subject and the corresponding value of the width of the Gaussian blur. As can be seen in the results for two subjects shown in Fig. 4, the model succeeds in predicting the overall time course of latency changes quite satisfactorily, including the surprising rise of latency during the last 175–250 ms of the foreperiod, which is in fact an inevitable consequence of such uncertainty. In addition, simulated distributions of latencies for each subject under all conditions generated excellent fits with observed distributions (for subjects A–F: A, \( P = 0.26; \) B, \( P = 0.17; \) C, \( P = 0.63; \) D, \( P = 0.55; \) E, \( P = 0.28; \) F, \( P = 0.49 \), using the K-S one-sample test; Fig. 6 shows two representative distributions). Finally, there...
was a strong correlation for all subjects between observed and predicted latencies (Fig. 6: $R = 0.98$); it appears that the model is capable of modeling both average saccadic latencies and their distributions at different times during an aging foreperiod.

**DISCUSSION**

Although we have a reasonably good idea of how static values of the decision parameters may influence response times and are beginning to understand what happens in response to step changes in these static values (for instance, see Anderson and Carpenter 2006), what is lacking is an understanding of how, on a much shorter timescale, decision mechanisms deal with dynamic changes of their parameters. An important example in an experimental setting that frequently tends to be overlooked and forms the basis of our enquiry is the role of stimulus timing. Normally experimenters arrange for the stimulus to appear after a random delay or foreperiod, after the onset of a warning cue. Here we manipulated the statistics of the randomization to generate different functions of expectation that can be directly inferred by measuring corresponding latencies.

From these three experiments it is possible to come to a number of conclusions.

1) That in a nonaging foreperiod the duration of a particular foreperiod has no systematic influence on reaction time, implying that subjective expectation is constant.

2) That, conversely, reaction time varies with the lapse of time during a conventional aging foreperiod; the observed concomitant swiveling of the latency distributions implies that the changes in reaction time indeed arise from changes in expectation.

3) That the final rise in expectation toward the end of a nonaging foreperiod is not as sharp as would be expected from a strict calculation of the hazard rate, suggesting that there is a degree of temporal uncertainty or blur in the stored representation of expectation.

4) That this blurring is Gaussian in shape, with a width of some 350 ms. When included with a conventional LATER unit it generates predicted latencies for different aging foreperiods that are extremely similar to those actually observed.

**Constancy of expectation with nonaging foreperiods**

For the nonaging foreperiod, where $E(t)$ is constant, we observed that mean latencies and their distributions were independent of foreperiod duration, as predicted. Interestingly, a previous study noted that response times may increase steadily as a function of nonaging foreperiod duration (Näätänen 1970).
In that study only three possible foreperiods were investigated within a range of 1–5 s: the differences in mean response time observed were not statistically significant for several subjects and conditions and were of the order of 10–12 ms, a value that falls within the range of variability for this experiment (Fig. 3). Perplexingly, a later study (Naäätänen 1971) noted that response times increase as a function of foreperiod duration when the mean foreperiod duration is 5 s, but are independent of foreperiod for mean foreperiod durations of ≥10 s. Two possible reasons for the increase in latency with foreperiod duration have been suggested, of a rather general kind. The first is that a subject’s estimation of the passage of time and therefore expectation is degraded by an uncertainty that is proportional to elapsed time, so that expectation is continually decreasing with foreperiod duration (Woodrow 1930). The second is fatigue, resulting from the requirement of maintaining a state of readiness (Karlin 1959). Neither explanation lends itself to quantitative evaluation, nor explains the specific timing of this phenomenon, which may in any case be a result of using longer foreperiods than those used in the current study, which seemed to us as large as would be likely to be regarded as convenient by most experiments. In the absence of this effect in our own measurements, further speculation is probably of little value.

Increase of expectancy during aging foreperiods

We found that successive latency distributions in the aging foreperiod produced swivel about an infinite-time intercept on the reciprobit plots, indicating—as predicted—dynamic alterations of expectation throughout the foreperiod. A curious feature of this variation is that mean latencies initially decreased, but then rose for all subjects at longer foreperiods, the peak ranging between 750 and 825 ms. To an extent this may reflect the subject’s uncertainty as to whether the stimulus is to appear at all, rising excitement being tempered by the dawning realization of possible disappointment. Previous investigations of aging foreperiods tended to yield ambiguous results. Some studies report that response times decrease steeply initially before leveling off at larger foreperiod values (Baumeister and Joubert 1969), whereas others suggest that response times increase consistently with prolongation of the foreperiod (Hermelin 1964; Nickerson and Burnham 1969). It is important to point out, however, that in the latter studies, the time interval between the possible foreperiod values increased progressively with the foreperiod duration. Consequently, foreperiods shorter than the mean were more frequently presented than those longer than the mean, inevitably resulting in a bias of expectation toward the shorter foreperi-

