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Contrast, Probability, and Saccadic Latency: Evidence for Independence of Detection and Decision

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Summary

Many factors influence how long it takes to respond to a visual stimulus. The lowest-level factors, such as luminance and contrast, determine how easily different elements of a target can be detected. Higher-level factors are to do with whether these elements constitute a stimulus requiring a response; they include prior probability and urgency. It is natural to think of these two processes, detection and decision, as occurring in series, so that overall reaction time is essentially the sum of the contributions of each stage. Here, measurements of saccadic latency to visual targets whose contrast and prior probability are systematically manipulated demonstrate that there are indeed separable stages of detection and decision. Both can be quantitatively described by rise-to-threshold mechanisms; the average rate of rise of the first is a simple logarithmic function of target contrast, whereas the second shows the linear rise characteristic of the LATER model of neural decision making. The implication is that under normal, high-contrast conditions, in which detection is very fast, the random variability that is characteristic of all reaction times is not caused by sensory noise but is gratuitously introduced by the brain itself; paradoxically, by conferring unpredictability it may aid an organism's survival.

Results and Discussion

Like other reaction times, saccadic latency varies randomly from trial to trial. For easily visible targets, the reciprocal of this reaction time is generally normally distributed [1], suggesting a model of the underlying process (the linear approach to threshold with ergodic rate [LATER] model) in which a decision signal rises linearly toward a threshold for initiating the response and the rate of rise on different trials follows a normal distribution.

One may think of this decision signal as a neural estimate of the log probability of the target being present, with the starting level representing prior log probability and the threshold representing a criterion level at which the likelihood of the target is so high as to compel a response. Measuring the distribution of latencies while altering the prior probabilities [2], giving subjects instructions that lead to alterations in criterion level [3], or manipulating the rate of provision of information [4] strengthens this interpretation; in each case the distributions alter in the way that LATER predicts.

Recordings from the frontal eye field of monkeys [5] have demonstrated some neurons whose activity preceding a saccade is remarkably similar in that it rises linearly until it reaches a level corresponding to the LATER threshold. In repeated trials this level is constant, but the rate of rise varies from trial to trial, which explains the corresponding variability of saccadic latency itself. Similar "rise-to-threshold" behavior is shown by superior-colliculus neurons, whose initial firing level often reflects target probability [6] and by parietal-cortex neurons, whose rate of rise seems to reflect the supply of information [7–9].

One might at first take this rise to threshold to represent something like a sequential statistical test of significance, the most efficient way of determining the existence of a stimulus in the presence of sensory noise [10]. But there are several features of reaction times that do not fit such a notion. Substantial reaction times, with substantial random variation, are observed with high-contrast stimuli for which the signal-to-noise ratio is so high that their detection must be very rapid indeed. Furthermore, such a process gives rise not to a linear rise to threshold but to a random walk, which would not generate the distributions actually observed under high-contrast conditions. Nevertheless, it is clear that a certain time is required to distinguish a target from its background, and many studies have shown that reaction times increase markedly as stimuli approach their threshold [11–13]. This suggests that there may be two processes here in series. The first would be a mechanism, perhaps of the random-walk type, that is concerned with *detection* of individual stimulus fragments. The second would be a process that embodies a linear rise to threshold and might be called a *decision* mechanism; it decides whether the existence of an entire object requires a particular response, given the existence of these fragments and the degree to which the object is expected [14]. The existence of two such processing stages that precede the initiation of a saccade is implied by further experiments by Schall and his colleagues in monkey frontal eye field [15–18].

Under high-contrast conditions, when targets are far from threshold, the second stage would be expected to dominate, with distributions obeying the LATER model. However, when targets are hard to detect, the time required for detection would predominate, leading to behavior more like the random-walk or diffusion models often proposed to explain the time taken to detect signals in the presence of noise [19, 20].

