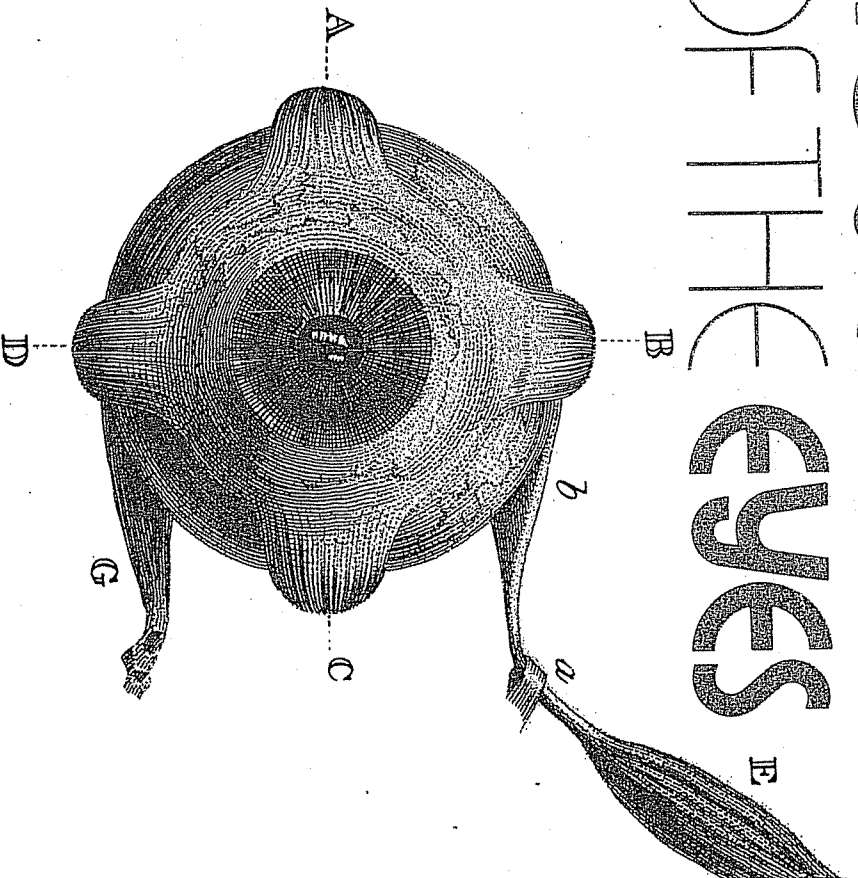


MOVEMENTS  
OF THE EYES

# MOVEMENTS OF THE EYES



RHS CARPENTER

2ND EDITION

2ND EDITION  
REVISED AND ENLARGED

**R**

**RHS CARPENTER**

A rather clear-cut demonstration of the relative strength of errors of retinal velocity and position is given by the open-loop response to a target that steps to the left at the same time as starting to move at constant velocity to the right (Pola and Wyatt, 1980): the initial target movement is to the left, even though this actually *increases* retinal slip velocity. Smooth responses to target position are considered by Pola and Wyatt (1985) to be a property of 'active' foveal pursuit, and not of the 'passive' optokinetic kind. A phenomenon that may well be related to smooth position control is the involuntary drift towards a target that is about to be fixated, described by Kowler et al (1984a); there is probably also a connection with *slow correction* ('corrective drift': section 6.3.2). Torsion in response to a tilted visual stimulus, once denied but undoubtedly real though rather small in magnitude ( $1^\circ$  at most; Howard and Templeton, 1964; Crone, 1975; Goodenough et al, 1979; Merker and Held, 1981), is superficially similar but rather different in its dynamic properties.

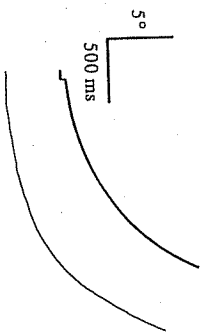


Figure 3.26. Human open-loop responses to a small step displacement of the target. The thick line represents target position, the thin line eye position; the accelerating nature of the response is evident (after Robinson, 1965).

## Saccades

"To be short, they be wholly given to follow the motions of the minde, they doe change themselves in a moment, they doe alter and conforme themselves unto it in such manner, as that *Bienor* the Arabian, and *Syrenus* the Phisition of Cypres, thought it no absurditie to affirme that the soule dwelt in the eyes ..."

In the strictest sense, saccades are the fast movements of the eyes that are used to bring a new part of the visual field to the foveal region. They are essentially voluntary, and indeed are the only voluntary eye movements that one can make without special training. However, some other fast eye movements, less voluntary in character, share many properties with voluntary saccades and are almost certainly generated by the same mechanism. These include the quick phase of vestibular or optokinetic nystagmus and the microsaccades which can be observed during fixation, to be described in chapter 6. The voluntary torsional movements of up to  $30^\circ$  that subjects can be trained to execute are also partly saccadic in nature (Balliet and Nakayama, 1978). The word 'saccade' appears first to have been used in the oculomotor sense by Javal (1879). Westheimer (1973) has briefly reviewed the historical development of ideas about this kind of eye movement.

### 4.1 The time course of saccades

Saccades are remarkably stereotyped: for a particular subject, the time course of a saccade of a given amplitude is largely independent of the means by which it is evoked, whether voluntarily to an existing visual target, or involuntarily in response to the sudden appearance of a target; its *latency* on the other hand is subject to considerable random variation. Saccades are so fast that there is normally no time for visual feedback to guide the eye to its final position: except in the case of the very largest saccades, the delay in the visual feedback loop is longer than the duration of the movement itself. The saccade control system must therefore calculate in advance a pattern of muscle activation that will throw the eye exactly to the desired position. The resultant movement is thus preprogrammed or *ballistic* (the same property that distinguishes ballistic missiles from guided missiles), in the sense that alterations in the target occurring during a saccade cannot modify its trajectory. (This should not be taken to imply that a saccade, once under way, cannot be modified. Although the time course of a saccade is normally quite rigidly determined by the stimulus that evoked it, under special conditions a subsequent visual stimulus, provided that it occurs soon enough, may modify the movement in midflight: section 4.1.3 below.) The way in which the time course of this movement 'package' varies for saccades of different sizes can tell us something about how the control system performs what is, on the face of it, a complex calculation in which distances across the retina have to be converted into temporal patterns of muscle activity.

#### 4.1.1. Amplitude-velocity-duration relationships

Figure 4.1 shows the time courses of a number of human saccades of different amplitudes in the horizontal plane: saccades in other meridians, including torsional saccades, do not differ in their essential characteristics (Gurevich, 1961; Ballet and Nakayama, 1978), nor is much interspecies variation observed [thus very similar results are found in the goldfish: see Hermann and Constantine (1971) and Easter (1975)]. A notable feature of such records is how fast the eye moves, often reaching more than  $7000^{\circ} \text{ s}^{-1}$  for large amplitudes. Not all recording techniques are suitable for measuring such high velocities: slippage of contact lenses may lead to underestimates (Byford, 1962), as does electro-oculography (Byford, 1963; Stryker and Blakemore, 1972; Bogen et al, 1974). It can also be seen that the duration of the complete movement is not constant, but increases with increasing amplitude (figure 4.2); the duration of saccades larger than some  $5^{\circ}$  in amplitude is roughly 20–30 ms plus about 2 ms for every degree of amplitude (Dodge and Cline, 1901; Hyde, 1959; Robinson, 1964).

This dependence of duration on amplitude has sometimes—mistakenly—been taken to imply that the system is in a sense nonlinear. But we cannot tell whether a system is linear or not simply by looking at a sample of its output: we must also know what the corresponding *input* was that produced it. The implicit assumption here is that the input that produces saccades of different sizes is a step function of varying height: if this were true, then differences in response duration would indeed imply some kind of nonlinearity. But records of the electrical activity of the motor nerves show that the fast rising part of the saccade is generated not by a step of activity of variable height, but by a *pulse* of essentially constant height whose *duration*

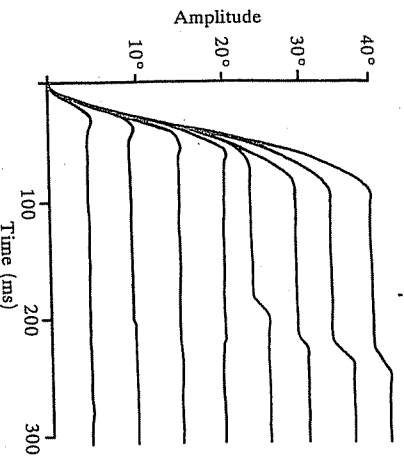


Figure 4.1. Human saccades of different sizes. The traces have been superimposed so that the beginning of each movement is at time zero. The dependence of the duration of the saccade on its amplitude can be seen, as can second correction saccades for larger amplitudes, at around  $t = 200$  ms (Robinson, 1964).

determines the amplitude of the saccade (see section 7.5.5). Such a pulse, acting on a linear model of the mechanical properties of the eye, produces amplitude-duration relationships very similar to those observed in actual voluntary saccades (Robinson, 1964). For a small saccade the pulse is very short and the response is dominated by the mechanical properties of the eye, so that the movement has a nearly constant duration; under these circumstances the peak velocity varies in proportion to the amplitude. The situation is rather like that of a man falling off a cliff: at first, acceleration dominates, and his peak velocity depends on how far he falls. But if his drop is a long one, most of the way he will be falling at his terminal velocity, so the duration of his fall will be in proportion to the height of the cliff. Either way, his initial trajectory will be the same. In the case of the eye, one can observe almost identical patterns of acceleration at the *beginning* of the movement, whatever its amplitude (Hyde, 1959). Larger saccades show a levelling-off of peak velocity as a function of amplitude, though it never becomes completely flat (figure 4.3).

