The main sequence of saccades optimizes speed-accuracy trade-off

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Abstract

In primates, it is well known that there is a consistent relationship between the duration, peak velocity and amplitude of saccadic eye movements, known as the 'main sequence'. The reason why such a stereotyped relationship evolved is unknown. We propose that a fundamental constraint on the deployment of foveal vision lies in the motor system that is perturbed by signal-dependent noise on the motor command. This noise imposes a compromise between the speed and accuracy of an eye movement. We propose that saccade trajectories have evolved to optimize a trade-off between the accuracy and duration of the movement. Taking a semi-analytical approach we use Pontryagin's minimum principle to show that there is an optimal trajectory for a given amplitude and duration; and that there is an optimal duration for a given amplitude. It follows that the peak velocity is also fixed for a given amplitude. These predictions are in good agreement with observed saccade trajectories and the main sequence. Moreover, this model predicts a small saccadic dead-zone in which it is better to stay eccentric of target than make a saccade onto target. We conclude that the main sequence has evolved as a strategy to optimize the trade-off between accuracy and speed.

1 Introduction

The ability to see an object well depends on the density of retinal photoreceptors and retinal ganglion cells deployed to transduce the retinal image. The evolution of the foveate retina raised maximum visual acuity enormously compared to a spatially homogeneous retina with the same total number of receptors. A price to pay for this non-uniformity is that the fovea must be constantly redirected at different visual targets. In primates this is usually accomplished by fast saccadic eye movements. The high speed of saccades precludes visual feedback, yet saccades have remarkably stereotyped trajectories (Bahill et al. 1975; Collewijn et al. 1988; Harwood et al. 1999). The peak velocity and the duration increase systematically with the amplitude of the movement, and these relationships have been called the 'main sequence' (Bahill et al. 1975). Here we investigate the origins of the main sequence.

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There are two complementary ways in which saccadic behavior can be modeled. First, there are models which simulate the neural mechanisms that generate observed behavior. By modeling neural systems such as superior colliculus these models aim to explain *how* saccades are generated (for example, Quaia et al. 1999). These models aim to recreate the neural mechanisms necessary to produce saccades, abstracting the important principles from the neural circuitry. Such models are extremely important for understanding neural processing

The second form of model attempts to simulate saccadic behavior based on principles that arise either through evolution or learning. These models ask *why* the behaviors have evolved to be the way they are. This approach assumes that stereotyped behaviors do not occur by accident but have emerged because they are evolutionary advantageous to the organism. The fundamental assumption is that evolution selects for overall fitness, and that sub-classes of behavior such as movement will also form part of fitness. Individuals whose movements are in some way better than others will have more chance of passing their genes on to the next generation. The goal of this approach is to find the physical and neural constraints placed on the system and the measure of fitness (or its inverse cost), of a particular way of moving. The framework used for such a model is that of optimal control theory. In this framework, a cost is assigned to each possible way of moving and, based on this cost, the theoretically optimal movement is found and compared to empirical observations. The idea is to find the biologically relevant costs and constraints by predicting observed behaviors as optimal. These models do not show how the behavior is neurally instantiated, although they may inform why certain functions are found.

Optimal control models have had a powerful influence on the field of skeletomotor control and have been successfully used to model arm movements (Flash and Hogan 1985; Harris and Wolpert 1998; Hogan 1984; Nelson 1983;Todorov and Jordan 2002; Uno et al. 1989), walking (for a review see Pandy 2001) and posture (Kuo 1995).We suggest that movement costs have four fundamental components - time, accuracy, stability and energy - with the relative weighting of the components depending on both the task and the body system under control. Movements such as walking have been accurately modeled by assuming that we choose to move so as to reduce energy consumption (e.g. Pandy 2001) Arm movements have been modeled by assuming that movements are chosen to be accurate, or to achieve the task at hand, in the presence of motor output noise (Hamilton and Wolpert 2002; Harris and Wolpert 1998; van Beers et al. 2002, 2004). Some models have suggested that movements are made to be as fast as possible, putting a cost on time (Enderle and Wolfe 1987; Happee 1992). Recently it has been shown that subjects can control the stiffness, that is stability to external perturbations, of their arm to optimally match task requirements (Burdet et al. 2001). In general there is a tension between these four types of cost. For example, it is possible to be fast but not accurate leading to the speed-accuracy trade-off. In general any task can be thought of as a weighted combination of these four types of cost.

In the eye movement literature, the notion of overall cost for eye movement has been less extensively explored. Early studies attempted to model saccade trajectories as minimum time using bang-bang optimal control time (Clark and Stark 1975; Enderle and Wolfe 1987). More recently we have shown that trajectories are better modeled as minimum variance profiles (Harris and Wolpert 1998; Harwood et al. 1999). However, to our knowledge, there has been no attempt to explain the main sequence as an optimal strategy. That is, why does a saccade of a given amplitude have a stereotyped duration and peak velocity? In this paper, we propose that both saccadic trajectory shapes *and* the main sequence have evolved to optimize visibility in the presence of motor noise, specifically optimizing the trade-off between the duration of the eye movement and end-point variability of the saccade. Unlike arm or leg movements, we assume that energy costs are not a significant factor (saccades are

remarkably resistant to fatigue, Fuchs and Binder 1983), nor do we consider instability an issue, as the oculomotor plant is highly overdamped. We suggest that the neural circuitry of saccade has evolved to optimize the trade-off between duration and accuracy.

