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Relative damping improves linear mass-spring models of goal-directed movements

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Abstract

A limitation of a simple linear mass-spring model in describing goal directed movements is that it generates rather slow movements when the parameters are kept within a realistic range. Does this imply that the control of fast movements cannot be approximated by a linear system? In servo-control theory, it has been proposed that an optimal controller should control movement velocity in addition to position. Instead of explicitly controlling the velocity, we propose to modify a simple linear mass-spring model. We replaced the damping relative to the environment (absolute damping) with damping with respect to the velocity of the equilibrium point (relative damping). This gives the limb a tendency to move as fast as the equilibrium point. We show that such extremely simple models can generate rapid single-joint movements. The resulting maximal movement velocities were almost equal to those of the equilibrium point, which provides a simple mechanism for the control of movement speed. We further show that peculiar experimental results, such as an 'N-shaped' equilibrium trajectory and the difficulties to measure damping in dynamic conditions, may result from fitting a model with absolute damping where one with relative damping would be more appropriate. Finally, we show that the model with relative damping can be used to model subtle differences between multi-joint interceptions. The model with relative damping fits the data much better than a version of the model with absolute damping. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The hypothesis of equilibrium point control of posture and movement (Feldman, 1966) proposes that the commands that the brain produces to generate a limb movement do not encode the forces that are needed, but rather task-related parameters such as positions or postures of the limb. This feature makes the hypothesis attractive, for it suggests that the brain does not need to perform complex inverse-dynamical computations to generate a movement. The dynamics of the movement arise automatically from the interaction of the mechanics of the limb with the set equilibrium position: the position to which one wants to move. (Detailed descriptions of the equilibrium point hypothesis and of several equilibrium point models can be found in Bellomo & Inbar (1997), Gribble, Ostry, Sanguineti, & Laboissière (1998), and Shadmehr, Mussa-Ivaldi, & Bizzi (1993).)

An important prediction of the hypothesis of equilibrium point control is that the limb's final position is insensitive to (transient) perturbations of the limb during the movement. Indeed, the endpoint of a reach with a monkey's unseen arm was insensitive to perturbations that it could not feel because the monkey was deafferented (Bizzi, Accornero, Chapple, & Hogan, 1984). Comparable findings have been reported for perturbed movements of healthy human subjects (when they were asked not to intervene voluntarily with the perturbation; Gottlieb, 1994; Gribble & Ostry, 2000; Shadmehr et al., 1993). When one moves the hand while sitting in a slowly rotating room, coriolis forces act on the arm during the movement, but not during rest (before and after the movement). The equilibrium point hypothesis therefore predicts that unexpected coriolis forces will affect the shape of the movement path but not the end position. When subjects made reaching movement towards remembered targets in a dark, rotating room, the path was perturbed. Nevertheless, at the end of the movement, the final error was negligible as long as subjects did not touch the table surface. In an experiment in which subjects did touch the table surface, the target was missed (Lackner & DiZio, 1994). In the latter case the movements may have been stopped by the table surface before the equilibrium position was reached. This interpretation of the latter experiment is not generally accepted (Feldman, Ostry, Levin, Gribble, & Mitnitsky, 1998; Lackner & DiZio, 1994), but it explains why the influence of unexpected coriolis forces can appear to be inconsistent with the equilibrium point hypothesis. Although the equilibrium hypothesis is an elegant description for many movements, there are tasks, such as jumping, exerting a specific force, or adapting to moving in a new kind of force field, for which other kinds of models for motor control might be more appropriate.

At present there are a number of equilibrium point models, which all have in common that the moving limb is attracted towards an equilibrium position or posture (e.g., Barto, Fagg, Sitkoff, & Houk, 1999; Gribble et al., 1998; Latash & Gottlieb, 1991; McIntyre & Bizzi, 1993; Shadmehr et al., 1993; St-Onge, Adamovich, & Feldman, 1997). The models differ considerably in how they damp the movement. The purpose of damping is to stop the movement without endless oscillations around the equilibrium point. The damping parameters affect the shape of the movement path and the velocity profile. Strong damping is needed to limit the extent to which the limb overshoots the target. However, in order to be able to move rapidly, the movement should not be too heavily damped.