This relatively fixed relation between amplitude, duration, and peak velocity for different saccades leads naturally to the idea of a sort of saccadic norm by which one can judge whether a particular saccade is aberrant, whether indeed it *really* is a saccade. [By analogy with the astronomers' classification of stars that is based on a similarly normative relation between brightness and temperature, this set of saccadic data has been called the *main sequence* (Bahill et al, 1975; 1981).] Thus very similar relationships between amplitude, duration, and velocity have been reported for microsaccades and for the quick phase of nystagmus (Mackensen and Schumacher, 1960; Ron et al, 1972; Guitton and Mandi, 1980a), which lends weight to the notion that these movements are essentially no different

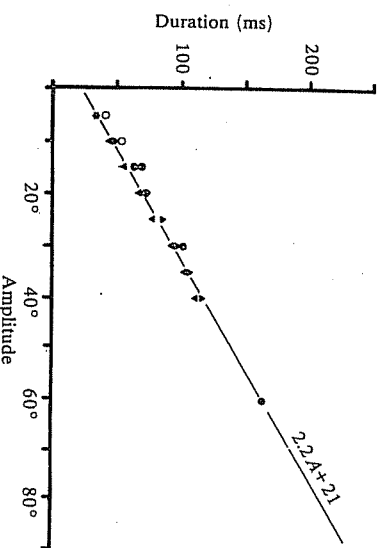


Figure 4.2. Saccade duration as a function of amplitude:  $\blacktriangle$  nasal saccades and  $\blacktriangledown$  temporal saccades (Robinson, 1964);  $\circ$  Yarbuss (1956);  $\bullet$  calculated from Hyde's (1959) records. The line represents the function  $(2.2A + 21)$  ms, where  $A$  is the saccade amplitude in degrees.

from ordinary saccades. Under natural conditions, with the subject moving freely in his normal surroundings, a histogram of the frequency of occurrence of fast eye movements (taking saccades and quick phases together) as a function of their amplitudes appears to show a single population, following a simple exponential function with a characteristic amplitude of around  $7^\circ$  (Bahill et al, 1975a) (figure 4.4). Thus more than 85% of natural saccades have amplitudes of less than  $15^\circ$  [as also noted much earlier by Lancaster (1941); a similar relationship is found in the rabbit and in the cat (Collewijn, 1970b; 1977a; 1977b)], and again, saccades and quick phases seem to fall into a single statistical population.

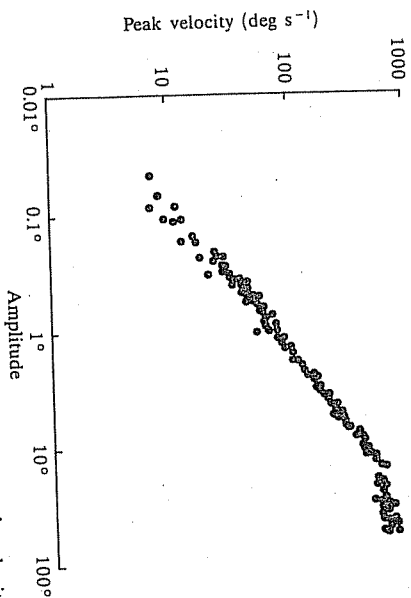


Figure 4.3. The main sequence, a graph of the peak velocity of human saccades as a function of their duration (Bahill et al, 1975c).

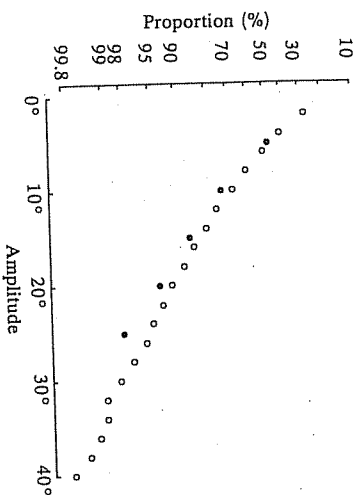


Figure 4.4. Distributions of saccadic amplitude under natural conditions. The graph shows the proportion of saccades that are less than or equal to the amplitudes shown on the abscissa, for: ● average of three human subjects (Bahill et al, 1975a), ○ cat (Collewijn, 1977a; 1977b).

Saccades that are slower than the main sequence would predict are found in infants (Hainline, 1984; Hainline et al, 1984), with auditory rather than visual targets, or in the dark (Becker and Fuchs, 1969; Riggs et al, 1974; Koerner, 1975; Zambardi et al, 1981; 1982), as a result of alcohol or barbiturates (Aschoff, 1968; Franck and Kuhlo, 1970; Gentles and Lewellyn Thomas, 1971; Wilkinson et al, 1974; Bittencourt et al, 1981), or as a result of voluntary control (Crawford, 1984), in certain clinical conditions (Starkman et al, 1972; see Leigh and Zee, 1983), and perhaps with fatigue (Bahill and Stark, 1975b; Fuchs and Binder, 1983). Age appears to have little effect (Abel et al, 1983), nor blindness (Leigh and Zee, 1980). Differences are also found in more extreme lateral eye positions, which may be explained by the mechanical properties of the eye (Abel et al, 1979). In cats, peak velocities are smaller, and the saccadic parameters tend to be more variable (Evinger and Fuchs, 1978). One might wonder whether the normal duration-velocity relation would still be seen when a saccade is made on a continuing background of smooth pursuit, or whether the smooth pursuit velocity would not add on to the saccadic velocity. Summation of this kind is not in fact seen (Jürgens and Becker, 1975) suggesting that here, as noted in section 2.3.2 in the case of the vestibulo-ocular reflex, other inputs to the oculomotor system are in effect switched off during saccades. Another situation where some deviation from the main sequence might perhaps have been expected is after damage to the oculomotor nerves; it turns out, however, that subjects learn to overcome the resultant weakness by generating longer pulse durations for a given amplitude, the velocity-duration relationship remaining normal (Abel et al, 1978).

Differences in the velocity of saccades made in different directions have sometimes been noted, though not always consistently (for a summary see Fuchs, 1971). In the case of oblique saccades—those involving more than one pair of muscles—one might wonder whether each pair of muscles receives a command of equal duration, but of a size scaled according to its contribution, or whether the horizontal and vertical components of the movement are of different durations. Experiments show that it is the first of these possibilities that actually happens, and that the smaller component is

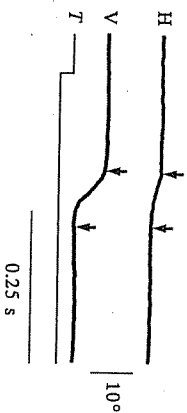


Figure 4.5. Horizontal (H) and vertical (V) components of an oblique saccade made by a cat. T is target displacement. The durations of each component (marked by arrows) are approximately equal (Evinger et al, 1981a).

stretched and slowed in such a way that both components finish more or less simultaneously (Viviani and Berthoz, 1977; Blakemore and Donaghy, 1980; Guitton and Mandl, 1980b; Evinger et al, 1981a; van Gisbergen et al, 1985) (figure 4.5). Possible ways in which the oculomotor system may do this are considered in chapter 12.

Comparisons with other kinds of movement can be instructive. Quite similar relationships between velocity, amplitude, and duration are found for voluntary movements of the wrist (Fortuin, 1982), suggesting that here too the size of a movement is essentially encoded in the duration of a motor command. Head movements, however, appear to be programmed differently: velocity increases more markedly with amplitude, and duration is virtually constant (Stark et al, 1980; Dieringer et al, 1982).

#### 4.1.2 The termination of saccades

The pulse of activity that drives the eye to its new position must be followed by a steady (and lower) level of stimulation that will hold it there. If these two components, the *pulse* and the *step*, are not matched correctly to one another, at the end of the saccade the eye will move from the position to which the pulse has thrown it, to the position corresponding to the size of the step component. Movements of this kind are rather slow, taking as much as a second to reach completion, and are called *glissades*: their time course corresponds with the step response of the eye mechanics (Weber and Daroff, 1972; Easter, 1973; Bahill et al, 1975d; 1976). If the pulse is too long in relation to the size of the step, an overshoot with glissadic return will be seen; if too small, glissadic undershoot (figure 4.6). In addition to this mismatch between the step and pulse components of activation of any one muscle, there may be differences of timing or amplitude between its activity and that of its antagonist. In particular, there is some evidence that saccades

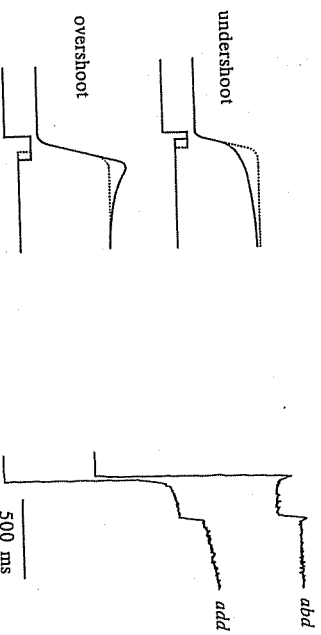


Figure 4.6. Modes of saccade termination. Left, glissadic undershoot and overshoot compared with a normal saccade, together with the corresponding idealised neural commands. Right, binocular recording of human 5° saccades showing dynamic overshoot in the abducting eye (*abd*) and postsaccadic drift in the adducting eye (*add*) (after Kapoula et al, 1986).

may be braked by a pulse of activity in the antagonist at the end of the movement (chapter 7), and this may also provide a source of error. Mismatch of this kind is believed to account for a different kind of behaviour seen in a substantial proportion of saccades called *dynamic overshoot*. Here the eye returns to its final position within 15–20 ms at a velocity that is much higher than in the case of a glissade (figure 4.6) (Westheimer, 1954a; Thomas, 1961; Fuchs, 1967a; Bahill et al, 1975b; 1976; Leigh and Stark, 1983; Kapoula et al, 1986). It is more commonly seen in the abducting eye, and is often associated with dynamic undershoot in the adducting one; it is characteristic of certain diseases of the periphery such as myasthenia gravis (Feldon et al, 1982). A third category of behaviour after a saccade is *postsaccadic drift*, more common in the abducting eye, and more like a glissade: the eye moves very slowly and at a more constant velocity (Kapoula et al, 1986). Whereas the glissade is the result of the eye settling to a new steady level of excitation, postsaccadic drift is thought to be the result of slow changes in the excitation itself, very likely as the result of drift in the saccadic integrator, moderated by the mechanism of slow visual oculomotor control (described in section 6.3.2: see for example Kowler and Steinman, 1979a; 1979b), and perhaps also by vergence. Thus postsaccadic drift is a prominent feature of the saccades of patients who have become blind well after birth (Leigh and Zee, 1980), demonstrating that in this case at least, postsaccadic drift is not primarily driven by vergence. A curious feature of the way in which the oculomotor

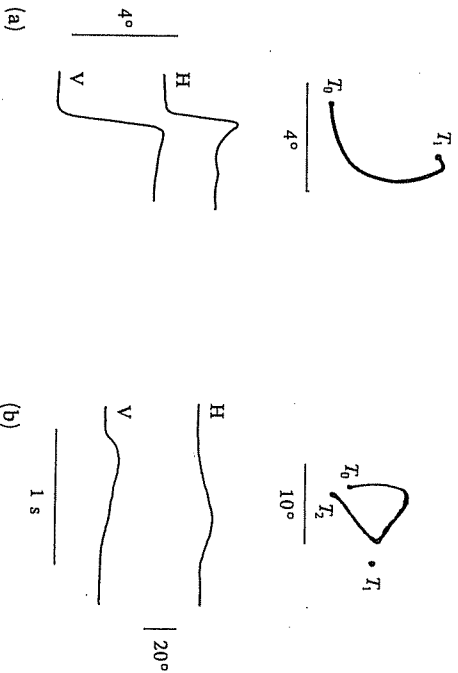


Figure 4.7. Two-dimensional trajectories of oblique saccades: (a) in man (after Bahill and Stark, 1979); and (b) in the cat (Evinger and Fuchs, 1978). The records underneath show the corresponding horizontal (H) and vertical (V) components as a function of time. The cat saccade is an aberrant one, the saccade being modified in midflight.  $T_0$  is the initial target position,  $T_1$  and  $T_2$  are successive ones.

system copes with peripheral defects of the mechanics is that modification of the pulse-step pattern can apparently only be made for *both eyes equally*: with unilateral weakness, one eye will make accurate saccades at the expense of the other, which shows overshoot and a prominent postsaccadic drift (Kommerell et al, 1976; Optican, 1985).