If there are indeed two mechanisms of this kind in series, it should be possible to demonstrate that fact by showing that overall reaction time is the sum of one component that is a function of prior probability but not of contrast and another that is a function of stimulus contrast but not of prior probability. The experiments described here therefore combined the technique of training subjects to expect saccadic targets on the left

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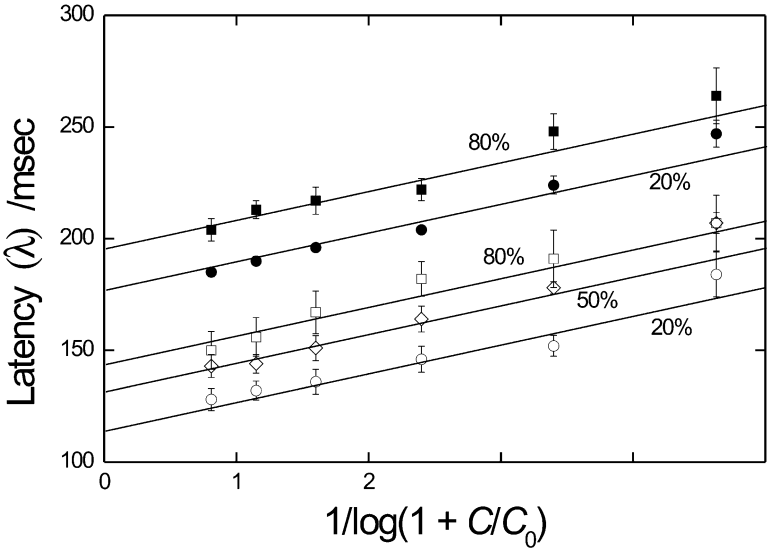

Figure 1. Latency as a Function of Contrast and Probability

Representative results for step (filled symbols) and gap (open symbols) tasks with different target probabilities for one subject show the relation between saccadic latency λ and the function $1/\log(1 + C/C_0)$, which represents the model's prediction of λ_0, the time taken to detect a stimulus of contrast C. The lines represent the function $\lambda = K/\log(C/C_0) + \lambda_1$, where λ_1 is different for step and gap tasks and for different probabilities, but K and C_0 are constant for any one subject.

or right with different probabilities [2] with simultaneous manipulation of target contrast. As well as conventional step tasks (in which the fixation spot is extinguished at the same time that the target is presented), we used gap tasks, in which the extinction of the fixation light precedes the appearance of the target and thus increases expectation still further.

It is helpful to consider first the expectations in this experiment because they suggest informative ways of analyzing and plotting the data. We want to know whether the overall latency λ can be expressed in the form $\lambda = \lambda_0 + \lambda_1$, where λ_0 is the contribution of the first, contrast-dependent detection stage and λ_1 is that of the second, probability-dependent decision stage, plus transport delay and other factors that do not vary significantly over the time course of an experiment. If the detection stage does indeed consist of a random-walk rise to threshold, then $(1/\lambda_0)$ represents its mean rate of rise, which must be some function $\phi(C)$ of stimulus contrast; λ_0 will then be proportional to $1/\phi$. It is natural to choose a logarithmic function for ϕ, more specifically one that encodes the difference between the signal when the target is present and when it is not [21]. If we assume the presence of background noise C_0, which combines additively with the signal [22, 23], then the simplest formulation is $\phi = \log(C + C_0) - \log(C_0)$, or $\log(1 + C/C_0)$. Thus:

$$\lambda_0 = \frac{K}{\log_{10}\left(1 + \frac{C}{C_0}\right)} \quad (1)$$

where the constants C_0 and K are the same for all data sets for any one subject but will be expected to vary between subjects. Thus, the prediction is that a plot of latency as a function of the reciprocal of the log contrast ratio should yield a straight line, from which values of the parameters can be estimated.

Figure 1 shows the raw results, plotted in this way, for one subject for all combinations of probability, task type, and contrast. The lines are of the form $\lambda = K/\log_{10}(1 + C/C_0) + \lambda_1$, where λ_1 is different for each task condition (probability, or step versus gap) but K and C_0 are identical for all conditions. Minimizing the sum of squares of deviations from linearity gave these values, and no data set from any subject deviated significantly (ANOVA, $p = 0.05$) from linearity. For different subjects the best-fit values of K vary somewhat, from around 7.5–13 ms per log unit of contrast (Table 1).