In the models mentioned above, this conflict between the damping requirements is solved by making the parameters in the model time- or speed-dependent (apart from Flash, 1987, who only modelled slow movements). This was done either by pulsestep control (Barto et al., 1999), by letting stiffness and damping change during the movement (St-Onge et al., 1997), by introducing non-linear muscle properties (Gribble et al., 1998), or by introducing a non-monotonic shift of the equilibrium point (Latash & Gottlieb, 1991). Unfortunately, much of the attractiveness of equilibrium point models is lost by this, because the brain will have to compute some sort of complex inverse dynamics after all (DiZio & Lackner, 1995; Gottlieb, 1998).

In the field of servo-control, *velocity feedback* is well known and commonly applied to regulate the speed of movement or to stabilise a system against perturbations. The idea to control velocity in addition to position was also proposed for the control of arm movements (McIntyre & Bizzi, 1993). Schouten, de Vlugt, van der Helm, and Brouwn (2001) showed that active velocity feedback plays indeed an important role in the control of posture in the human arm. This solution has been used to model an optimal controller in studies on motor learning (e.g., Shadmehr & Mussa-Ivaldi, 1994), but has not had any impact on equilibrium-point models (apart from McIntyre & Bizzi, 1993). Neither were its advantages discussed by critics of equilibrium point control. In the present paper we chose to apply velocity-feedback in the simplest kind of equilibrium-point model, a linear mass-spring model. The advantages of such a very simple model are the few parameters and the comprehensibility of its behaviour. We will show that such models can benefit greatly from a modified concept of damping without any extra parameters.

As we argued in the preceding, the damping in the existing equilibrium-point models usually counteracts the limb's (or joint's) velocity, as if the limb moves through a basin of water or oil. Indeed, muscles do have velocity-dependent properties (Hill, 1938). However, two underlying concepts of the equilibrium-point hypothesis are that reflexes contribute significantly to the mechanical behaviour of the motor system, and that reflexes function relative to the desired movement (Feldman, 1966, 1986). Modelling damping relative to the *environment* (joint) is inconsistent with this concept. An alternative is a damping term that acts on the hand's movement with respect to the *desired movement velocity* (the velocity of the equilibrium point). We will call the first (conventional) kind *absolute damping* (in parallel with the spring element) and the latter *relative damping* (in series with the spring element) (Fig. 1). This relative damping gives the limb a tendency to move at the same velocity as the equilibrium point, and can be understood as damping with respect to the equilibrium point, both kinds of damping are the same when the equilibrium point is stationary, but they differ when the equilibrium point moves.

We will evaluate the performance of models with absolute and relative damping by modelling the movement of a single-joint human arm (Fig. 1). This kind of movement has frequently been used to test mass-spring models. Besides being used to model whole movements, linear models can also be applied to a limited range of a non-linear system (Bennett, Hollerbach, Xu, & Hunter, 1992). As a second test,



Fig. 1. Illustration of a simple elbow model with the two kinds of damping. Drawn are an upper arm and a forearm with hand. Each model contains linear stiffness (the spring), linear viscous damping (the dash pot) and is powered through moving the equilibrium point (the circle with arrow). Various models for equilibrium point control differ considerably as to where they allocate the spring and damping elements (McIntyre & Bizzi, 1993): e.g., to the muscles' non-linear force–velocity properties (Bizzi et al., 1984) or to the level of reflexes (the stretch reflex, Feldman & Levin, 1995).

we will therefore model differences between rapid multi-joint interceptive movements. For this test we use Smeets and Brenner's (1995a) model to compare the effect of absolute and relative damping in these movements.