Finally, it should perhaps be borne in mind that some of the postsaccadic behaviour that has been described may possibly be caused by movements of the eye other than simple deviations, in particular the retraction and torsion that has been described by Emright (1987). An observation that reinforces this view is that neurons in the oculomotor nuclei sometimes show slow postsaccadic changes in firing rate that are *not* accompanied by corresponding deviations of the eye (Mays et al, 1985).

One consequence of all this irregular behaviour is that the two-dimensional trajectory of an oblique saccade is generally far from straight, despite the pulse-stretching mechanism described in the previous section; this is exacerbated by the lack of synchrony between the onset of activity in the two pairs of muscles that is sometimes observed (figure 4.7).

#### 4.1.3 Latency

The complexity of the calculation necessary to transform retinal distances into eye movements is reflected in the rather long reaction times associated with saccadic movements. A common experimental arrangement is for the subject to fixate a stimulus light that is suddenly switched off while a nearby light is simultaneously switched on: the saccade the subject then makes to the new target typically does not begin until about a fifth of a second later. A puzzling feature of saccadic latencies is their random *variability*: latency histograms in such an experiment typically stretch from some 120 ms up to 350 ms or more. The distribution is skewed, with a long tail towards longer latencies: by plotting it not as a function of latency but of its reciprocal (*promptness*), a curve that is very close to a normal distribution is obtained (figure 4.8) (Carpenter, 1981), generating a straight line on probit paper. A very similar relationship is found for many other kinds of reaction time data, and leads one to ask what type of mechanism might give rise to such a distribution.

The simple notion of transport delays along a chain of neurons seems out of the question, since the number of neurons in such a chain would have to be considerably greater than any plausible estimate of the neural length from retina to eye muscles; and in any case, the very large degree of *variability* would be hard to explain in such a scheme. Nor does it seem likely to be the result of the time it takes to calculate the neural signal necessary to move the eye to the required position. We shall see later that visual information arriving as little as 50 ms before the saccade can be used to help compute its size (Barnack, 1970b), and short-latency saccades on the whole show no more scatter than long (Becker and Jürgens, 1979). Rather, this delay seems to have to do with the task of deciding whether in fact there

is a target at all, and if so, whether to look at it, something altogether more high-level and complex. The complexity of such a process may not seem so obvious in the very artificial laboratory situation of a single light that may either be illuminated or not, but is immediately evident when we consider saccades under natural conditions. Here we are surrounded by a rich variety

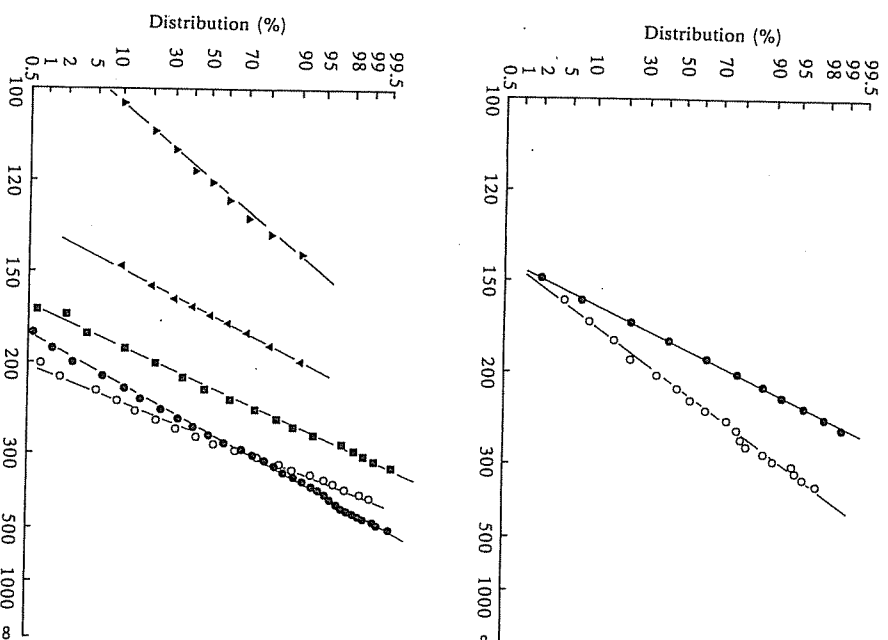


Figure 4.8. Top, cumulative distributions of latency for human (●) and simian (○) saccades, plotted on scales such that a normal distribution of reciprocal latency (*promptness*) would result in a straight line (data from Fuchs, 1967a; Carpenter, 1981). Bottom, reaction times for some very different tasks plotted in the same way, to show the generality of the relationship. ● pressing one of two keys in response to lights (Welford, 1959); ▲ responding to a 100 dB or ▼ 50 dB auditory stimulus (McGill, 1963); ■ responding to a tactile stimulus (Kiesow, 1904); and ○ in a visual discrimination task (Johnson, 1918).

of possible objects, which do not obligingly signal themselves by lighting up in the manner of laboratory targets, and whose relative importance depends on their meaning: are they *worth* looking at? That it is this kind of decision process that ultimately determines saccadic latencies is evident from experiments where the subject is required to make an oculomotor response to a visual target that is not simply that of looking at it. The subject may for example be required to make a saccade that is deliberately directed in the opposite direction to the stimulus (an 'antisaccade': Hallett, 1978; Hallett and Adams, 1980), or a colour change in the fixation light may tell the subject which of two alternative targets to fixate: in all such cases, as in those where the target is difficult to detect because of reduced contrast or higher noise-levels, latencies are greatly increased. How might such decisions be made?

One plausible notion is that for each possible action that might be taken, there is a corresponding *decision signal* that increases in response to stimuli that make that action appear more desirable and decreases with those that seem to make it less so. When this signal reaches some predetermined threshold, the command to carry out the action is given, and the decision signals of all the possible actions are reset to zero (figure 4.9). In effect, the system runs a race between the different possibilities, the first one to reach threshold being the one that determines the response. The rate of rise of such a signal will be expected to depend on the rate at which information is received (itself depending on the signal-to-noise ratio), but may also be expected to have a deliberate *random* element, to prevent responses from becoming too stereotyped. If this random component is taken to be Gaussian, the distribution of latencies expected from such a model in response to a novel stimulus is precisely of the rather odd kind previously noted, namely normal with respect to reciprocal latency rather than to

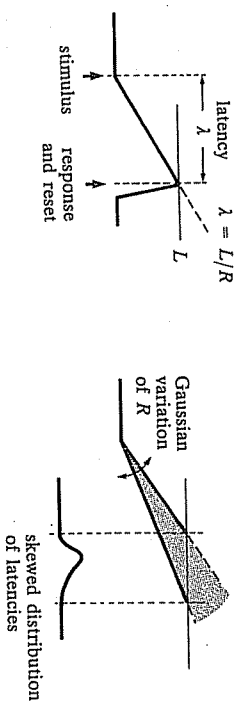


Figure 4.9. A model of the saccadic latency process. Left, the activity of a decision unit rises linearly at a rate  $R$  on presentation of the stimulus, and initiates a saccade when its activity reaches a predetermined level,  $L$ ; it then resets all other units. Thus the first unit to reach its threshold determines the choice of target and the latency. Right, if  $R$  is subject to random Gaussian variability, the resulting distribution of latencies will be Gaussian with respect to the *reciprocal* of the reaction time, rather than to the reaction time itself.

latency itself (Carpenter, 1981). The variability is on a rather short time scale: there is no detectable correlation between the latencies to two target jumps 500 ms apart. Its origin is certainly central rather than peripheral, at a rather high hierarchical level: latencies are generally identical in the two eyes (Williams and Fender, 1977), and during many kinds of complex natural movements, such as reaching out for an object, there is a very strong correlation between saccadic latency and that of head and arm movements (Herman et al, 1981; Biguer et al, 1982; Zangemeister and Stark, 1982a). In the same way, if a subject is asked both to look at, and also to reach out for, one of a pair of targets simultaneously presented, both eye and hand make the same choice (Gielen et al, 1984); the decision mechanism is evidently not merely a part of the oculomotor system. Possible neural mechanisms that might correspond to such a decision process are considered in chapter 12.

Cumulative plots of the distribution of saccadic latency as a function of promptness greatly facilitate the comparison of the effects of various stimulus conditions on saccadic latency. With reduced illumination, latencies are increased (figure 4.10) (Wheless et al, 1967), although the effects here are not very marked until the luminance of the target is actually below foveal threshold, introducing an obvious difficulty of interpretation! Latency increases to some extent with increased saccade amplitude, for example by some 40 ms for a  $40^\circ$  movement (figure 4.11, left) (White et al, 1962; Bartz, 1962). Paradoxically, it also increases if the required amplitude is

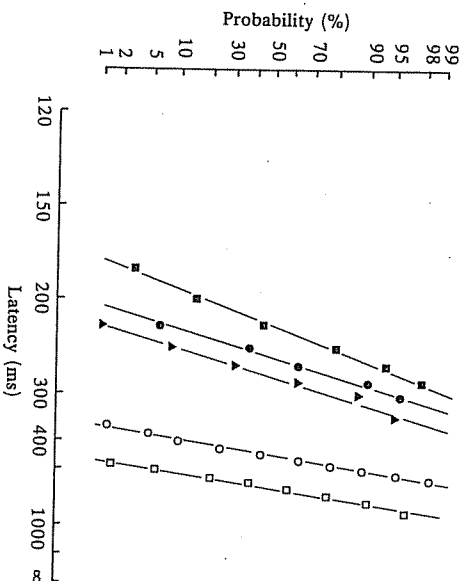


Figure 4.10. Saccade latency and luminance: cumulative latency probabilities are plotted as in figure 4.8 for five different luminance conditions: ▲ target luminance equal to the foveal threshold; ● 1 log unit; ■ 2 log units above foveal threshold; ○ 1 log unit; □ 1.5 log units below foveal threshold (data from Wheless et al, 1967).

reduced (figure 4.11, right) (Wyman and Steinman, 1973b); it seems that the probability (per unit time) of making the saccade falls sharply if the size of the positional error is very small. It is probably true to say that no target displacement is so small that it will not eventually evoke a saccade: certainly saccades can be repeatedly elicited by target movements rather less than  $10^\circ$  of arc in amplitude (Timberlake et al, 1972; Wyman and Steinman, 1973a; Haddad and Steinman, 1973; see section 6.4).

