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Bachelor's thesis

Upright posture control in changing gravity conditions

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Abstract

In order to be able to withstand and to take advantage of external forces and to be able to direct motor actions, living organisms developed ability to sense environmental impacts. For instance, proprioceptors and cutaneous receptors allow vertebrates to take into account, above all, gravitational influences. These receptors participate in planning and correcting posture, locomotion and other movements. In this thesis mechanisms of equilibrium control in changing gravity conditions were studied by means of literature analysis and analysis of data obtained in parabolic flight. This analysis revealed that standing balance in overloading is likely controlled in a manner resembling a single-link inverted pendulum. Such behavior could be beneficial to take advantage of passive body structures and to more actively involve foot receptors in balance regulation in challenging conditions. This adaptation also resembles typical postural responses in balance perturbation tasks. The latter were then studied in more detail. Further literature overview supported the suggestion that plantar foot receptors play an essential role in dynamic stability of upright posture. The obtained conclusions allowed to formulate possible mechanisms of sway and balance control and make suggestions on possible implementation of these mechanisms into the neuromusculoskeletal human model proposed by Walter, Günther, Haeufle, and Schmitt (2021) in order to make equilibrium control of this model robuster.

Zusammenfassung

Um äußeren Kräften widerstehen und diese nutzen, sowie motorische Handlungen steuern zu können, entwickelten Lebewesen die Fähigkeit, Umwelteinflüsse zu spüren und wahrzunehmen. Zum Beispiel ermöglichen Propriozeptoren und Hautrezeptoren es Wirbeltieren, unter anderem Gravitationseinflüsse zu berücksichtigen. Diese Rezeptoren sind somit an der Planung und Korrektur der Körperhaltung, Fortbewegung und anderer Bewegungen beteiligt. In dieser Arbeit wurden Mechanismen der Gleichgewichtskontrolle unter veränderlichen Gravitationsbedingungen mittels Literaturanalyse und Analyse von Parabelflugdaten untersucht. Diese Analyse ergab, dass das Gleichgewicht beim Stehen unter Überlastung wahrscheinlich auf eine Weise gesteuert wird, die einem einsegmentalen Inverted-Pendulum ähnelt. Ein solches Verhalten könnte vorteilhaft sein, um passive Körperstrukturen und Fußrezeptoren in die Gleichgewichtsregulation unter herausfordernden Bedingungen aktiver einzubeziehen. Diese Anpassung ähnelt auch typischen Reaktionen bei Balancestörungen. Die Letzteren wurden dann genauer untersucht. Ein weiterer Literaturüberblick unterstützte die Vermutung, dass plantare Fußrezeptoren eine wesentliche Rolle bei der dynamischen Stabilität des Stehens spielen. Die gewonnenen Schlussfolgerungen ermöglichten es, potentielle Mechanismen der Schwankungs- und Gleichgewichtskontrolle zu formulieren und Vorschläge für eine mögliche Implementierung dieser Mechanismen in das von Walter et al. (2021) vorgeschlagene neuromuskuloskelettale Menschenmodell zu machen, um die Gleichgewichtskontrolle dieses Modells robuster zu machen.

1 Introduction

All living systems on Earth phylogenetically evolved under the influence of external forces and interact with them continuously. In order to withstand external disturbances and to take advantage of the properties of the environment, living organisms developed abundant sensory systems being able to detect external stimuli of different modalities. Among such systems are the olfactory, gustatory, auditory, visual, vestibular and somatosensory systems in vertebrates. All these systems can direct and modify motor actions, but the letter three are considered to be of the highest importance (Deliagina, Beloozerova, Orlovsky, & Zelenin, 2014; Grillner & El Manira, 2020). Their mutual contribution to the generation of a particular action can however vary. For example, visual information is crucial while walking on a narrow beam (Grillner & El Manira, 2020), whereas the vestibular and somatosensory systems are dominant in control of upright quiet stance (Deliagina et al., 2014).

In order to correctly plan a motor action and to set an appropriate level of its stability and flexibility, the nervous system has to anticipate possible perturbations that it can undergo (Gerasimenko et al., 2017). For this purpose and, if needed, to correct the ongoing action, signals from somatosensory receptors such as muscle spindles, Golgi tendon organs and cutaneous receptors are used. It is intriguing how exactly information from these receptors is utilized and integrated by the nervous system, in particular, during maintenance of upright posture equilibrium – one of the most frequent motor tasks.

The main external force acting on the body during standing is the force of gravity. To keep the multi-segmental body erect and to avoid collapsing, muscles must exert anti-gravity thrust. In case of external perturbations, gravity force torque changes, and muscle forces must be adapted accordingly in order to keep a set body orientation. The goals of this thesis are twofold. First, to gain a deeper understanding and to give an overview of how such gravitational influences are taken into account and counteracted by the nervous system. Second, based on these findings, to make suggestions on how to make the equilibrium control robuster in the musculoskeletal model by Walter et al. (2021).

The thesis consists of four parts. Basic neural principles and mechanisms of postural

control and load sensing are described in section 2. An overview of neural aspects of postural control seems to be interesting in itself, but it is also useful to provide a better understanding of the control architecture of the musculoskeletal model considered in section 5. In section 3, data obtained in parabolic flight are analyzed. Parabolic flight is a flight with alternating phases of weightlessness and overloading. Therefore, it gives a unique opportunity to study load sensing. It is shown that postural behavior changes in altered weight force conditions and in overloading it resembles postural responses in perturbation tasks. This observation serves as a motivation for a deeper study of such responses, which is done in section 4. Additional literature investigation together with the analysis of the parabolic flight data, allows to conjecture that receptors of the foot sole play an essential role in triggering these postural reactions. The results of the literature and data analysis allows to make suggestions on how the control architecture can be modified to enhance the robustness of the musculoskeletal model in postural tasks. The model, control architecture and suggestions on its modification are described in section 5.

2 Neural mechanisms of postural control and load sensing

2.1 Selection of literature

In order to deeper understand the role of load receptors in equilibrium control, literature investigation was performed. Since this scientific area is extremely broad, some constrains were imposed on the search. Only reviews articles in English regarding postural control in humans and other mammals were considered. The articles were searched in the database PubMed and the following retrieval requests were used:

1. (postural control[Title/Abstract]) AND (english[Language]) AND (review[Publication Type]),
2. ((upright[Title/Abstract]) AND ((stance[Title/Abstract]) OR (posture[Title/Abstract]))) AND (english[Language]) AND (review[Publication Type]).
3. ((load receptor[Title/Abstract]) OR (Golgi tendon organ[Title/Abstract])) AND (english[Language]) AND (review[Publication Type]),
4. (sensory[Title/Abstract]) AND (load[Title/Abstract]) AND (english[Language]) AND (review[Publication Type]),

5. (proprioception[Title/Abstract]) AND (load[Title/Abstract]) AND (english[Language]) AND (review[Publication Type]),

These requests aimed at identifying works where such word combinations as ”postural control”, ”upright stance”, ”upright posture”, ”load receptor”, ”Golgi tendon organ”, ”sensory”+”load” or ”proprioception”+”load” were used in the title or in the abstract. The use of these requests resulted in lists of correspondingly 467, 242, 18, 112 and 0 review articles. Some additional criteria were applied to exclude the following types of articles from consideration:

- studies not directly concerning neural mechanisms of motor control (e.g. studies in cognitive or perception psychology, surgery, ergonomics, virtual reality and sensory augmentation research etc.);
- studies regarding any kind of neurodegeneration and neurological deficits or diseases (e.g. multiple sclerosis, Parkinson, cerebral palsy);
- studies dealing with conditions such as trisomy 21, autism, blindness, obesity, diabetes etc.;
- studies regarding other diseases of a wide spectrum (e.g. pulmonary, coronary diseases, strokes) or psychological conditions (e.g. anxiety);
- studies considering exclusively age-related features of postural control (in infants, toddlers or elderly persons);
- studies related to orthopedics (ankle instability), injuries or diseases of the musculoskeletal system (e.g. knee injuries), prosthetics;
- fatigue-related studies;
- studies considering postural control of specific body parts (e.g. mandible), in specific conditions (e.g. labour) or in specific occupation types (e.g. singers);
- studies exclusively on rehabilitation, physio- and psychotherapy or sport training;
- developmental and phylogenetic studies;
- encyclopedic or biographical articles.

Table 1: The list of review articles selected to summarize the neural mechanisms of load sensing in postural control.