Due to the extrafoveal fall-off in photoreceptor density, visibility of a visual target decreases rapidly with foveal eccentricity as small as a few minutes of arc, as measured by contrast sensitivity or letter acuity (Herse and Bedell 1989; Ludvigh 1941). Thus, position error decreases visibility. Visibility of an object also decreases when its image moves across the retina (retinal slip). The contrast sensitivity of a moving image is a complex function of the spatial frequency content of the image (Burr and Ross 1982) and the exposure time (Morgan et al. 1983), but when retinal slip exceeds a few degrees per second, contrast of small objects decreases rapidly (Burr and Ross 1982; Westheimer and McKee 1975), and little if any useful information can be gathered. We propose that such poor vision is an evolutionary cost.

Now consider a small stationary visual target imaged on the peripheral retina. How should the eye move to minimize the visual cost associated with this target? In principle, the optimal strategy would be to move the eye instantaneously to eliminate positional error. In addition to the limits on such motion placed by the non-zero response time of extraocular muscles, we have proposed that an additional constraint is imposed by signal dependent noise (SDN) perturbing the aggregate neural command (Harris and Wolpert 1998). With SDN, the standard deviation of the noise increases with the mean level of the signal. Moving more quickly requires larger command signals, which induce greater noise, and hence lead to an increased endpoint variance. Whereas, moving slowly may decrease errors, it does so at the price of spending more time with poor vision. Thus, movement time and positional error are in conflict, and there is a speed accuracy trade-off. We propose that the cost of losing vision during the movement added to the error over the subsequent fixation period, is optimized and this leads to both a unique optimal trajectory and duration of movement for each possible amplitude.

2 Methods

The problem is to find the optimal trajectory that minimizes the total cost associated with moving the eye to a target imaged on the retina at a specified foveal eccentricity. By making some simplifying assumptions, we solve this semi-analytically using Pontryagin's minimum principle (Bryson and Ho 1975).

We approximate the total cost of an eye movement integrated over the movement as being composed of two components. First, there is the cost associated with retinal slip, or movement cost. Here we assume that cost is all or nothing, so that once the saccade has begun and vision is lost the cost is a constant α per unit time until the saccade ends. After the movement ends there is a second cost per unit time associated with positional error over the post-movement period, F, which we call the fixation cost. We assume that in the vicinity of the fovea the cost is a quadratic function of eccentricity given by $\beta e(t)^2$, where $e(t)$ is the foveal eccentricity of the target at time t and β is a constant. It is well known that psychophysical threshold measures of acuity fall off approximately linearly with foveal eccentricity, and strictly speaking there should be a discontinuity at the foveola. However, we would expect a small object to yield a smooth threshold sensitivity around the fovea as it will be integrated by a region of foveal ganglion cell receptive fields. Thus the assumption of a quadratic minimum in the vicinity of the fovea seems reasonable.

In visual scanning the fixation period is highly variable, but here we assume a mean value of $F = 300$ ms and that the fixation error is not corrected by a secondary movement before a

movement to the next visual target is made (see Sect. 4). For a movement of duration T, the total integrated cost is therefore:

$$\text{Cost} = \underbrace{\int_0^T \alpha \, dt}_{\text{Movement cost}} + \underbrace{\int_T^{T+F} \beta \, e(t)^2 \, dt}_{\text{Fixation cost}}$$

(1)

where α and β are positive constants reflecting the relative importance of speed and accuracy. The values of these constants are assumed to be unknown and may ultimately reflect evolutionary penalties for the organism (see Sect. 4).

We now consider the mathematical problem of optimizing saccades to a target of fixed eccentricity A. We consider that two stochastic processes play into the generation of saccades. First, we assume that the aggregate neural command, $u(t)$, is perturbed by SDN, which is a zero-mean additive white noise process with instantaneous standard deviation proportional to the mean,

$$\sigma_u(t) = k|u(t)| \quad (2)$$

where k is the coefficient of variation of the SDN. Second, we assume that the desired amplitude of the saccade, P, need not be the target eccentricity and that P can vary from movement to movement for a fixed A. This is included for the sake of generality to take into account the possibility that the gain, $g = P/A$, may also be a stochastic process with the possibility of a non-unity mean, $\bar{g}$ (such as undershoot bias) and non-zero variance, σ_g^2, (such as localization error which could vary from trial to trial).

We denote the eye position at time t for a movement made of desired amplitude P, as $x_P(t)$. It follows from the linearity of SDN in a linear system that $x_P(t) = g\, x_A(t)$ where we consider the gain g as a random variable. Therefore, over repeated saccades of the same target eccentricity and duration, the expected value of the cost given in (1)

$$\begin{aligned} J &= E\{\text{Cost}\} \\ &= \alpha T + \beta \int_T^{T+F} \left(A - \bar{g}\, A\right)^2 + \text{Var}\{g \quad x_A(t)\} \, dt \quad (3) \end{aligned}$$

where we have decomposed the average squared error in the fixation cost, $E\{e(t)^2\}$, into its two components, the (expected bias)^2 and variance. We assume that the noise process in g and the SDN are independent and therefore expanding $\text{Var}\{g\, x_A(t)\}$ gives

$$J = \alpha T + \beta \int_T^{T+F} \left(A - \bar{g}\, A\right)^2 + \sigma_g^2 A^2 + \left(\bar{g}^2 + \sigma_g^2\right) \times \text{Var}\{x_A(t)\} \, dt \quad (4)$$

$$= \alpha T + \beta' \int_{T}^{T+F} \sigma_x^2(t)\,\mathrm{d}t + \gamma \quad (5)$$

where $\sigma_x^2(t)$ is the variance of the eye position in the fixation period, $\beta' = \left(\bar{g}^{-2} + \sigma_g^2\right)\beta$ and