But the greatest changes in latency are caused by providing the subject with prior information about the saccadic target. If the subject knows in advance *where* the target is going to appear, he or she tends to anticipate and shows shorter latencies than if the target can appear in one of two possible positions. [On the other hand, the latency to a target that has just been looked at is found to be increased slightly (Vaughan, 1984).] However, if the number of possible target positions is increased beyond two, the reaction time is apparently not correspondingly increased (Saslow, 1967b); saccadic reaction times thus differ in this respect from what is found in other reaction time experiments as the number of possible responses is increased (see for example Edwards, 1969). If the subject knows both where and *when* the stimulus is to appear—as for example in tracking a spot that is jumping back and forth at regular intervals—performance rapidly improves, and after a few cycles the subject can produce saccades that are virtually in synchrony with the stimulus movement (Westheimer, 1954b; Stark et al, 1962; Dallos and Jones, 1963; Fuchs, 1967b) (figure 4.12). As was previously noted in the case of sinusoidal tracking, monkeys are apparently unable to make use of this kind of redundancy in the input, and the saccades they make to repetitive stimuli show no improvement with time (Fuchs, 1967b).

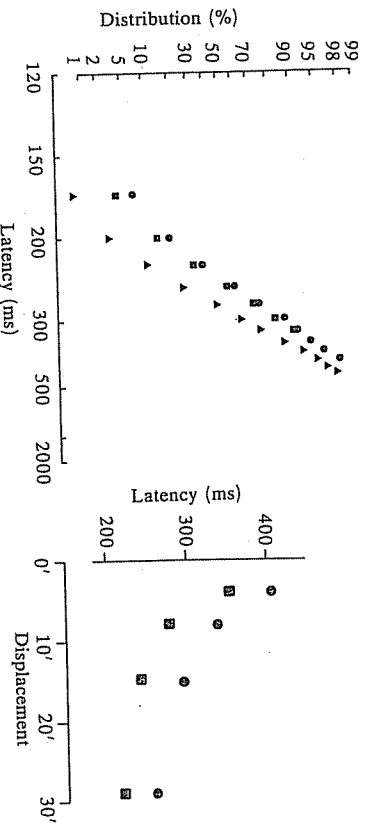


Figure 4.11. Left, cumulative plots of promptness, as in figure 4.8, of saccades of different amplitudes:  $\circ$   $10^\circ$ ;  $\square$   $20^\circ$ ;  $\blacktriangle$   $40^\circ$  (data from White et al, 1962). Right, average latencies (for two subjects) of saccades in response to rather small target displacements, as a function of their size (data from Wyman and Steinman, 1973b).

In the same way, any kind of *warning* signal before a saccadic stimulus, that helps the subject to predict when the target will appear, reduces latency (Ross and Ross, 1980). The warning may simply consist of extinction of the fixation light at a fixed interval before illumination of the target; in this situation saccades with unusually short latencies ('express saccades') are observed both in human subjects and monkeys, particularly if the target location is also known in advance (figure 4.13) (Saslow, 1967a; Becker, 1972; Findlay, 1981a; Boch et al, 1984; Fischer and Rampeger, 1984; Fischer et al, 1984). Histograms recorded under such conditions tend to be bimodal, the longer mode being nearly normal and the shorter one corresponding to anticipations. Indeed, even in the classical saccadic latency

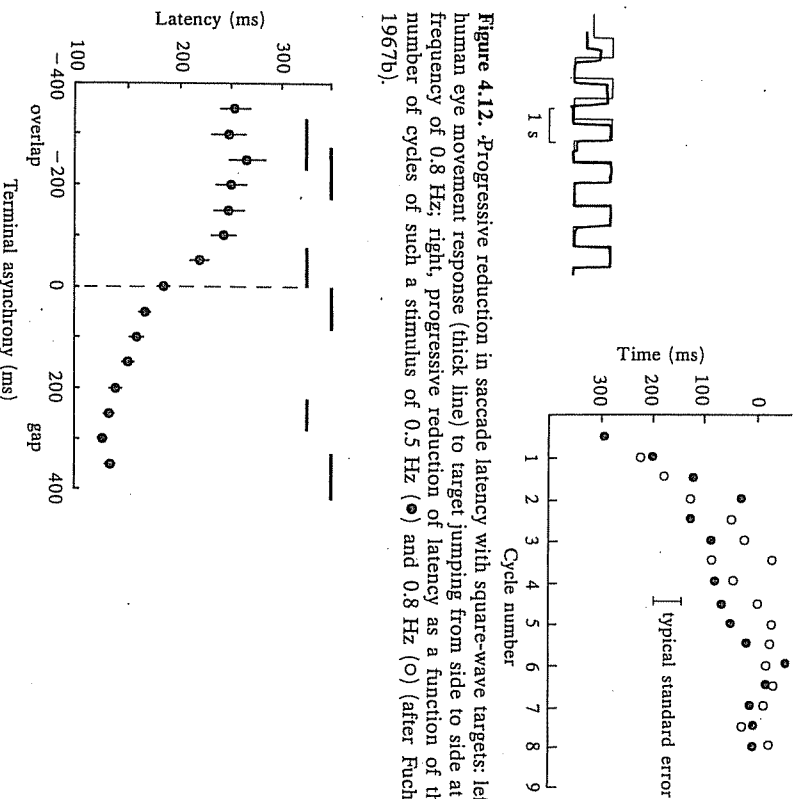


Figure 4.12. Progressive reduction in saccade latency with square-wave targets: left, human eye movement response (thin line) to target jumping from side to side at a frequency of 0.8 Hz; right, progressive reduction of latency as a function of the number of cycles of such a stimulus of 0.5 Hz ( $\circ$ ) and 0.8 Hz ( $\square$ ) (after Fuchs, 1967b).

Figure 4.13. Mean saccadic latency for different relationships between the time of extinguishing the fixation light and of illuminating the target. On the abscissa, negative times correspond to the case where the fixation light is extinguished before presentation of the target ('gap'), and positive times to when it is after ('overlap') (data from Saslow, 1967a).



experiment in which the fixation light is extinguished at the same moment as the appearance of the target, this extinction still serves as an extra cue that reduces saccadic latency. If the fixation light is left on, so that the stimulus is simply the extra appearance of the target, latencies are increased by 100 ms or more (figure 4.13) (Saslow, 1967a; Ross and Ross, 1980; Reulen, 1984a). It is arguable in fact that this form of saccadic stimulus is both simpler than the traditional one, and also more natural: it is not often in everyday life that something we are looking at happens to vanish at the very same instant that another object suddenly appears elsewhere in our visual field! The classical stimulus is really one of sudden *movement* rather than of simple stimulation of a particular retinal locus, and from the point of view of latency the extinction of the fixation light seems to be more important than the appearance of the target.

Another factor influencing the latency of saccadic movements is the apparent *refractoriness* that is observed after a saccade: as a rule, one saccade cannot follow another with an interval of less than some 180 ms. This can most easily be demonstrated by arranging for the visual target to switch back to the centre again after the initial displacement, providing a brief pulse of displacement rather than the step used in conventional saccade measurements (figure 4.14). If the duration of this displacement pulse is less than some 150 ms, one of two responses may occur: either the eye simply ignores the brief excursion, and does not move, or it makes a full saccade to the eccentric target, followed by a return movement. This return movement is not separated from the excursion by a time equal to the width of the pulse, as would be expected from a simple delay, but by a relatively fixed interval of some 150–200 ms (Westheimer, 1954b). It makes little difference if the second saccade is in a different meridian from the first (Feinstein and Williams, 1972). However, examination of large numbers of responses to short pulses of this kind, or to pairs of target displacements in the same direction (*double steps*) shows that refractoriness is not always strictly observed, and that a second saccade may be initiated before the first

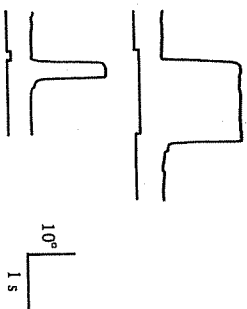


Figure 4.14. Saccadic responses to long and short pulses of displacement. In the second case it is clear that the initial saccadic response is unaffected by the fact that it is completely inappropriate—the target has already returned to its starting position—and the latency of the return saccade is very greatly increased.

would normally have finished: this modification of the first may occur within 80 msec of the second step, a time that is considerably less than the normal latency (Bahill and Stark, 1975b; Becker and Jürgens, 1975; Evinger and Fuchs, 1978; Findlay and Harris, 1984) [see figure 4.7(b)].

A similar refractoriness is observed in the microsaccades of fixation (Nachmias, 1959), a fact which raises a doubt as to whether conventional measurements of saccade latencies really measure reaction times at all. For if, in the course of fixating the central target, the subject happens to have executed a microsaccade very shortly before the target movement occurs, the saccade will be delayed by an interval representing the refractory period, rather than the true reaction time. Indeed, one could imagine a microsaccade occurring up to one reaction time *after* the moment of target motion (correcting for where the target *was*), resulting in a maximum latency of one refractory period plus one true reaction time; the minimum possible latency is of course the reaction time. Finally, one can demonstrate refractoriness of the quick phase of nystagmus after voluntary saccades (Judge, 1973), underlining once again the probable identity of these two movements. However, a quick phase does *not* apparently delay a subsequent saccade in the expected manner, perhaps because a novel visual stimulus in some way suppresses the more primitive nystagmus mechanism. The possibility that refractoriness is the result of some kind of intermittent gating process is discussed in section 4.2.2 below. But it is also a direct consequence of the decision mechanism proposed above, since it will take a certain period of time after all the decision units have been reset at the initiation of a saccade for any of them once more to reach threshold.