1	Grillner, S., & El Manira, A. (2020). Current principles of motor control, with special reference to vertebrate locomotion. *Physiological Reviews, 100*(1), 271-320.
2	Ivanenko, Y., & Gurfinkel, V. S. (2018). Human postural control. *Frontiers in Neuroscience, 12*, 171.
3	Rasman, B. G., Forbes, P. A., Tisserand, R., & Blouin, J. S. (2018). Sensorimotor manipulations of the balance control loop–beyond imposed external perturbations. *Frontiers in Neurology, 9*, 899.
4	Nonnekes, J., Carpenter, M. G., Inglis, J. T., Duysens, J., & Weerdesteyn, V. (2015). What startles tell us about control of posture and gait. *Neuroscience & Biobehavioral Reviews, 53*, 131-138.
5	Prochazka, A. (2015). Sensory control of normal movement and of movement aided by neural prostheses. *Journal of Anatomy, 227*(2), 167-177.
6	Deliagina, T. G., Beloozerova, I. N., Orlovsky, G. N., & Zelenin, P. V. (2014). Contribution of supraspinal systems to generation of automatic postural responses. *Frontiers in Integrative Neuroscience, 8*, 76.
7	Earhart, G. M. (2013). Dynamic control of posture across locomotor tasks. *Movement Disorders, 28*(11), 1501-1508.
8	Giladi, N., Horak, F. B., & Hausdorff, J. M. (2013). Classification of gait disturbances: Distinguishing between continuous and episodic changes. *Movement Disorders, 28*(11), 1469-1473.
9	Ting, L. H., Chvatal, S. A., Safavynia, S. A., & Lucas McKay, J. (2012). Review and perspective: Neuromechanical considerations for predicting muscle activation patterns for movement. *International Journal for Numerical Methods in Biomedical Engineering, 28*(10), 1003-1014.
10	Deliagina, T. G., Zelenin, P. V., & Orlovsky, G. N. (2012). Physiological and circuit mechanisms of postural control. *Current Opinion in Neurobiology, 22*(4), 646-652.
11	Chen, Y. S., & Zhou, S. (2011). Soleus H-reflex and its relation to static postural control. *Gait & Posture, 33*(2), 169-178.
12	Chiel, H. J., Ting, L. H., Ekeberg, Ö., & Hartmann, M. J. (2009). The brain in its body: Motor control and sensing in a biomechanical context. *Journal of Neuroscience, 29*(41), 12807-12814.
13	Deliagina, T. G., Beloozerova, I. N., Zelenin, P. V., & Orlovsky, G. N. (2008). Spinal and supraspinal postural networks. *Brain Research Reviews, 57*(1), 212-221.
14	Deliagina, T. G., Zelenin, P. V., Beloozerova, I. N., & Orlovsky, G. N. (2007). Nervous mechanisms controlling body posture. *Physiology & Behavior, 92*(1-2), 148-154.
15	Windhorst, U. (2007). Muscle proprioceptive feedback and spinal networks. *Brain Research Bulletin, 73*(4-6), 155-202.
16	Horak, F. B. (2006). Postural orientation and equilibrium: What do we need to know about neural control of balance to prevent falls? *Age and Ageing, 35*(S2), ii7-ii11.
17	Deliagina, T. G., Orlovsky, G. N., Zelenin, P. V., & Beloozerova, I. N. (2006). Neural bases of postural control. *Physiology, 21*(3), 216-225.
18	Macefield, V. G. (2005). Physiological characteristics of low-threshold mechanoreceptors in joints, muscle and skin in human subjects. *Clinical and Experimental Pharmacology and Physiology, 32*(1-2), 135-144.
19	Deliagina, T. G., & Orlovsky, G. N. (2002). Comparative neurobiology of postural control. *Current Opinion in Neurobiology, 12*(6), 652-657.
20	Van Emmerik, R. E., & Van Wegen, E. E. (2002). On the functional aspects of variability in postural control. *Exercise and Sport Sciences Reviews, 30*(4), 177-183.
21	Dietz, V., & Duysens, J. (2000). Significance of load receptor input during locomotion: A review. *Gait & Posture, 11*(2), 102-110.
22	Duysens, J., Clarac, F., & Cruse, H. (2000). Load-regulating mechanisms in gait and posture: Comparative aspects. *Physiological Reviews, 80*(1), 83-133.
23	Zehr, E. P., & Stein, R. B. (1999). What functions do reflexes serve during human locomotion? *Progress in Neurobiology, 58*(2), 185-205.
24	Dietz, V. (1998). Evidence for a load receptor contribution to the control of posture and locomotion. *Neuroscience & Biobehavioral Reviews, 22*(4), 495-499.
25	Pozzo, T., Papaxanthis, C., Stapley, P., & Berthoz, A. (1998). The sensorimotor and cognitive integration of gravity. *Brain Research Reviews, 28*(1-2), 92-101.
26	Pearson, K. G., Misiaszek, J. E., & Fouad, K. (1998). Enhancement and resetting of locomotor activity by muscle afferents. *Annals of the New York Academy of Sciences, 860*(1), 203-215.
27	Horak, F. B., Henry, S. M., & Shumway-Cook, A. (1997). Postural perturbations: New insights for treatment of balance disorders. *Physical Therapy, 77*(5), 517-533.
28	Massion, J. (1994). Postural control system. *Current Opinion in Neurobiology, 4*(6), 877-887.
29	Lestienne, F. G., & Gurfinkel, V. S. (1988). Postural control in weightlessness: A dual process underlying adaptation to an unusual environment. *Trends in Neurosciences, 11*(8), 359-363.

Since Golgi tendon organs and cutaneous receptors were assumed to be main load receptors (Dietz, Horstmann, Trippel, & Gollhofer, 1989; Dietz, Gollhofer, Kleiber, & Trippel, 1992) and, thus, represent the primary interest of the thesis, articles devoted exclusively to the vestibular, visual and/or auditory systems were also excluded. Unsuitable works were eliminated on the stage of reading titles or abstracts. Further, one more criterion was used with regard to the article's accessibility: the article must have been published in an open-access journal, in a journal accessible online from the University of Stuttgart or accessible freely on resources such as ResearchGate. After application of all the criteria mentioned above only 29 reviews were left [Table 1]. These articles were thoroughly read and the most relevant of them, as well as some articles from their reference lists, are summarized in sections 2.2 and 2.3.

2.2 Supraspinal mechanisms of postural control

Postural control system can be considered as consisting of two principal subsystems: orientation control subsystem and equilibrium control subsystem (Massion, 1994; Deliagina et al., 2014). The visual, vestibular and somatosensory systems actively interact with each other, and sensory information from these systems seems to play an important role both in orientation and equilibrium control (Deliagina et al., 2014; Horak, 2006). The visual system provides information which is predominantly needed for anticipatory, feedforward control (Krishnan & Aruin, 2011), while veridical vestibular and somatosensory information is crucial for normal feedforward control as well as for adequate rapid postural corrections (Horak, Nashner, & Diener, 1990; Mohapatra, Krishnan, & Aruin, 2012; Deliagina et al., 2014). Both supraspinal and spinal neural networks are involved in postural control [Fig. 1] (Deliagina et al., 2014).

Supraspinal networks seem to be important for setting body orientation as well as for equilibrium control in challenging conditions (Deliagina et al., 2014; Solopova, Kazennikov, Deniskina, Levik, & Ivanenko, 2003; Ivanenko & Gurfinkel, 2018), in particular, in case of a fast or large surface displacements (Horak & Nashner, 1986; Horak et al., 1990; Horak, Henry, & Shumway-Cook, 1997). Neurons of the corticospinal, vestibulospinal, reticulospinal and rubrospinal tracts were shown to be active during postural tasks. This means that all main supraspinal structures [motor cortex, cerebellum and brain stem] possibly participate in postural control (Deliagina et al., 2014).

The exact role of each of these structures is not completely understood yet. It is,

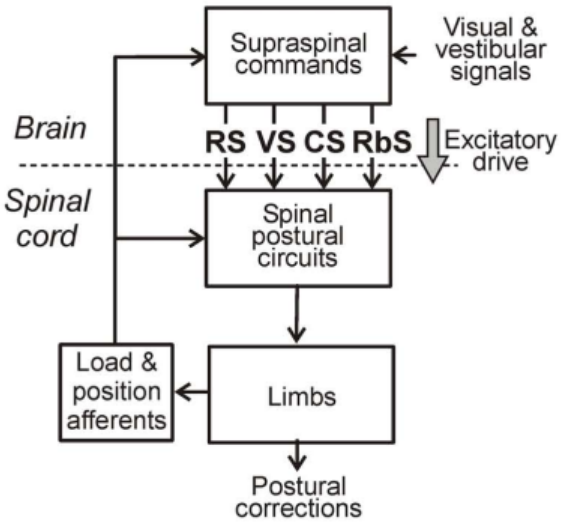

Fig. 1: Spinal neural circuits controlling limb and trunk muscles are activated by tonic stimulation from supraspinal structures [thick gray arrow]. They can modify their activity due to sensory signals from limb receptors [block "Load & position afferents"] as well as from supraspinal structures via reticulospinal [RS], vestibulospinal [VS], corticospinal [CS] and rubrospinal [RbS] tracts. Reprinted from Deliagina et al. (2014).

however, known that decerebrated animals can stand up, maintain a posture and equilibrium as intact animals do, as though EMG magnitude of their postural responses can be significantly reduced (Musienko, Zelenin, Lyalka, Orlovsky, & Deliagina, 2008; Honeycutt, Gottschall, & Nichols, 2009; Deliagina et al., 2014). Moreover, animals can restore the ability to counteract external perturbations after the dissection of the dorsolateral part of spinal cord containing the corticospinal tract within 3 weeks. This could mean that signals from motor cortex can provide additional excitation of spinal networks, but they are not strictly essential for postural control at least in basic postural tasks. This can be potentially explained by similarities in activity of neurons of the corticospinal and rubrospinal systems: the vast majority of studied corticospinal neurons and almost the half of studied rubrospinal neurons fired in a correlated manner during tasks requiring balance maintenance on a tilting platform (Deliagina et al., 2014).

Reticulospinal neurons also make a contribution to postural control. They produce the tonic excitation of spinal circuits and help to adjust a body orientation. Reticulospinal neurons were studied in cats. They fired in tasks requiring weight redistribution when a support surface under one of the limb was suddenly removed. Some of the neurons were active in a limb-specific manner while some others were active irre-

spective of the limb under which the support surface was removed. But the majority [about three quarters] of the neurons were activated by the removal of the support surface under two or three limbs. These observations allow to suggest that reticulospinal neurons play an important role in orientation control (Deliagina et al., 2014).