2. Models with absolute and with relative damping

We will now derive the equations for the mass-spring models. Let q(t) be the equilibrium position and x(t) be the hand's position (with either metric or angular units). Their time derivatives, velocity and acceleration, will be represented with one or two dots over the variable. The differential equation of a linear mass-spring system with viscous damping and parameters mass (M), damping (B) and stiffness (K) is for absolute damping

$$M\ddot{\mathbf{x}} + B\dot{\mathbf{x}} + K(\mathbf{x} - q) = 0,\tag{1}$$

and for relative damping

$$M\ddot{x} + B(\dot{x} - \dot{q}) + K(x - q) = 0.$$
(2)

We are only interested in systems with a stable (i.e., attracting) equilibrium point, so K > 0, $B \ge 0$ (and M > 0). The number of constant parameters is redundant, which means that each of the equations can be written as a function of just two constant parameters. This can be achieved by dividing all parameters by M and defining new constants, b and k (with units seconds⁻¹ and seconds⁻², respectively). This yields for absolute damping

$$\ddot{\mathbf{x}} + b\dot{\mathbf{x}} + k(\mathbf{x} - q) = 0,\tag{3}$$

and for relative damping

$$\ddot{x} + b(\dot{x} - \dot{q}) + k(x - q) = 0.$$
 (4)

We need the solution for (3) and (4) for an equilibrium that moves at a constant velocity $q(t) = q_0 + \dot{q}t$. This solution can be found in many textbooks on mathematics or physics. With boundary conditions $x(0) = x_0$ and $\dot{x}(0) = \dot{x}_0$, the solution can be written for the *underdamped* case (i.e., $k > b^2/4$) as

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$$x = \dot{q}t + \hat{q} - e^{-t/\tau} \left((\hat{q} - x_0) \cos(\omega t) + \left(\frac{\dot{q} - \dot{x}_0}{\omega} + \frac{\hat{q} - x_0}{\omega \tau} \right) \sin(\omega t) \right),$$
(5a)

where

$$\tau = 2/b$$
 and $\omega = \sqrt{k - \frac{1}{4}b^2}$,

and for the *overdamped* case (i.e., $k < b^2/4$) as

$$x = \dot{q}t + \hat{q} - \frac{\tau_1}{\tau_1 - \tau_2} ((\dot{q} - \dot{x}_0)\tau_2 + \hat{q} - x_0)e^{-t/\tau_1} + \frac{\tau_1}{\tau_1 - \tau_2} ((\dot{q} - \dot{x}_0)\tau_1 + \hat{q} - x_0)e^{-t/\tau_2},$$
(5b)

where

$$1/\tau_1 = \frac{1}{2}b + \sqrt{\frac{1}{4}b^2 - k}$$
 and $1/\tau_2 = \frac{1}{2}b - \sqrt{\frac{1}{4}b^2 - k}$.

Note that (5a) and (5b) are valid for both absolute and relative damping. For absolute damping, $\hat{q} = q_0 - (b/k)\dot{q}$, whereas for relative damping $\hat{q} = q_0$. Eq. (5a) is the equation for a gradually damping out oscillation, and (5b) contains the sum of two exponential functions that both approach zero (though at different rates). It may appear strange that (5a) and (5b) for absolute damping contain equilibrium velocity (\dot{q}) , whereas (1) does not. The reason for this is that q in (1) is not a constant, but changes at a rate \dot{q} .

3. Modelling a single joint movement

The modelling of a single joint elbow movement was aimed to demonstrate that relative damping makes it possible to generate fast movements with a linear massspring model. We compared the models with absolute and relative damping for a range of values of *b* and *k*. Apart from this, we modelled 'typical examples' of movements, programmed in Matlab[®]. For these predictions we used reasonable estimates for *b* and *k*. The elbow stiffness has been estimated by Bennett et al. (1992) for rhythmic single-joint elbow movements, and by Gomi and Kawato (1997) for discrete twojoint (shoulder and elbow) movements. Assuming a lower arm length of 0.4 m, we estimated the average value of *k* in the elbow to have been about 20 seconds⁻² in both studies. For the typical examples of movements that we simulated with our mass-spring model we therefore used k = 20 seconds⁻². For these examples we used a value for *b* that resulted in about 10% overshoot of the target. This was b =5 seconds⁻¹ for absolute damping, and b = 10 seconds⁻¹ for relative damping. Note that the first results in an underdamped system, whereas the latter results in a slightly overdamped system.

We assume the simplest velocity profile of the equilibrium point: the equilibrium point moves at a constant velocity from the start to the target, where it stays. The

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movement time (MT) is defined as the time between the beginning of the movement and the moment at which 90% of the distance to the target is covered. This measure also yields interpretable results for overdamped movements that undershoot the target. For underdamped movements the overshoot is defined as the maximal elbow angle beyond the target, expressed as a percentage of target angle.