It is apparent that different probability levels, both for step and gap conditions, produce a parallel shift of what is otherwise a straight-line relationship (parallelity was tested by an F test on the ratio of residual sums of squares for individual versus group fitting of the lines [24] and confirmed at $p = 0.05$ for all data from all subjects). This implies that there are indeed two separable additive components to latency, one dependent on prior probability and the other on contrast. The intercept gives the value of λ_1 and is plotted in Figure 2 as a function of log probability; a previous study [2], with constant contrast, demonstrated a linear relation between λ and log probability, although here, with fewer probabilities, smaller data sets, and extra conditions, the relationship is less precise.

The equations for the best linear-fit lines are of the form $\lambda_1 = T_0 - k \log_{10}(p)$, where $k = 37.5$ ms/log unit for the step task and 66.7 for the gap task; the values for T_0 were respectively 234 and 239 ms and were not significantly different ($p > 0.1$). It is interesting to note that the effect of having the gap condition rather than a step is approximately to double the effect of any given

Table 1. Least Squares Best-Fit Values of the Parameters K and C_0 for Each Subject

Subject	K (ms/log unit)	C_0 (Percent)
A	12.17	13.94
B	8.85	16.82
C	7.51	17.90
D	12.72	11.96
Mean	10.31	15.16

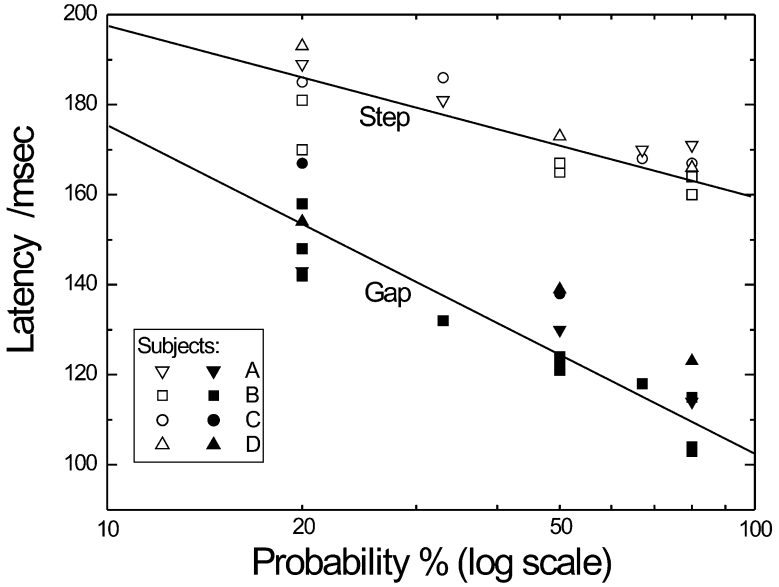

Figure 2. Latency as a Function of Probability Alone

Values of λ_1 for a number of different data sets are plotted for all subjects, and for gap and step tasks, as a function of the log of the prior probability of the target appearing. The two lines show the best apparent linear fits for step tasks (step: 234 ms − 37.5 ms/log unit, $R = 0.782$, $p < 0.0001$; gap: 239 ms − 66.7 ms/log unit, $R = 0.908$, $p < 0.0001$).

probability. The observed slope for the step task is similar to those reported recently for very similar conditions (A. Anderson and R.H.S. Carpenter, 2004, J. Physiol., abstract) but smaller than the 76 ms/log unit found under different conditions by Carpenter and Williams [2]. If one were to assume that λ_1 is zero when the target is always on the same side, then after extrapolating the line for the gap task to p = 100%, one might predict fixed delays in the system to amount to something like 100 ms; however, this is certainly an overestimate because even if the target is always on the same side, there is still uncertainty as to the *time* it appears, and in any case one cannot be sure that some other kind of prior warning might not have reduced latencies even more than a gap of this particular duration. Under these conditions, these considerations put an upper bound of 100 ms on such delays. Finally, in Figure 3, $1/\lambda_0$ is plotted as a function of log contrast, for all subjects under all conditions, together with the function $\log(1 + C/C_0)/K$, which, if this is model is correct, should predict $1/\lambda_0$.