General factors that increase latency include age (Abel et al, 1983), mental state (Kapoula, 1984), and certain kinds of psychopathology such as schizophrenia; in this respect saccadic reaction times behave very similarly to other kinds (Nettelbeck, 1980; Done and Frith, 1984). Increased latency can also be characteristic of amblyopia (Chiffreda et al, 1978a; 1978b).

#### 4.2 The control of saccades in relation to the visual stimulus

##### 4.2.1 Correction saccades

A rather puzzling feature of large saccades is that they almost invariably fall short of their targets, and are followed—after the expected refractory period—by a secondary, or *correction*, saccade (figure 4.1). Making a saccade to a target is thus not unlike taking a hole at golf. For target amplitudes greater than some 20° the size of the correction saccade is typically about 10% of that of the primary component, though there is a tendency for correction saccades to the midline to be smaller than when the movement is to the periphery (Becker, 1972; Kapoula and Robinson, 1986). As the target amplitude is reduced, the percentage is also reduced: at around 5–10° the primary saccade is accurate, and below that amplitude *overshoot* rather than undershoot is seen (Clark, 1936; Weber and Daroff, 1971; 1972; Henson, 1978; 1979; Fischer and Kunz, 1981; Kapoula, 1985). However, there is an

oddity about these observations, which is that the crossover point on the graph of primary saccadic amplitude against target amplitude depends on the range of target amplitudes presented in any particular session, under-shoot and overshoot depending to some extent on whether an amplitude is *relatively* bigger or smaller than others in the range recently presented [the *range effect*, commonly observed in manual tasks as well (Kapoula, 1985; Kapoula and Robinson, 1986)].

Are such saccades genuinely corrective, the result of seeing at the end of the primary saccade that there is still some way to go? If so, then in the case of the largest saccades, which can last 100 ms or more, it would imply a very short reaction time (rather less than 100 ms) for the generation of the correction saccade, though one that is perfectly compatible with latencies seen when, as here, the *time* of the saccadic stimulus is predictable. Perhaps indeed this is the explanation for having a refractory period at all: the system must obviously ensure that the eye has stopped moving at the time the estimate of the error is made, and this could perhaps be arranged most easily by holding up the calculation until some fixed time has elapsed after the beginning of the last one, long enough to allow for even the largest eye movements. One might suppose that it would be more efficient to allow more settling time for larger saccades than for smaller: but this does not seem to occur. The latency of the correction as measured from the *end* of the main saccade is greater, the smaller the size of the original movement (Becker, 1972); but the latency as measured from the *beginning* of the main saccade is roughly constant whatever its size.

However, a number of experiments indicate that the correction saccades seen in large movements are not in fact the result of sensing a visual error. They are still observed in total darkness, when of course no visual monitoring is possible (Becker and Fuchs, 1969), and also in 'antisaccades', where again there can be no direct error information from the retina (Hallett, 1978). Extinguishing the target just before the primary saccade does not abolish correction saccades, although they may then be less accurate: although visual feedback is not necessary, it can be used to increase accuracy provided it is available some 60 ms before the time of the secondary saccade (Pernier et al, 1969; Barnes and Gresty, 1973; Prablanc et al, 1978; Deubel et al, 1982). But in any case, the characteristics of the error in the first saccade do not suggest that the system is doing its best to get it right first time. If it were, we would surely expect the endpoint of the first saccade to be randomly distributed about the target, whereas in fact the first saccade shows rather little random variation and appears to be deliberately and quite accurately aimed short of the target (Becker, 1972). Nor is it simply that the eye is incapable of executing a single saccade of more than a certain amplitude: a saccade of 30° is executed in two stages, even though the first component of a 40° saccade is itself a saccade of more than 30° (figure 4.1). Further evidence that the eye is very deliberately

undershooting comes from experiments in which the target is moved back a little way at the moment of each primary saccade, so that what was previously an undershoot now lands on target. Far from being contented with the resultant hole-in-one, the saccadic control system quite rapidly adapts to the new state of affairs by reducing the amplitude of the primary component so as to require secondary saccades exactly as before (Henson, 1978).

Why are large saccades executed in this peculiar way? One might argue that undershoot simplifies the calculation of the secondary saccade, since at least its *direction* is known; perhaps also it is helpful for the same side of the brain to be involved as for the primary saccade (Becker 1972; Henson, 1978). Or perhaps it is that by providing a comparison of expected error with actual error, undershoot can help the system to optimise its parameters in relation to the oculomotor plant; deliberate errors are sometimes used for a similar purpose in man-made control systems (Elgerd, 1967; Optican, 1982). But while it is quite plausible that the system might deliberately miss the target so as to improve its *theoretical* performance in the long term, it is perhaps less plausible that the system should choose to play educational games with itself at the very moment when it is required to to perform as well as possible. Another suggestion is that undershoot is the result of the head being constrained: under natural conditions a head movement is initiated in parallel with the saccade, and it may very well be that the oculomotor system is trying to make allowance for a part of this expected contribution by the head. However, the sequence of saccades often seen with large shifts of gaze when the head is free suggests that this is not the case (see for example Guitton et al, 1984). A final possibility comes from a consideration of natural saccadic targets. As was emphasised earlier, targets do not commonly jump instantaneously from one fixed position to another in the real world. Usually a new target appears in the periphery, and it appears there because it is *moving into* the visual field. Perhaps then the undershoot in fixating sudden peripheral targets arises through anticipation of this movement, the saccadic system assuming that by the time the saccade occurs, the target will be that much nearer the centre.

But in addition to these rather pathological correction saccades following large eye movements, there are also those associated with much smaller movements, that are certainly simply the result of sensing an error of fixation. One way of demonstrating this is by opening the intrinsic visual feedback loop (in the manner described in the previous chapter) so that every time the eye makes a saccade toward the target, the target simultaneously jumps away from the eye by the same amount. One then finds that the response of the eye to an initial step displacement consists of a regular series of saccades of equal amplitude, forming a staircase in which the treads are some 200 ms long [figure 4.15(f)] (Young and Stark, 1963; Robinson, 1965; Fuchs, 1967a; Fleming et al, 1969; Evinger and Fuchs, 1978). If the negative feedback is increased beyond its natural value of -1, a step displacement of the target produces oscillations (again, as in the case of the

smooth pursuit mechanism) which either die away or increase in amplitude, depending on the value of the feedback gain [figure 4.15(a)-(c)]. For a gain of  $-2$  they neither grow nor shrink, and the result is a stable oscillation; with larger negative gains, around  $-2.3$  to  $-5$ , spontaneous oscillation is seen. All this is of course only what would be expected if the saccade size is matched accurately to the perceived target error, and tells us little new about the system beyond confirming that correction saccades can be generated by visual feedback, and really are corrective. The correctness of microsaccades is considered in section 6.4.

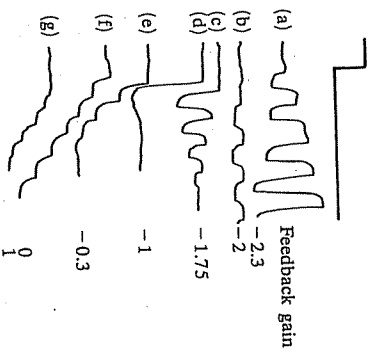


Figure 4.15. Saccadic responses to a step of target position (top trace) under different artificial feedback conditions:  $-1$  is the natural condition (after Young and Stark, 1963).

#### 4.2.2 Saccadic intermittency

Given that saccades are discrete, prepackaged, events, one might wonder whether the visual information used to generate them is also obtained in a similarly discontinuous manner. Is the visual scene *sampled*? The fact that every eye movement causes a shift of the visual world puts certain bounds on the periods of time preceding a saccade during which visual information about the position of a target is actually useful. Information obtained before a previous saccade is clearly out of date; equally, information acquired within one reaction time of the new saccade is too late. Thus there is a definite time window outside which visual information about target position is of little use. Note, however, that this does not necessarily apply to *velocity* information, which is not rendered out-of-date by an intervening saccade: this point is considered in the next section. It is also true that for *flashed* targets, information acquired during or even before a prior saccade might be better than none at all (see for example Hallett and Lightstone, 1976a; 1976b; and section 11.1): but the argument presented here concerns 'natural' objects that are continuously visible. Furthermore, not all the

information gathered during this window is equally useful: clearly more weight ought to be attached to the most recent information. In fact, in a noise-free situation (where the target is not subject to relatively fast random motion, and where the monitoring device has perfect certainty of the target's position at any instant) the best strategy is to make a rather short sample of the visual information, at the last possible moment. The greater the noise in the system, the longer this sampling interval will have to be for accurate performance. A simple way of meeting all these requirements would be to sample the visual scene briefly at regular intervals of time, the intervals being chosen to be greater than the sum of the reaction time and the duration of the longest saccades, that is, of the order of 200 ms. More than forty years ago, the desirability of this kind of intermittency in motor control in general had been identified by Craik (1966): "It is possible here that a system inevitably containing time-lags (for example, a human being) acts best if it acts discontinuously, so that its actions are always based on the last 'static' situation (that is, the instant when the last response, with its time-lag, has taken effect and the comparison of that with the situation to be met is observable) rather than on a shifting and misleading state of affairs". The suggestion that intermittent sampling might be used by the oculomotor system seems first to have been made by Vossius (1960) and by Young (1962; Young and Stark, 1963). Does it in fact occur?

The experiments that best support the notion of intermittent sampling are those that involve pulses of target displacement, of the kind described above in connection with the demonstration of the refractory period (for example Westheimer, 1954b). If the sampling pulse happens to coincide with the brief displacement of the target, one would expect the system to respond with a saccade; if not, no movement would be expected. This is exactly what is observed: on some trials a saccade is made to the pulsed target, whereas on others nothing happens at all. On the whole the responses are 'all-or-none', implying a rather short sampling period, although sometimes one may observe saccades of intermediate size.