$\gamma = F\beta\left[\left(A - \bar{g}\,A\right)^2 + \sigma_g^2 A^2\right]$. With SDN during the movement, the variance in the fixation period depends on the movement duration T, the precise trajectory of the saccade, the dynamics of the extraocular muscles (ocular plant), and the coefficient of variability of the noise k. The key point is that with SDN the two components in Eq. (5) cannot be minimized independently because reducing movement duration, T, reduces the first component but increases the second. We propose that the saccadic trajectory profile and movement duration, T be both selected to minimize the expected cost in Eq. (5).

To solve this optimization problem for a given movement amplitude, we first hold the duration T fixed and find the optimal trajectory. With T fixed the optimal trajectory is the one that minimizes the fixation cost of Eq. (5). We have previously shown numerically the trajectory that minimizes this cost (Harris and Wolpert 1998). Here we show that for a linear plant, the optimal trajectory and its variance can be derived analytically. We then vary the movement duration T, and for each T we find the optimal trajectory and compute the fixation cost, that is the integrated variance over the fixation period. For each amplitude, the optimal saccade duration is found that minimizes the overall cost.

We denote eye position as $x(t)$ which is the output of a linear pole-only ocular motor plant, with impulse response $p(t)$, whose input is a single scalar aggregate mean neural command $u(t)$. To represent signal dependent noise on the motor command we assume the motor command is corrupted by zero-mean white noise with an instantaneous standard deviation proportional to the absolute motor command $\sigma_u(t) = k|u(t)|$, where k is the constant coefficient of variation. The average trajectory is then given by

$$E[x(t)] = \int_{0}^{t} u(\tau)\,p(t-\tau)\,\mathrm{d}\tau \quad (6)$$

and from basic analysis, it follows that the variance of the eye position is given by the new convolution (Harris 1998)

$$\sigma_x^2(t) = \mathrm{Var}[x(t)] \quad = \int_{0}^{t} \mathrm{Var}[u(\tau)\,p(t-\tau)]\,\mathrm{d}\tau$$
$$= \int_{0}^{t} \mathrm{Var}[u(\tau)]\,p^2(t-\tau)\,\mathrm{d}\tau \quad (7)$$
$$= \int_{0}^{t} k^2 u^2(\tau)\,p^2(t-\tau)\,\mathrm{d}\tau$$

From Eq. (5) the expected cost of movement is

$$J \quad =\gamma+\alpha T+\beta' \int\limits_{T}^{T+F} \sigma_x^2(t) \, \mathrm{d}t$$

$$=\gamma+\alpha T+\beta' \int\limits_{T}^{T+F} \left[\int\limits_{0}^{t} k^2 u^2(\tau) \, p^2(t-\tau) \, \mathrm{d}\tau \right] \mathrm{d}t \qquad (8)$$

We can rewrite this to split the cost due to the noise during the saccade ($0 \leq t < T$) and that due to the noise in the fixation period ($T \leq t \leq T+F$),

$$J=\gamma+\alpha T+\beta' k^2 \int\limits_{T}^{T+F} \left[\int\limits_{0}^{T} u^2(\tau) \, p^2(t-\tau) \, \mathrm{d}\tau + \int\limits_{T}^{t} u^2(\tau) \, p^2(t-\tau) \, \mathrm{d}\tau \right] \mathrm{d}t \quad (9)$$

As we assume that after time T (the saccade duration) average eye position is at gA during the fixation period of duration F, the last component of J is the same for all possible trajectories and can be replaced by the constant κ:

$$J=\gamma+\alpha T+\beta' k^2 \int\limits_{0}^{T} u^2(\tau) \, q_T(\tau) \, \mathrm{d}\tau+\kappa \quad (10)$$

where $q_T(\tau) = \int_{T}^{T+F} p^2(t-\tau) \, \mathrm{d}t$.

We solve this optimal control problem for an order n state space model of the eye plant

$$\dot{\mathbf{x}}(t) = A\mathbf{x}(t) + Bu(t). \quad (11)$$

From Pontryagin's minimum principle the optimal control signal is given by minimizing the Hamiltonian with respect to u:

$$H(\mathbf{x}, u, t) = \alpha + \beta' k^2 u^2(t) \, q_T(t) + \Lambda^T(t) \left[A\mathbf{x}(t) + Bu(t) \right] \quad (12)$$

where Λ is the costate vector given by the solution of the costate equation:

$$-\dot{\Lambda}(t) = \frac{\partial H}{\partial \mathbf{x}} \quad (13)$$

Since J is independent of the state $\mathbf{x}$, the costate equation will be a homogeneous differential equation of order n, with a solution of n exponentials and hence will be continuous over $(0, T)$. Minimizing H with respect to u, requires solving

$$\frac{\partial H}{\partial u} = 2\beta' k^2 u q_T + \Lambda^T B = 0 \quad (14)$$

