INTRODUCTION

Stretch reflexes are generally known to have an important regulatory function in posture and locomotion. Investigation of the influence of these stretch reflexes (including reciprocal inhibition) on the behavior of musculo-skeletal systems is performed with the help of bifurcation analysis. The goal is to establish how reflexive feedback of muscle lengthening, velocity and the time delays, present in the reflex arcs, can lead to stable equilibria (i.e. posture) and stable limit cycles (e.g. gait, ankle clonus). Mathematical concepts from the bifurcation analysis are linked to known biomechanical concepts, such as stiffness. The presented musculo-skeletal model represents standing posture.

METHODS

The model of stance consists of an inverted pendulum with an antagonistic muscle pair, representing the ankle flexors and extensors (Fig.1). The Hill-type muscles possess activation and contraction dynamics. Two types of feedback are incorporated in the model: intrinsic feedback (force-length and force-velocity relations in the model) and reflexive feedback of muscle length and velocity with gain \(k_p\) and \(k_v\), and delay \(\tau\) (50 ms). Co-contraction of muscles is a very energy consuming way of creating joint stiffness relative to reflexive feedback. Therefore, only a co-contraction of 10% is assumed, which is not enough to maintain a stable posture without reflexive feedback. The considered equilibrium is standing upright, which corresponds to zero angle, zero angular velocity, and for both muscles constant, equal, active states and lengths of the CE’s. The model is used to calculate reflex gains in standing posture with experimental data from literature.

The model has 6 states in total: the angle \(\theta\), the angular velocity \(\omega\), the active states of the tibialis anterior and the soleus, \(a_{ta}\) and \(a_{sol}\), and the lengths of the CE’s of both muscles, \(l_{ce,ta}\) and \(l_{ce,sol}\). The delayed feedback of muscle length and velocity causes the angle and angular velocity also appear in delayed form, \(\theta(t-\tau)\) and \(\omega(t-\tau)\). The influence of stretch reflexes on postural stability is investigated by analysis of two types of bifurcations: the fold and the Hopf bifurcation. The fold bifurcation is recognized by one eigenvalue of the considered equilibrium (i.e. stance), passing zero with nonzero speed. Hopf bifurcation occurs when a conjugated pair of eigenvalues crosses the imaginary axis with nonzero speed. Accurate definitions of fold and Hopf bifurcations can be found in Kuznetsov (1995). After supercritical Hopf bifurcations, stable limit cycles emerge. The stable limit cycles, found for high reflex gains in the posture model, are linked to a neural deficiency, called ankle clonus.

The delay in the reflex arcs makes bifurcation analysis more difficult and for that reason a Matlab package, specialised in dealing with delayed differential equations, was used to calculate the bifurcations. This package is called BIFTOOL (Engelborghs 2000).

RESULTS AND DISCUSSION

In this section the influence of stretch reflexes including reciprocal inhibition, time delays, co-contraction and force feedback on the behaviour of the musculo-skeletal model of stance is shown. Stability regions of posture and periodic movement in parameter space (\(k_p\) versus \(k_v\)) will be distinguished with the help of bifurcation analysis.

To begin our analysis a reference parameter set has to be chosen, which defines the reference equilibrium in state space and accompanying eigenvalues. The reference parameter set is \([u \ k_p \ k_v \ \tau]\)=[0.1 50 10 50e-3]T, where \(u\) is the value of both neural inputs, \(k_p\), \(k_v\) and \(\tau\) are the reflexive feedback gains of the muscle length change, velocity and force, respectively, and \(\tau\) is the time delay present in the reflex arcs. A small amount of neural input (\(u=0.1\)) is chosen, which is not enough to stabilize the posture without reflexive feedback. The influence of stretch reflexes is studied first, thus the force feedback gain \(k_f\) is initially set to zero. The reference gains \(k_p=50\) and \(k_v=10\) stabilize the posture. A reference delay \(\tau\) of 50 ms is chosen, because this is typical for the short latency reflexes found in human ankle flexors and extensors (Sinkjaer et al 1988). These parameters give equilibrium at

\[
X_{eq, ref} = \begin{pmatrix} a_{ta} & a_{sol} & l_{ce,ta} & l_{ce,sol} & \theta & \omega \end{pmatrix}^T
\]

\[
= \begin{pmatrix} 0.1 & 0.1 & 0.936 & 0.936 & 0 & 0 \end{pmatrix}^T
\]
with accompanying rightmost eigenvalues

$$\lambda_{\text{rm,ref}} = -1.46 \pm 4.54j$$

(i.e. posture is stable). The states of the equilibrium $x_{eq}$ only depend on the value of the neural inputs $u$. The stability of the equilibrium, however, also depends on the positional feedback gain $k_p$, the velocity feedback gain $k_v$, and the delay $\tau$ of the reflex arc.