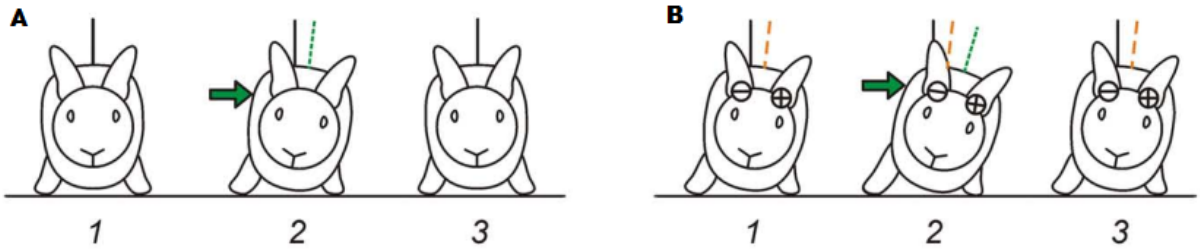

Fig. 2: Equilibrium position [1], deviation from [2] and return back into this position after the perturbation [3] in case of symmetrical [A] and asymmetrical [B] excitation of labyrinth organs. Reprinted from Deliagina et al. (2014).

The vestibular system also seems to be of very high importance for the establishment of body orientation and for the elicitation of balance responses. Vestibular afferents steadily fire and tonically excite α-motoneurons of extensor muscles and interneurons regulating their activation. Elimination of tonic stimulation can drastically change membrane properties of α-motoneurons (Hyngstrom, Johnson, Schuster, & Heckman, 2008) and alter activity of interneurons (Deliagina et al., 2014). Furthermore, modulation of vestibular signals by means of galvanic vestibular stimulation can significantly modify muscle tone. Excitation of afferent signals from one labyrinth organ and inhibition of afferent signals from the other one lead to establishing a stable asymmetrical equilibrium orientation to the side of inhibited afferents. After a deviation, the animal returns into this asymmetrical equilibrium position [Fig. 2]. Ablation of only one labyrinth leads to the continuous rolling towards the damaged side which can be stopped by electrical stimulation of the vestibular nerve. Moreover, dissection of ventral part of spinal cord containing the vestibulospinal tract leads to the irreversible disability to maintain balance (Deliagina et al., 2014). Thus, vestibular information seems to be a crucial source of tonic excitation of spinal circuits. At the same time, although patients with vestibular loss can exert balance responses when counteracting external perturbations, their responses are different from those in healthy subjects (Horak et al., 1990). This stresses the necessity of veridical vestibular information for equilibrium control.

2.3 Spinal and peripheral mechanisms of postural control

Besides supraspinal networks, spinal circuits are also strongly engaged in orientation and equilibrium control. They are responsible not only for ”simple” excitation of limb muscles but also seem to control disturbances of moderate difficulty. It was proposed that spinal networks exhibit some level of independence in controlling motor actions (Gelfand, Gurfinkel, Tsetlin, & Shik, 1966) and are are responsible for spatial distribution of activity between muscles (Ting, Chvatal, Safavynia, & Lucas McKay, 2012). In addition, studies indirectly indicating at the existence of spinal cord neural networks responsible for postural corrections (Ting & Macpherson, 2005; Torres-Oviedo & Ting, 2007), there studies showing that postural responses can be at least partially restored by means of direct electrical stimulation of spinal cord after their disappearance caused by spinalization (Musienko, Zelenin, Orlovsky, & Deliagina, 2010; Deliagina et al., 2014). The structure and function of these networks can potentially be similar to those responsible for locomotion (Bizzi, Cheung, d'Avella, Saltiel, & Tresch, 2008; Kiehn, 2016; Grillner & El Manira, 2020). The autonomy of postural spinal networks was conjectured to be based on and enhanced by peripheral afferent signals (Gelfand et al., 1966). Muscle spindles residing in muscles, Golgi tendon organs located in muscle-tendon junctions and cutaneous receptors of the sole of the foot/paw must be the main sources of peripheral information.

The role of each receptor type is not clear enough. Typically, muscle spindles are considered as sensors of muscle length and its change while Golgi tendon organs are considered to be sensors coding muscle tension/force, and foot receptors are considered as touch, pressure and skin stretch sensors (Pearson & Gordon, 2013; Schmidt & Schaible, 2006, pp. 203-216). Although muscle spindles, Golgi tendon organs and cutaneous foot receptors indeed react on changes in muscle length, force and skin deformation respectively, there is a rising doubt that the nervous system can interpret these variables individually. For example, convergence of Ia afferents [from muscle spindles] and Ib afferents [from Golgi tendon organs] on the same subsets of spinal interneurons could indicate that the nervous system strives to control some global variables (Windhorst, 2007). Due to complexity of sensorimotor connections even between distant muscles, it was suggested that joint or limb/leg stiffness could be one of such more global variables (Nichols, Bunderson, & Lyle, 2016). Some ”hidden” even more

global variables such as reciprocal and coactivation commands on different control levels could also exist (Latash, 2021), and joint or leg stiffness might, in its turn, be their component. Nevertheless, it is important to study the role of individual types of afferents in motor control despite the fact that this role might be extreme complex and ambiguous.

Particularly in regard to postural control, all three types of receptors mentioned above are of exceptional importance. For example, it was demonstrated on mice that genetic elimination of both muscle spindles and Golgi tendon organs or muscle spindles alone prevents the ability to correctly position limbs during movements (Ernfors, Lee, Kucera, & Jaenisch, 1994; Akay, Tourtellotte, Arber, & Jessell, 2014). Elimination of muscle spindles does not affect activity of extensor muscles during the stance phase of locomotion but leads to prolonged firing of flexor muscles and, thus, to increased joint stiffness in the end of the swing phase. (Akay et al., 2014; Grillner & El Manira, 2020). Further, studies on Earth (Roll et al., 1998; Kavounoudias, Roll, & Roll, 2001; Thompson, Bélanger, & Fung, 2007, 2011) and in spaceflight [when gravitational influences are counteracted by the centrifugal force] (Roll et al., 1998) demonstrated the alteration of body orientation when vibration was applied to different muscle-tendon units. Since application of muscle and tendon vibration is supposed to influence signaling of muscle spindles, one can assume that muscle spindles are the peripheral structures that are in charge of body orientation control. This suggestion is corroborated by the observation that cosmonauts can hold a standing position similar to the terrestrial one [especially if vision is not occluded], and differences between these positions gradually diminish within few days of spaceflight (Clement, Gurfinkel, Lestienne, Lipshits, & Popov, 1984; Lestienne & Gurfinkel, 1988a).

If one assumes that muscle spindles encode exclusively muscle length and its rate of change and Golgi tendon organ encode exclusively force, and only muscle spindles are responsible for orientation control, then some experiments (Lackner, DiZio, & Fisk, 1992; Fisk, Lackner, & DiZio, 1993) made in weightlessness and overloading seem to deliver confusing results. The experiments showed that accuracy of slow arm movements decreases with decreasing level of weight force. This could mean that either muscle spindles encode external load, or that Golgi tendon organs [and possibly other types of receptors] influence activity of γ-motoneurons and, therefore, sensitivity

of muscle spindles, and thus likely participate in orientation control. Both suggestions seem plausible. As noted by Duysens, Clarac, and Cruse (2000), any elastic component can be potentially considered as force sensor. Attenuation of H-reflex during walking in comparison with standing and during running in comparison with walking (Windhorst, 2007; Chen & Zhou, 2011) may indirectly indicate that force sensitivity of muscle spindles increases with increasing load. This suggestion conforms with the increase of thixotropic properties in a passive muscles [and, thus, likely in muscle spindles] and their decrease in an active muscle (Lakie & Campbell, 2019). Moreover, the ability of muscle spindles to encode load was recently demonstrated (Blum, Lamotte D'Incamps, Zytnicki, & Ting, 2017). Similarly, one can assume that signals from Golgi tendon organs can be interpreted by the central nervous system as encoding contraction velocity, simply because muscle contraction must lead to an increase in tension at the muscle-tendon junction. Moreover, influence of tendon vibration on body orientation was shown to be smaller in weightlessness than in normogravity (Roll et al., 1998) [that can be, however, explained also by changes in vestibular signaling]. From the said above, one can make a suggestion that both muscle spindles and Golgi tendon organs participate in active orientation control. So, it can be concluded with caution that muscle spindles with a possible participation of Golgi tendon organs are involved in setting of a body orientation when the latter make muscles generate additional anti-gravity thrust. This suggestion must be, however, investigated in more detail.

