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Models of ensemble firing of muscle spindle afferents recorded during normal locomotion in cats

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1. The aim of this work was to compare the ability of several mathematical models to predict the firing characteristics of muscle spindle primary afferents recorded chronically during normal stepping in cats.
2. Ensemble firing profiles of nine hamstring spindle primary (presumed group Ia) afferents were compiled from stored data from 132 step cycles. Three sets of profiles corresponding to slow, medium and fast steps were generated by averaging groups of step cycles aligned to peak muscle length in each cycle.
3. Five models obtained from the literature were compared. Each of these models was used to predict the spindle firing profiles from the averaged muscle length signals. The models were also used in the reverse direction, namely to predict muscle length from the firing profiles. A sixth model incorporating some key aspects of the other models was also included in the comparisons.
4. Five of the models predicted spindle firing well, with root mean square (r.m.s.) errors lower than 14% of the modulation depth of the target profiles. The key variable in achieving good predictions was muscle velocity, the best fits being obtained with power-law functions of velocity, with an exponent of 0.5 or 0.6 (i.e. spindle firing rate is approximately proportional to the square root of muscle velocity). The fits were slightly improved by adding small components of EMG signal to mimic fusimotor action linked to muscle activation. The modest relative size of EMG-linked fusimotor action may be related to the fact that hamstring muscles are not strongly recruited in stepping.
5. Length was predicted very accurately from firing profiles with the inverse of the above models, indicating that the nervous system could in principle process spindle firing in a relatively simple way to give accurate information on muscle length.
6. The responses of the models to standard ramp-and-hold displacements at 10 mm s^{-1} were also studied (i.e. velocities that were an order of magnitude lower than that during stepping). In these cases components of spindle primary response related to length as well as velocity were needed for good fits. Because these length-related components detracted from rather than improved predictions of the step cycle data, an attenuation of length dependence at high muscle velocities emerged as a possibility.
7. We conclude that in this study we have identified models and parameters that may be used to predict spindle afferent firing from the time course of muscle length in the cat step cycle.

In spite of many years of research there is still much uncertainty regarding the nature of proprioceptive signals and the role of these signals in kinaesthesia and movement control. The uncertainty mainly concerns the firing characteristics of the most numerous proprioceptors, the muscle spindles. From many studies in anaesthetized animals it is known that mammalian muscle spindle afferents respond to muscle displacement and velocity and that these responses are strongly modulated by γ -fusimotor activity

emanating from the central nervous system. Fusimotor action not only increases the firing rate of spindle afferents at a given muscle length ('bias'), it also controls the sensitivity of the afferents to changes in muscle length ('gain'). Just how the mammalian nervous system controls fusimotor action in daily life remains the subject of controversy (for review, see Prochazka, 1996). The firing rate of muscle spindles can also be affected by mechanical factors such as tendon strain, changes in pennation angle,

unloading and 'bounce' of muscles in rapid movements (Amis, Prochazka, Short, Trend & Ward, 1987; Hoffer, Caputi, Pose & Griffiths, 1989; Griffiths, 1991).

Starting in the late 1960s, several acute studies were aimed at deriving mathematical models of spindle response characteristics. The resulting models fall into three classes: linear transfer functions (Matthews & Stein, 1969; Chen & Poppele, 1978), non-linear functions based on curve-fitting (Houk, Rymer & Crago, 1981; Hasan, 1983) and non-linear models based on biological mechanisms of the muscle spindle (Otten, Scheepstra & Hulliger, 1995). The predictive power of the various models has never been directly compared, either in acute experiments or in relation to afferent recordings from awake animals or humans. In the absence of such comparative data, modellers have tended to choose the simplest spindle models for their systems, deferring validation to a later time.

Over the last two decades it has been possible to record from single afferent nerve fibres in awake humans, cats and monkeys. The techniques are difficult and generally the number of afferents recorded from in a particular study has been low. Thus although dozens of individual reports on afferent firing properties have been published, they nearly all concern the responses of small, somewhat heterogeneous groups of afferents in specific motor tasks or under specific experimental conditions. There have been few attempts to collate *population* responses of muscle afferents whose type and muscle of origin have been identified. Yet it is the population behaviour in well-defined and reproducible motor tasks that is the most valuable when testing mathematical models intended for use in control system descriptions of the motor system.

Fortunately, it has been possible in the last few years to assemble the beginnings of a 'look-up chart' of afferent firing profiles in the cat step cycle (Prochazka, Trend, Hulliger & Vincent, 1989). In this and the following paper we present some of these profiles, up-dated with data recorded since the first publication. We have found that after the profiles of five or six afferents have been averaged into a particular ensemble response, the addition of further data does not significantly change the population response profile (Prochazka *et al.* 1989). On this basis, we felt that the available data on spindle primary afferents of two main muscle groups, the hamstrings and triceps surae, were now sufficiently representative that testing of the available spindle models was justified.

In this first report we compare predictions of ensemble spindle primary afferent firing derived from muscle length with the use of six mathematical models. Despite fundamental differences in the structure of the models, most of them provided good predictions of firing from the length profiles and in some cases excellent predictions in the reverse direction, i.e. predictions of length changes from firing profiles. Statistical comparisons indicated that a simple hybrid model that combined linear and non-linear

features of existing models provided the best fits over a wide range of muscle velocities. In the companion paper (Prochazka & Gorassini, 1998) we present the updated look-up chart of ensemble afferent firing in different muscles and we use the hybrid model to make some indirect inferences regarding underlying fusimotor action. The main new insight is that the variations in muscle velocity in normal locomotor movements in the cat are very large and dominate in the shaping of spindle Ia firing profiles. We suspect that the same would be true in humans performing normal movements and this may explain the puzzling discrepancies between spindle responses recorded in human neurography where movements are very slow and in those observed in freely moving animals.

METHODS

The chronic data in this report were obtained in previous studies in our laboratory from nine freely moving adult cats. All of the surgical and recording techniques used have been described in detail previously (Gorassini, Prochazka & Taylor, 1993), so only a summary is presented here. Ethics approval for the chronic experiments was obtained from the Health Sciences Animal Welfare Committee at the University of Alberta and all surgical procedures were performed under strict supervision of veterinarians from the animal facility (Heritage Lab Animal Services).

Implantation

In one surgical procedure, performed with pentobarbitone anaesthesia (40 mg kg⁻¹ i.p., then i.v. pentobarbitone maintenance doses), and with antiseptic precautions, four 17 µm diameter enamelled nickel-chrome micro-wires were implanted so that the de-insulated, bevelled tips of the wires were positioned in the L7 and S1 dorsal root ganglia, with a connecting cable leading subcutaneously to a dental acrylic headpiece. Pairs of electromyogram (EMG) electrodes were implanted into the lateral gastrocnemius and posterior biceps femoris muscles. Nylon monofilaments were embedded into the bony points of origin and insertion of these muscles, the far ends emerging percutaneously along the line of the muscle, to provide attachment points for external length gauges. A silicone rubber cannula was implanted in the right external jugular allowing antibiotic (flucloxacillin) and short-acting anaesthetic (thiopentone) drugs to be administered in the days and weeks following recovery. Cats recovered from the procedures over a 12–24 h period in a humidified chamber. A potent analgesic (buprenorphine) was administered intramuscularly at 12 h intervals in the first 36 h of recovery to minimize discomfort. After 1–3 days, the cats bore the small implants with no sign of discomfort or motor deficit. At the end of each study, the animal was killed by a lethal intravenous injection of pentobarbitone.

Chronic recordings

Single-fibre neuronal recordings were obtained when the tips of the implanted dorsal root wires migrated into favourable positions near cell bodies or axons in the dorsal root ganglion. The neurogram electrodes were checked twice daily for single-unit activity. This was done by attaching a small three-channel radio telemetry device to a plastic socket embedded in the headpiece, and making connections with each neurogram terminal in turn. The neuronal activity was monitored with the use of a nearby radio receiver, and the length and EMG were monitored with a second receiver. For the purposes of the present study, only units in muscle groups whose length and EMG were available were included. When such a unit

appeared, a saline length gauge was attached to the appropriate fixation threads and the fine connecting wires were led to the telemeter. The cat was then allowed to move freely about the floor of a small room.