**Influence of stretch reflexes including reciprocal inhibition**

The influence of stretch reflex gains on the behaviour of the model is explored by looking at bifurcations in parameter space, with the positional gain $k_p$ on one axis and the velocity gain $k_v$ on the other. A bifurcation point is found by varying one parameter, while looking at the rightmost eigenvalues of the equilibrium, because they dominate the system behaviour. Figure 2 shows the real part of the rightmost eigenvalues $\lambda_{\text{rm}}$ in dependence of $k_p$, while the other parameters are kept constant at their reference value.

The real part of the rightmost eigenvalues versus the positional feedback gain $k_p$. The other parameters are kept constant at reference values. The left marking represents a fold bifurcation (one eigenvalue through zero), the right marking represents a Hopf bifurcation (conjugated pair of eigenvalues through imaginary axis).

The events for which the rightmost eigenvalue(s) goes through the imaginary axis are marked in the figure by circles and they correspond to a fold and a Hopf bifurcation. Distinguishing between a Hopf and a fold bifurcation from this figure is not possible; looking at the eigenvalues will reveal the nature of the bifurcation.

A fold and a Hopf branch are continued in parameter space, with the previously determined bifurcation points as starting points. Figure 3 shows the fold and the Hopf branch as well as the starting points. The fold branch is a vertical line, indicating its independence with respect to $k_v$; it depends merely on $k_p$.

The fold and Hopf branches divide parameter space into four regions, marked I, II, III and IV in the figure. The intrinsic stiffness of the muscles, induced by a co-contraction of 10 percent, is too small to compensate for the negative stiffness caused by the gravitational force. Thus, without reflexive feedback ($[k_p, k_v] = [0, 0]$ in the figure) the pendulum will fall to $\pm \pi$ (the muscles have no parallel element). Feedback of the muscle length change will increase the muscle stiffness and the vertical fold bifurcation line represents the minimal positional feedback gain $k_{p,\text{min}}$ to compensate for the negative 'gravitational stiffness' $K_g$. Thus, in region I and II the person falls, because his ankle stiffness, caused by intrinsic and reflexive stiffness of the muscles, is too low.

For stable posture, besides the minimal positional feedback gain $k_{p,\text{min}}$, a minimal velocity feedback gain $k_{v,\text{min}}$ is also necessary. Velocity feedback is necessary to compensate for the phase lag caused by time delay in the reflex arcs, muscle activation dynamics and the presence of a relative compliant SE. Figure 4 shows the minimal feedback gains to be $[k_{p,\text{min}}, k_{v,\text{min}}] = [11.74, 0.53e-2]$. This point is an intersection of the fold and Hopf branch and has a double zero as rightmost eigenvalues. It is in fact a Bogdanov-Takens (BT) bifurcation (Kuznetsov 1995) and it is the start of the Hopf branch in parameter space. The lower part of the Hopf branch, up till the turn, represents all possible positional feedback gains $k_p$ with accompanying minimal velocity feedback gains $k_v$. For higher velocity gains the posture is stable. However, if velocity gains increase too much the reflex loop becomes unstable. The upper part of the Hopf branch is associated with these maximal velocity feedback gains. To the right of the turning point of the Hopf branch the posture is also unstable, because the positional feedback is too high for any velocity feedback. Thus, in region III the posture is stable, because the lack of intrinsic stiffness is compensated by a large enough positional feedback and the phase lag, introduced most of all by time delay, is compensated by a velocity feedback.

If one travels from region III to IV across the Hopf branch the phase and/or gain margin depletes and the stability of the posture vanishes. In stead a limit cycle originates around the equilibrium states of the previously stable posture. The
Floquet multipliers of the limit cycles were calculated and the absolute values were always less than unity, indicating stable limit cycles just beyond the Hopf branch in all of region IV. In figure 5 the size of the imaginary part of the conjugated pair of eigenvalues, associated with the Hopf bifurcation (i.e. on the imaginary axis), is shown. The size of the imaginary part $Im$ is directly related to the period $T$ of the sinusoidal periodic solutions just beyond these Hopf points ($T=2\pi/Im$).

Along the Hopf branch, for increasing velocity gain $k_v$, $Im$ increases (i.e. $T$ decreases) from 0 [rad/s] at the BT to 16.0 [rad/s] at the second intersection of the fold and Hopf branch. This intersection has a zero and a conjugated pair of eigenvalues on the imaginary axis and is in fact a fold-Hopf (FH) bifurcation. Left from the FH, in region I, the limit cycles are unstable. In the neighbourhood of the BT and FH bifurcations, complex dynamical behaviour can be expected, such as homoclinic cycles (BT) and tori (FH). However, analysis of these complex behaviours is not within the scope of this paper. See Kuznetsov (1995) for more information on BT and FH bifurcations and the possible system behaviour in their neighbourhoods.