The investigation of what is the contribution of muscle and cutaneous receptors to equilibrium control is seemingly also far from complete. Some researchers argue that postural corrections at least in simple balance tasks can be elicited predominantly by Ia afferents from muscle spindles (Musienko et al., 2010) which underlie muscle stretch reflex that represents a negative feedback loop and can be considered as some sort of servomechanism (Pearson & Gordon, 2013). Musienko et al. (2010) assumed that forces generated [in spinal rabbits] are not sufficient to reverse Ib inhibition into Ib excitation. This view can be supported by the observation that motor units most actively involved in postural tasks have the strongest monosynaptic [autogenic] excitation (Windhorst, 2007). On the other hand, this statement can also be questioned. First, Golgi tendon organs are extremely sensitive receptors that can register very small changes in force (Duysens et al., 2000). Second, Ib excitation can seem-

ingly occur also in postural tasks. Loram, Maganaris, and Lakie (2004) showed that length of soleus varies within 2 mm and length of gastrocnemius medialis varies within 4 mm during purposeful sway. Consequently, muscle contractions can be considered as nearly isometric during standing and small perturbations. Although it was shown that stimulation of Ib afferents in isometrically contracting muscles leads to inhibition of motoneurons of the parent muscle and its synergists, this inhibition is normally short-lasting and can be shifted to Ib excitation. This reversal effect is thought to be due to presynaptic inhibition of Ib terminals (Duysens et al., 2000). It is interesting to note that common convergence of Ia and Ib afferents on spinal interneurons can in general have either co-excitatory or co-inhibitory, or mixed effects on α-motoneurons (Windhorst, 2007; Duysens et al., 2000). To complicate things even more, Ib afferents can provoke not only autogenic excitation. Golgi tendon organs innervating plantarflexors [ankle extensors] and knee extensors can elicit excitation also in dorsiflexors [ankle flexors] (Nichols et al., 2016). It is also worth noting that some complexity in regulation of activity of synergistic muscles was observed in previous studies. Normally, soleus and gastrocnemii are activated simultaneously. However, it was found that strong activation of gastrocnemii can be accompanied by inhibition of soleus in activities requiring fast or high force contractions of plantarflexors (Duysens et al., 2000). [In this case, muscle comprising triceps surae must be considered as synergistic not in the classical sense but in sense of Gelfand and Latash (1998).] From all said above, one can conclude that muscle spindles and Golgi tendon organs can have extremely diverse effects on α-motoneurons on parent, synergistic [in the classical sense] and antagonistic muscles and very flexibly regulate joint and leg stiffness.

Due to excitatory effects of Golgi tendon organs, due to existence of medium- and long-latency responses in balance tasks and attenuation of these responses during unloading, Golgi tendon organs were proposed to be the main load receptors (Dietz et al., 1989, 1992; Dietz & Duysens, 2000). Dietz et al. (1989) found that activity of gastrocnemius medialis decreases proportionally to the degree of body unloading and suggested that Golgi tendon organs might ”measure” toppling torques acting on the body during standing. From this, one could also suggest that Ib afferents might indirectly provide the central nervous system with information about the degree of the translation of the body center of mass relative to its vertical projection onto the ground. But from studies just cited, one cannot rule out that receptors of the foot sole also

have a strong impact on postural reactions. For instance, Horak et al. (1990) simulated cutaneous sensory loss while leaving function of muscle receptors unaffected. Although subjects were able to keep balance after a perturbation, they exhibited postural strategies that differed from those observed before and after the intervention. It was also shown that direct stimulation of plantar cutaneous receptors or nerves innervating the plantar surface of the foot can facilitate muscle activity (Fallon, Bent, McNulty, & Macefield, 2005), alter body orientation (Kavounoudias, Roll, & Roll, 1998, 1999; Kavounoudias et al., 2001), significantly increase force output during plantarflexion (Pearcey, Sun, & Zehr, 2020) and postpone the onset of fatigue during prolonged submaximal plantarflexion (Smith, Power, & Bent, 2020). Based on that, one can assume that stimulation of plantar foot receptors might represent a mechanism for maintenance of stable upright posture. Indeed, foot receptors have a widely distributed projections onto spinal cord networks, they can inhibit interneurons inhibiting extensor muscles by means of mitigation of Ia pre-synaptic inhibition and of Ib inhibition (Duysens et al., 2000; Pearcey et al., 2020) and/or by means of reduction of input from group III/IV afferents onto extensor motoneurons (Smith et al., 2020). Among other potential effects of cutaneous stimulation are increased excitability of spinal networks in response to descending commands and some violation of Henneman's motor units recruitment principle (Pearcey et al., 2020).

In conclusion, one can see that besides supraspinal networks afferent signals actively participate in postural control. While orientation control in intact animals and humans appears to be predominantly directed by muscle spindles and Golgi tendon organs, equilibrium is controlled by both of these receptor types and by plantar foot receptors as well. Thus, all these receptors can be considered as load receptors, however their mutual contribution in different tasks can vary. In the next section, some changes in neural control of upright posture in response to changing weight force will be studied. Possible influence of foot receptors on postural responses in sagittal plane will be analyzed in more detail in section 4.

3 Analysis of parabolic flight data

Parabolic flight provides an absolutely unique opportunity to investigate how motor behavior changes with a change in weight force acting on the body. The influence of apparent gravity alterations on leg muscle activity when keeping upright posture are

analysed in this section.

3.1 Methods

Experimental set-up and data acquisition

For the analysis of postural behavior in changing weight force conditions raw data recorded by Waldvogel et al. (2021) in parabolic flight were used. In the experiment took part 17 subjects, and 31 parabolas were flown during an approximately three-hour flight (Waldvogel et al., 2021). Only the data of one subject [subject 15, male] from parabolas 14 and 15 were provided for the analysis of upright stance. During parabola 14 subject's eyes were open, during parabola 15 subject's eyes were closed.

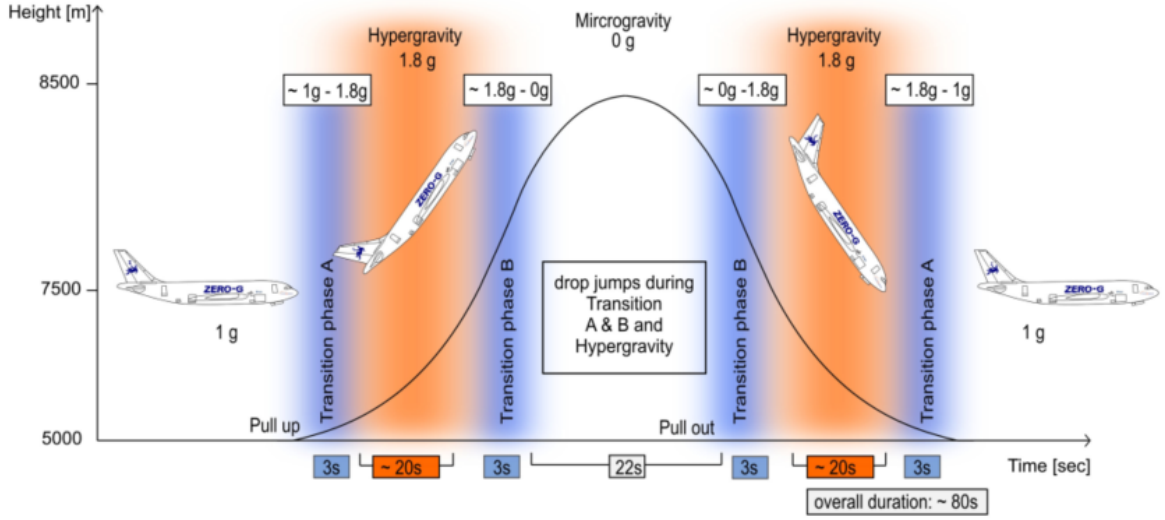

Fig. 3: Schematic representation of weight force phases in parabolic flight. Reprinted from Waldvogel et al. (2021).

Each parabola in the parabolic flight [Fig. 3] consisted of two periods of normogravity [1g], two periods of overloading [about 1,8g], one period of weightlessness [0g], as well as four transition periods [1g $\rightarrow$ 1,8g, 1,8g $\rightarrow$ 0g, 0g $\rightarrow$ 1,8g, 1,8g $\rightarrow$ 1g]. Electromyographic activity of main flexor and extensor muscles of the right leg [M. soleus, M. gastrocnemius medialis, M. gastrocnemius lateralis, M. tibialis anterior, M. vastus medialis, M. vastus lateralis, M. rectus femoris, M. biceps femoris] were transmitted via shielded cables to the amplifier [band-pass filter 20 Hz to 1 kHz, 200x amplified] and recorded at 2 kHz [A/D-converter National Instruments PCI-6229 DAQcard, Austin, TX, USA, 16 bit resolution]. Bipolar Ag/AgCl surface electrodes [Ambu Blue Sensor P, Ballerup, Denmark, diameter 9 mm, center-to-center distance 34 mm] placed according to SENIAM guidelines were used for data recordings (Waldvogel et al., 2021).

The level of weight force acting on the subject [g level] was measured with an accelerometer at 2000 Hz [model and manufacturer were not specified] (Waldvogel et al., 2021).

To assess leg kinematics in the sagittal plane, passive markers were placed at subject's iliac crest, greater trochanter, lateral femoral condyle, lateral malleolus, and fifth metatarsal [at the right side of the body]. Recordings were made with a high speed camera Basler ace acA1920 [Basler AG, Ahrensburg, Germany] at 100 Hz from 1 m distance and with SIMI Motion software [SIMI Reality Motions System GmbH, Unterschleißheim, Germany] (Waldvogel et al., 2021).

Data processing

Data processing and analysis[1] were performed with MATLAB® R2020b [MathWorks, Natick, MA, USA].

First of all, EMG activity for all eight muscles in both conditions [eyes open or closed] was plotted over time. Visual examination of the data showed that EMG of gastrocnemius lateralis, vastus medialis, vastus lateralis and rectus femoris in eyes closed conditions must be excluded from further consideration due to apparent issues during signal recording.