Much importance was attached to accurate identification of the afferents. When enough voluntary movement data had been obtained the cat was fully anaesthetized with intravenous thiopentone administered to effect. The sensory ending was located by palpation and joint manipulation. The responses of the afferent to length changes of various waveforms applied manually were then recorded. When enough data had been collected, an intravenous dose of suxamethonium ($200 \mu\text{g kg}^{-1}$) was administered and in the subsequent 3–4 min, a similar set of muscle length variations was applied. Muscle spindle primary and secondary afferents and tendon organ afferents are differently affected by suxamethonium, so this procedure is useful in differentiating between them. We classified units whose dynamic response was greatly increased by suxamethonium as spindle primary afferents. This is a reasonably secure criterion (Taylor, Rodgers, Fowle & Durbaba, 1992). However, Taylor *et al.* (1992) have shown that about half of the gastrocnemius spindles whose resting discharge is increased by suxamethonium, but whose dynamic response is not appreciably affected (i.e. units we would classify as spindle secondaries), have conduction velocities in the spindle primary afferent range. One of the triceps surae units we classified as a spindle primary had an equivocal response to suxamethonium (dynamic index only slightly elevated), so it could have been a b2c spindle primary ending (i.e. a primary afferent with sensory terminals on bag2 and chain intrafusal fibres, but not on bag1 fibres). One or more of the four units we classified as spindle secondaries could also have been b2c spindle primaries. All four of these units had a low variability of consecutive inter-spike intervals, which favours a secondary classification, but some uncertainty in this regard is acknowledged. Typically the identification tests took between 15 and 45 min.

All trials were video-taped (Sony SL-0HF900 Betamax video cassette recorder). Telemetered data were recorded on the stereo audio tracks of the video cassette tapes along with the video image of the animal. Subsequent analysis was performed by replaying the data and digitizing relevant segments with a Cambridge Electronic Design 1401 interface and a personal computer. The data acquisition software (DASA2) was developed by Mr Jamnan Law in A.P.'s laboratory. This program allowed segments of the recordings corresponding to single step cycles to be selected and averaged. The animals were free to vary the cadence and speed of gait, and so the kinematics of the step cycles varied somewhat, particularly at the onset and termination of a locomotor sequence. In selecting cycles, we attempted approximately to match cycle durations, favouring cycles in the middle of a sequence, whose muscle length variations were more reproducible and conformed to familiar and well-established profiles in the literature.

Mathematical modelling

Two additional software packages were used to analyse the averaged profiles on the basis of five mathematical models of spindle response from the literature (Matthews & Stein, 1969; Schäfer, 1974; Chen & Poppele, 1978; Houk *et al.* 1981; Hasan, 1983) and an additional hybrid model of our own. The basic analysis was performed with the Matlab 4.2c and Simulink 1.3c graphical simulation program (Mathworks Inc., Natick, MA, USA) which allowed the models to be implemented in graphical form (Fig. 7). The graphical representation of the models and the simulation routines in the Simulink software provide a convenient means of using the models, three of which were previously somewhat inaccessible to motor control researchers.

They may be downloaded from the following Internet website: <http://gpu.srv.ualberta.ca/~aprochaz/hpage.html>. Sigmaplot 3.1 and 4.0 and Sigmastat 1.0 software (SPSS Inc., Chicago, IL, USA) was used for statistical regression analysis of the modelled responses.

RESULTS

The firing profiles of nine hamstring muscle afferents recorded in awake cats during overground locomotion are analysed in this report. Figure 1A shows a segment of a recording from one such afferent recorded over two step cycles along with muscle length and EMG activity. The afferent activity is presented as an instantaneous firing rate where the ordinate of each point is the inverse of the last firing interval. The dotted vertical lines mark alignment times selected with the averaging program. We aligned cycles to peak muscle length, which occurred at the end of the swing phase of the step cycle, just prior to the foot making contact with the ground. In all the subsequent figures, averaged cycles are 800 ms in duration.

Figure 1B shows averaged profiles of EMG, length and afferent firing rate for nine hamstring spindle primary afferents. The averages were derived from step cycles aligned to peak muscle length (foot contact) as just described. Note that the firing rate is shown as a probability density function obtained by summing the action potentials occurring within consecutive bins and dividing by the bin width (0.01–0.02 s) to obtain mean rate per bin. Each afferent contributed five step cycles. The upper panel of Fig. 1C shows the predicted spindle Ia firing rate obtained by processing the length signal from Fig. 1B through a mathematical model, in this case $f = 4.3v^{0.6} + 82$, where f is the firing rate (s^{-1}), v is the muscle velocity (mm s^{-1}) and 82 is an offset equal to the mean firing rate (i.e. the overall mean of the probability density function) in Fig. 1B. Figure 1C (lower trace) shows the length predicted by passing the firing rate profile of Fig. 1B through the inverse of this model. The model in this case was based on the studies of Schäfer (1974) and Holm, Padeken & Schäfer (1981) and will be discussed in more detail below.

The predictions of Fig. 1C match well the actual recorded profiles in Fig. 1B, suggesting that muscle velocity was the main variable determining spindle primary afferent firing rate. However, this implies that other variables such as muscle length, phasic fusimotor action, tendon strain and intramuscular mechanical effects (Hoffer *et al.* 1989) were insignificant. The analysis below will show that the muscle velocities in the step cycles we studied were so large that they dominated over the other variables in modulating the spindle primary afferent firing.

Because of the emphasis in the literature on the linkage of fusimotor (γ - and β -motoneuronal) and skeletomotor (α -motoneuronal) activation, we tested for this by adding EMG-related components of signal to the predicted firing rate profiles. Figure 2 shows examples of this test. The

target data were obtained from a sub-group of step cycles with the fastest stretch velocities. Each of the nine spindle primary afferents contributed three cycles. First, the same model as in Fig. 1 was used to predict the firing rate from the length signal (Fig. 2A). This gave a very good fit, with a regression coefficient r^2 of 0.94 and r.m.s. error of 16 s^{-1} , equivalent to 8.8% of the peak-to-peak modulation depth of the target profile (182 s^{-1}). Three signals representing EMG-linked fusimotor action were then derived from the rectified, averaged EMG by computing proportional (Fig. 2Ba), differential (Fig. 2Ca) and integral (Fig. 2Da) versions of the EMG profile. The transfer functions of the differential and integral components were $(s + 0.5)/(s + 20)$ and $1/(s + 8)$, respectively, where s is the Laplace operator. The integrated component was time-advanced by 75 ms. This mimicked the fusimotor profiles in the literature, which are smoother, more extended, and encompass the duration of the EMG bursts (Taylor & Donga, 1989). The

parameters in these calculations were chosen by trial and error to give signals representative of α - γ linkage patterns described in the literature. These signals were added in turn to the predicted firing rate profile (Fig. 2Bb, Cb and Db) and scaled over many iterations to give the best possible fits. In the data of Fig. 2, the optimized scaling of the signals in Ba, Ca and Da had peak values of 15. Comparing the fits in Fig. 2B, C and D with that in Fig. 2A, the r^2 values were all slightly lower, indicating slight (though not statistically significant) deteriorations in linearity.

Note that in what follows, we will equate a high r^2 value with the term 'linearity', which we use in the restricted sense of how well the predicted and actual signals conform to a straight-line relationship. By its nature, the correlation coefficient r does not carry information on differences in amplitude of the predicted and target signals (i.e. non-unity slopes of the linear regressions). This means that the predicted signal could be many times the amplitude of the target and yet have an r^2 value close to unity. On our definition the relationship would be linear, yet the absolute errors

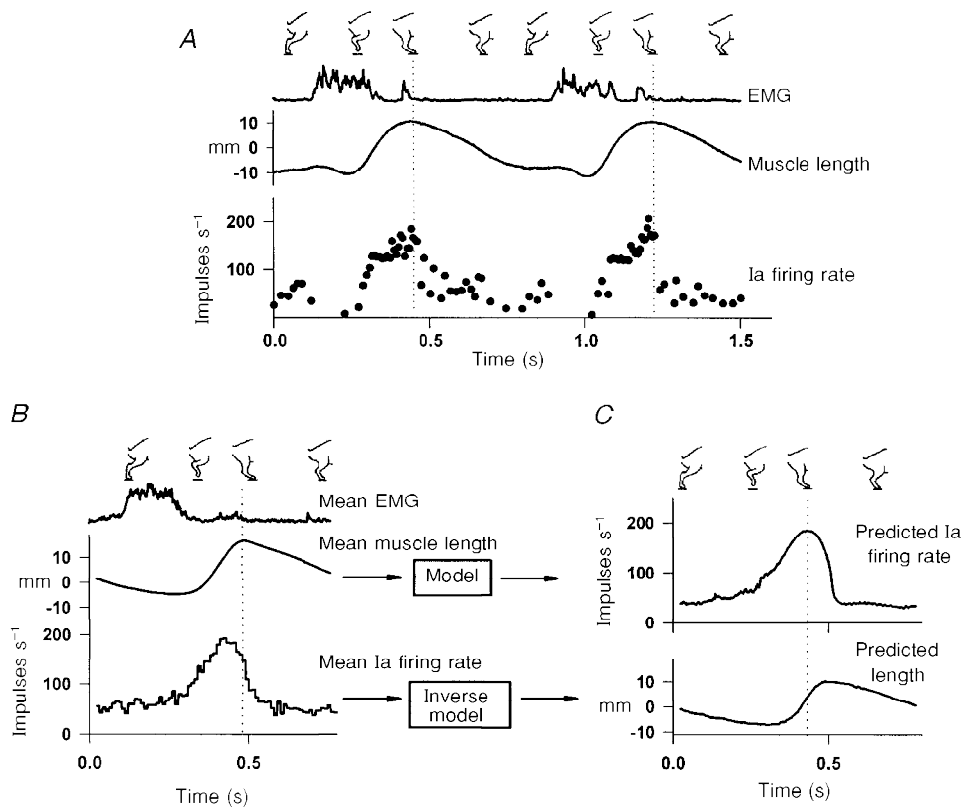


Figure 1. Method of computing ensemble activity during the step cycle and using mathematical models to predict either spindle firing rate from muscle length or muscle length from spindle firing rate