The optimal control is therefore given by:

$$u^*(t) = \sum_{r=1}^{n} c_r \frac{\exp(\gamma_r t)}{q_T(t)} \quad (0 < t < T) \quad (15)$$

where the γ_r are the n roots of the costate equation. For an overdamped ocular plant with distinct real roots, $\gamma_r = +1/t_r$ where t_r are the time constants of the plant. There are no constraints on $u(t)$, and in general there will be discontinuities in u at $t = 0$, and $t = T$. The

scalars c_r are determined by the boundary conditions on the state variables. We require that time derivatives up to order $n-1$ of eye position at T are zero:

$$\left.\frac{d^i x}{dt^i}\right|_T = 0 = \int_0^T u(t)\,\frac{d^i p(T-t)}{dp^i}\,dt, \quad i = 1, \ldots, n-1 \quad (16)$$

The remaining degree of freedom is given by the amplitude, P, of the movement

$$x(T) = P = \int_0^t u(t)\,p(T-t)\,dt. \quad (17)$$

This provides n simultaneous equations to solve for the c_r. Although it is possible to find explicit expressions for the c_r they are extremely cumbersome. Instead, we have solved them numerically. For simulations we have used a third-order linear model ($n = 3$) of the oculomotor plant with time constants 223, 14 and 4 ms (Harwood et al. 1999).

From Eq. (10) the optimal trajectory is independent of any constants added or subtracted from the cost J, and also independent of any multiplicative scale factor applied to J. Thus, the optimal trajectories will be independent of γ, κ, and will depend only on the ratio $a/(\beta\,k^2)$. Thus the weighting factors and the coefficient of variation of the noise collapse into one unknown.

3 Results

This fixation cost arising from SDN on the motor command with a coefficient of variability (k) of 0.7% is plotted against duration T for a unit amplitude saccade in Fig. 1a. This shows that the fixation cost at the end of the optimal movement is a rapidly decreasing function of the movement duration, reflecting a strong speed accuracy trade-off. Similar curves can be obtained for saccades of amplitude other than unity, because with SDN the standard deviation scales linearly with amplitude. Figure 1b shows the two components of the cost and the combined total cost for a 10 degree movement. The dotted line is the movement cost, which is a linearly increasing function of T with a slope of a. For a given duration, T, this component of the cost function does not change with the amplitude of the movement. The dashed line is the fixation cost which depends on the amplitude. The full cost (solid line) is given by the sum of these two components, which clearly has a minimum that represents the optimal movement duration, in this case around 50 ms. For movements of different amplitudes, this optimal duration increases with amplitude (Fig. 1c) and also depends on the single parameter trade-off ratio $a/(\beta\,k^2)$.

Figure 2a (solid line) shows the optimal duration as a function of amplitude for $a/(\beta\,k^2) = 26{,}500$ (for example, $a/\beta = 1.3$ and $k = 0.007$). This is a compressive function for very brief movements but becomes linear for longer movements, and is very similar to the empirically observed main sequence for duration (Fig. 2a, dots). Once the duration and amplitude are specified, the trajectory is fixed and therefore the peak velocity is determined (Harris and Wolpert 1998). Figure 2b shows a good fit for the main sequence for peak velocity as well. It must be emphasized that the compressive nature of the peak velocity function is not the result of any saturation in the control signal but arises from optimizing Eq. (5). It is also an empirical observation that the product of peak velocity and duration is proportional to amplitude, reflecting a constant ratio of peak to average velocity (Becker 1989). The model clearly captures this phenomenon as well (Fig. 2c). The optimal speed profiles for 5, 10 and 20 degree saccades from the optimal model with SDN are shown in

Fig. 2e showing symmetric bell shape trajectories, as previously described (Harris and Wolpert 1998)

The predicted main sequence depends on the trade-off between the movement and fixation costs and the noise, that is the ratio $\alpha/(\beta' k^2)$. Increasing the ratio penalizes duration more thus leading to shorter durations for a given amplitude, and conversely, decreasing the ratio leads to longer durations. For example, data published by Baloh et al. (1975) showed modestly longer durations than typically found in our lab (Fig. 2d). However, these data can still be well fit by the model but with $\alpha/(\beta' k^2) = 12, 200$. This could be attributed to individual differences such as approximately halving α or doubling β', or simply to more noise (increasing k by 40%). This also reveals that the predicted main sequence is not very sensitive to these parameters, so that similar main sequences across individuals would occur even with moderate individual differences in trade-off parameters.

Theoretically, for a given $\alpha/(\beta' k^2)$, the optimal main sequence should also depend on the fixation cost in Eq. (5). To explore this dependence we found the optimal main sequence when mean F was varied over an extreme tenfold range from 100 to 1,000 ms. As can be seen from Fig. 3, there is little change in the optimal main sequence. Although individual fixation durations are empirically highly variable (Buswell 1935), mean fixation duration is much less variable. Thus, we do not expect any strong relationship between physiological fixation durations and the main sequence.

