Self-stability in Biological Systems – Studies based on Biomechanical Models

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Summary. Mechanical properties of complex biological systems are non-linear, e.g. the force-velocity-length relation of muscles, activation dynamics, and the geometric arrangement of antagonistic pair of muscles. The control of such systems is a highly demanding task. Therefore, the question arises whether these mechanical properties of a muscle-skeletal system itself are able to support or guarantee for the stability of a desired movement, indicating self-stability. Self-stability of single joint biological systems were studied based on eigenvalues of the equation of motions and the basins of attraction were analysed using Lyapunov functions. In general, we found self-stability in single muscle contractions (e.g. frog, rat, cui), in human arm and leg movements, the human spine and even in the co-ordination of complex movements such as tennis or basketball. It seems that self-stability may be a general design criterion not only for the mechanical properties of biological systems but also for motor control.

1 Introduction

The basis for human and animal motion and locomotion are co-ordinated muscle contractions. Even for very simple movements, a huge number of muscles must be controlled. Therefore, we may ask how humans and animals are able to control such complex neuromusculoskeletal systems. Especially for humans, the easiest way to get an answer is to ask somebody. But we would not expect a meaningful answer because the motor control system acts almost without conscious control. The muscles must generate sufficient forces and moments at the joints. However, these forces and moments must be fine tuned in such a way that they can react upon sudden perturbations. This fine tuning may be guaranteed by mono- and poly-synaptic reflexes with negative and positive feedback-loops [5]. On the other hand, the mechanical properties of a musculoskeletal system itself may support or even guarantee for sufficient stability [7, 4]; in these cases motion or locomotion is self-stabilized [10, 2, 1]. Simple biomechanical models, e.g. single muscle contractions or one degree of freedom joint models, can be self-stabilized. But even if these subsystems are self-stabilized the global motion of the multi-body system may still be unstable. However, the global control of a locally self-stabilized system is easier compared to a locally unstable system. The purpose of this paper is to analyze and summarize the self-stabilizing properties of biological systems, i.e. single muscle contractions, single joint movements, and more complex arrangements like the human spine. This paper is a companion paper to Giesl and Wagner (this issue) where the mathematical details to analyse stability and basins of attraction of biomechanical models are given.

2 Single Muscle Quick Release Contractions

The first step in analyzing self-stability of musculoskeletal systems was to study whether mechanical properties of muscles themselves may provide self-stability. A simple method to investigate the self-stabilizing properties of dissected muscles is a quick-release experiment. In quick-release experiments dissected muscles are loaded with an external weight or force, which will be released suddenly [8]. Typically, after the release the muscles contracted and found a new equilibrium at shorter muscle lengths, indicating that the systems were stable (Fig. 1).

As a next step, the quick-release experiments were described and simulated by an equation of motion of a biomechanical model. Based on the equation of motion the stability could be analysed by the eigenvalues of the system. For the given experiments the eigenvalues were negative indicating self-stability. Furthermore, because of the simplicity of the model, the system could be

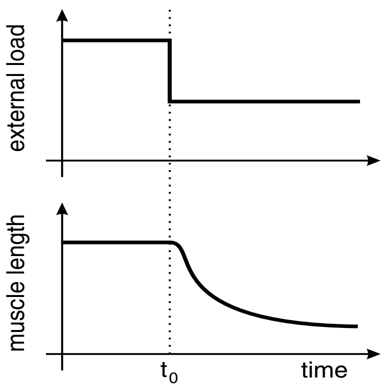

Fig. 1. Schematical representation of a quick-release experiment. At time t_0 the external load was released (*upper row*) and the muscle contracted until a new equilibrium was found between the external force and the muscle force

analysed analytically. From this it could be shown that the classical muscle properties, i.e. the force-velocity relation, force-length relation, are sufficient to provide self-stability. As the mechanical properties of dissected muscles support self-stability, the question arise whether muscles within a geometrical arrangement of joints are still able to achieve self-stability.

