CHAPTER 4

# VISUAL ORIENTING

## 4.1 Introduction

Visual orienting involves redirecting the gaze to a new location in the visual field. This process has been intensively studied, particularly in relation to the *target-elicited saccade*, the orienting saccadic eye movement that readily follows the appearance of a new target in the field of vision. One reason for the interest is the close correspondence between processes discovered in human behavioural studies and those shown in studies of primate brain physiology. To emphasize this correspondence, the chapter is sectioned so that the two principal variables in connection with a saccade, the latency and the metric properties, are treated in separate sections (Section 4.2 and Section 4.4) with each section followed by an account of the underlying physiology (Section 4.3 and Section 4.5).

In chapter 2, we emphasized that the foveal region provides a high acuity region for detail vision. For it to be used, it must be directed at the part of the visual world that is of current interest. This is the process of visual orienting. The gaze redirection may, for distant objects, involve movements of the body, head and eyes. The orienting mechanisms for head and eyes are closely coupled (Jeannerod, 1988). For close objects, manipulations may also occur which bring the object into the gaze direction rather than vice versa but these will not be given further consideration here.

A classic study by Sanders (1963) distinguished regions in which different combinations of effectors were used to achieve orienting. For an individual initially facing forward with gaze in the primary position, an *eye field* extends out to eccentricities of about 20°. Within this region, orienting is achieved by moving the eye only. Beyond this region, a *head field* extends out to eccentricities of about 90° where orienting involves both eye and head movements. For objects outside the head field, whole body movements are additionally employed. Sanders suggested that transitions between the different zones resulted in increased task load and performance decrements.

These regions are only loosely delineated, and other factors, both of an individual and a situational nature, may affect the way in which orienting is achieved. For example, individuals wearing spectacles may increase the

incidence of head movements, in order to maintain the gaze direction through an appropriate part of the spectacle lens. In Section 8.5, we discuss an individual whose orienting is entirely achieved with head movements.

A large number of studies on visual orienting have restricted consideration to orienting with the eyes alone. Orienting in this case is achieved using saccadic eye movements, and the study of the target-elicited saccade forms one of the major concerns of this chapter. Such saccades occur when a new target makes a sudden appearance in the parafoveal or peripheral regions of the visual field. Although clearly a voluntary response, saccadic orienting in this situation has an automatic and natural quality, ensuring that reliable data can readily be acquired.

Two other important paradigms can be mentioned at this point as both have been widely used to extend our knowledge of visual orienting. In the *anti-saccade* paradigm, discussed in Section 4.4.5, observers are instructed to respond to the target by moving the eyes in exactly the opposite direction. An anti-saccade requires suppression of the automatic orienting response and the creation of a different set of motor commands. Another paradigm requiring more voluntary activity on the part of the observer is the *memorised saccade* paradigm. Typically, a peripheral target is flashed briefly and the observer required to withhold the immediate orienting response, but to respond at the end of some period of time during which the location of the target must be held in short-term memory. This paradigm is discussed together with other work on saccades to remembered locations, in Section 9.2.4.

## 4.2 What determines the latency of orienting saccades?

In the target-elicited saccade paradigm, the observer is asked to make a saccadic orienting movement to a target that appears in some location in the peripheral visual field. A delay, termed the *latency* of the saccade, occurs between the appearance of the target and the time that the eyes start to move. This delay is the reaction time of the eye response and represents the cumulative time taken by the brain processes that enable orienting. We shall, in this chapter, show how study of these saccades can give insight into the underlying brain processes but a cautionary note is first in order. The brain is an integrated system and although saccadic orienting is a very automatic process, it is never completely independent of other brain activity. Zingale and Kowler (1987) demonstrated this point neatly by showing that, when a number of saccades were required, the latency of the first orienting saccade increased steadily with the length of the sequence. Likewise, saccade latencies are augmented when observers are required to do concurrent cognitive tasks (Takeda and Findlay, 1993).

### 4.2.1 Target properties

One might expect that the latency for an orienting saccade would be dependent on the properties of target to which the eye is moving. Several studies have shown this to be the case. For example, saccades to a bright target show

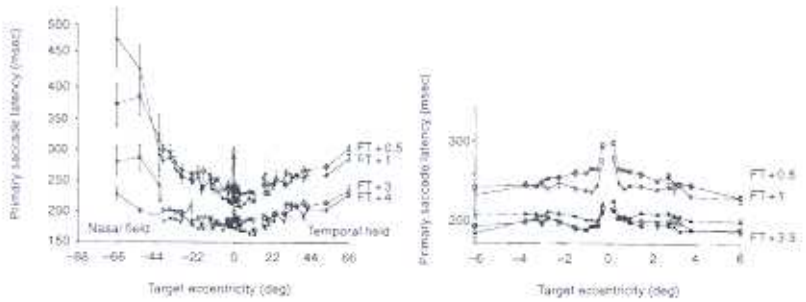


**Figure 4.1** Latency of target-elicited saccades plotted as a function of target eccentricity for targets of varying intensity (FT + 1 indicates 1 log unit above foveal threshold etc.). From Kalesnykas and Hallett (1994).

shorter latencies than those to a dim target (Kalesnykas and Hallett, 1994; Reuter-Lorenz *et al.*, 1991). Targets with little low spatial frequency information show prolonged latencies (Findlay *et al.*, 1993). However, the magnitude of these effects is rather small, except when the targets are close to threshold visibility.

The effect of target location is of some interest. In a review of a number of studies, Findlay (1983) concluded that the variation of latency as a function of target eccentricity was a bowl-shaped function. Over a broad range (approx. 1°–15°), latencies changed rather little while latencies increased for very small movements (less than about 1°; Wyman and Steinman, 1973) and for large movements (greater than about 15°). Orienting in the latter case almost invariably involves a corrective saccade (Section 4.4.5). A systematic study by Kalesnykas and Hallett (1994) confirmed this relationship, as shown in Fig. 4.1. (note however Hodgson, 2002)

### 4.2.2 The gap effect

Target-elicited saccades are often studied in an eye tracking task when an observer is required to follow a visual target which makes an unpredictable step movement. In this case, the target simultaneously disappears at the previously fixated location when it reappears at the new location. Saslow (1967) realised that, under these circumstances, the disappearance of the visual stimulus at the previously fixated location might contribute to the programming of the saccadic orienting movement. He studied this by treating the fixation target disappearance and the target appearance as separable visual events. He carried out an experiment in which the two events were not simultaneous, but were separated in time by a temporal offset. The fixation stimulus could disappear before the appearance of the peripheral target, leaving a *gap* period with no visual stimulation. Alternatively, the fixation stimulus might not disappear until after the appearance of the peripheral target, the *overlap* situation. Saslow found that this manipulation strongly affected the saccade latency.

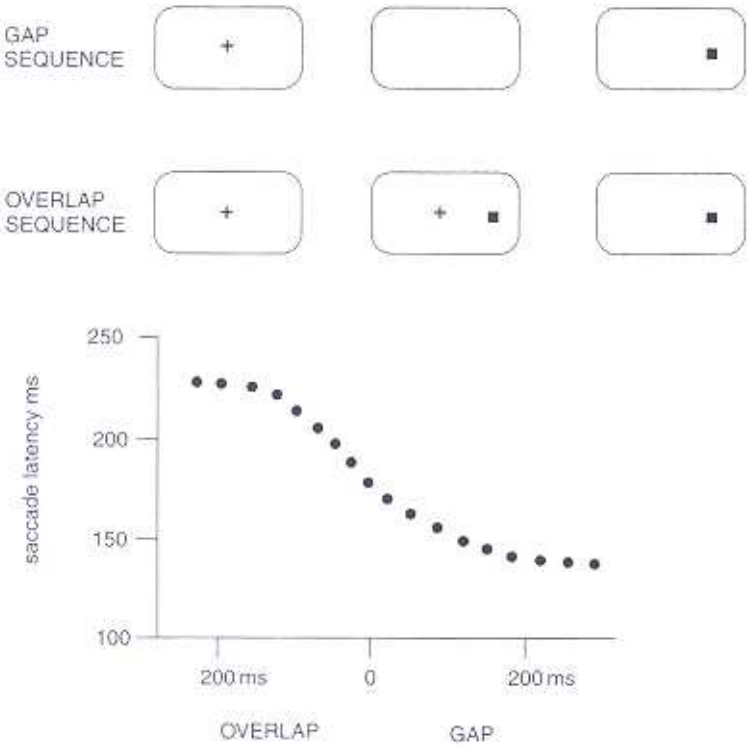


**Figure 4.2** The gap effect. Top panels show typical display sequences in gap and overlap conditions respectively. The task is always to initially fixate the centre and make an eye saccade to the target when it appears, either on the left or on the right of the screen. Latencies are measured from the target appearance. The lower panel shows schematically typical results from the paradigm.