Similar results have been obtained by using a slight modification of this arrangement, namely the *pulse-step* stimulus (Wheless et al, 1966; extended by Komoda et al, 1973; Carlow et al, 1975; Becker and Jürgens, 1979; and others). Here the target first jumps to one side of a central fixation spot, and then after a brief interval  $W$  jumps to the other side of it and stays there (figure 4.16): to prevent adaptational changes, this stimulus is randomly interleaved with suitable controls. The resultant response is again found to be probabilistic, the eye making a saccade either to one or to the other side of the centre. As the duration of the pulse is increased, the probability of the initial saccade being in the same direction as the pulse—a *type A* response—increases linearly (figure 4.16). [The exact relationship varies considerably from subject to subject, but this variability can be greatly reduced if allowance is made for the mean reaction times of different individuals (Lisberger et al, 1975).] Such a relationship is exactly what

would be expected if brief samples of the visual input were being made at regular intervals: the longer the pulse, the greater in proportion will be the probability that the sample will happen to fall within it. Even with a pulse lasting 200 ms, a substantial percentage of the responses do not follow it, suggesting that the sampling interval is somewhat longer than this. The fact that zero probability is reached with a pulse duration of some 40 ms might be taken to suggest that the sampling period is of about this size. This view is supported by the observation that both here and also in the case of double-step stimuli a few saccades of intermediate size can be observed in the transition region between the full-blooded type A and type B and responses (figure 4.17) (Becker and Jürgens, 1979; van Gisbergen et al, 1981a; Ottes et al, 1984), suggesting low-pass filtering of perceived target position of the kind that a finite sampling window would be expected to produce.

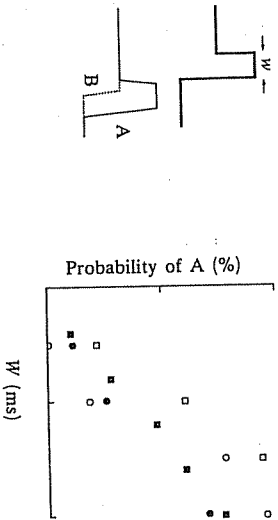


Figure 4.16. The pulse-step experiment. On the left, the upper trace shows the target movement: it steps to one side for a duration  $W$ , then steps back to the same distance on the other side of the midline. The eye (lower trace) either follows it back and forth (type A response), or moves only in the final direction (type B response). The graph shows the probability of a type A response as a function of  $W$  (● Wheelless et al, 1966; ■ Carlow et al, 1975; ○ Komoda et al, 1973; □ Becker and Jürgens, 1979).

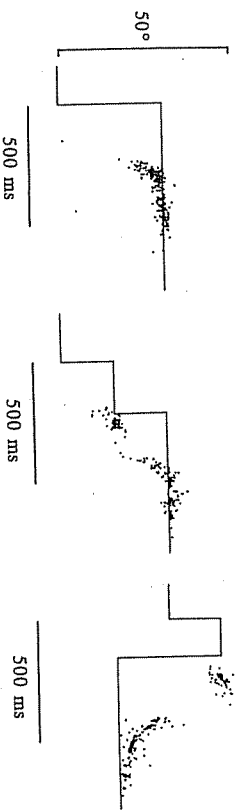


Figure 4.17. Transitional behaviour with step, double-step, and pulse-step targets. In each case, the endpoints of saccades that finished at particular times are shown as dots, superimposed on the time course of the stimulus itself (data from van Gisbergen et al, 1981a; subject JG).

These results clearly provide *prima facie* evidence for the idea of intermittent sampling. But if we start to look at what the model implies about the distribution of *latencies* in different saccadic tasks, it becomes obvious that there is something terribly wrong. Consider first an ordinary single target step: on different occasions a stimulus sample will occur with responses at different times relative to the step itself, so that we would expect to get a random variation of latencies with a spread of some 200 ms, which is perfectly true. But the expected *distribution* of these latencies will be a rectangular function, flat in the region  $\lambda_0$  to  $\lambda_0 + s$ , where  $\lambda_0$  is the reaction time of the system, and  $s$  is the intersample interval [figure 4.18(a)]. Actual latency distributions are not of this form, as we have seen, but it is likely that other sources of variation exist which will tend to round off the corners. (Latour claimed in 1967 that there was a *periodic* component to distributions of saccadic latency, linked to the EEG; but its frequency was an order of magnitude greater than the kind of clock being considered here.) Consider next a pulse-step stimulus in which the width of the pulse is  $W$ . The expectation then is that all responses whose latencies lie in the region  $\lambda_0$  to  $\lambda_0 + W$  will follow the pulse, whereas those in the region  $\lambda_0 + W$  to  $\lambda_0 + s$  will follow the step, resulting in a pair of distributions for the two responses, that do not overlap [figure 4.18(b)].

The actual distributions found in such experiments (figure 4.19) do not look like this. Although the number and distribution of pulse-following responses agree well with the model (as can be seen by comparing their cumulative distributions with those for the simple step stimulus: see also Lisberger et al, 1975, and Becker and Jürgens, 1979), the distribution of latencies for the responses that follow the step is markedly shifted to the right, by some 130 ms. Now if the *only* information available to the system about the position of the target was obtained by a series of samples more than 200 ms apart, the system could not possibly know that the step had

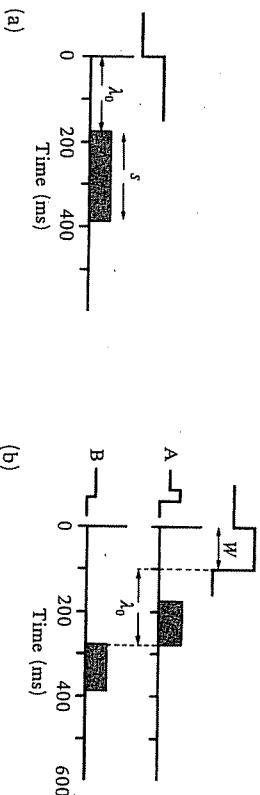


Figure 4.18. Distributions of reaction times expected in the Wheelless experiment, on the very simple hypothesis of regular sampling at an interval  $s$  (uncorrelated with the stimulus) and a simple reaction time: expected distribution (a) in response to a step of position, and (b) for each of the two kinds of response to the Wheelless stimulus;  $W$  is the duration of the stimulus pulse.

been preceded by a pulse in the opposite direction. Yet the system *must* in fact know that these are not just normal steps, for it responds to them with latencies that are enormously increased. One is therefore forced to conclude that the system does *not* rely solely on intermittent brief samples in calculating its saccades. In the pulse-step experiments the presence of the step can in some way cancel the pulse response that would otherwise have occurred, and conversely the presence of the pulse can profoundly modify the response to the ensuing step. Rather similar effects were shown by Becker and Fuchs (1969), using stimuli consisting of a large step followed by a smaller step. If the interval between the two is large enough for the second step to take place after the saccadic responses to the first, extremely large latencies—again of the order of 400 ms—are observed in the second saccade.

Observations of this kind do not rule out the notion of intermittent sampling altogether: but they imply that visual input is *continuously* available for the purpose of cancelling saccades that are in the course of elaboration and that are going to be inappropriate. A hypothetical system of this type is

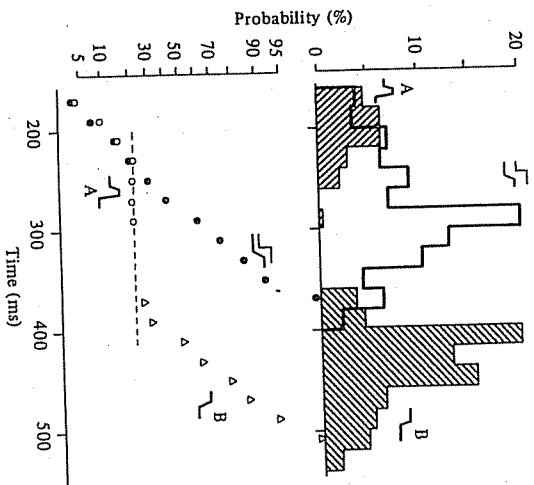


Figure 4.19. Statistical properties of the latencies in the experiment shown in figure 4.20. Above, the shaded areas show the observed latency histograms for the two kinds of response, type A and type B; the unshaded histogram is for a simple single step of the same amplitude under identical conditions. Below, the same data are plotted in the form of cumulative probabilities, showing that the type A responses lie on the curve for ordinary single-step saccades, whereas the latencies for type B responses are as if the single-step distribution were cut in two at around  $t = 230$  ms, and the later responses delayed as a whole by some 130 ms (data from Wheelless et al., 1966).

represented in figure 4.20. After experiencing a delay  $\lambda_v$ , visual information is used in two ways: it is intermittently allowed access to the process that calculates the next saccade, and it is also able at any time to cancel a calculation that is in progress, if some change in target position has occurred which means that the saccade is going to be wrong. Figure 4.21 shows the expected distributions from this model in the Wheelless experiment: with a suitable choice of parameters ( $s = 200$  ms,  $\lambda_v = 130$  ms,  $\lambda_p = 50$  ms) it accounts well for the time relations observed in the actual distributions, but not their shapes (because of the assumption of an essentially flat stochastic process). It is also necessary to assume that the cancel signal lasts at least 50 ms, as otherwise the earliest type B responses, due to samples occurring just after the second target displacement, would not be cancelled: the corresponding 'hole' in the distribution is obvious in the data of figure 4.17, but it is evidently not absolute. A similar mechanism of cancellation can also be used to explain the delayed responses, observed when a subject is

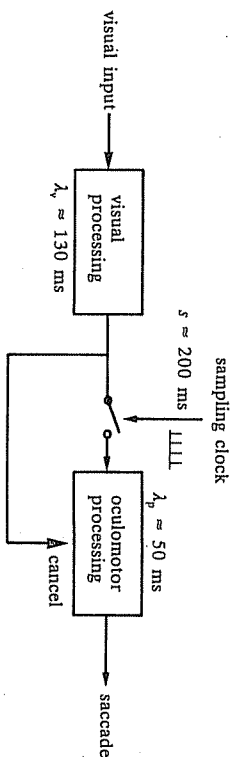


Figure 4.20. A hypothetical model that shows some of the features observed in the saccadic responses to pulse-step target movement.

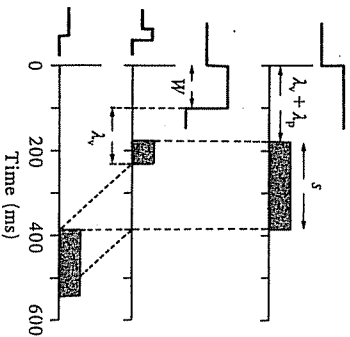


Figure 4.21. Latency distributions that would be predicted by the model of figure 4.20: above, expected distribution of latencies to a single-step movement; below, expected latencies of the two kinds of response to pulse-step stimuli, for  $W = 100$  ms.

required to make an 'antisaccadic' response to a target (section 4.1.3) (Hallett and Adams, 1980).