3 One Degree of Freedom Joint Models

In models consisting of a muscle and a simple one-degree of freedom rotational joint the interactions between the muscle and joint properties influence the stability of the system. In general, the inner muscle moment arm as well as the moment arm according to the external force vector depended on the flexion angle of joints. The individual shapes of these dependencies were influencing the mechanical stability of the system. We performed quick-release experiments with the elbow-joints of rats and cuis, while the extensor muscles were stimulated [8]. Here again, the systems found new equilibriums after the release of the external loads, indicating stability. A stability analysis based on a biomechanical model resulted in negative eigenvalues, indicating asymptotic stability likewise. For flexor muscles of an elbow joint the moment arms can be calculated from simple trigonometric assumptions, whereas the moment-arms of extensor muscles depends on individual geometrical arrangements. Based on an analytical analysis of the eigenvalues (Giesl and Wagner, this issue) it can be estimated that the derivative $\frac{\partial h_{ext}}{\partial \beta}$ of the geometric function h_{ext} with respect to the flexion angle β must be positive to support stability. This is guaranteed around elbow flexion angles below ca. 90° (Fig. 2).

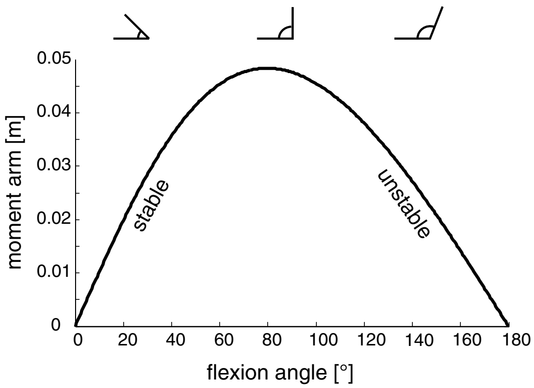

Fig. 2. Representation of the flexor moment arm at an elbow joint (length humerus = 0.27 m, length ulna = 0.26 m, insertion of the muscle at the ulna = 0.048 m). The slope of the curve indicates that stability is supported for flexion angles below ca. 90°

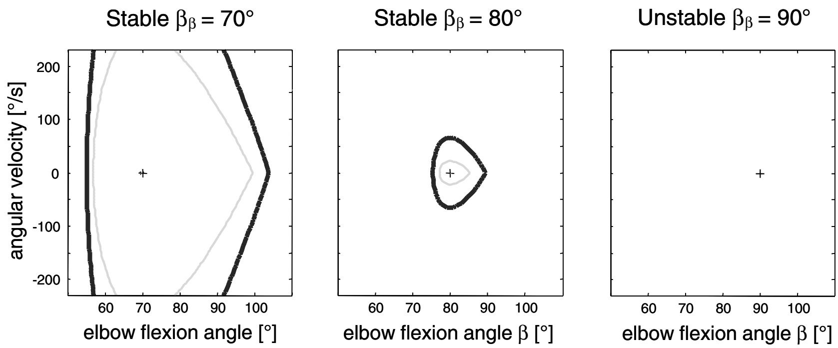

Fig. 3. The basins of attraction of equilibrium points in the phase-plane were calculated with Lyapunov-functions of the systems (Giesl and Wagner this issue). The basins of attraction (black lines – extensor activation 50% of maximum voluntary contraction) were reduced with increasing elbow angles (*left*: equilibrium at $\beta_0 = 70°$; *middle*: $\beta_0 = 80°$; *right*: $\beta_0 = 90°$). Furthermore, the basins of attraction were reduced with decreasing level of co-activation (*thin gray lines* – extensor activation 25% of maximum voluntary contraction)

Experiments with humans supported this result [6]. Here, we determined individual muscle properties of the flexor and extensor muscles. Then the subjects performed quick-release contractions [12]. As a result, the subjects found new equilibriums at lower elbow flexion angles, which was in accordance with the animal experiments. The stability analysis of the experiments resulted in negative eigenvalues for flexion angles below ca. 90°, indicating stability. Furthermore, basins of attraction were calculated based on the theory of Lyapunov functions. We found considerable large basins of attraction at low elbow flexion angles and unstable situations for more extended elbows (Fig. 3). Furthermore, the areas of the basins of attraction depended on the co-activation level of the antagonistic muscles.