As Fig. 4.2 shows, saccade latencies become progressively shorter in the gap situation with increasing temporal offsets (up to gaps of about 200 ms) and conversely become progressively longer as more overlap occurs.

This effect, the *gap effect*, is highly reproducible and occurs irrespective of whether the observer can predict the direction in which the target will appear (Kingstone and Klein, 1993; Walker *et al.*, 1995). This suggests that the offset of the fixation point initiates some general preparatory process in connection with the saccadic movement, with the spatial metric of the saccade assigned at a late stage in the programming of the movement (Section 4.6). Work on the gap effect (Forbes and Klein, 1996; Reuter-Lorenz *et al.*, 1995) has led to the proposal that there are two general preparatory components. The first is a general alerting component found with any warning signal (Tam and Stelmach, 1993, showed that manual reactions benefit from this component).

The second effect is specific to ocular orienting and has been assigned a variety of terms (fixation offset, fixation release, fixation disengagement or ocular disengagement).

### 4.2.3 The remote distractor effect

Ross and Ross (1980) reported a related converse result in the situation where, rather than disappearance of the fixated material, a new stimulus appears at the point of fixation around the time of target onset. Such a stimulus onset resulted in a latency *increase* if it occurred simultaneously with the target appearance. If the onset occurred substantially before the appearance of the target, its effect reversed and a latency reduction occurred, presumably because it operated as a warning signal. The latency increase is a robust effect. Walker *et al.* (1995, 1997) carried out further studies of events where distractor stimuli occur simultaneously with target onset. They showed that, in a comparable way to the gap facilitation, the increase occurs

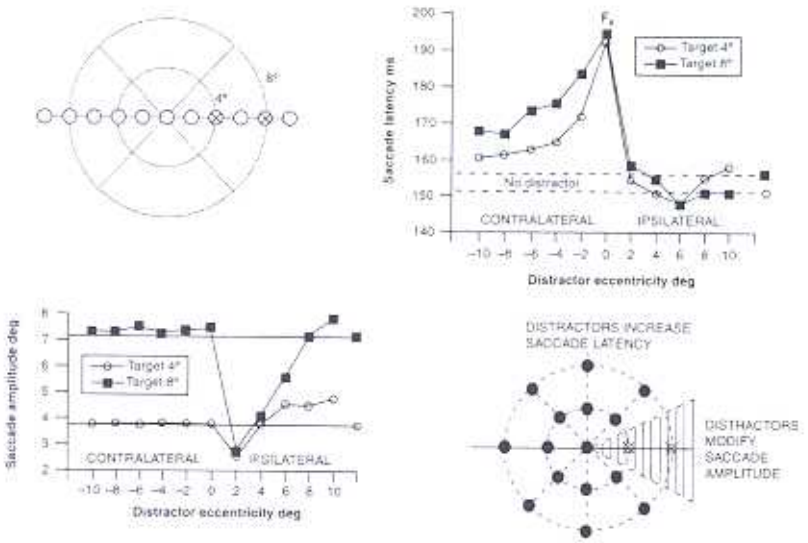


Figure 4.3 The remote distractor effect, studied by Walker *et al.* (1997). Targets appeared at either 4° or 8° on one side of fixation and were, on test trials, accompanied by a simultaneous distractor. In the experiment illustrated in the upper left panel, the distractor could appear in one of the eleven positions indicated by circles. On control trials, no distractor appeared. Distractors at fixation or on the contralateral side produced an increase in saccade latency, shown in the upper right panel. Distractors on the ipsilateral side did not affect the latency of the orienting saccade, but modified its amplitude, shown in the lower left panel. From this and similar experiments, the effect was shown to take the form shown in the lower right panel. Distractors within a narrow sector on either side of the saccade target axis modify saccade amplitudes, whereas distractors in the remainder of the visual field produce an increase in latency.

whether or not the subject has advantage knowledge of the direction in which the eyes will move. The increase in latency results from onsets in any region of the visual field except a sector close to the target (Fig. 4.3). Walker *et al.* introduced the term *remote distractor effect* to describe these findings. Distractors in this critical sector have no effect on the saccade latency but in contrast do affect the endpoint of the saccade, an instance of the global effect (Section 4.4.3). Figure 4.3 shows the highly systematic nature of the remote distractor effect.

The gap effect and remote distractor effect are highly robust and regular, suggesting that visual onsets and offsets have an access route to the saccade generation mechanisms that operates in a very automatic manner. A further result showing this was reported by Theeuwes *et al.* (1998). These workers have shown that if a visual onset occurs at the instant when an observer is about to make a voluntary saccade, there is often an unintended saccade towards this onset, rather than to the intended location.

### 4.2.4 Express saccades

In 1983, Fischer and Boch reported a remarkable finding. They trained monkeys to make target-elicited saccades in a gap paradigm and measured saccade latencies. They found that the monkeys frequently made saccades with extremely short latencies (80–100 ms). Since, at the time, figures of 200 ms or more were widely described in texts as the 'typical' saccade latency, such short latencies were newsworthy in their own right. A second finding concerned the distribution of saccade latencies over a large number of trials (Fig. 4.4). The short latency saccades very clearly formed a separate

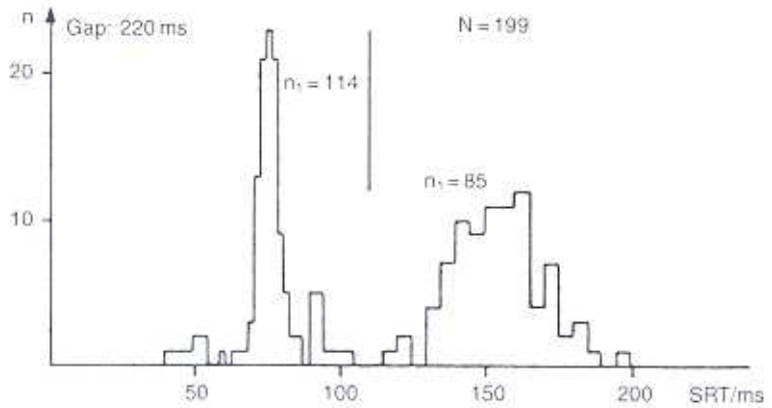


**Figure 4.4** The first demonstration of express saccades by Fischer and Boch (1983) in a study with monkeys. The monkey was trained to make an orienting saccade in the gap paradigm. The distribution of saccade latencies shows a separate sub-population of saccades with extremely short reaction times.

sub-population of the total, justifying their identification as a separate *express saccade* category.

In the following year Fischer and Ramsperger (1984) reported that that a similar phenomenon occurred in human subjects, although the latencies of the human express saccades were somewhat greater (100–130 ms) than those produced by the monkeys. Subsequent work has confirmed this finding (Jüttner and Wolf, 1992) although human subjects only rarely show the dramatic bimodality in latency distributions shown in Fig. 4.4 (Reuter-Lorenz *et al.* 1991; Wenban-Smith and Findlay, 1991). A lively debate about their properties and significance of these movements can be found in Fischer and Weber (1993). Express saccades show some unexpected properties; for example, they are less common when the saccade target is close to the fovea (Weber *et al.*, 1992). During free viewing, it is quite common to find fixations whose duration is very short (e.g. Section 4.4.4) and it seems likely that these may be a manifestation of the same phenomenon.

### 4.2.5 Variability in latencies

Even when testing conditions are controlled as carefully as possible, the latency of saccades varies in an apparently unpredictable way on a trial-by-trial basis. Over a series of trials, a cumulative distribution of latencies can be obtained. The nature of this distribution is of considerable interest. Carpenter (1981; Carpenter and Williams, 1995) has shown that the distributions of reaction times are positively skewed with the distributions of the reciprocal of latency closely approximating a Gaussian distribution.