A, firing of a hamstring spindle primary afferent during two steps. Schematics of hindlimb at top show approximate timing of phases of the step cycles. The afferent fired most during muscle lengthening in the swing phase. Dotted vertical lines show alignment points for averaging. B, mean EMG, muscle length and afferent firing rate computed as a probability density function of impulses occurring in 10 ms bins. Nine hamstring spindle primary afferents each contributed five cycles to the average. Top panel in C, spindle primary firing rate predicted from muscle length by a mathematical model. Bottom panel in C, muscle length predicted from afferent firing rate by the inverse of the same model. The model was a power-law function of muscle velocity (see text). Note the good correspondence between predictions in C and the corresponding 'real' length and rate profiles in B.

between the signals could be very large. Because we felt that the absolute error was the more relevant statistic in applications such as control systems modelling, we therefore also computed r.m.s. error in all plots.

The r.m.s. errors were slightly lower in *B* and *D* (significant, $P < 0.01$, Mann–Whitney rank sum test), partly because the α – γ profiles corrected for a small offset error in *A*. We conclude that the simple model accounted for about 91 % of the spindle primary afferent firing rate modulation in the step cycle and EMG-linked components of signal (adding up to about 15 s^{-1} peak) could slightly reduce this error (though without improving the linearity of the fits). As we will see

in the companion paper (Prochazka & Gorassini, 1998), simulated α – γ components *did* significantly improve the fits of spindle primary profiles in triceps surae, indicating that EMG-linked fusimotor action is stronger in this muscle group than in hamstrings. In the Discussion we posit that in quiet stepping, hamstring muscles are recruited far less than triceps surae muscles as a proportion of maximal possible recruitment and so the *linked* component of fusimotor activation is much smaller in hamstrings. The *tonic* components of fusimotor action must be quite potent in both muscle groups, however, to maintain spindle primary afferent firing at the rates seen during rapid muscle

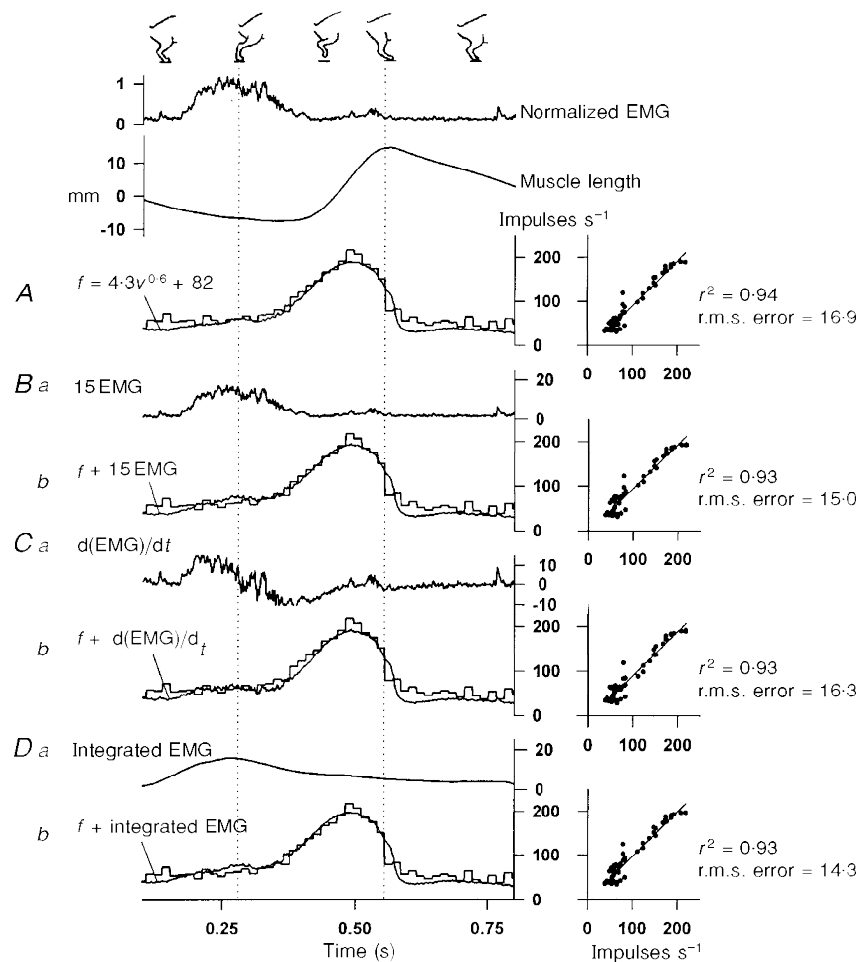


Figure 2. Predictions of hamstring spindle primary afferent firing with added components mimicking α – γ linkage

The normalized mean EMG, mean length and mean rate profiles were computed from a sub-group of fast step cycles shown in Fig. 1. The same power-law model as in Fig. 1 was used. *A*, mean spindle primary firing rate with prediction of model superimposed. Right: linear regression of predicted rate (ordinate) plotted against 'real' rate (abscissa), one sample per bin. Note the good fit (high correlation coefficient and low r.m.s. error in relation to overall modulation depth). *Ba*, scaled EMG signal (maximum value 15). *Bb*, result of adding the scaled EMG of *Ba* to the prediction in *A*. Linearity of fit (as judged by r^2 values) was not quite as good as in *A*, but r.m.s. error was slightly lower. *Ca*, differentiated version of EMG signal. *Cb*, addition of *Ca* signal to predicted signal in *A*. Regression parameters show a slight deterioration of the fit compared with *A*. *Da* and *b*, similar data for integrated EMG. This gave a small but significant improvement over *A*. On balance, the data supported the existence of a small component of afferent firing linked to the EMG activity.

shortening. The limitations of using the EMG to mimic α -linked components of γ activity are discussed in the companion paper.

Figure 3 shows the results of using six different models to predict the firing rate of spindle Ia afferents from the time course of the muscle length signal. The models are shown in Fig. 7 in the Appendix. They are of varying complexity, but each has specific parameters that determine gain and offset. For each model a gain was found that gave a unity slope of the linear regression of the model output against the target firing rate profile in Fig. 3. As in Fig. 2, the mean ensemble firing rate (82 s^{-1}) proved to be an appropriate choice of offset, giving y -axis intercepts close to zero in all models. This is not accidental: the firing-rate profile can be viewed as a cyclical modulation of a 'carrier' frequency that is itself a function of mean muscle length and background fusimotor action. The modulating variables length and velocity are fairly symmetrical about their means, so the mean firing rate is a reasonable approximation of the underlying carrier

frequency. The high value of the mean firing rate (82 s^{-1}) is consistent with strong, maintained static fusimotor action.

Note that the mean and 'carrier' frequencies are expected to diverge when the spindle response is non-linear and the length and velocity profiles are asymmetrical about their means. This may explain the small offsets of the predicted and actual profiles in Fig. 3C, E and F. It also explains why a rate offset of 93 s^{-1} rather than 82 s^{-1} was required to produce symmetrical length profiles in the inverse model in Fig. 8. Limitations in the concept of an underlying carrier frequency are discussed in the companion paper (Prochazka & Gorassini, 1998).