Finally, we analysed simple vertical oscillations of a human leg model [10, 11]. Here additionally, the self-stability was supported by a moving center of rotation at the knee joint, as well as a co-activation of bi-articular muscles, i.e. rectus and biceps femoris muscles.

While introducing a joint it is much more complicated to achieve self-stability. Therefore, several solutions to support the stability could be found in biological systems, e.g. co-activation of bi-articular muscles, moving center of rotations.

4 Varying Center of Rotation Model

In the previous section we have discussed the stabilizing behaviour of simple biomechanical models of extremities, i.e. elbow joint and knee joint. These models have a well defined location of the instantaneous center of rotation. In the following we will discuss models with simple one-degree of freedom rotational joints and varying center of rotations. As an example, we may think of lateral flexions of the human lumbar spine. Here we can not define one single center of rotation but depending on the intermuscular co-ordination of local inter-vertebral muscles the center of rotation will vary between the lowest (L5-S1) and the highest functional unit (L1-L2). As a simplification we analyzed rotations at one functional unit, e.g. L1-L2, while the other units were assumed to be stiff. How interactions between different joints of models with more than one degree of freedom may influence the stability of the system cannot be answered with the present simplified model. Is it still possible to self-stabilize such a model with a single pair of antagonistic muscles? First, we described the antagonistic muscles with a Hill-type model including a force-velocity relation, but excluding a force-length relation [9]. As a result two stable areas existed; one around L5-S1 with negative attachment angles of the muscles, e.g. obliquus internus muscle, and another one more cranially for positive attaching angles of the muscles, e.g. obliquus externus or multifidus muscles. But it was impossible to stabilize every center of rotation with only one antagonistic muscular arrangement. Therefore, we improved the model and included a force-length relation such that the muscle was acting on the ascending limb. Now, it was possible to self-stabilize the system at every location of the center of rotation (Fig. 4). We calculated the minimum physiological cross-sectional area (PCSA) of the acting muscles that still can stabilize the system. The physiological cross-sectional area is nearly proportional to the maximum isometric force of a muscle, therefore, a low minimum value of PCSA indicates that only low muscular force is necessary to stabilize the system. For oblique muscle arrangements a minimum physiological cross-sectional area (PCSA) between 50 and 80 cm^2 was found, whereas, muscles acting in parallel to the spine were able to stabilize the system with only 7 cm^2. Introducing additional antagonistic muscles could not reduce this minimum value of the PCSA.

5 Discussion

The purpose of this paper was to analyze and summarize the self-stabilizing properties of biological systems. We tried to draw a line from single muscle contractions, single joint movements, to more complex arrangements like the human spine. Single muscle contractions could be stabilized based on typical shapes of bio-mechanical properties, i.e. the force-velocity relation and the force-length relation of skeletal muscles. It could be shown analytically, that the typical shape of the force-velocity relation was essential for the stabilisation of single muscle contractions [8].

Furthermore, if acting on the ascending limb of the force-length relation, the typical shape of the active and passive force-length relation supports the self-stability of muscles. Especially for muscle lengths above the optimum