Such a distribution is capable of being explained by a remarkably simple generative mechanism, shown in Fig. 4.5, which Carpenter has termed the LATER model (linear approach to threshold with ergodic rate). On each trial, a hypothetical variable commences to increase at a linear rate. The saccade is

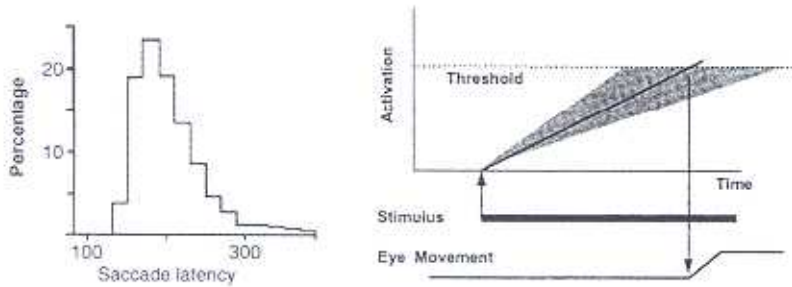


**Figure 4.5** The left hand panel shows a typical, positively skewed, distribution of saccade latencies in an orienting task. The right hand panel shows the principle of Carpenter's LATER model, in which the underlying generative process is a linear rise of activation to a fixed threshold level, with the rate of rise being a random variable with Gaussian distribution.

initiated when a certain threshold value is achieved with the time taken to reach the threshold corresponding to the saccade latency. The LATER model postulates that the rate of increase is a random variable with Gaussian distribution. This model is then able to predict a skewed distribution of latencies with the shape observed. Furthermore, differential instructions to aim for speed or for accuracy modifies the distribution of saccade latencies in a way that can be interpreted as a simple change of threshold level (Reddi and Carpenter, 2000). This model has also received support from physiological studies (Section 4.3.3).

## 4.3 Physiology of saccade initiation

One reason for the intense interest in target-elicited orienting movements is the close correspondence that can be found between the behavioural study of such movements, as described in the previous section, and physiological brain processes.

Primates show patterns of saccadic eye movement control that are similar in very many ways to those of humans. Monkeys can readily be trained in the laboratory to make orienting saccades as well as saccades in more complex tasks such as visual search. Our knowledge of the neurophysiology of the saccadic system has been particularly advanced by studies in several laboratories of the properties of brain cells when awake and alert monkeys carry out trained tasks.

Figure 4.6 shows a set of schematic diagrams of primate brain, illustrating the major regions and pathways important for the generation of saccadic eye movements. The eye muscles themselves are controlled by motor neurons leaving the midbrain and pontine regions via cranial nerves III, IV and VI. The cell bodies of these nerves are found in the corresponding oculomotor nuclei. Adjacent to these nuclei are the important premotor centres of the midbrain reticular formation (MRF) and the paramedian pontine reticular formation (PPRF) shown in Fig. 4.6. The descending input to these centres comes largely (although not exclusively) from the superior colliculus (SC). The SC contains cells responsive to visual stimuli and a partially overlapping set of cells which fire when saccades are made. It is a highly significant visuomotor centre in connection with saccadic eye movements and receives input from two areas of the cortex (LIP and FEF) important in saccade generation (Section 2.4.4).

### 4.3.1 Burst and pause cells in the reticular formation

Figure 4.7 shows schematically the neural processes occurring in oculomotor and immediate pre-motor regions of the brain. It provides a very simplified overview of a highly complex piece of neural machinery (for further detail see Fuchs *et al.*, 1985; Moschovakis and Highstein, 1994; Schall, 1991, 1995;

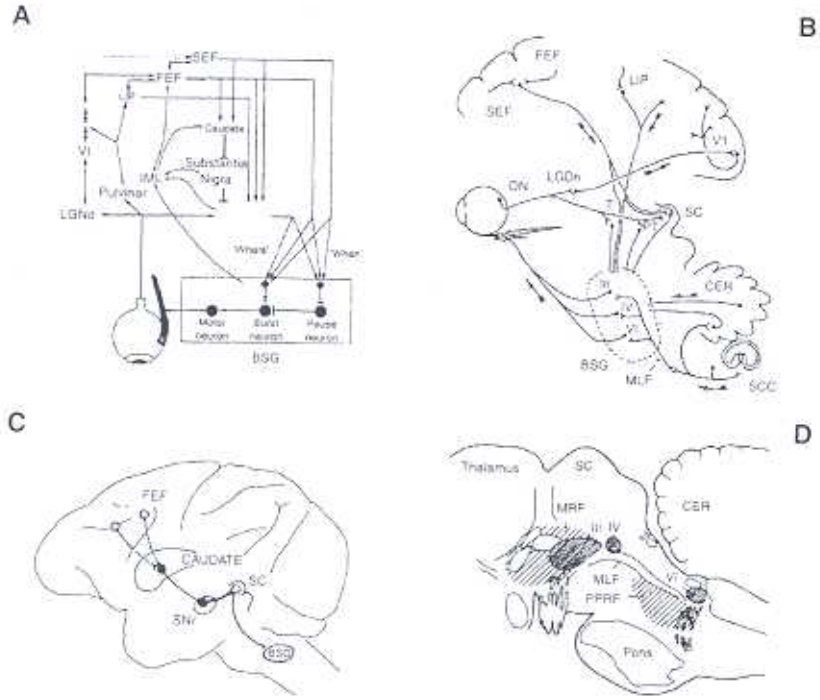


**Figure 4.6** Brain centres for saccade generation. (A) Diagram of pathways involved in saccade generation (Fig 2.17) from Schall (1995). (B) Schematic diagram of primate brain showing input visual pathways and output oculomotor pathways, as well as location of the cortical centres involved in saccade generation (modified from Robinson, 1968). (C) Diagram of primate brain showing the oculomotor pathway through the basal ganglia to the brainstem (modified from Hikosaka and Wurtz, 1989). (D) Schematic diagram of the brainstem saccade generator region (from Henn *et al.*, 1982.).

III, IV and VI are the third, fourth and sixth cranial nerve nuclei, the nuclei from which the ocular motor neurons originate, BSG-brainstem saccade generator (elaborated in diagram D), CER-cerebellum, FEF-frontal eye field, IML-internal medullary lamina of the thalamus, LGNd-dorsal part of the lateral geniculate nucleus, LIP-lateral intraparietal area, MLF-median longitudinal fasciculus, MRF-mesencephalic (midbrain) reticular formation, ON-optic nerve, PPRF-paramedian pontine reticular formation, PT-pretectum, SC-superior colliculus, SCC-semicircular canals, SEF-supplementary eye field, SNr-substantia nigra, pars reticulata, T-tectal nuclei, V1-cortical area Visual 1.

OCCULAR CAPTURE

Scudder *et al.*, 2002). When the eye is at rest, all oculomotor neurons show tonic activity, firing at a moderate rate that depends on the particular position of eyeball in the orbit. Typical activity in such a neuron during saccade generation is shown in the 'Motor neuron' trace of Fig. 4.7. To generate a saccade, the motor neurons to the appropriate agonist muscles switch

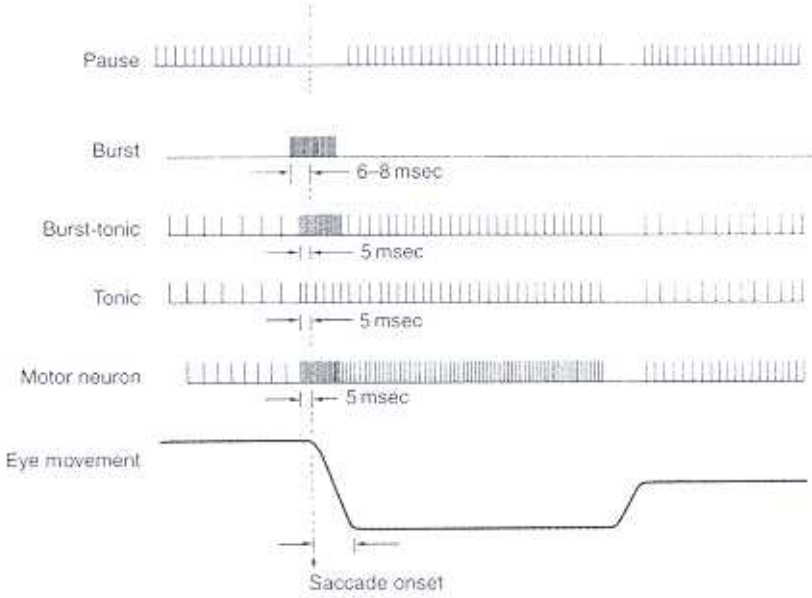


**Figure 4.7** Neural activity in various types of brainstem cells accompanying saccadic eye movements (redrawn from Gouras, 1985).

transiently to a very high rate of firing and then settle to a lower, but increased, rate appropriate for the new position. The term *pulse-step* pattern is often used to describe this innervation. The activation to the antagonist muscles consists of a pause in activation at the time of the pulse burst and a lower rate of subsequent activity. The hypothetical motor neuron shown controls the agonist for the first eye movement and shows the pulse-step pattern. For the second, reverse direction, movement, the motor neuron activity shows a pause, indicating that there is no driving signal to the antagonist movement in a saccade.