3.1. Results

Examples of the elbow movements predicted with absolute and relative damping are shown in Fig. 2B. The movement is much faster with relative damping than with



Fig. 2. *Panel A*: Fast elbow flexions towards targets at 50° eccentricity with a width of 3°, 6° and 12° (data from Gottlieb, Corcos, & Agarwal (1989): Fig. 4). *Panel B*: Examples of predicted single-joint elbow movements. Equilibrium MT = 0.15 seconds; k = 20 seconds⁻²; absolute b = 5 seconds⁻¹; relative b = 10 seconds⁻¹. *Panels C and D*: The predicted relation between the movement of the equilibrium point and that of the elbow. The values for *b* and *k* and target distance are as in panel B. The movements have an overshoot of about 10%, irrespective of the speed of the equilibrium point. Open and filled dots indicate the movements of panel B.

absolute damping. The difference in movement time between the movements predicted with absolute and with relative damping exists for a large range of the equilibrium point MTs (Fig. 2C). This is even so when the equilibrium point moves instantaneously (i.e., as the equilibrium point MT approaches 0). Using the above-mentioned values for b and k, the fastest movement with absolute damping is 0.5 seconds, whereas with relative damping it is less than 0.2 seconds (Fig. 2C). The latter MT is representative of a rapid human movement (Fig. 2A). In the model with relative damping, the elbow's movement time is almost the same as that of the equilibrium point (Fig. 2C).



Fig. 3. Predicted shortest possible movement times (equilibrium point MT approaches 0) for a range of values of *b* and *k*. *Left panels*: absolute damping; *Right panels*: relative damping. *Upper panels*: Continuous lines are contours of equal movement time. Dashed lines show the range of critical damping; to the left of these lines are overdamped movements and to the right underdamped movements. *Lower panels*: Predicted overshoot for the same conditions. Continuous lines are contours of equal overshoot. Note that the 0% line in the left panel (absolute damping) is the range of critical damping.

Fig. 2D shows that for the model with relative damping the peak velocity of the movement is almost equal to the equilibrium velocity over a large range of equilibrium velocities. In contrast, for the model with absolute damping the peak velocity only increases with the equilibrium velocity for slow movements.

In the above example, the difference between the lowest possible movement times with absolute and with relative damping is considerable (Fig. 2C). The contour plots in Fig. 3 (upper panels) show that this is the case for a range of values of b and k. For both kinds of damping, shorter movement times are obtained by increasing the stiffness. However, the effect of increasing the damping differs between the two kinds: increasing *absolute damping* increases the movement time, whereas increasing *relative damping* decreases the movement time.

The lower panels of Fig. 3 show that the amount of overshoot also depends on b and k. The overshoot is generally smaller with absolute damping than with relative damping. Increasing the amount of *absolute damping* decreases the overshoot and increases the movement time. In contrast, increasing the amount of *relative damping* decreases both the overshoot and the movement time, which is of course a favourable situation. Note that with absolute damping there is no overshoot in the overdamped range, whereas with relative damping there is always overshoot. This can be shown mathematically (Appendix A).

3.2. Discussion

Damping of the elbow from a stationary position has often been measured without problems in a posture control task (e.g., Flash, 1987). However, attempts to measure damping of the elbow during active arm movements have not been very successful (Bennett et al., 1992; Gomi & Kawato, 1997; Gomi, personal communication). One reason for this could be that such studies used a model with absolute damping. If the subject does not intend to move, the equilibrium point will remain stationary, so there is no difference between absolute and relative damping. During a movement, however, fitting a model with absolute damping to a system with mostly relative damping will result in a strong velocity dependency of the absolute damping parameter. Indeed, Bennett et al. (1992) found a velocity dependency of the absolute damping parameter.