We now consider another strategy of moving slowly to maintain vision at all times. Here we make the simplifying assumption that retinal slip below d° s^{-1} affects vision minimally so the cost of a drifting movement is caused only by the fixation cost and is given by

$$\text{Cost} = \beta' \int_0^F e(t)^2 \mathrm{d}t \quad (18)$$

where $e(t)$ reduces at the rate of d° s^{-1}. Provided $F > A/d$ the fovea will reach the target at $t = A/d$ and the cost is $A^3/3d$. If $F < A/4$ then the target is not reached during the fixation period and the cost is $A^2F - AdF^2 + d^2F^3/3$. It can be seen from Eq. (5) that for very small target eccentricities the cost of making a saccade could exceed the cost of slowly reducing eccentricity by d° s^{-1}. Figure 4 shows the cost of saccading and the cost of drifting at various values of d including no movement ($d = 0$) for various target eccentricities. As can be seen, for very small amplitudes it does not pay to make a saccade, but instead drift towards the target or even to maintain constant eccentric fixation. Above the intersection point of the saccade and drift curves it is optimal to make a fast movement. The precise location of this intersection point depends on the drift rate d that can be tolerated and the expected fixation duration F. Thus, SDN predicts that minimization of cost leads to two possible strategies depending on the target eccentricity and expected fixation duration or target longevity.

4 Discussion

It is a remarkable fact that in spite of the myriad of visual tasks that we carry out every day, we only make a few different types of eye movement. When we view a stationary scene at a fixed distance with the head still, only fixations or saccades occur, there are no 'in-between' types of eye movement. Moreover, saccades have a fixed relationship between their amplitude and the saccadic duration and peak velocity, known as the main sequence. We have shown that this stereotypicity could be an inevitable consequence of maximizing vision given the constraints of motor noise. There are two steps to our argument.

First, if the motor command is perturbed by SDN with the property that the standard deviation is proportional to the mean, then variance is accumulated during the movement leading to inaccurate fixation. For a given movement duration there is a unique trajectory that minimizes the cost of inaccurate fixation over the post-movement period [fixation cost in Eq. (1)]. As previously shown (Harris and Wolpert 1998), the shape of this optimal trajectory is in good agreement with empirical observation, but depends in detail on the dynamic response of the oculomotor plant and the duration of the post-movement period. We have chosen a third-order linear model because this provides an excellent fit to the trajectories when using the sensitive technique of Fourier analysis (Harwood et al. 1999). However, the general symmetrical bell-shaped profile for fast movements is not only insensitive to modest variations in the precise parameters and the order of linear plant models, but is also predicted by non-linear models (Harris and Wolpert 1998). This first step only tells us the optimal shape and does not tell us which duration is optimal for a given movement amplitude.

In the second step we attribute an additional cost due to loss of vision from image motion, which is proportional to the duration of the movement. The total cost of a movement is then composed of two components, the movement cost and the fixation cost. Minimizing the total cost reveals two distinct optimal strategies depending on the target eccentricity: (a) for very small eccentricities, it pays to drift slowly or not move the eye at all (fixation), and to tolerate the marginally poor vision due to imperfect foveation; and (b) for larger eccentricities, the optimum is to move quickly with the optimal saccadic trajectory, losing vision transiently during the movement, but reaching the target rapidly. Moreover, as target eccentricity increases, the optimal movement increases in both duration and in peak velocity in a fixed stereotyped way, which is in good agreement with the empirically observed main sequence (Fig. 2).

Although the empirical main sequence is stereotyped, it is not immutable. Saccades to acoustic (Zambarbieri et al. 1982) and tactile targets (Groh and Sparks 1996) are slower. The main sequence also depends on the subject's visual task such as just looking at visual targets or actually tapping the targets (Epelboim et al. 1997) or pointing to real or remembered targets (Smit et al. 1987). However, all these main sequences have a similar shape and the task may determine the relative weighting of movement and fixation cost. As can be seen from Eq. (10), changing the single parameter $\alpha/(\beta\ k^2)$ does not alter the shape of the relationship but acts to simply scale the shape along the amplitude axis. Thus differences in main sequences under different conditions and between individuals may reflect differences in the cost weightings (α and β), and/or the amount of SDN (k). At present we are unable to pre-specify α and β. It is possible that they are fundamentally experimentally indeterminate, depending on the precise evolutionary niche of the organism (i.e. how much slowness and error contribute to evolutionary fitness). However, it is possible that α and β reflect some as yet unknown underlying process that fixes the relationship between uncertainty and speed. Whether an information-theoretic approach will yield insight into this issue remains to be seen.

Our results do not depend on or assume that a saccade is accurate on average. In particular, if a saccade is programmed to undershoot the target with subsequent corrective movements, the main sequence is still optimal for each saccade and its post-movement period. We have assumed implicitly, however, that the cost of a saccade does not include the cost of subsequent corrective saccades. Although corrective saccades are undoubtedly commonplace in the laboratory when subjects make saccades to a single target, they appear to be much less frequent or even absent when viewing natural scenes (Buswell 1935). Therefore, we argue, it seems unlikely that the main sequence would have evolved to include costs for correctives. However, more experimental data are needed to corroborate

this conclusion. The reason for so many correctives in laboratory situations is unknown and controversial. One possibility is that they are simply an artifice of the laboratory, as we do not usually encounter single targets naturally. However, we have previously argued that the undershoot bias may also reflect a stratagem to minimize overall saccade flight time given that saccades are inaccurate (Harris 1995). If this is the case, then a parsimonious picture emerges in which the main sequence optimizes individual saccades, while adaptive gain control optimizes the overall sequence when correctives are needed.