These patterns of activation are in turn generated by neural circuitry in the adjacent areas of the MRF and PPRF. Within these regions are found two types of cells with very different properties. The *pause* or *omnipause* cells fire at a steady uniform rate at all times except that, when a saccade occurs, their firing stops completely for a brief period. The start of the pause of activity in fact precedes the start of the actual movement by 5–15 ms. The pause occurs irrespective of the size or direction of the saccade and thus the omnipause cells do not code the metric properties of the saccade in any way. Such metric coding occurs in other types of cells, in particular cells which show a brief *burst* of activity synchronised (and, as with the pause cells, briefly preceding) a saccadic movement. The burst cells, however, only fire for a certain direction

and size of movement; in other words, this type of cell is coding the metric properties of the movement. Some cells (long lead burst cells) show an increase in discharge rate considerably in advance of the actual movement. The MRF and PPRF are closely coupled regions (via the MLF), with the MRF burst cells relating to the vertical component of an eye movement and those in the PPRF to the horizontal component.

A very important principle demonstrated here is the separation of two streams of control information. Van Gisbergen *et al.* (1981) introduced the following terminology. The pause cells may be said to form a WHEN system because they are concerned with the point in time when a saccade will occur but not where it will move the eye. This is the concern of the burst cell system, which can therefore be termed the WHERE system. One plausible behavioural consequence of the WHEN/WHERE distinction is that preparatory processes for the initiation of a saccade can occur before the destination of the movement is specified (Section 4.2.2).

Pause cells are active at all times except when a saccade occurs and thus may be described as cells active during fixation. It is possible to envisage them as the late stage of a system that is concerned with fixation. Cells in the superior colliculus that code fixation will be discussed in the following section. Cells with similar properties are also found in cortical areas related to eye movements, such as the posterior parietal association cortex (Lynch *et al.*, 1977) and the dorsomedial region of the frontal cortex (Bon and Luchetti, 1992).

### 4.3.2 Fixation, burst and buildup neurons in the superior colliculus

The superior colliculus (SC) is the major region from which pathways descend to the midbrain and brainstem oculomotor generating centres described in the previous section. Its organisation has been considerably elucidated in recent years and shows some similar characteristics to that of the lower centres. The work of Daniel Guitton, Doug Munoz and Robert Wurtz has been of seminal importance and this section draws considerably on the lucid account given in Wurtz (1996). The presentation here emphasizes the direct pathways downstream from SC. It is becoming increasingly recognised that although these pathways appear adequate to generate saccades, accuracy and adaptability is maintained through parallel SC > brain stem pathways involving the cerebellum (Robinson and Fuchs, 2001).

The SC consists of multiple layers, stacked somewhat like the pages of a book. As elaborated below, the layers contain maps of visual and oculomotor space with each hemifield represented in the contralateral SC. The upper layers, termed the *superficial layers*, receive a direct visual projection from the retina. The lower layers (*intermediate and deep layers*) receive a separate cortical visual projection, as well as being connected to the saccadic generation centres. Studies of the details of these projections in terms of the visual pathways described in Section 2.2.1 shows the following. Activation of the SC

superficial layers comes from a homologue of the cat W-system, whereas activation in deep layers comes about mainly through M-cells but with some evidence for a P-contribution (Schiller, 1998). Paradoxically it is believed that the upper and deeper layers do not connect neurally. This visual mapping is anisotropic in a similar way to that of the retino-cortical projection. The central foveal region obtains the largest proportional representation and is mapped at the rostral end of the structure (the *rostral pole*). Upper space is represented medially and lower space laterally. The mappings are eye-centred and are independent of the position of the eye in the orbit although, as in other visual centres, eye position does affect the level of activity (Paré and Munoz, 2001).

The statement that the SC 'maps visual space' refers to the fact that cells, both in the upper and in the intermediate layers, have visual receptive fields whose locations are laid out topographically. The statement that the SC 'maps oculomotor space' refers to the fact that cells in the lower (deeper) layers have the property that electrical stimulation generates a saccadic eye movement with the size and direction of the eye movement dependent on the location of stimulation. Some cells have both visual and oculomotor responsiveness. A highly significant discovery was the fact that visual and oculomotor maps were in register (Schiller and Koerner, 1971; Robinson, 1972). Stimulation of a location in the deeper layers of the colliculus results in a saccade to precisely the region of space which is represented in the visual map at the same collicular location. The SC is thus clearly involved in the visuomotor co-ordination of orienting. Nevertheless, a period of doubt followed the early discovery of the register of the maps because it was unclear how the two maps might interact. Recent progress on the SC has concentrated on the events in the deep layers that precede a saccade, and in particular on the role of the rostral pole region.

The term *fixation centre* can be applied to the rostral pole region of the SC, the location corresponding to the foveal region on the visual map. Neurophysiological studies show that cells in this region show activity whenever the animal fixates and pause during saccadic eye movements (Munoz and Wurtz, 1993*a*). The region is GABA sensitive (Munoz and Wurtz, 1993*b*) so that injection of the GABA agonist muscimol into the region increases saccadic activity. An animal with such an injection has difficulty in maintaining fixation. Conversely, injection of the GABA antagonist bicuculline has the opposite effect. Animals produce fewer saccades and saccades with longer latencies than normal. The cells in this region have similar characteristics to those of the omnipause cells of the brainstem. A direct connection has been traced between the region and the brainstem omnipause cells (Paré and Guitton, 1994).

Two important cell types are found in the remaining parts of the deep layers. Both show neural activity preceding saccades but differ in important ways. The *buildup* cells show a pattern of increasing activity that commences

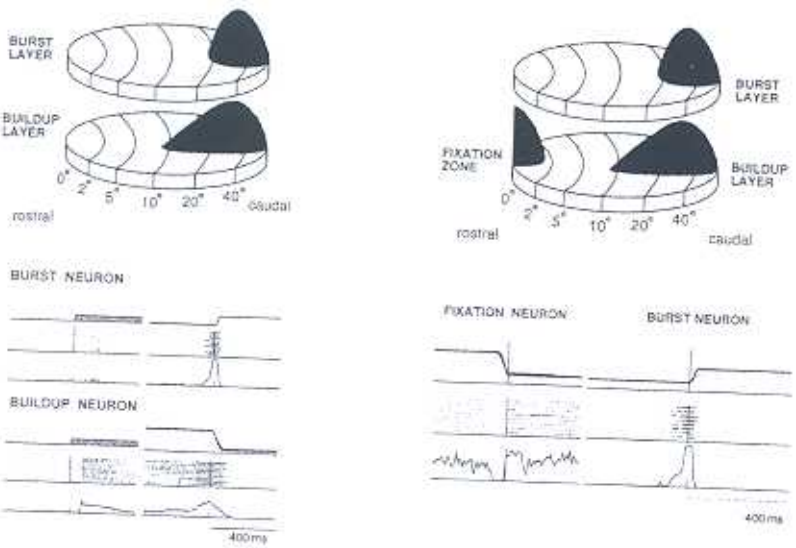


**Figure 4.8** Cartoon of activity in the superior colliculus relating to a saccade. The left hand top panel shows two layers of the SC, each topographically mapped. The dark mounds represent neural activity peaks in these two layers. The LH lower panel shows typical activity of neurons in these two layers. The left hand plots show activity in relation to the visual target and the right hand plots show activity in relation to the eye movement. The top plots show the event (visual target or saccade). The middle plots show neural activity in a raster display with each line of the raster corresponding to a successive trial. The bottom plots show averaged neural activity. The right hand panels show additionally the activity of neurons with the fixation zone at the rostral pole of the SC. (Modified from Wurtz, 1996).

well before the actual movement and reaches a peak just before the saccade is triggered. The *burst* cells are similar to their namesakes in the MRF and PPRF, in showing a brief burst of discharge just prior to the movement. In each case, activity is only found preceding movements in the appropriate direction for the oculomotor map, with the burst cells being more tightly tuned in this respect than the buildup cells.

The events in the SC that lead up to a saccade may be portrayed as follows (Fig. 4.8). In the region of the SC corresponding to the location in space to which the eyes will be directed, the buildup cells in the intermediate layers gradually increase their activity. This increase is presumed to occur because of activity in the various descending pathways (Fig. 4.6). At the same time, cells in the fixation region of the rostral pole show a decrease in activity. At some point, the activity balance reaches the point where an abrupt switch is triggered. At this point, rostral pole activity ceases, the burst cells start firing and the activity characteristic of saccades

occurs in MRF and PPRF. Whilst the activity in the buildup cells may reflect the very varied nature of the descending stimulation, the subsequent triggering process ensures that, when saccades are produced, they show a very stereotyped pattern. Although latencies will be affected by events both in the fixation region and in the buildup region, Dorris *et al.* (1997) found that, prior to express saccades, saccadic latencies correlated well with prior activity at the buildup location and not with prior activity in the fixation region.