Further processing [finding the linear envelope] succeeded according to the general scheme from Barzilay and Wolf (2011). Frequency spectra for all muscles were examined. Due to a relatively fast amplitude attenuation, bandwidth 20-650 Hz was chosen: amplitudes at 650 Hz did not exceed 5$\%$ of the maximal amplitude within frequencies larger than 20 Hz [20 Hz is the high pass frequency during recordings in Waldvogel et al. (2021)]. A 6th-order Butterworth low-pass filter [low pass cut-off frequency 650 Hz] and a 4th-order Butterworth high-pass filter [high pass cut-off frequency 20 Hz] were used for band filtering. Then, the signals were full-wave rectified and smoothed [moving average over 250 ms following Benoit, Lamontagne, Cerulli, and Liti (2003)]. After that, the linear envelope was found by means of a 1st-order Butterworth low-pass filter with the cut-off frequency 30 Hz as suggested by Barzilay and Wolf (2011). The orders of the three mentioned Butterworth filters were correspondingly computed as [$n_i \in \mathbb{N}$, $i = \overline{1,3}$]:

[1] All data and the source code are submitted together with an electronic version of the thesis.

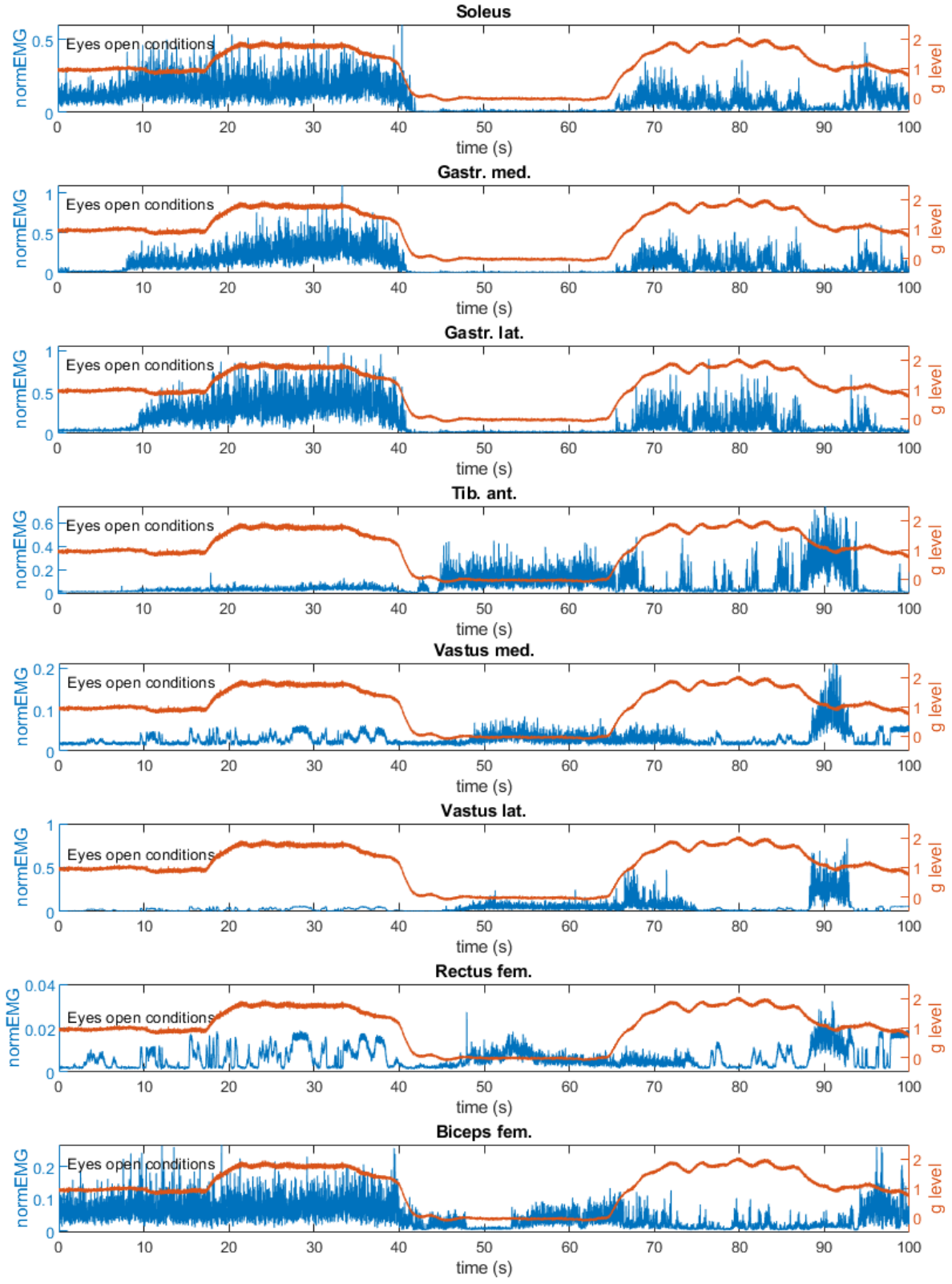

Fig. 4: EMG of muscles of the right shank and the right thigh [in blue] and g level [in orange] in eyes open conditions.

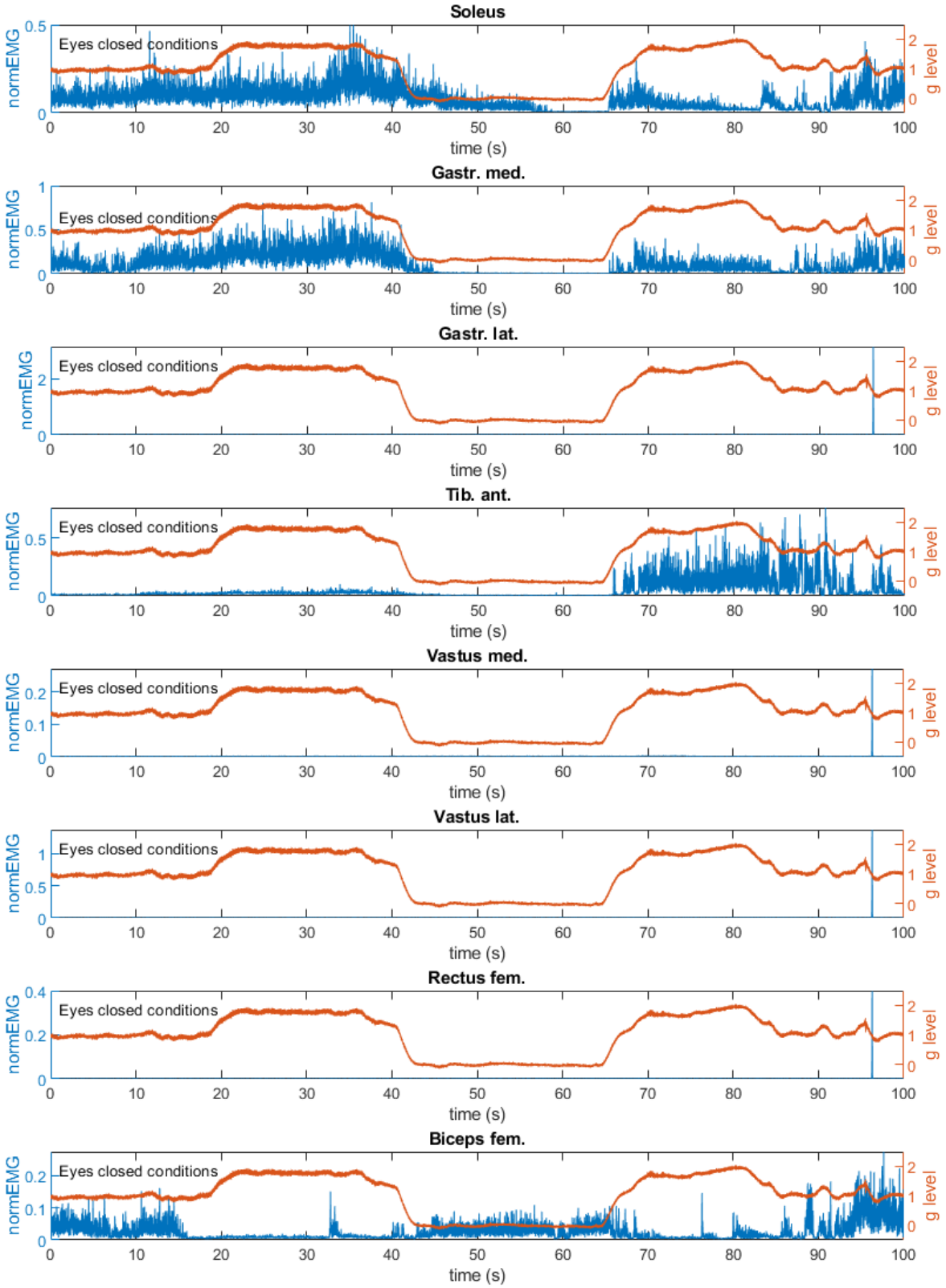

Fig. 5: EMG of muscles of the right shank and the right thigh [in blue] and g level [in orange] in eyes closed conditions.

$$n_1 \geqslant \frac{|\log(0,01)^{1/2}|}{\log(\frac{1000}{650})} \approx 5,3;\ n_2 \geqslant \frac{|\log(0,01)^{1/2}|}{\log(\frac{20}{20/2})} \approx 3,3;\ n_3 \geqslant \frac{\log(0,01)^{1/2}}{\log(\frac{1000}{30})} \approx 0,7.$$

EMG activity of all eight muscles, except rectus femoris, in both visual conditions [eyes open or closed] were normalized to EMG during a maximal isometric voluntary contraction [see Waldvogel et al. (2021) for details]. For rectus femoris, the value of the EMG signal for the maximal isometric voluntary contraction significantly exceeded EMG during normal standing. In this case, maximal EMG during a countermovement jump studied by Waldvogel et al. (2021) was taken for the signal normalization. Electromyographic activity is represented in Figs. 4 and 5. Please notice that activity of gastrocnemius lateralis, vastus medialis, vastus lateralis and rectus femoris in eyes closed conditions is absent on recordings.