All models with the exception of the linear transfer function of Matthews & Stein (1969) gave good fits ($r^2 = 0.85$ or greater). The three best fits were those in Fig. 3A (linear transfer function of Chen & Poppele, 1978), Fig. 3E (rate proportional to $v^{0.6}$ as in Figs 1 and 2) and Fig. 3F (rate proportional to $v^{0.6}$ and muscle displacement). In fact, a simple linear model, $f = 0.68v + 82$, not illustrated in Fig. 3, gave the best fit of all to the step cycle data ($r^2 = 0.95$, r.m.s. error = 11.6 s^{-1}). However, it was poor in

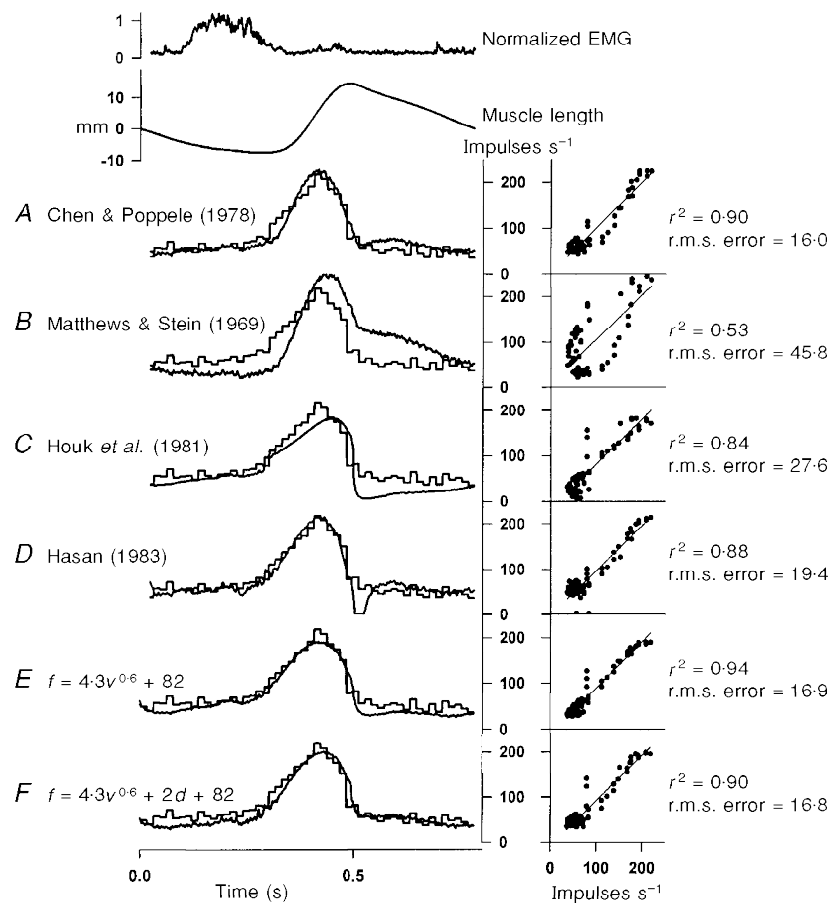


Figure 3. Comparison of the predictions of six models of the same Ia data as in Fig. 2

Figure 3E is identical to Fig. 2A. A and B, linear transfer function models. C–F, non-linear models incorporating power-law functions of velocity. All of the models gave reasonable predictions ($r^2 > 0.5$), though A, E and F were the best. The models in E and F were essentially slightly modified versions of the linear and power-law models in A–D. Though the length-sensitive term in model F slightly detracted from the fit achieved in E, it improved performance at low muscle velocities (see Fig. 7), i.e. it was more generally valid.

predicting responses at much lower stretch velocities (see Fig. 6) and so was discarded as a general model.

From acute experiments it is known that spindle primary afferents are velocity and length sensitive, so on this basis one might have expected the Matthews & Stein model to provide a better fit than the model of Fig. 3*F* and for that matter the simple velocity model. On the suspicion that the 10 rad s⁻¹ corner frequency in the Matthews & Stein model over-emphasized the length-sensitive component, we tried lower values of the turning point frequency. The goodness of fit began to approach that of the simple velocity model for turning points lower than 0.5 rad s⁻¹. The pros and cons of different values of the exponent 'exp' in summed velocity and length models of the form $f = \text{constant}_1 v^{\text{exp}} + \text{constant}_2 d$ will be taken up again in the Discussion.

Figure 3*C* and *D* shows predictions obtained with the use of two closely related models, those of Houk *et al.* (1981) and Hasan (1983). It should be stressed that Houk *et al.* (1981) did not define their model for negative velocities, nor did they claim its validity under these circumstances. In order to extend the use of this model to negative velocities we computed (absolute velocity)^{0.3} and then restored the negative sign (see Fig. 7, Appendix). The free parameters in this model are rate offset (r^*), length offset (x^*) and gain (K^*). We chose a rate offset of 82 s⁻¹ for consistency with the other models as discussed above. A maximal r^* value of 53 s⁻¹ was recommended by Houk *et al.* (1981), based on data from spindles recorded in decerebrate animals. The reasonable fits obtained with 82 s⁻¹, and the fact that we obtained the best fits with even higher offsets (of around 95 s⁻¹, not illustrated), is again consistent with significant fusimotor biasing in our step cycle data. A value of 25 mm for the length offset x^* gave good fits to our data (range recommended by Houk *et al.* (1981): 16–39 mm). A gain K^* of 0.6 gave a unity slope in the linear regression of Fig. 3*C*. No clear recommendation was given for this parameter in the original study.

The Hasan (1983) model is based on the Houk model, but incorporates position sensitivity (i.e. a length-dependent term independent of velocity), acceleration responses and fusimotor action. After some initial tests, we chose to modify the Hasan model in one important respect, namely changing the velocity exponent from 0.3 to 0.6. This was motivated by the better overall performance of $v^{0.6}$ models across a wide range of velocities (see Fig. 6). Note that 0.56 was the mean value of the velocity exponent in the study of Holm *et al.* (1983). The choice of 0.6 as the velocity exponent necessitated a change in Hasan's recommended value of the gain parameter a for static fusimotor drive, from 100 to 280. The 280 value resulted in unity slopes in our linear regressions as outlined above. Hasan's gain parameters b and h were set to the values recommended for static fusimotor drive: $b = 100$, $h = 200$. In fact the values recommended by Hasan for dynamic fusimotor drive (125, 250) did not significantly change the regression coefficients in our simulations. The product of the positional sensitivity (h/b)

and a length offset parameter c , determines the background firing rate in Hasan's model. The recommended value of c is -25 mm, which results in a background firing rate of 50 s⁻¹. As explained above, we had chosen a background firing rate of 82 s⁻¹ for all the models, which dictated a value of -41 mm for c . Hasan's parameter p determines the relative size of initial burst responses. As these are 'smeared' in population responses, we reduced the value of this parameter from the recommended value of 0.1 to 0.05.

The Houk and modified Hasan models did not perform quite as well as the simpler velocity-length models when judged solely on the basis of regression coefficients and r.m.s. errors in Fig. 3. However, the fits in the early parts of the cycles in Fig. 3*C* and *D*, where there are major transitions in velocity, were preferable to the corresponding sections of Fig. 3*B*, *E* and *F*. Moreover, the modified Hasan model predicted spindle Ia afferent firing in slow movements better than the other models (see discussion of Fig. 6 below), so in the final analysis the Hasan model was among the three preferred models in our study.

A crucial requirement of a good model is that it generalizes across different sets of data. Because muscle velocity was clearly an important variable, we split our step cycles into three groups encompassing as large a range of maximal velocities as the data would allow. The resultant averaged length and firing rate profiles are shown in Fig. 4, along with the corresponding fits obtained from the six models tested. The maximal velocities in the three sets of data were 205, 179 and 148 mm s⁻¹, respectively. Nine spindle primary afferents contributed to each of the three averages. Each afferent contributed three step cycles for the fast velocity group, five cycles for the medium velocity group and two cycles for the slow velocity group (i.e. the averaged profiles represented 27, 45 and 18 cycles respectively). The fast step cycle data (left column) are the same set illustrated in Fig. 3.

The gain parameters of the models were determined from the linear regression curves of the *fast* cycles. These same gains were then used for the *medium* and *slow* cycles to test for generality. The offset was also kept constant at 82 s⁻¹ throughout even though the mean firing rates in the medium and slow cycles were slightly lower (81 and 77 s⁻¹, respectively). Small improvements in r.m.s. error could have been obtained by appropriately adjusting the offset parameter in each regression of Fig. 4, as performed for the fits in Fig. 2, but we felt that this might give an unrealistic assessment of the models, which would normally be used with muscle length and EMG inputs only.