#### 4.3.3 Variability of saccade latencies

An interesting convergence has also occurred between theoretical work and neurophysiological studies concerned with the variability in saccade latencies. The LATER model proposed by Carpenter (Section 4.2.5) appears to be reflected quite well in processes occurring at the single cell level. Studies of cell activity within primate frontal eye field (Hanes and Schall, 1996; Schall and Hanes, 1998) showed that in the period immediately before a saccade, neural activity showed a steady increase. The rate of this increase correlated well with saccade latency, supporting an accumulator model whereby the initiation of the saccade occurring when this becomes sufficiently high. Similar correspondences have been reported at the level of the superior colliculus (Dorris *et al.*, 1997).

## 4.4 What determines the landing position of orienting saccades?

We are so familiar with the ability to direct our eyes to any target at will that we rarely reflect on the fact that this is a considerable achievement of neural processing although, as described in Chapter 8, the loss of this ability can be devastating. Many studies of target-elicited saccades have investigated the ability in detail (see Hallett, 1986 or Becker, 1989 for a fuller account). For targets within about the central 10 degrees of vision, the most common pattern is for a single saccade to move the gaze directly to the target. Such saccades show the stereotyped saccade trajectories described in Section 2.4 but their amplitudes are variable (the range is typically about 5–10 per cent of the movement amplitude; Kowler and Blaser, 1995). A small secondary, error correcting, saccade may follow the first, primary, saccade. With larger movements, undershoot and secondary saccades become more common. A widely held view is that saccadic undershoot of about 10 per cent is normal, although this has been challenged (Kapoula and Robinson, 1986). For small saccades, the occurrence of secondary corrective movements increases when a task requires scrutiny (Findlay and Kapoula, 1992). An occasional variant on the standard pattern is for the eye to move to the target in a series of small saccades (Crawford, 1991, Section 4.7).

### 4.4.1 Corrective saccades

Study of the corrective saccades that follow a primary orienting saccade has yielded some interesting insights. If the target for orienting is flashed briefly, so that it is no longer visible when the first saccade is made, corrective saccades are still found but less frequently (Becker, 1972). This suggests that corrective saccades may occur either on the basis of a pre-planned sequence or on the basis of a visual error sampled after the end of the first saccade. The latency of the corrective saccade, i.e. the duration of the fixation following the first saccade, is quite tightly dependent on the size of the gaze error remaining after the first saccade (Becker, 1989).

A typical experiment investigating orienting saccades will present a set of trials with targets at a set of varied different amplitudes. Subjects rapidly become aware of the properties of the set; this is demonstrated by saccades to the lower amplitude targets showing slight undershoot and those to higher amplitude targets slight overshoot (Kapoula, 1985). This is a familiar finding in motor response investigations, known as the *range effect*.

### 4.4.2 The double step paradigm

In the double step paradigm an observer is asked to follow with their eyes a target which makes two successive movements in a quick sequence. The idea behind the paradigm is to measure the effects of the second stimulus step on the programming of the saccade to the first step. A typical experiment would be designed to prevent, as far as possible, the observer predicting the stimulus properties. Double steps in varying direction and with varying intervals between them would typically occur unpredictably in a set of trials that also contained single target steps. The paradigm has been widely employed (Komoda *et al.*, 1973; Becker and Jürgens, 1979; Findlay and Harris, 1984, Aslin and Shea, 1987) and has been most informative.

Three principal outcomes occur on double step trials. First, the eye following can consist of a separate saccade to each step in turn. This situation will typically occur when the interval between the two steps is long and the response to the first step is complete before the perturbing influence of the second step is felt. At the opposite extreme, the eye may make a single saccade to the final position following the two steps, ignoring the pause at the intermediate position. This outcome is found when the pause between the two steps is very brief. The third possible outcome that is found is where the first saccade goes to neither target position but instead to a location intermediate between the target locations. Such a saccade would generally be followed by a second saccade to the target 2 location. A further option, that the saccade trajectory itself is modified, appears only to occur for large saccades (Section 2.4.1).

Becker and Jürgens (1979) showed that the most important determinant of the type of outcome was a variable measuring the time elapsing between the

second step and the initial saccade. They designated this variable D and, as shown in Fig. 4.9, under certain conditions an *amplitude transition function* may be plotted to show the systematic dependence of the first saccade end point on D. For small values of D, the perturbing second step does not affect the saccade. For large values of D, the eye moves to the new position following the second step. Thus the new step fully captures the saccade. Becker and Jürgens found that for an intermediate range of D values, a compromise saccade occurs with endpoints landing between the two positions occupied by the target and showing a smooth transition between the first and second step locations. The point at which this transition starts shows the last point in time at which it is possible influence a saccade about to be launched. For small saccades, this value is about 80 ms, although in the case of larger saccades, Becker and Jürgens reported higher values.

Amplitude transitions of the type shown in Fig. 4.9 are found when the two target positions are at different eccentricities along an axis away from fixation. A different pattern was found when one location was on the right and the

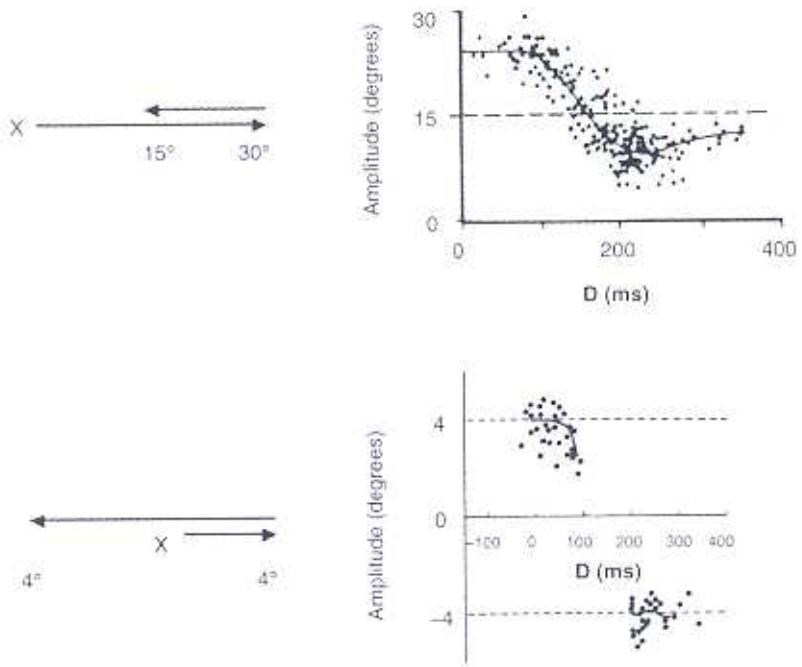


Figure 4.9 Amplitude transition functions found in a two-step tracking task. The successive steps made by the target are shown on the left hand side. In the right hand plots, each dot represents a single saccade. The amplitude of the saccade is plotted against the variable D, the time elapsing between the occurrence of the *second* target step and the initiation of the saccade. Top plot from Becker (1989) and lower plot from Findlay and Harris (1984).

other on the left (only horizontal saccades were considered in the Becker and Jürgens, 1979, study). In this case, as in the one just described, steps occurring with values of D less than about 80 ms had no effect. After this point, all saccades were directed to the second target (contralateral to the first). In the range of D values where the transition function was found in the ipsilateral case, no saccades at all were noted.