The main conclusion is that the variable part of saccadic reaction time can be decomposed into the sum of two independent delays, λ_0 and λ_1, influenced by distinct aspects of the circumstances of the experiment. When target visibility is high, λ_0 contributes little (for subject A, with a target of 100% contrast it is only some 13 ms) and λ_1 dominates the reaction time. However, as target contrast is reduced, λ_0 rises in a remarkably regular way (to some 62 ms for 8% contrast in subject A) and comes to dominate overall behavior. It should be pointed out that the data presented here are also compatible with some other contrast functions that have been postulated in the past [25–27], the differences introducing changes in the shape of the plots in the region of the threshold, where there is necessarily less experimental information. (Similar relationships have been observed empirically since the earliest days of reaction time studies [28, 29] and, more recently, in a study of manual responses to sinusoidal gratings [30].)

We can now sketch, in broad terms, a sequence of stages by which noisy visual signals are first transformed to a log scale, then integrated to drive a detection signal to a threshold level. This in turn triggers a second rise to threshold, which is linear rather than random-walk, with a rate of rise that varies greatly from trial to trial. Such a model has implications about the form of the distribution of latencies under low-contrast conditions, as well as their medians. An analysis of this kind requires more data than were available in the present study but is the subject of a current series of experiments.

The history of searching for empirical relationships between reaction time and such stimulus factors as intensity or contrast is a long one, dating back nearly 140 years [28, 31]. Donders' view was that reaction time could be analyzed in terms of consecutive processes (his "method of subtraction"), but this approach subsequently fell out of favor with psychologists, who preferred models that tried to describe reaction times in terms of a single process that often represented optimal detection of a stimulus in the presence of sensory noise. The development of these ideas has been thoroughly discussed by Luce [32]. However, apart from the obvious sense in which the neural processing of sensory information is necessarily serial, although stochastic considerations and the existence of numbers of neurons in parallel may blur the transition from one stage to the next, it is clear that the variability in reaction time under conditions of good visibility is vastly greater than can be explained in this way and comes not from detecting the stimulus but from the second stage, decision, with its linear rather than random-walk rise to threshold, which uses clues from sensory stimuli, circumstantial evidence, and past experience to decide between rival hypotheses about the presence of objects in the outside world [2]. In everyday life there would be many LATER decision units running in parallel, and the first to reach threshold would determine the response to a particular set of stimuli, a general arrangement first suggested by Robinson [33]. An aspect of this that may seem less