Taking all the data in Fig. 4 into account, the best overall fits were obtained with the Chen & Poppele linear transfer function (Fig. 4*A*), and the two $v^{0.6}$ functions (Fig. 4*E* and *F*). There was little to choose between the latter two models, either in terms of linearity (r^2 range, 0.88–0.94) or r.m.s. error (14.1–18.4 s⁻¹, i.e. 9.2–14.7% of modulation depth). The shape distortions evident in the predictions of the Houk

model (Fig. 4C) indicate that the exponent 0.3 in the relationship $v^{0.3}$ attenuated the spindle primary afferent responses to high velocities too much. This is also indicated by the overestimate of peak firing rate in the slow steps (Fig. 4C, right panel). For values of the exponent of 0.6 (Fig. 4E), 0.8 and 1.0 (not illustrated) the predicted peak rates matched those in the target profiles in the three sets of data better, but these models underestimated the dynamic components of response when much slower cycles were simulated (Fig. 6). The Hasan model (Fig. 4D), modified so that the exponent was 0.6 rather than 0.3, gave excellent fits except for an over-emphasis of the fall in firing rate just after muscle length reached its peak. This feature persisted over a wide range of parameters and must therefore be seen as a slight drawback of the model for ensemble data of this type. With the use of the originally recommended exponent (0.3) in the Hasan model, there was the same over-emphasis of the initial step response at the onset of the rapid stretch seen in the simulations using the Houk model (not illustrated).

Figure 5 shows the results of using the models in the reverse direction (i.e. computing length from the firing rate profile). The Hasan model is not represented because it was not obvious to us how to implement the inverse of this fairly complex model with the Simulink software available. The best fits were again obtained with the Chen & Poppele model and the $v^{0.6}$ model. The r^2 values in these cases were 0.97 and 0.99, respectively, indicating excellent linearity. The corresponding r.m.s. errors were 1.5 and 0.8 mm, representing 7.5 and 4% of the total length excursion, respectively. The accuracy of the predictions of length from firing rate are consistent with the good fits in the forward direction (predicting firing rate from length). In physiological terms, the significance of these results is that even with a fairly simple decoding mechanism the nervous system would be able to derive muscle length with great accuracy from ensemble spindle input. Because the mathematical process in this case is essentially simple integration, the predicted curves are smooth.

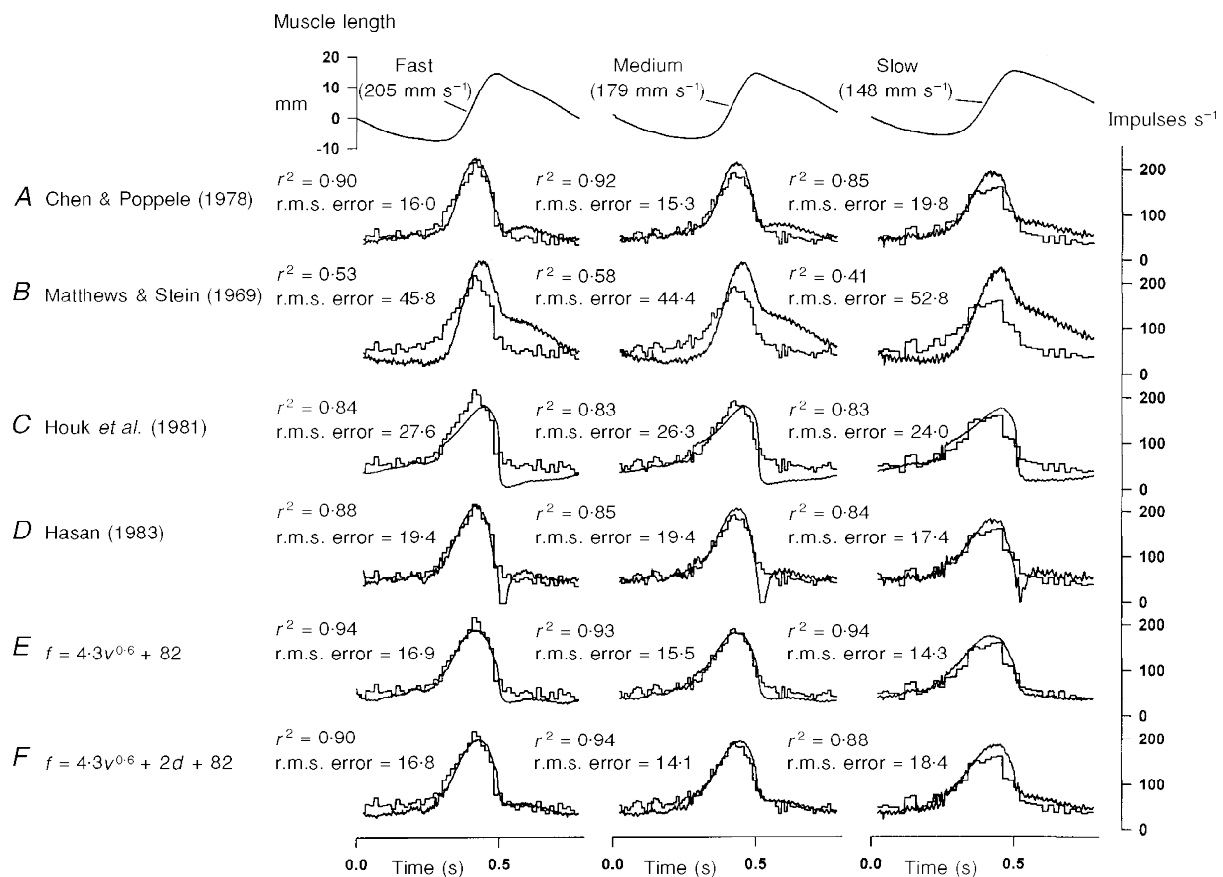


Figure 4. Comparison of the various spindle primary models in step cycles of different speeds

Predictions for data from the same nine afferents as in Figs 1–3 but with the cycles selected into three groups according to muscle velocities (see peak muscle velocity values in upper panels). The aim was to compare how well the models generalized across data when muscle velocity varied. Left column same as in Fig. 3. The r.m.s. errors in the two linear models (A and B) increased in the slow cycles whereas those of the power-law functions tended to reduce. This indicates that the power-law functions tracked velocity changes better. The best fits were seen in E and F.

The range of maximal muscle velocities in the chronic step cycle data was insufficient to give a clear picture of the generality of the models for very slow movements. We considered using recordings from the same spindles obtained during slow imposed movements for this purpose. However, the available data were inconsistent with regard to the time course of the imposed movements. Furthermore, it was clear from the very high firing rates evoked that imposed movements were associated with high levels of dynamic fusimotor action as previously verified in acute experiments (Prochazka, Hulliger, Zangger & Appenteng, 1985). We therefore opted to compare responses of the models with profiles synthesized on the basis of parameters obtained from the literature. The population data of Holm *et al.* (1983) indicated dynamic responses (decrements in firing 2.5 s after the end of 10 mm s⁻¹ stretches) of between 6 s⁻¹ and 60 s⁻¹ for spindle Ia afferents under static fusimotor drive and 10 s⁻¹ and 100 s⁻¹ for Ia afferents under dynamic fusimotor drive. Based on these and other data in the literature (Crowe & Matthews, 1964; Brown, Lawrence & Matthews, 1969; Holm *et al.* 1981; Banks, Hulliger, Scheepstra & Otten, 1997) as well as a large population study of Dr Manuel Hulliger (unpublished, personal communication), we felt that dynamic responses in the range 20–30 s⁻¹ and positional sensitivities ranging from 1.5 to 5 mm s⁻¹ would provide a representative range of mean

Ia afferent response profiles to 10 mm s⁻¹ stretches under the moderate levels of static fusimotor drive that we believe pertain during locomotion. Profiles synthesized according to these parameters are shown dotted in Fig. 6 along with the predictions of the six models considered in our study. The general form of Ia responses to ramp-and-hold stretches is an initial step reflecting the velocity component, and a ramp, the slope of which reflects displacement sensitivity. In all cases the predictions were obtained with the same parameters used for the step cycle data of Figs 1–5. In Fig. 6*A*, the initial step response and slope of the prediction of the Chen & Poppele model were both at the lower end of the expected range. The Matthews & Stein model (Fig. 6*B*) had too small an initial step and too large a slope. The opposite was true of the Houk model (Fig. 6*C*) and the $v^{0.6}$ model (Fig. 6*E*). The modified Hasan model (Fig. 6*D*) and the hybrid $v^{0.6}$ model (Fig. 6*F*) were close to the middle of the target range, though in both cases the sizes of the step and slope components were somewhat less than ideal. This indicates that values of the exponent slightly lower than 0.6 might prove more general, because they would emphasize the step component at low stretch velocities more. We tried $f = 6.75 v^{0.5} + 2d + 82$, where d is displacement (mm) and although this did have the desired effect of increasing the step component for the slow stretches, it slightly detracted from the goodness of fit in the step cycle data ($r^2 = 0.90$