On the basis of their findings, Becker and Jürgens (1979) proposed a two stage model of saccade generation. The two stages are shown schematically in Fig. 4.10. The decision stage has the responsibility of deciding when the eyes are to move and in which direction. When the decision is made, a signal is sent to the amplitude computation stage, which is responsible for the magnitude of the movement. The amplitude computation stage works in a completely automatic manner to compute the desired amplitude by sampling the target information. The sampling is not made on an instantaneous basis but integrates whatever information is available within a temporal window. The duration of the amplitude transition function corresponds to the duration of this window. If, during this integration period, the target changes position, the resultant amplitude that

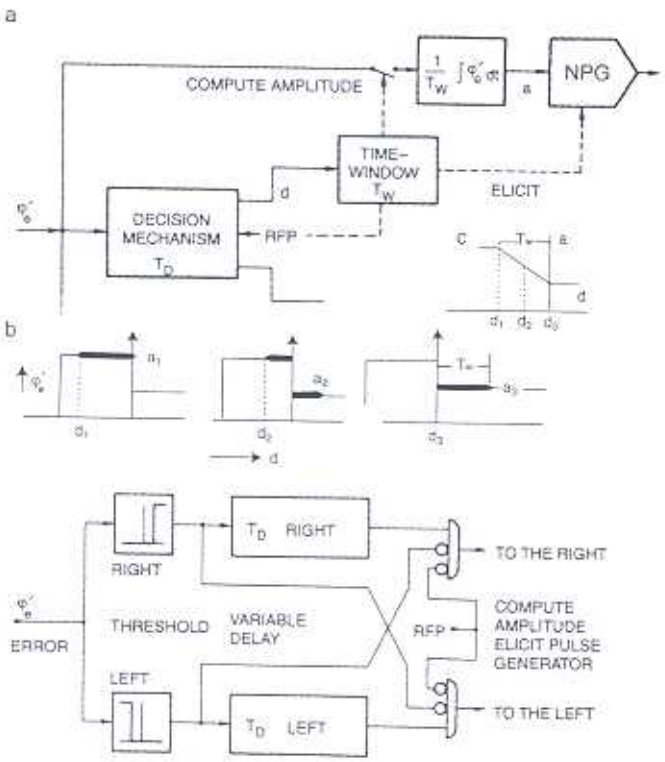


Figure 4.10 The model for the generation of saccades proposed by Becker and Jürgens (1979).

emerges is from a weighted integration of the two target positions. This integration process accounts for the saccades directed to intermediate locations.

The model has affinities with the WHERE/WHEN separation discussed in earlier sections of this chapter. However Becker and Jürgens associated part of the WHEN computation in the decision stage of their model. The model accounts very well for findings from the two-step paradigm and other paradigms in connection with horizontal saccades but runs into some problems when the more general case of saccades in two-dimensional space is considered. Findlay and Harris (1984), and Aslin and Shea (1987) found transition functions for both amplitude and direction in experiments using the double-step paradigm in the two-dimensional case. Findlay and Walker (1999) have argued that the delay in responding to a contralateral step is an instance of the remote distractor effect (Section 4.3.2) rather than representing a specific direction re-programming. They offer an alternative model in which amplitude and direction are not separately programmed but all programming comes about through selection on a 2D spatial map (Section 4.6).

### 4.4.3 The double target paradigm

Another well studied variant of the target-elicited saccade paradigm has two targets appearing simultaneously. A frequent finding, as noted already in Section 4.2.3, is that, when the stimuli are in reasonably close proximity, the orienting saccade goes to an intermediate location between the targets rather than accurately to either individual target. Following the interpretation of the comparable finding in the two-step paradigm, an explanation may be offered that the saccade amplitude computation is based on stimulation integrated over a wide area of visual space; the term *global effect* reflects this aspect of the finding. The relative properties of the targets such as size and brightness influence the saccade landing position in such a way that the effect is often appropriately described as a *centre-of-gravity* effect (Deubel *et al.*, 1984; Findlay, 1982; Findlay *et al.*, 1993; Ottes *et al.*, 1984). The effect has been demonstrated and studied in monkeys (Schiller, 1998; Chou *et al.*, 1999). These findings show that the effect is one that involves integration of the visual signal in a relatively 'raw' form. Nevertheless, various findings suggest that the effect should be assigned to a relatively late stage in the visuomotor pathways.

He and Kowler (1989) carried out a double target experiment in the form of a search task. Two stimuli were presented that differed in form (+ vs. ×) and one was designated as the search target. Subjects showed no ability to use peripheral vision sufficiently well to direct their eyes to the search target. Saccades generally landed at intermediate locations but the landing positions were systematically affected by prior knowledge about the most likely location for the search target. He and Kowler argued from this finding that the global effect was dependent on high level strategies. A more appropriate interpretation would appear to be that of Ottes *et al.* (1985) who suggest that the global effect represents a default

option for the saccadic system but may be modulated by higher level search or cognitive strategies. The main studies of the global effect have been in connection with visual orienting but claims have been made that the effect plays a role in the choice of saccade landing points in text reading (Vitu, 1991*a* see Chapter 5).

### 4.4.4 Parallel processing of saccades

In the section on corrective saccades (Section 4.4.1), it was noted that such saccades were occasionally found even when the target was no longer visible after the end of the first saccade. This implies that the second saccade was pre-programmed. Another result suggesting that more than one saccade can be processed at a time is the occurrence of very short fixations (<100 ms) in visual tasks. Becker and Jürgens (1979) noted such short latency second saccades in the double step paradigm discussed above and also proposed that saccades may be prepared in a paired manner. For a pair of saccades to be directed accurately, it is necessary that the second saccade takes account of the eye rotation achieved by the first, raising some important questions which we return to in Chapter 9.

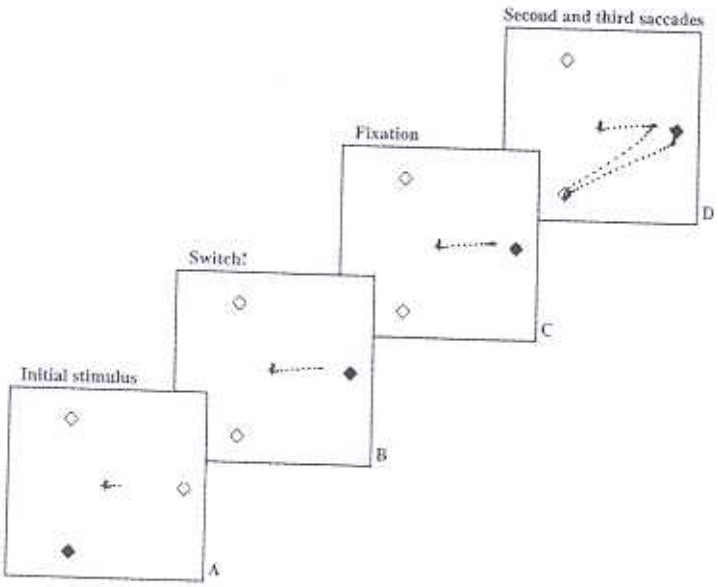


**Figure 4.11** Display sequence used by McPeek *et al.* (2000) with superimposed example eye record. The subject is instructed to make a saccadic movement to the target defined as the odd one of the three (actual displays used red and green shapes). On some trials, two of the shapes were switched. The trace shows an example where the switch brings the target to the saccade destination. Nevertheless, the saccade stops short and a further saccade is made to the former target location before a final saccade on to the target at the new location.

Interest in the phenomenon has recently revived with the discovery that short duration fixations occur commonly in scanning and visual search tasks (Findlay *et al.*, 2001; McPeek *et al.*, 2000; Sommer, 1994). This form of programming is also reported for within word refixations in reading (Section 5.6) and may be more common than previously thought. McPeek *et al.* (2000) studied saccades in an oddity search task (Section 6.1). On each trial, a display consisting of three elements occurred, either two red and one green, or two green and one red. The task was to move the eyes to the target with the unique colour. First saccades were frequently misdirected but in many cases, a second saccade to the target occurred following a very brief fixation. McPeek *et al.* combined this task with a saccade-contingent manipulation such that the display changed during the course of the first saccade. The change reversed the colours of the two items away from the direction of the saccade (Fig. 4.11). When the fixation before the second saccade was brief, the second saccade went towards the first location occupied by the target, showing that the target location was registered on the initial fixation. Surprisingly however, such 'memory directed' saccades occurred after normal and even relatively long fixations also. Only when the fixation duration was greater than 250 ms, was the colour switch taken into account. This suggests that pipelined double programming of saccades may be much more common than previously suspected.

### 4.4.5 Antisaccades

The antisaccade task was first developed by Peter Hallett (Hallett, 1978; Hallett and Adams, 1980). In the task, the participant is required to respond to a visual target by making a saccadic movement to a position in space located at the opposite side to the target. So, for example, if the target is on the right hand side of fixation then the correct response is to make a leftward saccade to the mirror image location. The task is of value for two reasons: first, as a means of investigating the interaction of reflex and voluntary control of saccadic movements; second, as a marker for diverse neurological conditions (Section 8.4). A review of both normal and clinical findings was made by Everling and Fischer (1998). Successful performance in the antisaccade task, requires participants to suppress the natural tendency to make an orienting saccade to the target. In discussions concerned with antisaccades, these reflex-like erroneous orienting movements are frequently termed *prosaccades*.