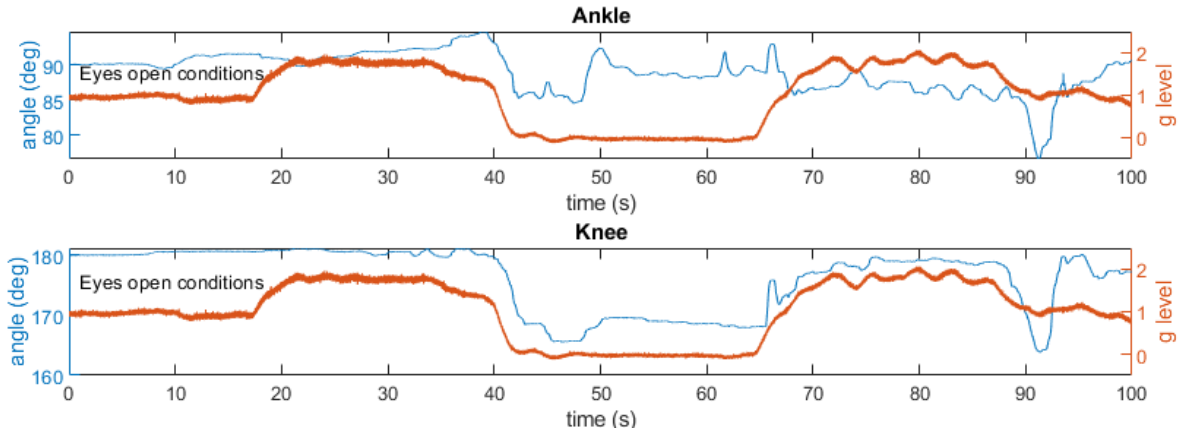

Fig. 6: Joint angles [right ankle and knee] and g level in eyes open conditions. A decrease in the ankle angle means a plantar flexion, an increase means a dorsal extension; a decrease in the knee angle means a knee flexion, an increase means a knee extension.

The first 100 s of the recording in eyes-open conditions and the time period from 23 to 123 s of the recording in eyes-closed conditions were taken for further analysis. Time intervals for both visual conditions included the whole parabola, i.e. periods of normogravity [prior to the parabolic maneuver], both overloading periods and the period of weightlessness between them [Figs. 4 and 5].

Accelerometer data [g level] were smoothed with the moving average [over 250 ms, i.e. 500 samples, following EMG smoothing].

Joint angles data were smoothed with the moving average [over 250 ms, i.e. 500 samples, following EMG smoothing] and are presented in Fig 6 and 7.

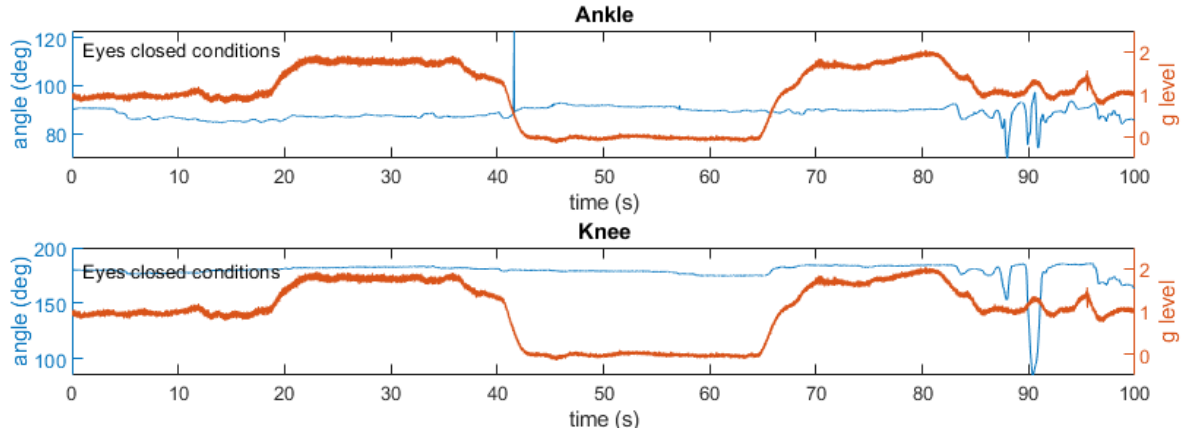

Fig. 7: Joint angles [right ankle and knee] and g level in eyes closed conditions. A decrease in the ankle angle means a plantar flexion [an increase means a dorsal extension]; a decrease in the knee angle means a knee flexion [an increase means a knee extension].

It is worth noting that joint angles in Figs. 6 and 7 represent rather general changes in joint kinematics. They are not precise due to a too close placement of the camera [1 m to the subject] and due to a quite strong subject's foot eversion/pronation [what can be seen on the video of the experiment].

Data analysis

For the further analysis, 100-second time intervals mentioned above were divided into 0,1-second subintervals and mean normalized EMG values for all considered muscles were calculated for each subinterval. The latter was calculated as the integral [trapezoid method] of the normalized EMG signal divided by the length of the subinterval [i.e. 0,1 s; in the following formula, $t_{i,0}$ and $t_{i,1}$ stand for the ends of the i-th time subinterval, $i = \overline{1, 1000}$]:

$$EMG_{norm,mean,i} = \frac{1}{t_{i,1} - t_{i,0}} \int_{t_{i,0}}^{t_{i,1}} EMG_{norm}(t)dt.$$

Then, three 9-second time periods corresponding to three different g levels were taken for each condition: 0-9 s [1g], 21,5-30,5 s [1,8g] and 46-55 s [0g] for eyes open and 0-9 s [1g], 22,5-31,5 s [1,8g] and 47,5-56,5 s [0g] for eyes closed. Mean values of the normalized EMG signal were then considered as a random variable, and Krauskal-Wallis test was applied to this variable in order to test differences in the EMG signal at the given time periods. Wilcoxon rank sum test was applied to the pairs of conditions [1g vs. 1,8g, 1g vs. 0g, 2g vs. 0g], when Krauskal-Wallis test showed an influence of

g level.

As the next step, when appropriate, a linear regression model was applied to all EMG subintervals [i.e. to mean normalized EMG over 0,1 s] in order to investigate how EMG activity changes in concordance with changes in g level.

After that, muscle coactivation was evaluated by means of a linear regression model analogous to Nashner (1977). This was made for muscles considered from the classical anatomical standpoint as agonists and antagonists acting around a joint [triceps surae and tibialis anterior, quadriceps femoris and biceps femoris]. The same was made for the pair of quadriceps femoris and tibialis anterior and for the pair of triceps surae and biceps femoris that could potentially coactivate in order to stop swaying backward and to initiate swaying forward and vice versa, respectively. In eyes open conditions, this analysis was performed for all combinations of muscles making up corresponding muscle groups, as well as for their summed activity. In eyes closed conditions, the assessments were made only for the pair soleus and tibialis anterior and for the pair soleus and biceps femoris due to issues mentioned in section 3.1.

3.2 Results

Eyes open conditions

For all eight muscles Krauskal-Wallis test showed an influence of g level [$p < 0,001$]. Wilcoxon rank sum test used as a *post hoc* test with the Bonferroni correction showed significant differences [$p < 0,00033$] for all pairs of g levels for all muscles except 2g vs. 0g for vastus medialis [$p = 0,658$] and rectus femoris [$p = 0,257$].

EMG activity of all plantarflexors [ankle extensors] increased in overloading, but an increase relative to normogravity was much more pronounced in fast-twitch two-joint gastrocnemii [approximately 9 times] in comparison with slow-twitch one-joint soleus [approximately 1,5 times]. In weightlessness, EMG activity of plantarflexors was lower relative to normogravity [about 2-3 times in gastrocnemii and about 11 times in soleus]. Two-joint biceps femoris [hip extensor and knee flexor] demonstrated similar behavior: its activity was slightly higher in overloading [about 1,1 times] and was depressed in weightlessness [about 4,5 times].

The reaction of tibialis anterior [dorsi-/ankle flexor], rectus femoris [hip flexor and knee extensor] and both vasti [knee extensors] to changed force conditions was dif-