We have assumed that the movement cost per unit time is constant at a throughout the saccade, which implies that there is an abrupt step in cost when there is any retinal slip. This is a simplification that allows us to relate cost to movement duration by the simple integral in Eq. (1). Threshold measures for small visual targets would indicate a rapid but not step-like rise in cost once slip exceeds some critical velocity (Burr and Ross 1982). For small visual targets this critical velocity is often cited as about $3° \text{ s}^{-1}$ (Westheimer and McKee 1975). However the effect of slip velocity on visibility is complex. For single exposures of about 200 ms, contrast sensitivity is only marginally affected for slips below $3° \text{ s}^{-1}$ (Westheimer and McKee 1975), but for repeated exposure as might be expected in visual scanning, contrast sensitivity decreases at lower slip velocities (Morgan et al. 1983). Further complications arise because the critical velocity increases with larger visual targets (Burr and Ross 1982), and if the object is already blurred, image motion may actually improve contrast (Hammett et al. 1998). Again, it is plausible that the relative values of the movement and fixation costs, and hence the optimal main sequence, could depend on the spatial frequency content of the peripheral target. A more elaborate model of cost could also take into account how the visibility of a moving target scales with foveal eccentricity (Chung and Bedell 1998). Thus, relating the visibility to image motion is very complicated. In any case, the proportion of movement time during most saccades at these low velocities is small.

We have also examined the strategy of moving the eyes very slowly so as to maintain visibility during the movement. In this case the cost of movement increases rapidly with foveal eccentricity of a target, while the cost of a saccade is a compressive function (Fig. 4). Thus, there will always be a target eccentricity above which it pays to make a saccade and below which it pays to drift slowly or not move at all. The precise size of this 'deadzone' depends on the choice of a/β and the level of noise, and on the fixation period F. For longer fixation periods, the cost of eccentric fixation is proportional to the fixation period while the cost of a saccade increases sub-linearly. Therefore the saccadic deadzone decreases as the fixation duration increases. Although a saccade deadzone of about $0.2°$ was originally proposed (Rashbass 1961), it was subsequently shown that saccades as small as $0.05°$ could be elicited by a visual target (Wyman and Steinman 1973a,b). However, these microsaccades tended to have latencies longer than the typical 200 ms, which appeared to depend not on visual processing of targets at such small eccentricities, but rather on the programming or execution of the saccade (Wyman and Steinman 1973a). It also has been shown that express saccades, which have a much shorter latency, do exhibit a deadzone of about $0.5°$ (Weber et al. 1992). These findings suggest that the saccade deadzone may decreases with longer latency, which is not inconsistent with our model. Thus, the longer a stimulus is expected to be present, the smaller the deadzone becomes until a movement is eventually triggered.

For the SDN we have proposed that the standard deviation of the neuromotor command noise is proportional to the mean level of the command, giving a constant coefficient of variation. At least for limb movements this type of SDN is in accord with data from both motoneuronal recording (Matthews 1996) and force production studies (Schmidt et al. 1979). We have shown that such SDN arises from a combination of a renewal process at the

motoneurons and the recruitment properties of muscles (Jones et al. 2002). It is also in general accordance with known psychophysical relationships implicit in Fitt's law and Weber's law. We predict that a similar noise dependency exists in the oculomotor system, and may arise at the single neuronal level, as an emergent property of neuronal networks, or at the neuromuscular level or as a consequence of motor unit recruitment. Consistent with the idea of SDN is that the standard deviation of saccadic endpoints increases monotonically with saccadic amplitude (van Opstal and van Gisbergen 1989). Recent scleral coil recordings in humans of variability of the initial 150 ms of post-saccadic fixation to targets or varying eccentricity shows that this variability within a saccade increases with eccentricities (and hence muscle tension) supporting the idea of SDN (van Beers 2003). Although we have focused on noise on the aggregate neural command throughout a saccadic movement, it is possible that the noise arises from a different process such as variability in planning or variability of muscle excitability. For example, we can consider instead that the motor command $u(t)$ on any given movement is noise-free but that the gain, g, of the motor command varies from trial to trial with unity mean and standard deviation σ_g. Across an ensemble of movements the variance of the motor aggregate command is

$\mathrm{Var}\{gu(t)\} = \sigma_g^2 u(t)^2$. Therefore once again we have SDN across the ensemble of movements and the mathematics follows as before. It is also possible that the dynamic response of the muscle plant also fluctuates in time. This leads to more complicated expressions, but essentially leads to a similar problem (Harris 2002).

The fixed relation between amplitude and duration for saccades is in sharp distinction to the variable relation seem in arm movement. Some of the earliest studies of movement examined how we select the duration of a movement. The relationship between the movement amplitude, the accuracy requirement of the movement (as determined by target width) and the movement duration is described by Fitts law (Fitts 1954). This law relates the duration of a movement to the accuracy requirement of a task, as determined by the target width and amplitude of the movement, and has been shown to apply for a range of task such as reaching to targets, placing pegs in hole and picking up an object. We have previously modeled this relation by assuming that in the presence of SDN, subjects aim for a fixed success rate, that is probability, of getting on target given the target width and target amplitude (Harris and Wolpert 1998). Why then is there only one duration for each amplitude for saccades? One possibility is that in saccades the fovea is equivalent to target width. An object of interest in the visual scene needs to be placed within the target of the fovea. Therefore the saccadic system can be considered equivalent to the arm always pointing towards a fixed size target leading to a fixed amplitude-duration relationship.