Participants are normally able to generate antisaccades, however across trials errors do occur in the form of a reflex prosaccade to the target. Interestingly, subjects are often unaware that an erroneous prosaccade has been made (Mokler and Fischer, 1999). The proportion of prosaccade errors decreases with practice, to typically around 20 per cent, although with considerable individual variability, as demonstrated in a large scale study on over 2000 young conscripts by Evokimidis *et al.* (2002). Mean reaction times for antisaccades are somewhat greater than for prosaccades and no antisaccades ever

occur with latencies in the express range described in Section 4.2.4 (Fischer and Weber, 1992). Error rates increase and latencies decrease systematically as the target amplitude increases from 1° to 12° (Fischer and Weber, 1996). Krappman (1998) carried out a study of antisaccades in the eight principal directions and showed that the variability in landing positions was high although saccade direction was generally roughly appropriate. Corrective saccades occurred but resulted in only a small improvement in accuracy.

As discussed in Section 8.4, patients with frontal lobe damage experience difficulty in suppressing erroneous prosaccades. This has led to the suggestion (e.g. Walker *et al.*, 1998) that to generate an antisaccade it is necessary for a frontal system to send a signal to the superior colliculus to inhibit the natural reflexive saccade before the antisaccade is programmed. Nevertheless given the increasing evidence for parallel processing of saccades, it seems likely that both prosaccade and antisaccade are prepared in parallel (Section 4.4.4), as proposed by Mokler and Fischer (1999). This would then account for the relatively short latency difference between pro and antisaccades. Zhang and Barash (2000) conclude that the transformation needed to generate the antisaccade is 'visual' rather than 'visuomotor', on the basis of their finding of the early appearance (50 ms after target onset) of increased neural activity in the parietal cortex at the location of the target for the antisaccade.

## 4.5 Physiology of the WHERE system

In Section 4.4, the role played by the superior colliculus in saccade generation was outlined. Selection of the saccade target was achieved by selecting the point on the oculomotor map at which burst activity took place. An important property of the visual representation in the SC is the fact that although a series of precise maps are present at different layers of the structure, in the layers at which visual and motor systems make contact, the spatial coding occurs in a highly distributed manner. This means that the visual receptive fields are large and overlapping so that any cell maps an extensive region of visual field and the representation of a point target extends over a considerable region of the collicular map. The SC thus uses a distributed population code to represent visual and oculomotor direction, a property first remarked on by McIlwain (1976; see also McIlwain, 1991). Experimental studies such as that of Lee *et al.* (1988), illustrated in Fig. 4.12, have confirmed these findings. Robinson (1972) and others have shown that simultaneous stimulation of two separate locations in the motor map of the SC will produce a saccade which is a vector average, in much the same way as that seen in behavioural experiments (see also Glimcher and Sparks, 1993).

This distributed representation assists in the conversion of a spatial, retinotopically mapped visual signal to an appropriate temporal code for the

OCCULAR CAPTURE

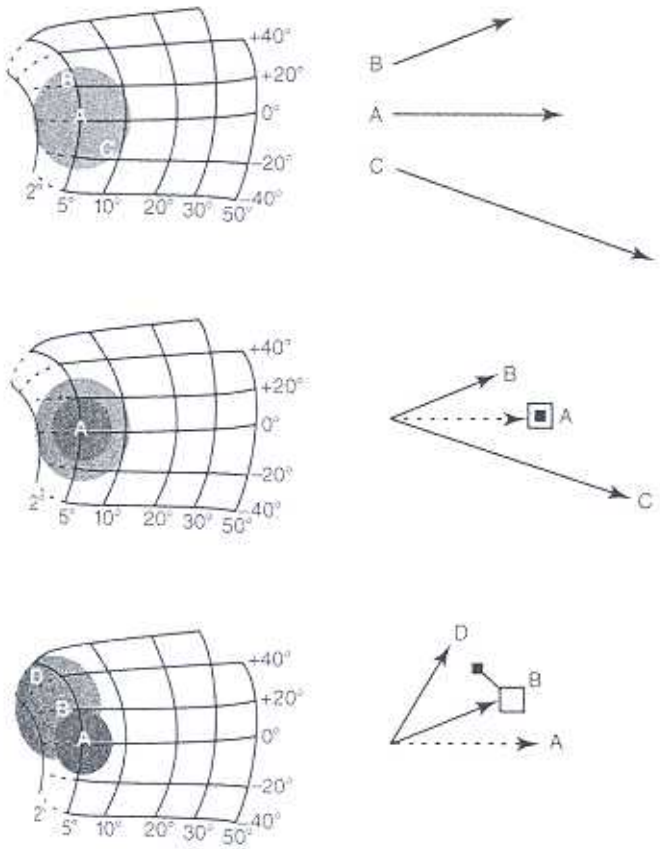


**Figure 4.12** Demonstration of distributed coding in the monkey superior colliculus. The left hand column shows schematically the collicular motor map. Stimulation at locations A, B and C respectively leads to saccades with the vectors shown in the top row. The light grey area shows the region of colliculus active before the 5° rightwards saccade obtained by stimulation at A. The lower two rows shows the result of stimulation following an injection of lidocaine centred at point A. The dark grey area estimates the affected region. Stimulation at A (centre) still results in saccades 5° rightwards, because the result of vector averaging from the unaffected regions sums to this vector. However, stimulation at B now results in a saccade displaced towards the direction obtained through stimulation at point D, since the dark shaded region no longer contributes to the vector summation. From Lee *et al.* (1988).

activation of the eye muscles, the details of which process are outside the scope of this volume (see McIlwain, 1976 and Van Gisbergen *et al.*, 1987 for implementation suggestions). When only a single target is considered, distributed representations are as accurate as point-to-point ones. However two co-occurring targets will tend to form a single representation, exactly the feature found in the global effect (Section 4.4.3).

### 4.5.1 Spatial coding and the saccadic system

An extremely influential article by Robinson (1975) affected much subsequent thinking about the saccadic system. Robinson noted the evidence that saccades were directed towards some internal goal state and proposed that this goal state was a location in a mental representation of space having a head-centred organisation. Support for this came, amongst other reasons, from the demonstrated ability to make a saccade towards the source of a sound (Zambarbieri *et al.*, 1982, Zahn *et al.*, 1978). Sound localisation is dependent principally on the difference in sound characteristics arriving at each ear and is thus initially coded with respect to the head direction.

A further finding which supported Robinson's position was that of Mays and Sparks (1980). Mays and Sparks trained monkeys to saccade to a flashed target in an otherwise dark room. Immediately after the target flash, they electrically stimulated a location in the SC. This has the effect of generating an artificial saccadic movement. The idea was to generate this movement in the latency period of the target elicited saccade and examine whether the manipulation changed the saccade characteristics. The results were unequivocal. The monkey produced the saccade required to reach the target location from the new position of the eyes following the stimulation saccade. In some way, this displacement had been 'taken into account' as the movement was prepared.

The idea of a head centred co-ordinate system has encountered some problems however. Signals in neural centres related to saccadic eye movements seem invariably to use oculocentric, rather than head-centred, co-ordinates (Moschovakis and Highstein, 1994, but see Section 9.3.3). An alternative interpretation of the Mays and Sparks result by Droulez and Berthoz (1990, 1991) emphasizes motor memory. This suggestion involves memory relating to space being encoded in terms of related motor activity so that memory for a visual field location would be encoded in terms of the command signals to direct the eyes at the location. This suggestion has support from the finding of Jay and Sparks (1987) that the auditory representation of space in the superior colliculus shifts with changes in eye position. Thus it is a representation that allows the eyes to be directed to a sound source, rather than having any absolute framework. Recent work, discussed in Chapter 9, shows that the same process occurs also with the visual representation.

## 4.6 The Findlay and Walker model

Findlay and Walker (1999) proposed that the insights gained into the organisation of the orienting system could be captured by the model shown in Fig. 4.13.