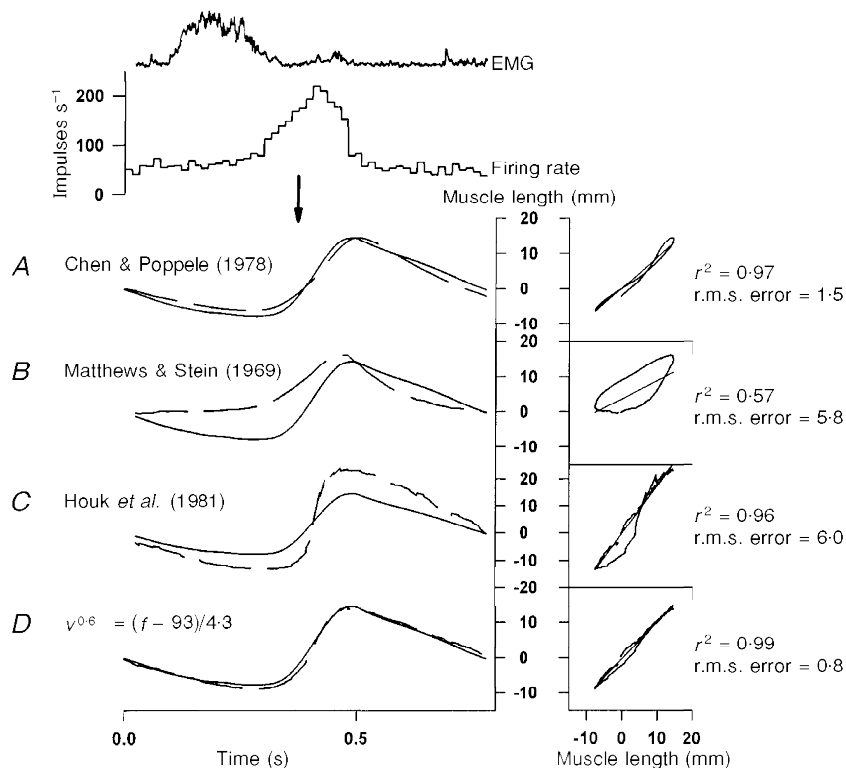


Figure 5. Predictions of muscle length from spindle primary firing profiles

These were obtained by using the inverse of the models used earlier. The regression parameters in *A* and *D* indicate excellent goodness of fit. The analysis shows that in principle, the central nervous system could derive accurate estimates of muscle length from ensemble spindle primary firing rate.

compared with $r^2 = 0.91$ for an exponent of 0.6 in Fig. 3*F*). The simplest velocity model alluded to earlier ($f = 0.68v + 82$), though performing very well on the step cycle data, produced far too small a step (6.8 s^{-1}) and no ramp in the test of Fig. 6 (response not illustrated), and so was dropped from further consideration as a general model.

DISCUSSION

In previous studies in our laboratory, we used the Chen & Poppele (1978) model to predict responses of spindle primary afferents to variations in muscle length (Gorassini *et al.* 1993). Though the modelling was adequate for the purpose at the time, certain inaccuracies were noted. In the present study we therefore compared the performance of six available models, including the Chen & Poppele model, in predicting spindle primary afferent firing rate from muscle length in ensemble data from freely moving cats. In theory, a simple relationship between length and spindle firing was hardly to be expected, as other influences, including phasic fusimotor action, would probably also modulate spindle firing. Yet in the case of hamstring spindle primaries, we found that ensemble firing rate was predicted quite accurately from the time course of muscle length alone. The predictions were not improved by adding components of firing rate that mimicked EMG-linked fusimotor action, indicating that to all intents and purposes α -linked components of fusimotor action could be neglected. This was not true of ensemble spindle primary data from triceps surae muscles, as is shown in the following paper (Prochazka & Gorassini, 1998). In the case of hamstring muscles, the recruitment of α -motoneurons in quiet stepping is probably

at quite a low level: for example the phasic bursts of EMG in the step cycle are very small when compared with those in voluntary contractions when the cat tries to free its foot from a firm grasp (Prochazka, 1986, Fig. 2). From a modelling point of view the important point is that the fusimotor action underlying hamstring spindle primary afferent firing appears to have been essentially tonic throughout the step cycle. The maintained firing during the rapid muscle shortening in the early stance phase indicated γ_s action at a fairly strong level (in the fast steps of Fig. 4 the maximal shortening velocity was around 50 mm s^{-1} , which would require firing rates of single γ_s -motoneurons of around 100 s^{-1} to maintain Ia firing in the range $50\text{--}100 \text{ s}^{-1}$: Appenteng, Prochazka, Proske & Wand, 1982). We argued above that the mean Ia firing rate reflected the background firing rate or 'carrier frequency', which in turn was a function of mean length and fusimotor action. The mean rate was around 80 s^{-1} in all the groups of step cycles analysed, which again suggests significant fusimotor action (Jansen & Matthews, 1962).

All of the models except that of Matthews & Stein (1969) predicted spindle primary afferent firing with r^2 values in the range $0.83\text{--}0.96$ (Fig. 4). Surprisingly, the simplest model (rate proportional to velocity) produced the best fits overall, closely followed by a modified version of the Schäfer model (rate proportional to velocity^{0.6}). All four power-law models (Houk, Hasan, Schäfer and hybrid models) reproduced the portions of the firing rate profiles around the transition from shortening to lengthening the best. This is significant, because it is in this region that velocity changed the most. In general, the effect of the power functions was to distort

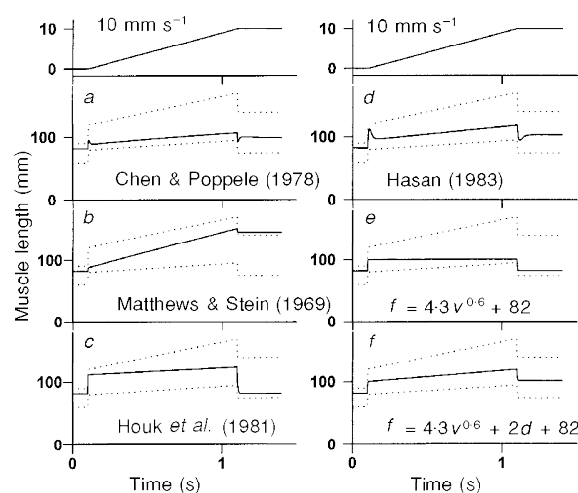


Figure 6. Predictions of the models of spindle primary responses to ramp-and-hold stretches at much lower velocities than those recorded in locomotion

Dotted lines show the range of spindle primary responses under moderate static fusimotor drive, estimated from the literature (see text). Models without length-sensitive terms (e.g. *c* and *e*) did not reproduce the ramp increase in firing rate during stretch, so cannot be considered general. The responses in *d* and *f* fall in the middle of the expected range and have appropriate step and ramp components, indicating that their velocity and positional sensitivities are correctly scaled. These models also predicted the step data well (see earlier figures).

the rate–velocity relationship so that the lower velocities were emphasized. The lower the exponent, the greater this low-velocity emphasis. The exponent recommended in the Houk and the unmodified Hasan models is 0.3, which over-emphasized the responses in the low-velocity portions of our data (compare Figs 4 and 6). The exponent 0.6, which we used in implementing the Hasan model, was less severe in this regard and produced the best fits of the step cycle data and in particular the firing rate profiles in the transition from shortening to lengthening. An exponent of 0.5 produced the most representative responses to simulated slow stretches (10 mm s^{-1}). Taking all of this together, our results suggest that a power-law relationship with an exponent in the range 0.5–0.6 would generalize the best over the range of velocities encountered in most movements. This agrees well with the mean value of 0.56 of the velocity exponent that best fitted the dynamic response data of Holm *et al.* (1981). It should be acknowledged, however, that our step cycle data are not very discriminative in this regard, because changes in the exponent from 0.4 to 1.0, with appropriate adjustments of the gain factor, gave only small changes in goodness of fit (r^2 changing from 0.90 to 0.94).

It should also be noted that our aim was to identify the models that best fitted the ensemble data. Transients in the response of individual afferents, such as initial bursts, which occur at slightly different lengths in different spindles, are smoothed out in the population data. The Chen & Poppele model and the Hasan model (with the p parameter set to 0.1) emphasize initial bursts, which would give these models an advantage in predicting single unit response profiles.