The model with relative damping is not only a simple way to generate fast movements, it can also help to interpret some peculiar experimental findings. Latash and Gottlieb (1991) reconstructed the time-course of the equilibrium-position by fitting a linear model without damping to perturbed elbow movements. For fast movements, they found that the equilibrium point moves forth, back and forth again, two times changing its direction (they termed it an 'N-shaped virtual trajectory'). Our proposal of relative damping gives an alternative interpretation for Latash and Gottlieb's (1991) results. In our view, the 'N'-shape of the equilibrium trajectory originates from fitting an inappropriate model. If one fits a model without damping to a system with non-negligible damping, the damping forces will be attributed to shifts in the equilibrium point's position. An example is given in Fig. 4. We generated a movement with our model with relative damping ($b = 10 \text{ seconds}^{-1}$). Subsequently, we determined at each time the equilibrium position assuming that b = 0 (following



Fig. 4. An N-shaped 'virtual trajectory' (dashed line) is found when applying the method of Latash and Gottlieb (1991) to a movement generated with our model (dotted line), using a ramp-shaped equilibrium trajectory (solid line). Equilibrium MT = 0.15 seconds; k = 20 seconds⁻²; relative b = 10 seconds⁻¹.

the method of Latash & Gottlieb, 1991). Fig. 4 shows that our model with relative damping predicts that the method of Latash and Gottlieb (1991) yields an 'N-shaped virtual trajectory' in rapid movements.

The results of Bellomo and Inbar (1997) can be interpreted as evidence that the damping in elbow movements is indeed relative damping. They used a ' λ -equilibrium model' (Feldman, 1986), which is a non-linear model in which the threshold activity of the muscles is controlled. This threshold depends not only on the equilibrium position, but also on the movement velocity (absolute damping). Bellomo and Inbar (1997) used EMG activity as a measure of muscle activity. They measured how the model parameters changed during elbow movement with different loads. For an equilibrium point that moves with a continuous velocity to the target, the 'absolute damping' depended on the difference between the hand's velocity and the virtual velocity. This is the same as a *constant relative damping*. This shows that relative damping not only improves a simple linear model, but also improves a non-linear model such as the lambda model.

In one aspect, the final slowing down phase, the mass-spring movements do not look very realistic (compare Fig. 2A and B). There is a rather large overshoot of the target followed by a slow return, irrespective of the kind of damping. We could undoubtedly improve this for instance by introducing a smoother movement of the equilibrium point. However, we will not do so because a simple model is valuable for providing insight into the general pattern of behaviour, rather than for giving an exact fit of the observed behaviour.

4. Modelling the effect of moving targets in a fast interception

A linear mass-spring model can also be used to model small variations in a nonlinear system. To investigate whether relative damping also improves the model's performance in such applications, we used the data from experiment 3 in Smeets and Brenner (1995a). Subjects had to hit static and moving spiders on a screen in front of them (Fig. 5A) in a rapid, unrestrained 3-D movement. The mass-spring model is used to describe the control of the hand's movements in the same component that the targets moved in (from left to right).

Kinematic data of the 3-D hand movements were averaged over subjects for each condition. These averages were calculated (in the left–right direction) over points in the paths that were at the same distance from the screen. To obtain the responses to the targets' positions and velocities, the average path towards the stationary target at 0 cm was subtracted from each path (Fig. 5B). The movements started on average 38 cm from the screen. The movement component towards the screen approximated a constant acceleration. Consequently, at half the MT the hand had moved one-quarter of the distance towards the hitting screen, so that it was 28.5 cm from the screen.



Fig. 5. *Panel A*: Lateral (left–right) positions of stationary (solid lines) and moving (dashed lines) targets that were presented in random order (Smeets & Brenner, 1995a). The stationary ones appeared at -3, 0 or 3 cm with respect to the hand's current lateral position. The moving ones appeared at -8 cm, moving at a velocity of 6, 9, 12, 15 or 18 cm/seconds to the right. Time = 0 is when the hand started to move. The start and end of each line indicate the average times at which the target appeared and at which the screen was reached. *Panel B*: Experimental paths, averaged over 12 subjects. The path towards the target at 0 cm was subtracted from the others (data from Smeets & Brenner, 1995a). Numbers near the dashed lines indicate the target's velocity (cm/seconds). *Panels C and D*: Model fits of the lateral movement component. The forward component was modelled as a continuous acceleration.

In all conditions, a position 28.5 cm from the screen was reached (on average) within 5 ms of half of the MT.