The model is primarily a functional account but is also designed to be compatible with the emerging physiological knowledge of the brain pathways involved in orienting. A principal feature is the separation of the pathways controlling WHEN and WHERE information. This shown by the two vertical streams of the model. The WHERE stream is a set of interconnected activity

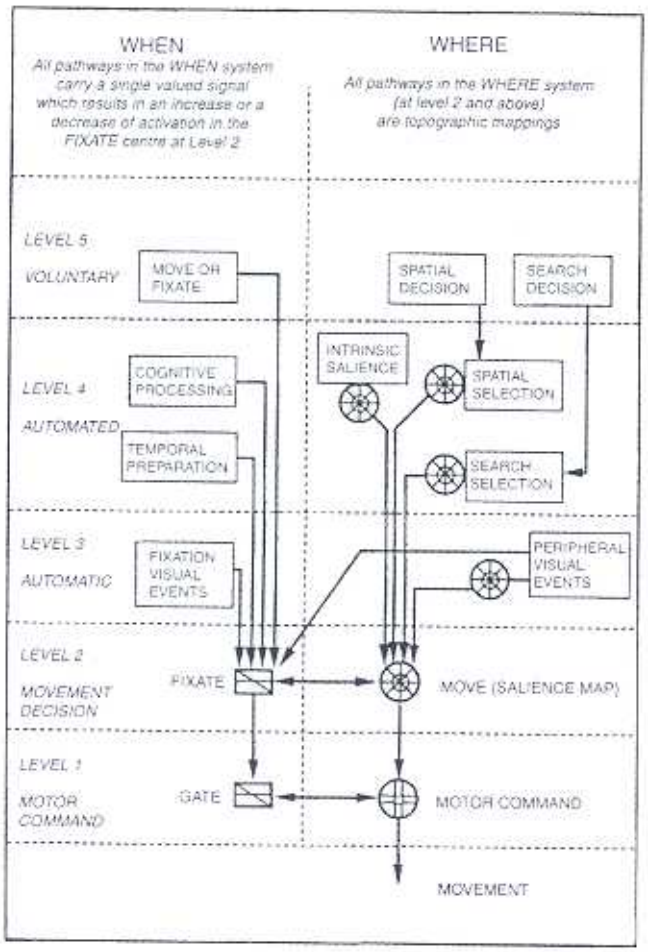


**Figure 4.13** The framework for saccadic eye movement generation presented by Findlay and Walker (1999).

maps, resulting in a 'salience map' from which the saccadic target location is selected. The idea of a salience map has figured strongly in theories of visual search (Section 6.4.3). Location coding in the activity maps occurs in a distributed manner. In contrast, the WHEN stream is envisaged as a single individual signal whose activity level varies. The horizontal bands represent processing levels that become progressively less automatic ascending up the hierarchy from bottom to top. Interaction between the two streams occurs at the lower levels in terms of reciprocal competitive inhibition.

Level 1 is specifically designed to capture the interaction in the brain stem between described in Section 4.3.1, with the burst cell system and the pause cell system interacting reciprocally to trigger each saccadic movement. When

the balance crosses some critical level, the saccade is irrevocably triggered. This level 1 interaction is in turn influenced by the next level in the hierarchy. At level 2, a push-pull competitive interaction occurs between the *fixate centre* and the *move centre*. The operations at level 2 are similar to those at level 1 but whereas level 1 operates in a highly automatic manner to effect a rapid movement, level 2 works by a slower and more variable build up in one centre and declines in the other. This time consuming process is largely responsible for the exact point in time at which the saccade is generated. Although level 2 shows obvious similarities to the processing in the superior colliculus (Section 4.3.2), Findlay and Walker avoid the exclusive identification with SC processes and suggest that similar competitive interaction may also occur in other brain centres.

Level 3 reflects the fact that transient visual events appear to have automatic and unavoidable influences on the orienting process. Events at the point currently fixated have a substantial and unavoidable effect on the fixation system. Events in the periphery have an automatic effect on the salience map of the move centre, although whether this leads to overt orienting depends on the state of the level 2 fixate/move balance. Events in the periphery also influence the *fixate* system, shown as a cross-linking pathway. Level 4 and level 5 are much more loosely designated and sketch how higher order influences might play a role.

The model accounted for a number of well-established findings in saccadic orienting, specifically the gap effect, express saccades, the remote distractor effect and the global effect. The model was presented in a journal with open peer commentary, most of which was supportive of the approach, often proposing more detailed schemes of implementation. Indeed two such schemes have appeared in subsequent publications (Clark, 1999; Trappenberg *et al.*, 2001). An interesting detail suggestion from physiological workers derives from the proposal originally made by Krauzlis *et al.* (1997) that fixation cells and build-up cells form a continuum. This offers a more integrated account of level 2 processes in which a single activity map projects differentially to level 1; projections in the WHEN pathway being mainly but not exclusively from the region representing the fovea and projections in the WHERE pathway being from the remainder of the map. A final point to note is that the model cannot, as formulated, offer any account of paired programming (Section 4.4.4).

## 4.7 Development and plasticity

The account given in the previous sections has described a set of smoothly functioning neural processes that are now rather well understood. In this section we review first evidence that these orienting mechanisms are present in some form at a very early stage of life and finally discuss adaptive mechanisms that maintain the accuracy of orienting.

The development of visual orienting has been the subject of much systematic study. Orienting responses to salient peripheral targets are present from birth, at least within the central 30 degrees of the periphery (Maurer and Lewis, 1998). The probability of an orienting response occurring depends upon stimulus variables such as size and contrast. With age, the area of the visual field that provokes orienting expands and the latencies of orienting responses decrease. Aslin and Salapatek (1975) reported that infants in the first two months of life oriented by using a staircase pattern of small saccades rather than a single one, although there is also evidence that more adult-like saccadic responses occur with more realistic stimulus material (Hainline, 1998). Evidence that competition between stimuli at fixation and peripheral targets appears from a very early age comes from the demonstration that the gap effect (Section 4.2.1) is found with young infants (Hood and Atkinson, 1993). A particularly interesting phenomenon termed 'sticky fixation' often occurs at around 1–2 months of age where babies can show great reluctance to move away from a central target (Hood *et al.*, 1998).

One aim in studying visual development is to relate behavioural findings to knowledge about neurological maturation. An influential paper by Bronson (1974) suggested that, below about two months of age, all visual processing was carried out subcortically and that the SC formed the major orienting centre in infants. This position has gradually become less tenable with the appreciation that the retino-collicular pathway is probably not connected to the collicular orienting centres (Section 4.3.2), and demonstrations of infant capacities beyond those previously used by Bronson support his argument (Slater *et al.*, 1982). Johnson (1997) has articulated a position more in line with current understanding of brain orienting processes.

The orienting response achieves a transformation from an input signal, the location of the visual target on the retina, to an output signal, the oculomotor command. Eye saccades are ballistic and stereotyped (Section 2.4) so that the immediate response is deterministic. However over longer time periods, the coupling between input and output can be adjusted. Such adjustment maintains the accuracy of the orienting and allows the system to work effectively in spite of changes in muscle strength, both normal and pathological.

An impressive early demonstration of these adaptive mechanisms occurred in a study by Kommerell *et al.* (1976). These workers studied a patient who had a muscle paresis (weakness) in one eye only. When an eye patch was placed over the normal eye, it was found that, following a period of a few hours, the amplitude of the saccades elicited by a target (presented in either eye) had increased. Switching the patch over to the abnormal eye reversed the process and a gradual decrease in the size of movements occurred. In some way the system was able to adjust to the information that the eye was not reaching its desired target.

Similar adaptation can readily be shown in the laboratory with an ingenious paradigm first introduced by McLoughlin (1967). A target is displayed on a screen to initiate a saccade. The observer's eye position is monitored and, as

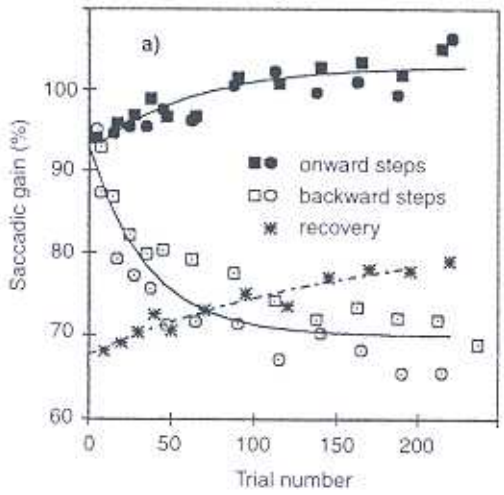


**Figure 4.14** Adaptation of saccade gain resulting from displacement of the target during an orienting saccade. The plot shows the steady incremental change in saccade gain (saccade amplitude ÷ target displacement). From Deubel (1991).

soon as the orienting saccade starts, the target is moved to a new location. Saccadic suppression (Section 2.4.3) ensures that such a change is undetectable to the observer. Nevertheless, as shown in Fig. 4.14, if such a manipulation occurs regularly over a series of saccades, adaptation is found. The significance of this finding is taken up again in Chapter 9.

Deubel (1987, 1991, 1995) has demonstrated a number of properties of this adaptation. Generalisation tests involve adapting to changes made to saccades to one specific target location, and testing the effect on target-elicited saccades at a variety of locations. These show that adaptation generalises only to a small set of directions adjacent to that experienced during the adaptation period. In contrast, adaptation of saccades at one particular amplitude demonstrates substantial transfer to saccade of different amplitude in the same direction. Separate adaptation mechanisms can be demonstrated for target-elicited saccades and for volitional saccades.