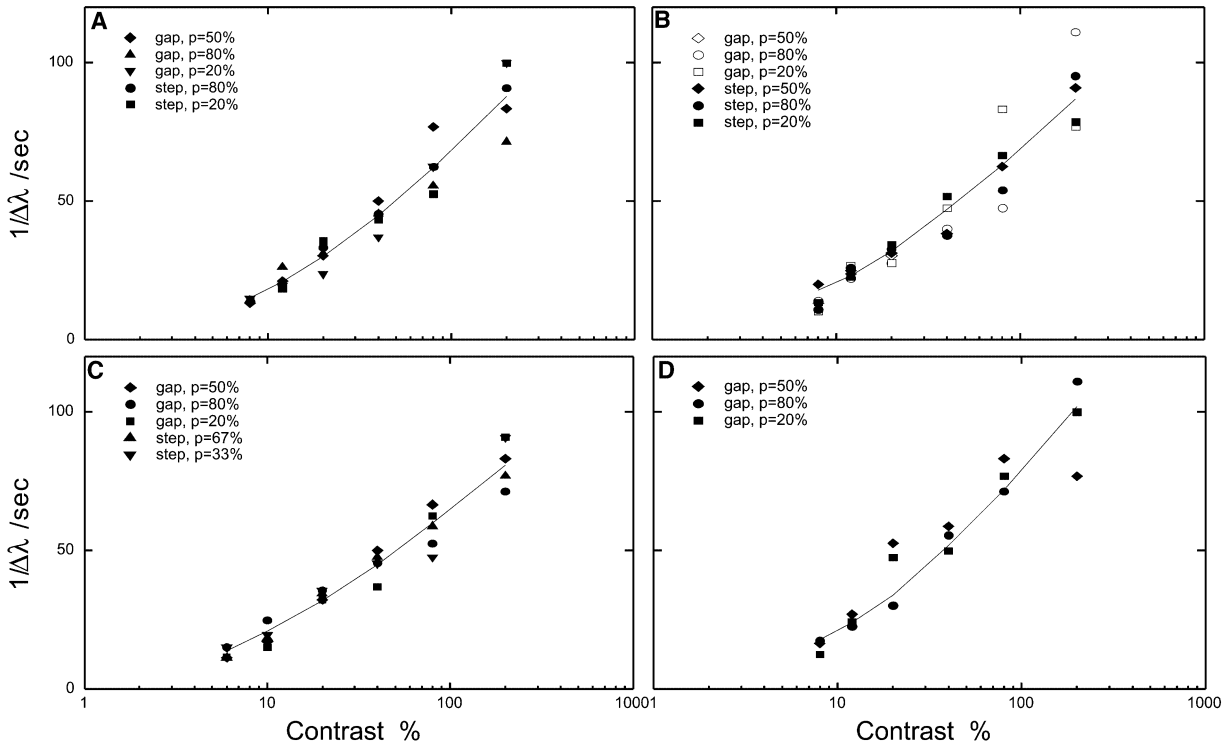

Figure 3. Latency as a Function of Contrast Alone

The points show observed values of $1/\lambda_0$; the values are plotted as a function of log contrast for all subjects and all conditions. The lines show the predicted relationship, if the mean rate of rise in the detection stage is given by $K/(\log(1 + C/C_0)$, where K and C_0 are constant for each subject over all probabilities and task types and are given by the best-fit values shown in Table I.

plausible is the gratuitous random component, which dominates the variability of reaction times when the stimuli are easily detectable. Although it is difficult to see the benefit of variability of reaction time per se, individual variability in the rate of rise must, in a competitive system of this kind, necessarily be translated into randomness of *choice* of response; it generates, in fact, unpredictable behavior. In a precedence task, in which competing targets are presented with a small temporal offset [34], LATER provides a quantitative description of the stochastic choice behavior as well as simply of the reaction times. One might well wonder what possible advantage there could be in deliberately introducing the neural equivalent of a roulette wheel into the decision process. Biologically speaking, there are many reasons why unpredictability of behavior is desirable [35]; it encourages exploration, both literal and metaphorical, and by embodying the well-known principle from game theory [36], that randomness is the best strategy for both attacker and defendant, it assists both predator and prey.

Experimental Procedures

Four subjects contributed with informed consent to the experiments, which had approval from the local ethical committee. They were presented in each run with targets chosen at random from a repertoire of six possible contrast levels; the targets were displayed on the left or on the right with different probabilities. After the subjects trained until their performance appeared to level off, test runs were used to measure median latency for each combination of probability and contrast.

The stimuli were three yellow rectangular LEDs subtending a 14 × 23 min arc: a central fixation LED and targets at 4.5° horizontally on each side. They were optically superimposed on a uniform 4.5 cd m^{-2} extended background and visually matched in color to the LEDs, whose luminance was pulse width modulated at 100 Hz (9 cd m^{-2} maximum, i.e., 200% contrast). An infrared scleral reflection oculometer [37] was used with a computer system, SPIC [38], that recorded, stored, and analyzed eye movements and also controlled the presentation of stimuli. Runs were of blocks of 100 trials, and subjects normally undertook nine such blocks for each probability, after at least 100 and up to 300 preliminary trials for which the data were discarded, which established a stable level of response for the prevailing probabilities. Each trial started with a random wait period in the range of 0.5–1.5 s and then extinction of the fixation LED. In step trials, either the left or right target, chosen at random with specified probabilities, was simultaneously illuminated; in gap trials there was an intervening period of 100 ms. After a run, records were examined so that trials contaminated by blinks or other irregularities could be eliminated.

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