4.1. The models

We used the model as a linear approximation of the non-linear behaviour of the arm. To do so, we only modelled the differences between the responses to the targets, i.e., the differences in the lateral (left–right) component of the hand's movements. Note that the lateral component was much smaller than the forward component (Fig. 5B), but that it is the only direction in which the positions and velocities of the spiders differed (Fig. 5A). We chose the stationary 0-cm target as a reference, that is, we only modelled the differences with respect to the paths made in this condition. The modelled paths are therefore directly comparable to the experimental ones when displayed as in Fig. 5B.

Fast interceptive movements are not ballistic, which means that information about the target continuously influences the hand's movement (Prablanc, Pélisson, & Goodale, 1986; Smeets & Brenner, 1995b). Fig. 5B shows that moving and static spiders were not hit in the same way: the trajectories towards the 6 cm/seconds targets and the 18 cm/seconds targets are less curved than the paths towards stationary spiders. A possible explanation for this is that the subjects did not use the spider's velocity to predict where it will be hit (Smeets & Brenner, 1995a), but instead used an expected velocity (this may be the preceding spider's velocity: de Lussanet, Smeets, & Brenner, 2001). Smeets and Brenner (1995a) proposed that the subjects continuously predicted how far ahead of the spider's current position they would hit it.

Let s, x and q be the lateral positions of, respectively, the spider, the hand and the equilibrium point. With a stationary spider, we assume that the equilibrium position is simply the spider's position: q = s. The position of the equilibrium point (q) at a given instant is the sum of the spider's actual position (s) and the subject's prediction for how much further the spider will move (in the remainder of the movement time). The spider's position changes at its actual velocity (s), whereas the prediction is made with the expected velocity (v), so that q in (3), (4), and (5a), (5b) is substituted with:

$$q = s_{-RT} + \dot{s}(RT + t) + v(MT - t), \tag{6}$$

where the time t = 0 is when the hand starts to move, and t = RT (reaction time) is the time between when the spider appears and when the hand starts to move.

The model with *absolute damping* is given in (3) with q according to (6). In the model with *relative damping* (4), not only (6) is substituted but also the velocity of the equilibrium point ($\dot{q} = \dot{s} - v$). This is the velocity at which the subject's prediction of where the target will be hit (the equilibrium point), moves. This means that the target's final *position* is continuously updated on the basis of the expected velocity, and relative damping drives the hand in the direction of the difference between the target's velocity and the expected velocity. In de Lussanet et al. (2001), we presented evidence that this expected velocity is equal to the preceding target's velocity (which on average is the average velocity of all the targets in a randomised experiment).

For modelling the differences in the lateral component of the interceptions, the speed of the target dictates the movement of the equilibrium point. Stationary spiders appeared at their position well before the hand started to move, so the equilibrium point was stationary during the hand's movement. This implies that the models with absolute and relative damping do not yield different results for stationary targets.

4.2. Fitting procedure

The root of the mean squared difference (RMS error) between the model and the measured paths was minimised. We first fitted the model to the two eccentric stationary targets (thick paths in Fig. 5B) to obtain *b* and *k*. Therefore the RMS error was minimised at 28.5 and 0 cm from the screen (corresponding with half and the end of the MT). This resulted in b = 7.96 seconds⁻¹ and k = 61.0 seconds⁻² (RMS error = 0.18 cm). These values of *b* and *k* were used to fit the expected velocity *v* in each model to the conditions with moving targets.

4.3. Results and discussion

Fig. 5C and D show the results. The paths for the stationary targets are the same in both panels and show the best fit of b and k to the conditions with stationary targets (see fitting procedure). For v we expect a value that is close to the average velocity of the (preceding) spiders, which was 10.125 cm/seconds (in the experiment there were additional conditions that we do not treat here). The best fit for the model with absolute damping was obtained with v = 10.6 cm/seconds (RMS error = 0.49) cm). ¹ The best fit for the model with relative damping was v = 9.5 cm/seconds (RMS error = 0.19 cm). So both models yielded a value for v that was close to the expected value. The model with relative damping describes the data better than does the model with absolute damping. This can be seen when comparing the dashed lines (for the moving targets) in Fig. 5C and D with those in panel B. Moreover, the model with relative damping describes the paths towards the moving targets as well as those to the static targets (the RMS errors are almost the same). However, for the static conditions, two parameters were fitted, whereas just one parameter was fitted for the moving ones. This means that the model with relative damping describes the moving target conditions very well, compared to the fit of the static conditions.