In summary, we have argued that without any neuroanatomical constraints other than SDN, the saccadic system may have evolved to optimize the speed-accuracy trade-off. This model only addresses the overall goal of the saccadic system and does not specify the neural mechanisms which generate the saccades. We propose that saccades optimize this trade-off at two levels. First, for any given amplitude and duration of movement there is an optimal trajectory, which is given by the minimum variance trajectory (Harris and Wolpert 1998; Harwood et al. 1999). We believe this principle is shared by other aimed movements such as arm movements. Second, there is also a fixed speed-accuracy trade-off for saccades of different amplitudes. This leads to an optimal relationship between duration and amplitude, which we call the main sequence.

Acknowledgments

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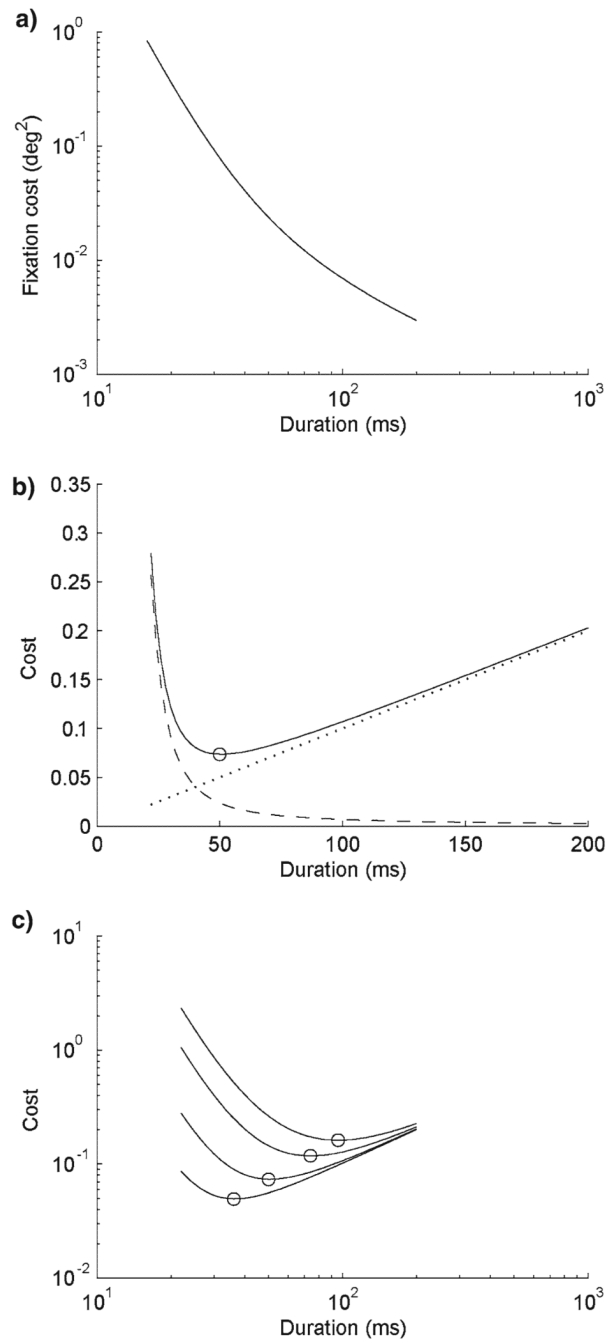
Fig. 1.
a The fixation cost (see Eq. (1)) of making a unit amplitude saccade as a function of movement duration, T, plotted on a log-log scale ($F = 300$ ms). Note that cost decreases for longer duration for a given amplitude. **b** A linear-linear plot of the total cost of a 10 degree saccade as a function of duration, T. The total cost (*solid line*) is made up of two components (see Eq. (1)): the movement cost which increases linearly with duration (*dotted line*) and the fixation cost which decreases with duration, as in (**a**) (*dashed line*). The optimum cost is the minimum total cost, shown by the *circle*. **c** The total cost for movements

of different amplitudes (5°, 10°, 20° and 30°) shows an increase in optimal duration (*circles*) with amplitude, as seen empirically in the duration main sequence
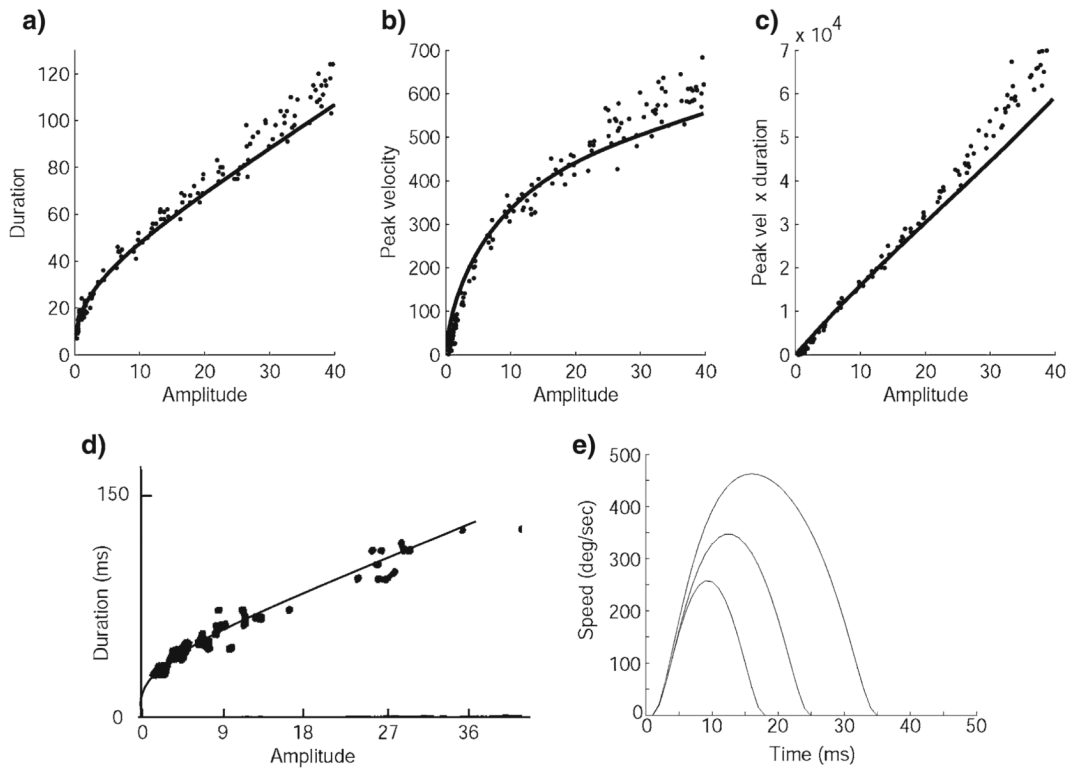
Fig. 2.