However, there is another respect in which the idea of intermittent sampling must be modified. If the sampling clock is ticking away at a constant rate, regardless of any visual stimuli or saccadic responses, then there should be a strong correlation between the latencies to two consecutive target steps—in fact the two saccades should always be separated by an exact multiple of the clock interval. Tümer (1975) found some evidence for this tendency in certain of his subjects, though its contribution was small in relation to the overall variability of the latency of the second saccade. With a pulse-step stimulus, Becker and Jürgens (1975) found that the smaller the interval between the second step and the first saccade the longer, on average, the interval between the two saccades—as would be expected if the second response latency were effectively uncorrelated with the first—whereas longer intervals tend to lead to single saccades that jump immediately to the final position of the target. The most critical test of the idea of a regular sampling clock is to arrange for the second step of a double-step stimulus to be triggered at a fixed time after the first saccade, rather than after the first target step (a DT stimulus). This ought in effect to synchronise the second step to the supposed clock, and should therefore entirely abolish (or at least greatly reduce) the variability of the second latency. This simply does not happen: the scatter of the second latencies is about the same as that of the first (figure 4.22). Sampling does *not* occur at regular intervals of time.

So does it occur at all? In particular, is there some other way of explaining the probabilistic nature of the responses to pulse-step targets?

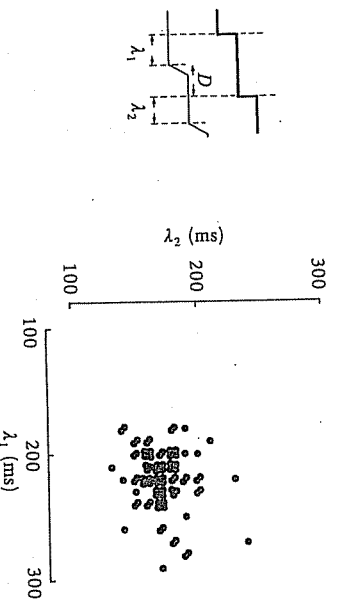


Figure 4.22. Saccadic latencies for one subject in a DT experiment, where the second target step is triggered by the first saccade. The latency of the second saccade is plotted as a function of that of the first; the interval,  $D$ , between the beginning of the first saccade and the appearance of the target was 250 ms. The scatter of the second response is evidently no less than that of the first, and there is no obvious correlation between the two.

Robinson (1973a) has presented a model of saccadic timing that postulates no clocks or sampling, but is still consistent with the kinds of observations described above. In essence, he proposes an array of independent processors acting in parallel and corresponding to different points on the retina. Each takes a certain time to reach its decision about the command to be issued, and when the decision is reached, it both initiates a saccade, and cancels any decisionmaking activity that may be going on in the other units. The time needed for any particular unit to make its decision is subject to random variation: thus if—as in the Wheelless experiments—one unit is activated only a short period of time after another, it may nevertheless complete its operations sooner and thus produce a saccade that jumps immediately to the final target position. By choosing plausible probability functions for the decision times of the individual units, it is possible to make quantitative predictions of many kinds of double-step responses, without having to postulate the existence of a regular sampling process. In particular, if each decision unit works in the way suggested in section 4.1.3 above (Carpenter, 1981), one may obtain quantitative descriptions of the latency distributions that are actually observed.

One factor that complicates the consideration of the responses to double steps is that the relative *directions* of the two components interact with one another in a complex way. Thus the observed amplitude-transition function (figure 4.17) is much wider when the two steps are in the same direction rather than in opposite directions (Becker and Jürgens, 1979), and the correlation of the latencies of the first and second response is different in the two cases (figure 4.23). When the target movement has both vertical and horizontal components the results are more complex still (Feinstein and

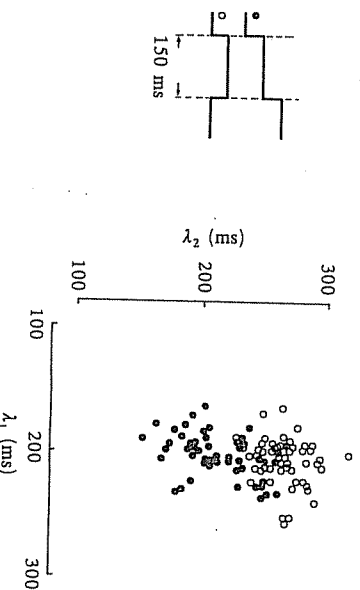


Figure 4.23. Correlation between first and second saccadic latencies plotted for one subject as in figure 4.22, but for an ordinary double-step experiment in which the interval between the steps was 150 ms, and the second step was either in the same direction as the first ( $\bullet$ ), or in the opposite direction ( $\circ$ ).

Williams, 1972; Lisberger et al, 1975; Hou and Fender, 1979; Findlay and Harris, 1984; Ohtes et al, 1984), suggesting that there are special subsystems that deal with direction and magnitude.

#### 4.2.3 Saccades to moving targets

We saw in the previous chapter that smooth pursuit is distinctly sluggish, exhibiting large phase lags even at quite moderate frequencies. In the case of a step change in target velocity, as when a target that is initially stationary moves off with constant velocity, this sluggishness implies that in the absence of any other mechanism, although the eye will quite soon reach the same *velocity* as the target, it should do so with a permanent error in *position* (figure 4.24). In practice, however, what happens is that the saccadic system intervenes, generating a saccade that is of exactly the right size to correct the positional error. The astonishing thing is that this correction saccade is typically initiated long before the positional error is fully manifest (Westheimer, 1954b; Rashbass, 1961). One is forced to conclude that the saccadic control system must estimate from the velocity of the target how large a correction is going to be required: in doing so it must also of course allow for the dynamic properties of the slow pursuit mechanism. It appears that this estimate is added to any other step displacement that may be required. If at the moment of moving off, the target is also simultaneously displaced, the resultant saccade is still of the right size to correct the total positional error (figure 4.25) (Fuchs, 1967a; Evinger and Fuchs, 1978). In particular, if the target is displaced backwards by a suitable amount at the



Figure 4.24. Response to a target moving off at constant velocity: left, response of smooth pursuit system alone leads to a permanent positional lag because of time required for the eye to approach the target velocity; right, diagrammatic representation of how a saccade of appropriate size can eliminate positional error of this kind.

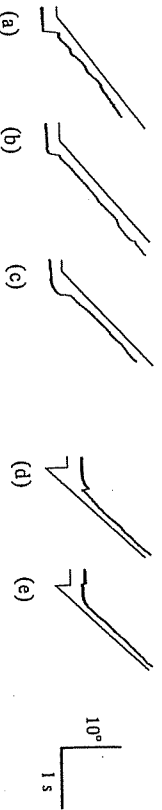


Figure 4.25. Monkey eye movements in response to ramp and ramp-step target motion: (a)-(c), ramps of  $10^\circ \text{ s}^{-1}$ , showing clear saccadic components; (d), (e), ramps of  $13^\circ \text{ s}^{-1}$  combined with backwards steps: the saccades are reduced or eliminated (Fuchs, 1967a).

start, no saccade at all is necessary—and none occurs. If the target is extinguished shortly before the first response, a saccade still takes place to the point where it would otherwise have arrived, and the eye continues for some 200 ms with the previously appropriate velocity (Westheimer, 1954b).

This seemingly intelligent behaviour could in fact be produced by quite a simple mechanism. All the system needs to do is to monitor the velocity of the target, and generate a saccade whose size is proportional to this velocity, since (if linear) the permanent positional lag of the pursuit system will vary directly with the velocity of the stimulus. One could conceive of a more sophisticated system that took into account not only the velocity of the target but also any acceleration it might have, to form a better estimate of its future position. But experiments with targets moving off with constant acceleration show that this does not in fact occur, and that in these circumstances the extra error due to the acceleration remains uncorrected (figure 4.26) (Fleming et al, 1969). If the target velocity is very high, so that there is still a residual *velocity* error by the time the saccade has taken effect, one or more additional saccades may be made to correct for the positional lag that will result from it (Fleming et al, 1969). One might perhaps expect that in these circumstances the system would simply have arranged for the whole ultimate error to be cancelled at a stroke; but this would result in a larger mean deviation of the eye over the whole movement than piecemeal correction by a number of smaller saccades. It may in any case be the result of the saturation nonlinearity of the smooth pursuit mechanism.

This particular mechanism also shows a certain degree of adaptive plasticity; if monkeys are repeatedly trained at one ramp velocity, on switching to a different ramp velocity they tend to persevere with the (inappropriate) previous saccade size (Barmack, 1970a). A similar observation in man is that if the target velocity is altered at the moment of the saccade, so that the eye movement has an inappropriate velocity, with training the eye learns to move with a velocity matched to the second target velocity rather than to the first. These adaptational aspects of saccades are discussed in chapter 13. *Attention* can also be used to select one moving target rather than another. If while tracking one moving spot across an oscilloscope screen, it becomes necessary to shift the gaze to another spot moving with a different velocity in a different part of the field, a saccade of appropriate magnitude is generated to reach it despite the powerful and

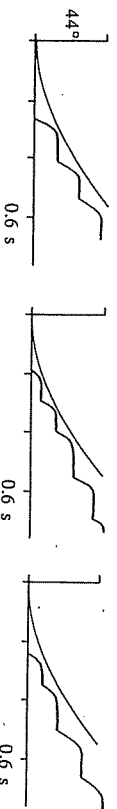


Figure 4.26. Human responses to targets moving off with constant acceleration, showing gradually increasing error despite a sequence of corrective saccades (after Fleming et al, 1969).



misleading visual slip signal being generated by the objectively stationary surroundings (Atkin, 1969).

It was argued in the last section that intermittent sampling of the velocity of visual targets was unnecessary, since velocity information is not rendered out of date by intervening saccades. A simple experiment (Barmack, 1970b) shows that even though it is used to control saccades, velocity information is indeed continuously monitored [at least, by *some* subjects; others apparently do not (Heywood and Churcher, 1981)]. If we arrange for a target to move off at constant velocity from an initial stationary position (as in the previous experiments), suddenly reducing its velocity shortly after it has set off, the resultant saccade is found to be correspondingly reduced, by more or less the right amount to bring the eye finally on to the trajectory of the target, so long as the change in velocity occurs more than some 50 ms before the saccade (Figure 4.27). It is difficult to avoid the conclusion that all the velocity information gathered for a considerable period of time before the saccade is available for the purpose of computing its size. It also seems that the latency for using it is very much shorter than that for positional information, a conclusion that is perhaps not so very surprising, bearing in mind the difference in complexity between velocity and position control that has repeatedly been urged in previous chapters.