An interesting aspect of the results is that in spite of basic differences in structure, the models gave fairly similar predictions. For example the predictions of the non-linear Hasan model did not differ markedly from those of the linear model of Chen & Poppele (1978). This may be because all of the models have velocity terms and all of the predictions were dominated by the large velocity peak during the swing phase of the cycle. In the Houk and Hasan models, because of the relatively large length offset required to match the mean firing rates (25 and 41 mm, respectively), the 20 mm modulation of length in the step cycle did not have as much effect on the predicted profiles as one might have expected (this was further illustrated in separate simulations in which the length term in the Houk model was held constant at 35 mm).

A rather surprising outcome was that length-dependent terms in the models were not an asset in predicting hamstring spindle primary afferent firing in the step cycle data, though they were clearly needed for predicting spindle primary afferent responses to slower stretches. In the relatively slow stretches used in classical acute experiments on spindle responses in the 1960s and 1970s where velocities were usually 10 mm s^{-1} (about 0.1 rest-length s^{-1}) or lower, Ia afferents were shown to have a significant static length sensitivity (Jansen & Matthews, 1962; Crowe & Matthews,

1964). The hamstring stretch velocities encountered in the cat step cycle are at least an order of magnitude greater, so it is not surprising that velocity is the predominant modulating variable. Nonetheless, length-dependent modulation should still have improved rather than detracted from the fits. The Matthews & Stein (1969) transfer function linearly sums length and velocity terms. We tried reducing the relative contribution of the length term in this model by using progressively lower turning points (from the recommended 10 rads s^{-1} to 6, 2, 1 and 0.5 rads s^{-1}) and although this did progressively improve the fits, the best fit was in fact obtained with a turning point of zero, i.e. when static length sensitivity was eliminated entirely. A similar trend was observed when length-dependent terms were added to the simple $v^{0.6}$ model (see the slight reduction in r^2 in Fig. 3*F* compared with Fig. 3*E*). On the other hand, the Hasan model did benefit from its length-dependent term (the pathway denoted 'x-c' in Fig. 7); predictions of the step cycle data deteriorated when this term was replaced with a constant (not illustrated). Because the range of velocities available from our data was quite restricted, we could not explore in detail the implied decline or abolition of static length sensitivity at high velocities. What is needed is a set of ensemble spindle primary afferent firing profiles obtained in acute experiments over a large range of stretch velocities (e.g. $1\text{--}500 \text{ mm s}^{-1}$) with controlled fusimotor stimulation. The analytical models could then be used to settle this issue. If length sensitivity does indeed decline at high velocities, it may be because of pacemaker switching (Banks *et al.* 1997) whereby spindle endings on bag1 intrafusal fibres take over the pacemaker function from endings on bag2 and chain fibres. Alternatively, during very slow stretches, there may be time for some stable cross-bridges to form in bag1 fibres thus increasing the stiffness of the polar regions of the spindle and increasing the positional sensitivity (Morgan, Prochazka & Proske, 1984).

Whatever the mechanism, the implication is that slightly different analytical models would perform best in different velocity ranges. In this regard it is also worth noting that the peak muscle velocities in human spindle recordings have rarely exceeded $0.1 \text{ rest-lengths s}^{-1}$. For example, in the ensemble data of Al-Falahe, Nagaoka & Vallbo (1990) muscle velocity was 20 deg s^{-1} , which we estimate is equivalent to about $0.08 \text{ rest-lengths s}^{-1}$, compared with the $2 \text{ rest-lengths s}^{-1}$ maximal velocity in our cat hamstring data. There has been much conjecture about the fact that spindle firing rates are much lower in human neurography than in animals performing tasks such as locomotion. Indeed of late there has been discussion of a basic species difference in this regard. Yet it has been known for some time that muscle velocities in the two types of data are radically different (Prochazka, Stephens & Wand, 1979). Our present results give a more quantitative idea of how important this is. With hindsight, it is not surprising at all that Ia responses, which are evidently so dependent on muscle velocity, should differ when the range of velocity increases by a factor of 20 or more. Given that the stretch sensitivity of human spindles

at low velocities are evidently similar to those of cats (Poppele & Kennedy, 1974), we feel it is reasonable to posit that in human movements with muscle velocities of around $0.5 \text{ rest-lengths s}^{-1}$ (e.g. locomotion at a cadence of 1 s^{-1}), spindle Ia mean firing rates and modulation depths are also in the same range as those in cats ($50\text{--}80$ and $100\text{--}180 \text{ s}^{-1}$, respectively).

What can be concluded about the relative merits of the different models we tested? To our knowledge, the models

have never been directly compared, whether on ensemble data recorded in freely moving animals, or, more surprisingly, on Ia firing profiles in acute experiments. Within the limited range of muscle velocities available in our data, the Chen & Poppele model, the modified Hasan model and the hybrid model ($f = 4.3v^{0.6} + 2d + 82$) performed the best, though acceptable fits were obtained with the Houk model. The predictions of responses to slow stretches (Fig. 6) indicated that length-dependent terms were required. Though the Chen & Poppele model does not

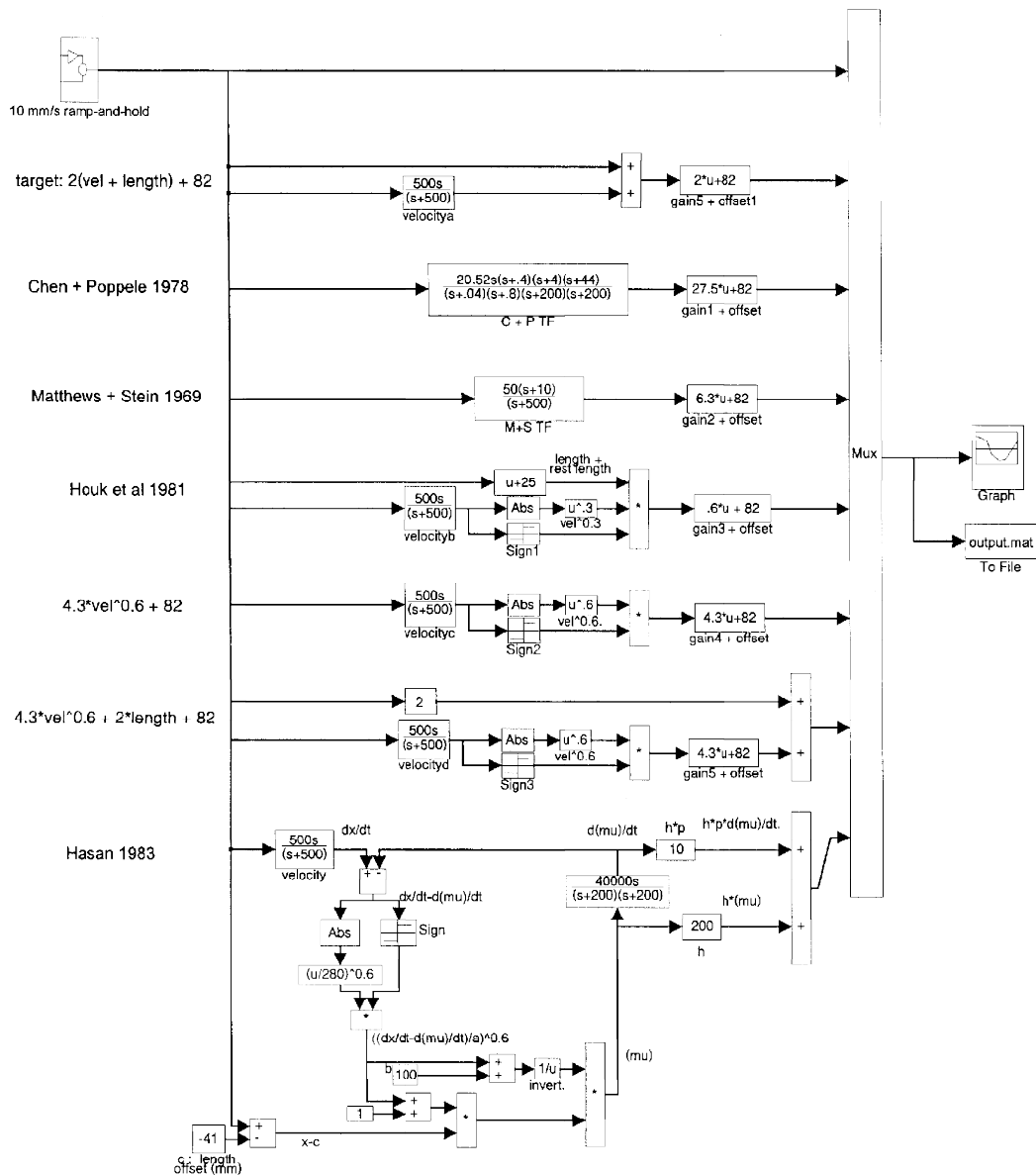


Figure 7. Graphical representation of the models used in this report

The analysis was performed using Matlab Simulink software. This graph can be downloaded from the Internet and a simulation run under Simulink without further programming (see Appendix text). Each model is represented as a few processing blocks, each block performing a mathematical operation on the input. These operations include computing Laplace transfer functions, implementing algebraic equations or performing simple non-linear operations such as returning an absolute value of the input signal. Presented in this form, models that were previously difficult to implement may be tested and modified with relative ease.