The observed limit cycles have nothing to do with the sway experienced during stance. They are more likely to be related to ankle clonus. Clonus is a rhythmic movement around joints that is stimulated through stretch reflexes and is often caused by injury of the central nervous system. Hidler and Rymer (1999, 2000) showed that the presence of two conditions lead to clonus, namely the presence of significant delays in the reflex paths and an increase in effective reflex gains, caused by a reduced motoneuron-firing threshold. The ankle is a distal joint, which leads to considerable time delays in the reflex arcs. This is why ankle clonus is a quite common type of clonus.

The limit cycles to the right and above the Hopf branch (Fig. 3 and 5) are caused by similar mechanisms to those causing ankle clonus, namely high reflex gains in combination with a considerable time delay in the reflex arcs. The period of the oscillations, associated with ankle clonus, depends on the feedback gains of muscle length change and velocity and varies between 1.8 and 2.5 Hz (Fig. 5). In literature frequencies of about 3 to 8 Hz are reported, but these were usually assessed when the patient was sitting. It is therefore not surprising that our simulated frequencies, assessed with a model of stance, are somewhat lower (moment of inertia about ankles is much larger).

**Influence of reflex delay**

The influence of time delay $\tau$ on the behaviour of the posture model is displayed in figure 6 in parameter space. The fold branch does not change for different delays, because it represents the muscle length feedback $kp_{min}$ for zero ankle stiffness and stiffness is defined at zero frequency. Time delay only adds phase lag proportional to frequency ($H_\tau=e^{\tau\omega}$) and has no influence on stiffness and therefore also not on the location of the fold bifurcation in parameter space. However, time delay has a tremendous influence on the Hopf branch. For increasing delay, the Hopf branch ‘shrinks’, because it becomes harder to compensate for the extra phase lag, introduced by this delay. This causes the region of reflex gains, for which the posture is stable (region III in Fig. 4) to become smaller.

![Figure 4: Zoom-in of figure 3. BT is a Bogdanov-Takens bifurcation, the first intersection of fold and Hopf branch and representing the minimal feedback gains $[kp_{min}, kv_{min}] = [11.74, 5.53e^{-2}]$ above which the posture will be stable (up to certain maximum gains).](image)

![Figure 5: Size of imaginary parts $Im$ of conjugated pair of eigenvalues related to the Hopf bifurcations are plotted along the Hopf branch. The period $T$ of limit cycles just beyond these Hopf points is about $T=2\pi/Im$.](image)

![Figure 6: Influence of time delays $\tau$ on fold and Hopf branches. Fold bifurcation branch is unaffected by delay. Hopf bifurcation branch shrinks with increasing delay.](image)
frequency of the oscillations, associated with ankle clonus, varies between 4.5 and 6.3 Hz for zero time delay, between 1.8 and 2.5 Hz for 50 ms time delay (as mentioned in previous section), between 1.1 and 1.7 Hz for 100 ms time delay and between 0.8 and 1.2 Hz for 150 ms time delay.

Figure 7 shows a zoom-in of parameter space at the BT point. The minimal velocity feedback gain \( k_{v,\text{min}} \), necessary for stable posture, increases for increasing time delay \( \tau \), because the extra phase lag of the time delay has to be compensated by extra velocity feedback. The figure also shows that without time delay, no velocity feedback would be necessary at all to obtain stable posture (although it still might give better transient response).

Model fit on data
To get a notion about the reflex gains experienced during posture, the model was fitted on data from literature about disturbance rejection and quiet stance in the sagittal plane. Mihelj et al (2000) measured the effective ankle stiffness (i.e. stiffness of ankles plus gravitational stiffness) in the sagittal plane in response to disturbances, relying mainly on ankle strategy. They found it to be between 9 and 12 Nm/deg. We estimated the relative damping factor to lie between 0.6 and 0.8, by taking the logarithmic decrement of the presented graphs. The combinations of reflex gains \([k_p, k_v]\) reflecting this data is shown in Figure 8 (light grey area).

If ankle stiffness, reflexive contributions in particular, is important in quiet stance is a question of debate at the moment. Some believe anticipatory control to give a major contribution to the stability during quiet stance. Nevertheless, we fitted our model to data of quiet stance in the sagittal plane with eyes closed (Winter et al. 1998) and also plotted it into figure 8 (dark grey area). Figure 9 shows a zoom-in on the areas of reflex gains. The figure shows that the areas of reflex gains for perturbed stance and quiet stance occlude each other.

REFERENCES