FIG. 4. Distributions of latencies recorded in four successive time intervals (0–250, 250–500, 500–750, and 750–1,000 ms) in an aging foreperiod of random duration 1,000 ms are shown for two participants. Solid lines represent best LATER fits to the main distribution subject to the constraint of a common infinite-time intercept (not shown), demonstrating the expected swiveling of the distributions about this point. Adjacent to each reciprobit is a corresponding plot showing mean latencies with their respective ±1 SE calculated for each 50-ms interval of the total 1,000-ms foreperiod. Filled circles represent observed values; the hollow circles are the latencies predicted from simulation (see DISCUSSION).
ods. Other studies point to an amalgamation of the above findings, such that response times initially decrease before rising again at foreperiods longer than the mean (Karlin 1959; Woodrow 1914), a description that seems most in accord with our results. Again, it is difficult—and probably not particularly enlightening—to try to determine the origin of these discrepancies between previously published findings.

FIG. 5. Temporal blurring of expectation. Subjects were presented with stimuli with a fixed foreperiod of 700 ms, although in occasional probe trials the foreperiod was different. The six graphs show average promptness (reciprocal latency) as a function of actual foreperiod. Curves are best-fit Gaussians (least squares; $R^2$ values as shown in each case), whose widths (2 SD) are shown for each participant in the bar chart at the bottom.

FIG. 6. Left: observed latencies in the aging foreperiod experiment for different values of the foreperiod plotted as a function of the latencies predicted from the model, showing the accuracy of the prediction ($R = 0.98$, $P < 0.0001$); the line shows the expected relationship for a perfect prediction. Right: reciprobit plots showing the simulated and observed latency distributions of two subjects for all foreperiod values in the aging foreperiod task. Statistical similarity of the observed and predicted distributions was confirmed using the K-S test (see RESULTS).
Temporal blur or uncertainty

The increase in latency at longer waits is puzzling: in a model in which \( E(t) \) translates directly into a change in \( S_0 \), one would expect latencies to continue to decrease because \( E(t) \) progressively rises to the very end of the range of foreperiods. A plausible explanation, as noted earlier, is that the internal representation of expectation as a function of time is itself subject to uncertainty. This explanation is reinforced by the observation that no time-dependent changes in latency are observed with a nonaging foreperiod, ruling out explanations based on fatigue or other extraneous time-dependent factors. Comparison of \( E(t) \) with the time course of the change in mean latency would suggest that \( E(t) \) is subject to a kind of blurring (Fig. 2); again, because under nonaging conditions \( E(t) \) is constant, blurring has no effect and consequently average latencies do not vary with foreperiod. We previously reported a similar blurring of prior probability in space to targets presented in adjacent loci (Adams et al. 2000) and a similar blurring was reported in the responses of neurons in monkey parietal cortex that appear to fire in relation to hazard rate (Janssen and Shadlen 2005).

Our experiments using a fixed foreperiod established that the blurring is quasi-Gaussian in nature with a width of about 350 ms, which is comparable to what was found by Janssen and Shadlen (2005). To incorporate the effect of this blur we convoluted the hazard function \( E(t) \) with Gaussians having the best-fitting mean \( \mu \) and variance \( \sigma^2 \) determined for each subject. Simulating the resulting function using LATER generated predicted latencies whose means and distributions were statistically indistinguishable from those actually observed. It was noted earlier that some previous studies suggested that temporal uncertainty obeys something like Weber’s law, such that the ratio of the magnitude of the uncertainty to elapsed time is roughly constant (Gibbon et al. 1997; Janssen and Shadlen 2005). The kind of model envisaged for instance by Gallistel and Gibbon (2000), with a LATER-like rise to threshold, would imply that uncertainty should increase with time lapse. However, we do not seem to find this phenomenon in our results: it would have manifested as a progressive increase in the variability of response latency for the nonaging foreperiod, which was not observed. Since the range of latencies explored for the nonaging foreperiod was more than double that investigated for the aging foreperiod, we can confidently say that—within the conditions of our experiments—temporal uncertainty does not vary with elapsed time. Although Weber-like behavior would be expected from a random-walk rise-to-threshold model, this is not true if the rise is linear, as in LATER. However, this linear rise clearly cannot continue indefinitely and it does seem from common experience that over much longer periods, at least, temporal uncertainty must eventually increase with the lapse of time: we clearly cannot estimate an interval of 1 h with a precision of 350 ms.

The neural mechanisms encoding the passage of time are still relatively poorly understood (Gallistel and Gibbon 2000; Gibbon et al. 1997), despite numerous neurophysiological studies having pointed to likely neuronal substrates, particularly neurons whose activity reflects time-dependent expectation (Basso and Wurtz 1997; Platt and Glimcher 1999). In particular, recent attention has focused on neurons in cortical area LIP (lateral intraparietal area), where recordings in mon-
REFERENCES

Woodrow H. The measurement of attention. Psychol Monogr 17: 1914.