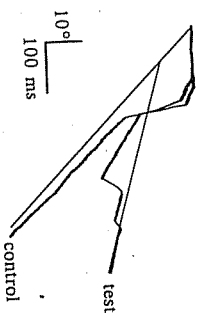


Figure 4.27. Latency of responses to altered target velocity. Thin lines show target movement, thick lines show the eye response. In the control experiment the target moves off at constant velocity and the eye responds in the usual way with a saccade of appropriate size. In test runs, the target velocity is altered soon after it has started to move: nevertheless the saccade size is correctly modified, with considerably reduced latency (after Barmack, 1970b).

#### 4.2.4 Selection of the saccadic goal

The question of how the saccadic system decides *what* to look at is obviously one that requires a consideration of topics like perception and attention that are well beyond the scope of this book. The subject has considerable applied interest, and much work has been done by psychologists on patterns of eye movements made when for example a jet pilot views his instrument panel, or a shopper scans the supermarket shelves. Tasks discussed in a recent symposium (Gale and Johnson, 1984) range from searching for lung tumours on radiographs and for blemishes on

apples to judging shot-putters and spotting tanks on battlefields. Although many experimenters have been interested in the *principles* that determine what features of a scene attract the gaze (for example Mackworth and Mackworth, 1958; Yarbus, 1967; Stark, 1971), their interests have tended to lie at a psychological rather than physiological level. Although Gould and Peeples (1970) claim that a subject's *interpretation* of a simple figure has no effect on the eye movements he makes when viewing it, and that it is only its 'physical attributes' that determine the movements, it is plain that this cannot be true of more complex targets such as photographs of faces, where the eye movements are obviously strongly influenced by the high-level perception of such 'attractive' features as the eyes and mouth (figure A1.11).

One physiological question that is of considerable interest is how, out of all the possible points on a particular visual object, the oculomotor system selects *one* point as the target for a saccade. Suppose for example that a subject is looking at a fixation spot with instructions to look at any visual target we may flash nearby on the screen. If the target we present consists simply of a small spot, then we know that the subject's gaze will jump quite accurately onto it. But if we give an extended object such as a triangle, it is not clear *a priori* whether the subject will fixate its centre, or an edge, or even one of the points. If we believe that the system behaves mechanistically, it must presumably have built into it some algorithm for converting two-dimensional retinal images into a single point which is the desired endpoint of saccades used for looking at it. An obvious approach to finding out how this algorithm works is to consider the simplest of all stimuli where the problem arises at all, namely a pair of simple targets presented simultaneously (Findlay, 1981b; 1982; Deubel et al, 1984). Under some conditions, an eye movement is made to a point lying between the two targets, generally nearer to the less peripheral target, to the bigger one, or to the brighter. Such results can be explained relatively simply by assuming that there are target-detectors with large receptive fields that are a function of retinal eccentricity; but such a model cannot easily be extrapolated to deal with edges and vertices and other salient aspects of more complex stimuli.

The model presented earlier, in which a large number of decision units compete in parallel to decide the next saccadic goal, can explain some aspects of the selection of saccadic targets. But these units cannot simply correspond to single points in the outside world: most of them must code for whole objects that cover an extended area of the retina. So how are their commands translated back into a single saccadic goal? For example, a subject can make saccades to fixate the vertices of a figure created by pairs of Julesz random-dot stereograms (Dimitrov et al, 1976), where the figure exists only at a high level in the brain and there is no corresponding retinal pattern that might be referred to. Similarly, the amplitudes of the eye movements made in scanning the pairs of intersections of the Müller-Lyer illusion figures show the same metrical changes as the perceived illusion



itself (figure 4.28) (Yarbus, 1967), and similar results are found for other illusions (see Coren's general review, 1981); again, there cannot here be reference back to the raw retinal image to determine the saccadic goal. On the other hand, if an illusory movement of a saccadic target is induced, by shifting a frame round it, the subsequent saccade is made to a position corresponding with the *retinal* rather than the perceived position: though if the retinal information is no longer present, so that the target position has to be remembered, the eye goes to the perceived location (Wong and Mack, 1981; Mack et al, 1985). It is not easy to formulate a plausible mechanism that will deal both with the global and with the local aspects of such a process.

Another experimental approach is to measure not the initial eye movements made in response to a figure suddenly presented, but rather the relative popularity of various parts of figures as resting places for the eye, as measured by the relative amounts of time spent there. For example, in free scanning of gratings the eye tends to spend more time at one part of each cycle than another, resulting in a pattern of average illumination that is itself grating-like (Arend and Skavenski, 1979). Earlier work by Kaufman and Richards (1969; see also Richards and Kaufman, 1969) showed that in simple line drawings the centre of gravity is attractive, as are also the edges and corners (figure 4.29); comparable findings have been presented by Lévy-Schoen (1973). Similarly, in scanning polygons (Bozkov et al, 1982)

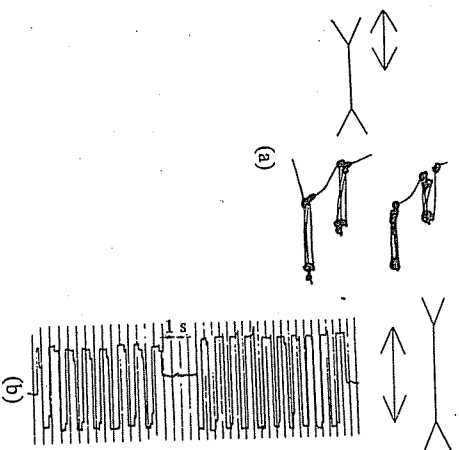


Figure 4.28 (a) Two-dimensional records of eye movements made when viewing Müller-Lyer illusion figures, showing that the amplitude of the eye movements corresponds on the whole to the illusory size. The comparison can be made more easily in (b), which shows the time course of the horizontal eye movements made by a subject instructed to scan his eyes between the intersections of each figure (Yarbus, 1967).

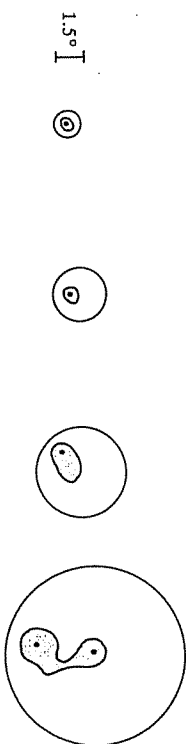


Figure 4.29. Fixational tendencies in prolonged viewing of extended discs: the shaded areas include 86% of recorded fixations by two observers, and the dots show mean fixation positions (after Kaufman and Richards, 1969).

A further aspect of scanning by the eye relates to the question of the extent to which the *recognition* of objects depends on recognising the pattern of eye movements that it evokes, the notion that 'you know what you see when you see what you do'. The idea seems first to have been proposed by Bain (1855), who considered that the perception of "... naked outlines, as in the diagrams of Euclid and the alphabetical characters, are to say the least of it, three parts muscular and one part optical". Subjects repeatedly viewing a set of pictures generate relatively stereotyped patterns of scan that are specific for each picture, and one may choose to think of such patterns as the eye looking in sequence at individual features of the picture which are then ticked off on a mental checklist (Noton and Stark, 1971). For very complex recognitions (*is this flower a meadowsweet?*) this kind of serial recognition process is evidently used (*are the leaves interruptedly pinnate? the terminal leaflets three-lobed, and downy white on the underside? the calyxes five-lobed?*); but equally, it is clear that even the most complex recognitions can ultimately be performed far more quickly than the time that would be required to make the requisite number of saccades. Faces presented tachistoscopically can still be recognised (Groner et al, 1984), and so of course can objects presented in mirror-reversal or at a different angle of view. One specific case where it might naturally be assumed that eye movements are used for recognition is *counting*: Landolt (1891) observed that objects closer than some 5' of arc apart could not be counted, and he supposed this to be due to an inability to make the necessary small voluntary saccades, which are of about the same size (Haddad and Steinman, 1973). However, direct experiment shows that accuracy is actually *improved* if saccades are suppressed (Kowler and Steinman, 1977), partly perhaps because of the danger of losing one's place if an inaccurate movement is made. But at a higher, more conscious level of thought, there is no doubt of the very strong connections between gaze and serial logical

analysis: they are particularly evident when recording the eye movements of someone playing chess (Tikhomirov and Poznyanskaya, 1967), when the contemplation of possible moves and their consequences is reflected in corresponding shifts of the gaze around the board.

One special and important case of visual scanning occurs of course in *reading*. Normal eye movements made while reading consist of a sequence of saccades along the text, at intervals of some 250 ms, with an amplitude and a frequency that depend on the skill of the reader, the difficulty of the reading matter, and details of the typography (for example Herring, 1879a; Erdmann and Dodge, 1898; Vernon, 1931; Gruber, 1962; McConkie and Zola, 1984) (figure 4.30). A curious feature of the saccades is that they are closely similar in skilled readers both of Chinese and English (Sun et al, 1985), despite the very different nature of the symbols in each case, and in direction of movement: it seems that typography has evolved in each case in such a way as to present information at a linear rate that suits the eye movement control system. Saccades do not have to be particularly closely tailored to the visual stimulus for comprehension to be possible: reading can be performed quite adequately if the subject fixates a stationary point, while the whole text is stepped sideways in a saccade-like fashion at an appropriate regular rate (Bouma and de Voogd, 1974).

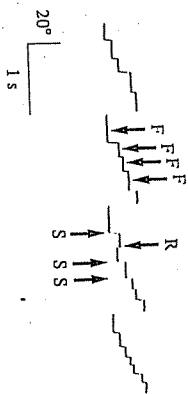


Figure 4.30. Typical eye movements made while reading, showing fixational pauses (F), interfixational saccades (S), and a regressional movement (R).

The control of eye movements in relation to the text being read presents many very interesting questions, particularly concerning *when* the eye chooses to move from one point to the next, and *where* it decides to move to. The dwell time for a fixation is not preset, but depends on the meaning of the word: but it would be unreasonably inefficient for the command for the eye to move to be issued only when all processing is complete, as the saccadic latent period would then be spent in idleness (Vonk, 1984; McConkie et al, 1984). Furthermore, while the word one is looking at is being processed, there must be simultaneous preliminary analysis, using parafoveal vision, of what is to come (Carpenter and Just, 1983; Jennings and Underwood, 1984). Saccades do not simply jump from one word to the next but are closely related to the information content of what is read, implying control at a very high level by the large-scale meaning of the text.

For example, the time spent fixating a pronoun that refers back to a previous noun depends on whether or not the reference is ambiguous (as in 'the put his hand on the stove because it was cold'), a distinction that clearly requires some knowledge of the properties of the real world (Kerr and Underwood, 1984). In situations of this kind, eye movements provide a subconscious running commentary on higher cognitive processes, opening up exciting possibilities for research.