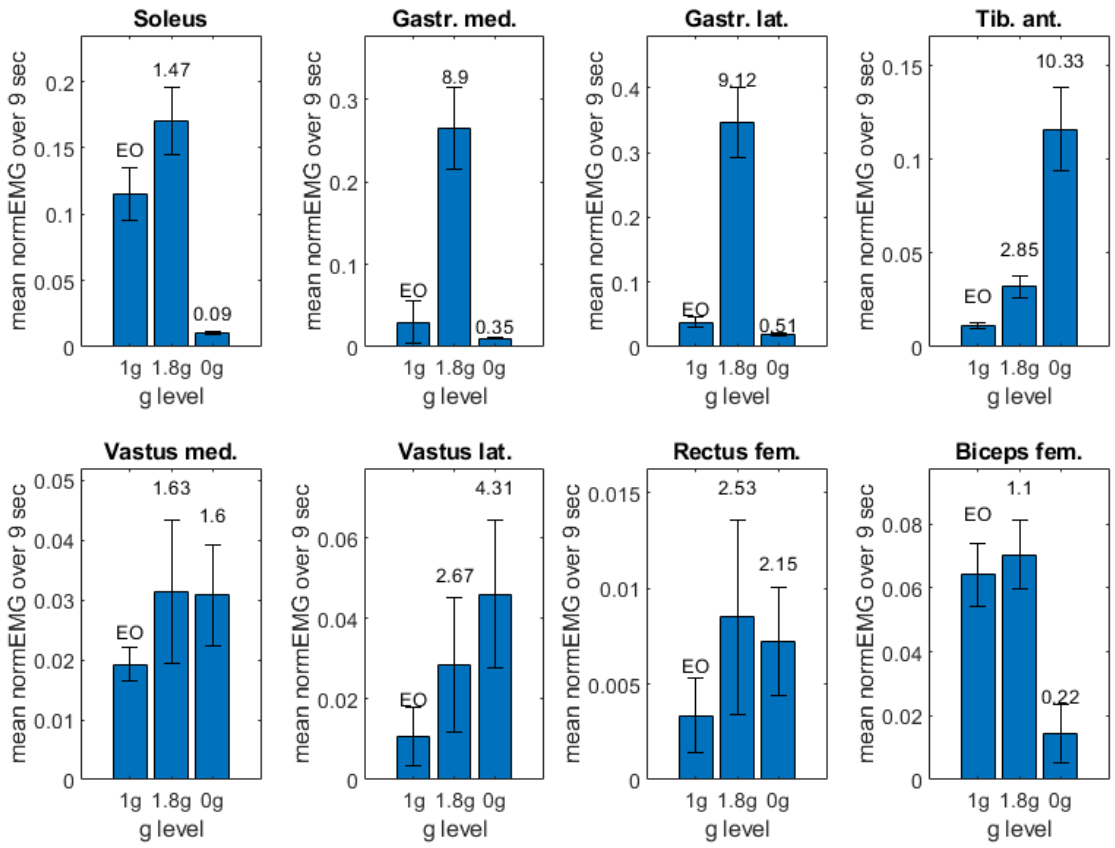

Fig. 8: Mean EMG values for different g levels in eyes open conditions. ”EO” above the left bar denotes ”eyes open”. Numbers above the central [1,8g] and right bars [0g] are the proportions of the corresponding EMG values to the EMG value in normogravity [1g, left bar].

ferent in comparison to that of hip and ankle extensors. Their activity in both altered conditions was heightened. Increases were equally high for both changed force conditions in vastus medialis [approximately 1,6 times], as well as in rectus femoris [approximately 2,2-2,5 times]. Tibialis anterior and vastus lateralis were stronger activated in weightlessness than in overloading [correspondingly about 10 and 2,8 times for tibialis anterior and 4,3 and 2,7 times for vastus lateralis]. The results for all muscles are presented in Fig. 8.

Monotonic changes in EMG activity of soleus, gastrocnemii and biceps femoris in dependence on g level allowed to apply a linear regression model to these muscles' activity [Fig. 9]. The goodness of fit was from very low for biceps femoris [$R^2 = 0,043$, $p < 0,001$] to moderate for soleus [$R^2 = 0,349$, $p < 0,001$], gastrocnemius medialis [$R^2 = 0,462$, $p < 0,001$] and lateralis [$R^2 = 0,431$, $p < 0,001$].

No significant coactivation of either quadriceps femoris and tibialis anterior or triceps surae and biceps femoris were observed [R^2 did not exceed 0,168 for any mus-

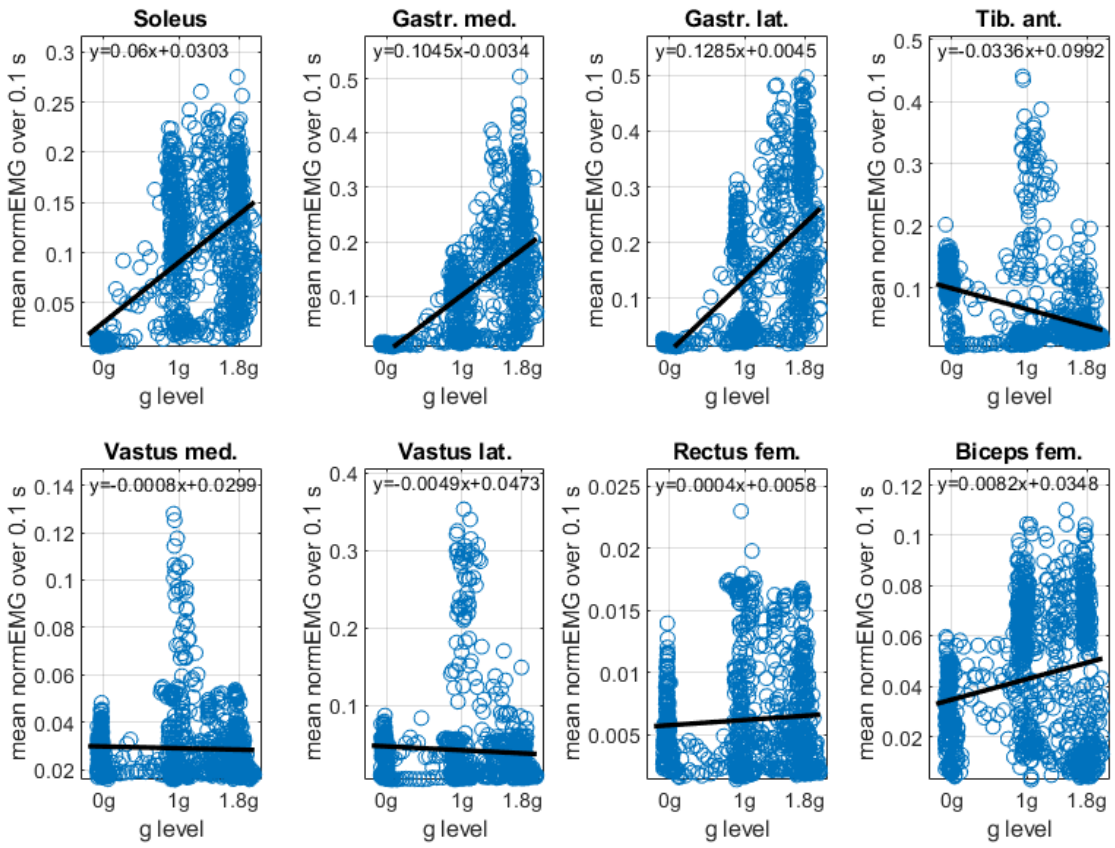

Fig. 9: Mean EMG values for different g levels and linear regression models in eyes open conditions. The equation of each linear regression model is given on the top of the corresponding graph.

cle pair in any gravitational condition]. In the case of agonist-antagonist coactivation, weak correlation was observed for the pair of soleus and tibialis anterior for 1g [$R^2 = 0,272$, $p < 0,001$], for the pair of gastrocnemius medialis and tibialis anterior for 1g [$R^2 = 0,268$, $p < 0,001$] and for 0g [$R^2 = 0,212$, $p < 0,001$] and for the pair of triceps surae [summed activity] and tibialis anterior for 1g [$R^2 = 0,371$, $p < 0,001$] and for 0g [$R^2 = 0,211$, $p < 0,001$]. Moderate correlation was observed between gastrocnemius lateralis and tibialis anterior in normogravity [$R^2 = 0,508$, $p < 0,001$]. For other muscle pairs for other g levels correlation was very low [R^2 did not exceed 0,173].

Eyes closed conditions

For all four muscles Krauskal-Wallis test showed an influence of g level [$p < 0,001$]. Wilcoxon rank sum test used as a *post hoc* test with the Bonferroni correction showed significant differences [$p < 0,00033$] for all pairs of g levels for all muscles except 1g vs. 0g for biceps femoris [$p = 0,591$].

EMG activity of ankle flexors in eyes closed conditions was qualitatively similar to that

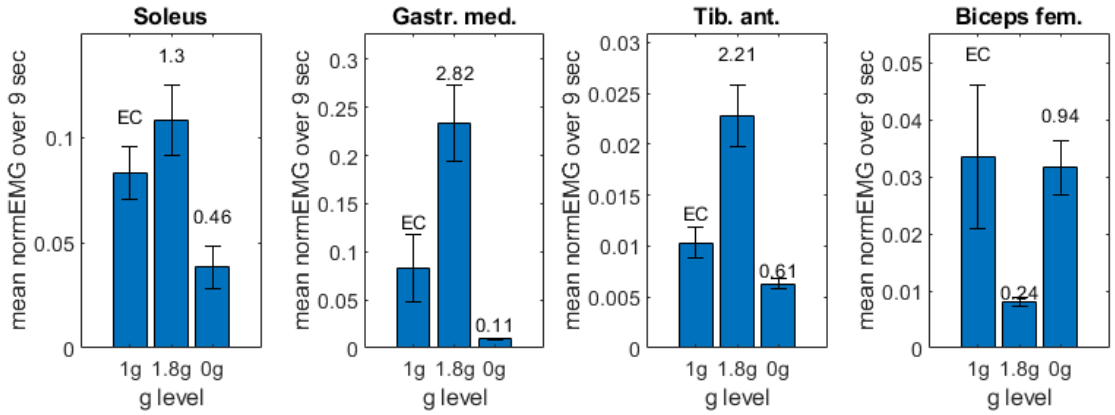

Fig. 10: Mean EMG values for different g levels in eyes closed conditions. ”EC” above the left bar denotes ”eyes closed”. Numbers above the central [1,8g] and right bars [0g] are the proportions of the corresponding EMG values to the EMG value in normogravity [1g, left bar].

with eyes open. However, an increase of the EMG signal from soleus in overloading and its decrease in weightlessness were milder [1,3 and 2,2 times respectively]. An increase of activity of gastrocnemius medialis was 2,8-folded in overloading relative to normogravity, and a decrease in weightlessness was approximately 9-folded.