5. General discussion

With a realistic value of stiffness and damping, a simple linear mass-spring model with absolute damping generates rather slow movements (Fig. 3). To obtain rapid

¹ The model with absolute damping fit the same data worse than it did in Smeets and Brenner (1995a). The reason for this is that differences in reaction time and movement between the conditions (Fig. 5A) were ignored when making the original fit. The good result of that original fit is therefore probably a coincidence.

movements, one has to assume that stiffness is higher than what is measured experimentally (Bennett et al., 1992; Gomi & Kawato, 1997). Previously, it has been proposed to 'solve' this problem by introducing non-linearities (such as a non-monotonic movement of the equilibrium-point) and extra parameters in the model. Apart from not being very elegant, such solutions suggest that the human motor system behaves non-linearly. An argument against such non-linearity is that people can easily scale-up their characteristic movement trajectories without changing the shape of the movements (Merton, 1972). This would be difficult with a non-linear motor control system. A solution from servo-control is to control the desired velocity of the movement in addition to the desired position (or trajectory). For human movements, this solution has been used for models with an optimal controller in the learning of goaldirected arm movements (Shadmehr & Mussa-Ivaldi, 1994), for interception in a model using a dynamical systems approach (Zaal, Bootsma, & van Wieringen, 1999) and for equilibrium point models of goal-directed movements (McIntvre & Bizzi, 1993). We showed that a similar performance can be obtained by a massspring model with relative damping.

The stiffness value that we obtained for the fast interception (Section 4: $k = 49.6 \text{ seconds}^{-2}$) was higher than the one that we used to model the single joint movement (Section 3: $k = 20 \text{ seconds}^{-2}$). The latter value was based on the literature (Bennett et al., 1992; Gomi & Kawato, 1997). Does that mean that the k obtained by fitting the model to interceptive movements is unrealistic? No, because the first value is the endpoint stiffness of a complete arm whereas the latter is the isolated elbow stiffness. Gomi and Kawato (1997) also measured the endpoint stiffness for an arm flexion towards the shoulder, opposite in direction from the hitting movement in Smeets and Brenner's experiment. From movement start to peak velocity, the lateral endpoint stiffness measured by Gomi and Kawato was fairly constant and remained within a range of 40–60 N/m (two subjects). Assuming similar stiffness values when moving in the opposite direction and assuming an effective mass of about 1 kg, this range of stiffness is equal to $k = 40-60 \text{ seconds}^{-2}$. Thus, the value that we estimated for k for the fast interception is within a realistic range.

The linear mass-spring model is a course simplification for a system that consists of both muscles and reflexes. As we mentioned in Section 1, the muscles have (nonlinear) *absolute damping* properties that we neglected. In addition, we neglected the delays of the reflex system. However, by keeping the model simple, we gained much insight into its behaviour. Moreover, the muscle reflex-system has such a complex structure that merely introducing reflex delays and a realistic muscle force–velocity relationship would not make the model appreciably more biologically realistic. On the other hand, a truly realistic model would be almost as incomprehensible as the muscle-reflex system itself.

Single joint movements have been modelled very often, because in such movements there are no dynamic interactive forces between the limb segments. The present paper gives evidence that relative damping provides a very simple explanation that can account for results that previously appeared to indicate that motor control is complex. It would be interesting and useful to reanalyse earlier data by Bellomo and Inbar (1997), Bennett et al. (1992), Gomi and Kawato (1997) and Latash and Gottlieb (1991) using models with relative damping. Given the present results, this may result in reliable estimates of the damping during the movement and may free Latash's version of the lambda model from the N-shaped equilibrium trajectory.

From the viewpoint of optimal control it does make sense that the muscle-reflex system forms a unit that behaves as a singular linear system. For example, the non-linear stretch reflex and non-linear stiffness were shown to provide a more linear muscle stiffness (Nichols & Houck, 1976). In addition, muscles without reflexes only behave spring-like for a limited duration, whereas reflexes act after a brief delay. The combination of the two time scales of muscle and reflex properties could potentially result in approximately linear behaviour over both time scales. The good results of the simple model with relative damping to predict the effects of differences in target velocity provides support for this view.