Comparison of theoretical optimal main sequence (*solid lines*) to empirical data (*dots*). **a** Duration against movement amplitude. **b** Peak velocity against movement amplitude. **c** The product of duration and peak velocity against movement amplitude. This typical main sequence was recorded from a healthy adult using an infra-red limbus eye-tracker at 1 kHz. The data were recorded in a previous study (Harwood et al. 1999). The ratio $\alpha/(\beta' k^2)$ was set to 25,500 (see text). **d** duration against amplitude plotted together with data from (Baloh et al. 1975) with $\alpha/(\beta' k^2) = 12,200$ (see text). **e** Optimal saccadic speed profiles for 5°, 10° and 20° saccades
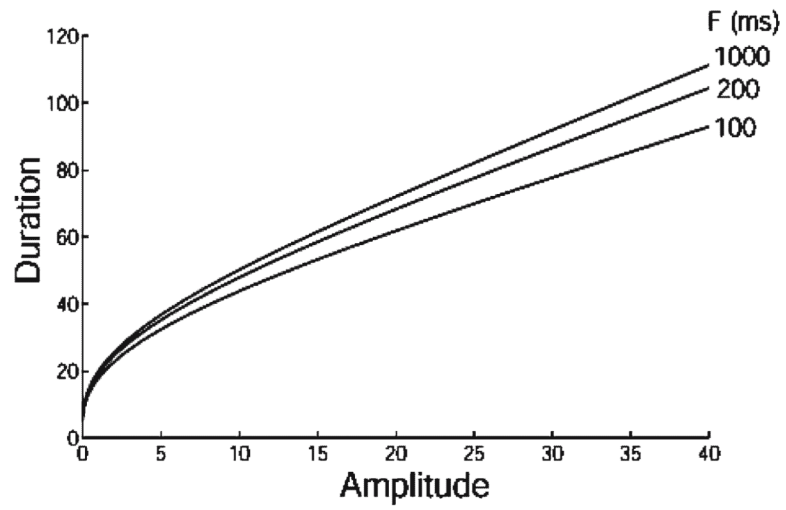
Fig. 3.
The optimal duration main sequence for mean fixation periods, *F* = 100, 200 and 1000 ms
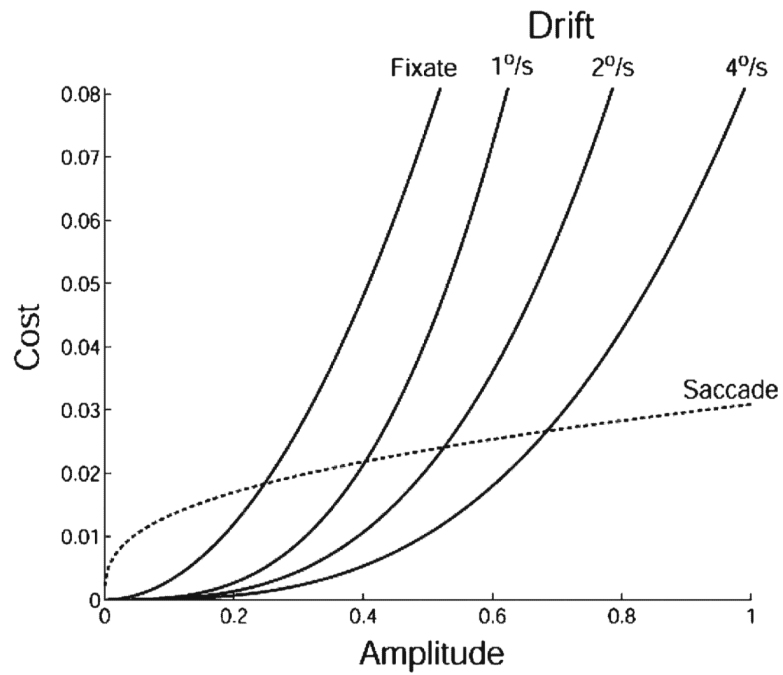
Fig. 4.
A comparison of total costs for two strategies of movement. The *dotted line* shows the cost for saccadic movements and the *solid lines* show the cost for drifting movements with different tolerated drift rates *d*. The intersection of each solid line with the dotted line represents the saccadic deadzone for the given drift rate *d*