Each box represents an input–output operation such as a transfer function (e.g. $500s/(s + 500)$, where s is the Laplace operator), addition (boxes with ‘+’ symbols), algebraic functions (e.g. box labelled $2*u + 82$, where ‘u’ symbolizes the input) or certain non-linear functions such as finding the absolute value of the input (boxes marked Abs), or sign detection whereby the output is either -1 or $+1$ depending on whether the input is negative or positive (boxes marked Sign1, Sign2 etc.). Where appropriate, outputs are further defined by small legends. As described above, in the power-law models, negative velocities were dealt with by computing the power function of the absolute value of the input variable and then restoring the negative sign using the product function (boxes with enclosed asterisks). The symbols a , b , c , h and p in the Hasan model were discussed in the text above. The box at the top left generates a 10 mm s^{-1} ramp-and-hold signal. The boxes at the right define an on-screen graph that displays the results of simulations and an output file to which the results are written. The results may then be converted into text files for further analysis with spreadsheet and graphical software. In our study all of the simulations were performed with the Euler algorithm selectable within Simulink, with a step size of 1 ms.

The graphical design exemplified in Fig. 7 is stored as a computer file, which is accessible over the Internet for use in other laboratories. The Internet address from which the Simulink graphs used in this study may be downloaded is: <http://gpu.srv.ualberta.ca/~aprochaz/hpage>.

An exemplar graphical design that gave rise to Fig. 3F is shown in Fig. 8. This schematic design includes three boxes on the left that represent the original averaged EMG, spindle primary afferent firing rate and length signals. Downloading this file from the Internet along with the three data files will allow simulations of this model to be executed by interested readers.

- AL-FALAHE, N. A., NAGAOKA, M. & VALLBO, A. B. (1990). Response profiles of human muscle afferents during active finger movements. *Brain* **113**, 325–346.
- AMIS, A., PROCHAZKA, A., SHORT, D., TREND, P. ST J. & WARD, A. (1987). Relative displacements in muscle and tendon during human arm movements. *Journal of Physiology* **389**, 37–44.
- APPENTENG, K., PROCHAZKA, A., PROSKE, U. & WAND, P. (1982). Effect of fusimotor stimulation on Ia discharge during shortening of cat soleus muscles at different speeds. *Journal of Physiology* **329**, 509–526.
- BANKS, R. W., HULLIGER, M., SCHEEPSTRA, K. A. & OTTEN, E. (1997). Pacemaker activity in a sensory ending with multiple encoding sites: the cat muscle spindle primary ending. *Journal of Physiology* **498**, 177–200.
- BROWN, M. C., LAWRENCE, D. G. & MATTHEWS, P. B. C. (1969). Static fusimotor fibres and the position sensitivity of muscle spindle receptors. *Brain Research* **14**, 173–187.
- CHEN, W. J. & POPPELE, R. E. (1978). Small-signal analysis of response of mammalian muscle spindles with fusimotor stimulation and a comparison with large-signal properties. *Journal of Neurophysiology* **41**, 15–27.
- CROWE, A. & MATTHEWS, P. B. C. (1964). The effects of stimulation of static and dynamic fusimotor fibres on the response to stretching of the primary endings of muscle spindles. *Journal of Physiology* **174**, 109–131.
- GORASSINI, M., PROCHAZKA, A. & TAYLOR, J. (1993). Cerebellar ataxia and muscle spindle sensitivity. *Journal of Neurophysiology* **70**, 1853–1862.
- GRIFFITHS, R. I. (1991). Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *Journal of Physiology* **436**, 219–236.
- HASAN, Z. (1983). A model of spindle afferent response to muscle stretch. *Journal of Neurophysiology* **49**, 989–1006.
- HOFFER, J. A., CAPUTI, A. A., POSE, I. E. & GRIFFITHS, R. I. (1989). Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. In *Afferent Control of Posture and Locomotion*, ed. ALLUM, J. H. J. & HULLIGER, M., *Progress in Brain Research*, vol. 80, pp. 75–85. Elsevier, Amsterdam.
- HOLM, W., PADEKEN, D. & SCHÄFER, S. S. (1981). Characteristic curves of the dynamic response of primary muscle spindle endings with and without gamma stimulation. *Pflügers Archiv* **391**, 163–170.
- HOUK, J. C., RYMER, W. Z. & CRAGO, P. E. (1981). Dependence of dynamic response of spindle receptors on muscle length and velocity. *Journal of Neurophysiology* **46**, 143–166.
- JANSEN, J. K. S. & MATTHEWS, P. B. C. (1962). The effects of fusimotor activity on the static responsiveness of primary and secondary endings of muscle spindles in the decerebrate cat. *Acta Physiologica Scandinavica* **55**, 376–386.
- MATTHEWS, P. B. C. & STEIN, R. B. (1969). The sensitivity of muscle spindle afferents to small sinusoidal changes of length. *Journal of Physiology* **200**, 723–743.
- MORGAN, D. L., PROCHAZKA, A. & PROSKE, U. (1984). The after-effects of stretch and fusimotor stimulation on the responses of primary endings of cat muscle spindles. *Journal of Physiology* **356**, 465–478.
- OTTEN, E., SCHEEPSTRA, K. A. & HULLIGER, M. (1995). An integrated model of the mammalian muscle spindle. In *Alpha and Gamma Motor Systems*, ed. TAYLOR, A., GLADDEN, M. H. & DURBABA, R., pp. 294–301. Plenum Press, New York.
- POPPELE, R. E. & KENNEDY, W. R. (1974). Comparison between behavior of human and cat muscle spindles recorded *in vitro*. *Brain Research* **75**, 316–319.
- PROCHAZKA, A. (1986). Proprioception during voluntary movement. *Canadian Journal of Physiology and Pharmacology* **64**, 499–504.
- PROCHAZKA, A. (1996). Proprioceptive feedback and movement regulation. In *Handbook of Physiology*, section 12, *Exercise: Regulation and Integration of Multiple Systems*, ed. ROWELL, L. & SHEPHERD, T., pp. 89–127. American Physiological Society, New York.
- PROCHAZKA, A., GILLARD, D. & BENNETT, D. J. (1997). Implications of positive force feedback in the control of movement. *Journal of Neurophysiology* (in the Press).
- PROCHAZKA, A. & GORASSINI, M. (1998). Ensemble firing of muscle afferents recorded during normal locomotion in cats. *Journal of Physiology* **507**, 293–304.

- PROCHAZKA, A., HULLIGER, M., ZANGGER, P. & APPENTENG, K. (1985). 'Fusimotor set': new evidence for α -independent control of γ -motoneurons during movement in the awake cat. *Brain Research* **339**, 136–140.
- PROCHAZKA, A., STEPHENS, J. A. & WAND, P. (1979). Muscle spindle discharge in normal and obstructed movements. *Journal of Physiology* **287**, 57–66.
- PROCHAZKA, A., TREND, P., HULLIGER, M. & VINCENT, S. (1989). Ensemble proprioceptive activity in the cat step cycle: towards a representative look-up chart. In *Afferent Control of Posture and Locomotion*, ed. ALLUM, J. H. J. & HULLIGER, M., *Progress in Brain Research*, vol. 80, pp. 61–74. Elsevier, Amsterdam.
- SCHÄFER, S. S. (1974). The discharge frequencies of primary muscle spindle endings during simultaneous stimulation of two fusimotor fibres. *Pflügers Archiv* **350**, 359–372.
- TAYLOR, A. & DONGA, R. (1989). Central mechanisms of selective fusimotor control. In *Afferent Control of Posture and Movement* ed. ALLUM, J. H. J. & HULLIGER, M., *Progress in Brain Research*, vol. 80, pp. 27–36. Elsevier, Amsterdam.
- TAYLOR, A., RODGERS, J. F., FOWLE, A. J. & DURBABA, R. (1992). The effect of succinylcholine on cat gastrocnemius muscle spindle afferents of different types. *Journal of Physiology* **456**, 629–644.

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Models of ensemble firing of muscle spindle afferents recorded during normal locomotion in cats

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