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Appendix A. Relative damping always gives overshoot

The model with relative damping for a single joint movement predicts that the target will be overshot even in the overdamped case (Fig. 3). Here we show mathematically that this is the case for all equilibrium MTs. We will regard positive damping and stiffness parameters.

The model is linear, so the target's distance does not change the shape of the trajectory (it only scales the trajectory). For simplicity we set the target distance at 1. Let the equilibrium MT be t_q , so while the equilibrium point moves, $\dot{q} = 1/t_q$. The initial values are $x_0 = \dot{x}_0 = q_0 = 0$. From (5b) it follows that at time t_q , when the equilibrium point reaches the target, the hand's position and velocity are

$$x(t_q) = 1 - \frac{\tau_1 \tau_2}{\tau_1 - \tau_2} \frac{1}{t_q} (e^{-t_q/\tau_1} - e^{-t_q/\tau_2}),$$
(A.1)

$$\dot{\mathbf{x}}(t_q) = \frac{1}{t_q} + \frac{1}{\tau_1 - \tau_2} \frac{1}{t_q} (\tau_2 \mathrm{e}^{-t_q/\tau_1} - \tau_1 \mathrm{e}^{-t_q/\tau_2}).$$
(A.2)

By definition $0 < \tau_1 < \tau_2 < \infty$ when b > 0. This means that $0 < x(t_q) < 1$, in other words, the hand never reaches the target before the equilibrium point does.

After the equilibrium point reaches the target, it remains there. The hand will then either slowly approach the target (but never reach it), or the hand will shoot past the target and return slowly. If there is always overshoot, the time t_{target} – when the hand

reaches the target – must be within the range $(t_q < t_{\text{target}} < \infty)$, regardless the values of b, k and t_q . After time t_q , the equilibrium point q = 1 and $\dot{q} = 0$, so

$$\mathbf{x}(t_{\text{target}}) = q = 1, \tag{A.3}$$

so (5b) becomes

$$1 - \frac{\tau_1}{\tau_1 - \tau_2} (-\dot{\mathbf{x}}_q \tau_2 + 1 - x_q) e^{-(t_{\text{target}} - t_q)/\tau_1} + \frac{\tau_2}{\tau_1 - \tau_2} (-\dot{\mathbf{x}}_q \tau_1 + 1 - x_q) e^{-(t_{\text{target}} - t_q)/\tau_2} = 1,$$
(A.4)

which can be rewritten as

$$\exp\left\{ (t_{\text{target}} - t_q) \left(\frac{1}{\tau_1} - \frac{1}{\tau_2} \right) \right\} = \frac{\tau_1}{\tau_2} \frac{\dot{x}_q \tau_2 - 1 + x_q}{\dot{x}_q \tau_1 - 1 + x_q}.$$
 (A.5)

When we substitute $x_q = x(t_q)$ and $\dot{x}_q = \dot{x}(t_q)$ as given in (A.1) and (A.2), we get

$$\exp\left\{ (t_{\text{target}} - t_q) \left(\frac{1}{\tau_1} - \frac{1}{\tau_2} \right) \right\} = \frac{1 - e^{-t_q/\tau_1}}{1 - e^{-t_q/\tau_2}}, \tag{A.6}$$

so

$$t_{\text{target}} = t_q + \frac{\ln(1 - e^{-t_q/\tau_1}) - \ln(1 - e^{-t_q/\tau_2})}{1/\tau_1 - 1/\tau_2}.$$
(A.7)

From (A.7) we can calculate t_{target} for positive damping (b > 0) to range from

$$t_{\text{target}} = \frac{\ln(\tau_1/\tau_2)}{1/\tau_1 - 1/\tau_2}$$

for $\lim_{t_q \downarrow 0}$, to $t_{\text{target}} = t_q$ for $\lim_{t_q \to \infty}$. This means that for any $0 < \tau_1 < \tau_2 < \infty$, there is a time $t_q < t_{\text{target}} < \infty$ when $x(t_{\text{target}}) = 0$. Thus there will be overshoot for all movements with positive relative damping.

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