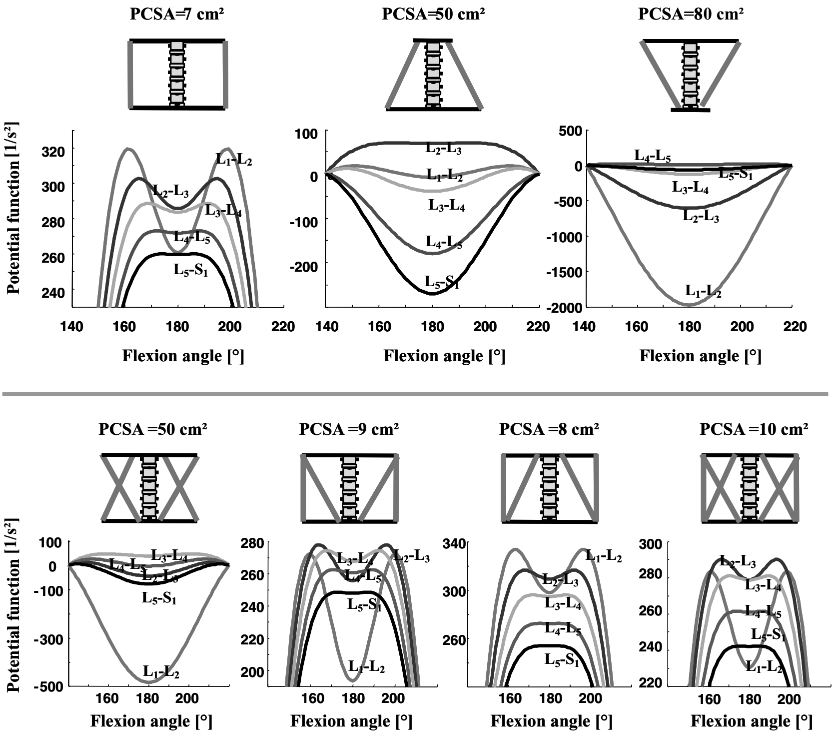

Fig. 4. Lyapunov-functions for different antagonistic muscle arrangements describing the lumbar spine. The centers of rotations were located at L1-L2, L2-L3, L3-L4, L4-L5, and L5-S1 [3]. For all situations a minimum PCSA for self-stability was calculated. The x-axis shows the flexion angle of the segment, while 180° represented the vertical position. The small icons represent the muscular arrangements of the different models and the minimum PCSA for each model is given at the top

length the passive properties were important. In sub-maximal contractions, the activation level of the muscle changes the slope of the force-velocity and force-length relation and thus changes the stability of the system. Therefore, sub-maximal co-ordination patterns in physiological motions and locomotion influences the self-stability of the system [11].

If the muscle was not dissected the geometrical arrangement of joints influenced the self-stability behaviour. The flexion angle of an elbow joint effected the stability of the system. Extending the elbow more than about 90° results in an unstable situation [6]. This simple geometrical dependency may influence simple movement tasks, e.g. imagine a waiter who should not spill the water in the glass while moving. But also throwing tasks are influenced by these geometric relations. Compare throwing a basketball with juggling. Whereas in the first case the basketball will be released with a nearly extended elbow joint, in the second case the juggling-ball leaves the hand with a more flexed elbow joint.

Especially the stabilisation of the human spine is a challenging task. Here the location of the center of rotation may vary depending on the activation pattern of intervertebral muscles. They are influencing the stiffness around the spine and therefore the location of the instantaneous center of rotation. However, the simulations support the assumption that even for this complicated situation the muscles can guarantee for the self-stabilizing function of the spine. Without changing the activation patterns of the trunk muscles, it seems to be possible to stabilize lateral flexions at different centers of rotations [9]. This analysis of the self-stabilizing behaviour of biological systems may influence different scientific areas, e.g. robotics and prosthetics, and it may hopefully have an effect for the medicine and physiotherapy. A profound understanding of the self-stabilizing properties of biological systems is important while investigating the motor control of complex movements of the whole body. Although the models analyzed here were very simple, we may assume that self-stability seems to be an important criterion for the evolution of humans and animals. If the basin of attraction of an equilibrium point or an envisioned trajectory is considerably large this may offer a great advantage for motor control systems. A self-stable system can be controlled much easier with simple reflexes compared to an unstable system. If the system is risking to move out off the basin of attraction a simple reflex may be sufficient to push it back into the stable basin. Especially for fast movements, which do not require a high precision, the neuronal system can be unburdened. Considering the control of legged robots this may reduce the requirements on the precision of the sensors and the controller systems.

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