Tibialis anterior and biceps femoris reacted differently in eyes closed conditions compared to eyes open conditions. The former was stronger activated in overloading [2,2 times] and somewhat inhibited in weightlessness [1,6 times]. The latter was inhibited in overloading [4,2 times], but its activity in weightlessness was equal to that in normogravity. The results are shown in Fig. 10.

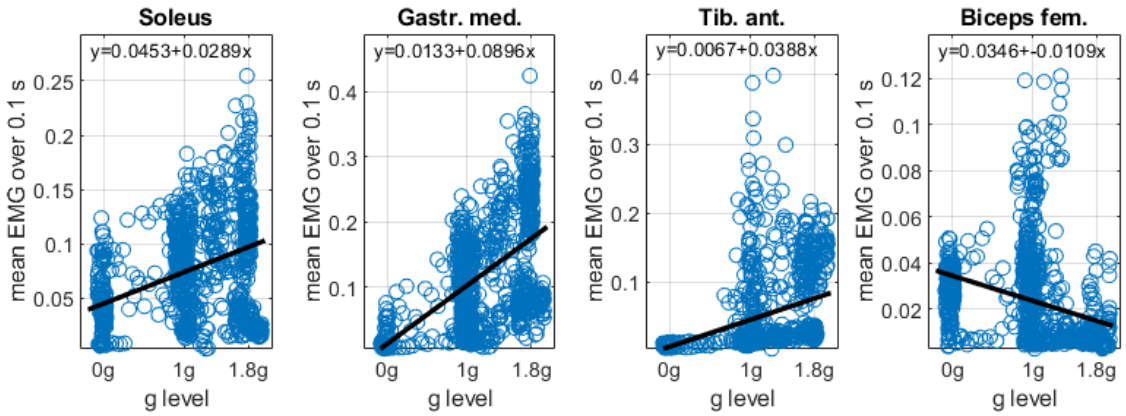

Fig. 11: Mean EMG values for different g levels and linear regression models in eyes closed conditions. On the top of the graph, the equation of the linear regression model is given.

These observations showed that a linear regression model can be used in the case of the shank muscles [Fig. 11]. For soleus and tibialis anterior the goodness of fit

is rather weak [$R^2 = 0,165$, $p < 0,001$ for soleus $R^2 = 0,187$, $p < 0,001$ for tibialis anterior], but for gastrocnemius medialis the goodness of fit is moderate [$R^2 = 0,440$, $p < 0,001$].

The analysis of muscle coactivation revealed only weak correlation between activities of soleus and tibialis anterior in weightlessness [$R^2 = 0,208$, $p < 0,001$]. In other cases, R^2 did not exceed 0,132.

Comparison of different visual conditions

By comparing muscle activity [of four muscles] in different visual conditions, one can see that muscles had different activity level from the beginning of the measurements. In normogravity, soleus, tibialis anterior and biceps femoris were stronger activated in the presence of vision [1,4, 1,1 and 1,9 times stronger respectively, Wilcoxon rank sum test, $p < 0,001$ in all cases]. Higher activity in these muscles in eyes open conditions was preserved in overloading [1,6, 1,4 and 8,7 times higher respectively, Wilcoxon rank sum test, $p < 0,001$ in all cases]. This is also true for tibialis anterior in weightlessness [18 times higher activity with eyes open]. EMG activity of soleus and biceps femoris in weightlessness was higher with eyes closed [3,7 and 2,2 times higher, Wilcoxon rank sum test, $p < 0,001$ in both cases].

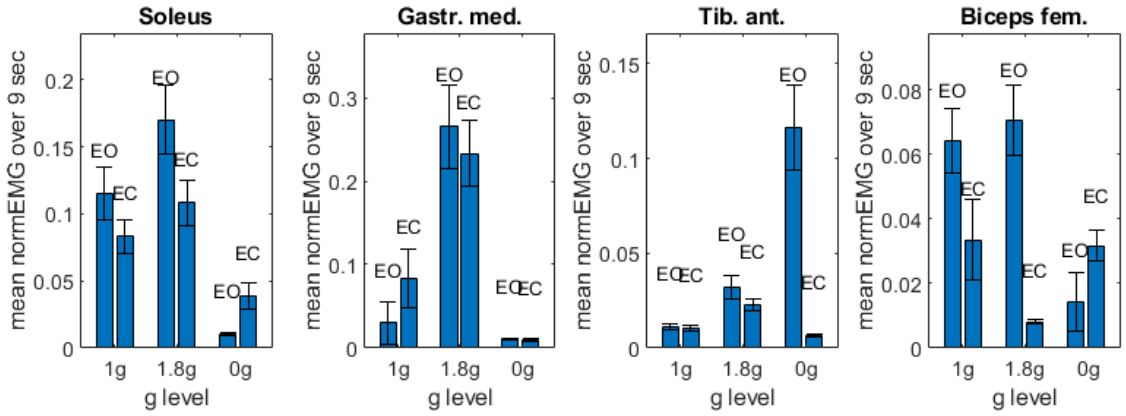

Fig. 12: Comparison of mean EMG values for different g levels. ”EO” and ”EC” above the bars denote ”eyes open” and ”eyes closed”, respectively.

Activity of gastrocnemius medialis in normogravity was stronger [2,8 times, Wilcoxon rank sum test, $p < 0,001$] when the subject stayed with eyes closed, but became slightly higher in eyes open conditions both in overloading [1,1 times, Wilcoxon rank sum test, $p < 0,001$] and in weightlessness [1,1 times, Wilcoxon rank sum test, $p < 0,001$]. The

results are summarized in Fig. 12.

3.3 Discussion

The aim of the data analysis was to estimate changes in electrophysiological activity of subject's leg muscles and a degree of these changes in conditions of altered apparent gravity.

In the case of eyes open conditions, one can see that tonic activity of plantarflexors rises with an increase of g level and is significantly decreased in weightlessness relative to normogravity. EMG activity of the dorsiflexor tibialis anterior is heightened both in overloading and weightlessness, with much stronger activation in weightlessness. EMG activity of knee and hip extensors was also heightened in overloading. After the transition from 1,8g to 0g flight phase, EMG activity of knee extensors stayed unchanged or increased while EMG activity of the hip extensor biceps femoris significantly decreased [Fig. 8].

It is worth noting that the activity of all muscles investigated was far from their maximum. Gastrocnemius lateralis in overloading was activated the most, reaching about 35% of its maximum. At the same time, muscle activation measurement during maximal voluntary contractions used in Waldvogel et al. (2021) as suggested by Roelants, Verschueren, Delecluse, Levin, and Stijnen (2006) and Wiley and Damiano (1998) were performed unilaterally. Given possible effects of bilateral deficit (Škarabot, Cronin, Strojnik, & Avela, 2016), normalized muscle activity in the described experiment would be likely higher if maximal voluntary contractions were performed with both extremities simultaneously. Moreover, in the papers cited above, maximal voluntary contractions were measured when the knee was flexed. Thus, quadriceps femoris was activated at the length close to its optimal sarcomere length and could contract stronger than with the knee extended (Becker & Awiszus, 2001). The subject also knew that he is attached to the aircraft cabin, i.e. the initial support also could attenuate the EMG responses (Horak et al., 1997).

Muscle coactivation and dependence of EMG activity on g level were studied here by using the linear regression model. This method does not account for some possible variations in latencies of mutual activity in the complex muscle system. Thus, it is perhaps not suitable for unveiling the real structure of muscle coactivation during standing in comparison with perturbation tasks (Nashner, 1977). Actual dependence of EMG

activity on g level can be in principle non-linear.

Visual conditions also influenced muscle activity, typically leading to stronger muscle activations in eyes open conditions. Among few exceptions are activations of soleus and biceps femoris in weightlessness and activation of gastrocnemius in normogravity. In these cases muscles were activated stronger in eyes closed conditions.

Overloading conditions

Our observations regarding activity of soleus and tibialis anterior agree with the observations of Clement and André-Deshays (1987) in parabolic flight. Heightened activity of plantarflexors in overloading can be explained by the increased forward toppling torques around talocrural joints. These torques act on the body center of mass due to the fact that its vertical projection is about 4,5 cm in front of talocrural joints (Gurfinkel, Kotz, & Shik, 1965, pp. 15-18). They are probably the main stimulus for the activity of calf muscles (Masani, Sayenko, & Vette, 2013). A very strong change in activity of gastrocnemii in overloading is accompanied by higher activity of vasti and rectus femoris. This can indicate increased torques acting around the knee leading to higher muscle force needed to keep it extended during upright standing. Stronger activation of biceps femoris can be similarly explained by increased hip torques in overloading. Thus, increased activity of all leg muscles tested can indicate increased stiffness of all three main leg joints. Since application of the linear regression model was not very successful in the investigation of the structure of muscle activity, the latter was additionally studied by means of computing of coactivation indices (Osternig, Hamill, Lander, & Robertson, 1986) and by means of the uncontrolled manifold analysis (Latash, Scholz, & Schöner, 2002, 2007).

Coactivation index is normally computed in dynamic tasks where muscles can be more or less unambiguously characterized as agonists and antagonists. During standing, it is not always easy to say which muscle acts as agonist and which as antagonist. This arrangement seems to be clear in case of the soleus-tibialis pair (Masani et al., 2013) but is questionable in case of multi-joint muscles such as rectus femoris and biceps femoris. Nevertheless, this method could be helpful for better understanding of mutual muscle activity in postural tasks. According to Osternig et al. (1986), the level of agonist [AG] and antagonist [ANT] muscle coactivation [coactivation index, CI] can

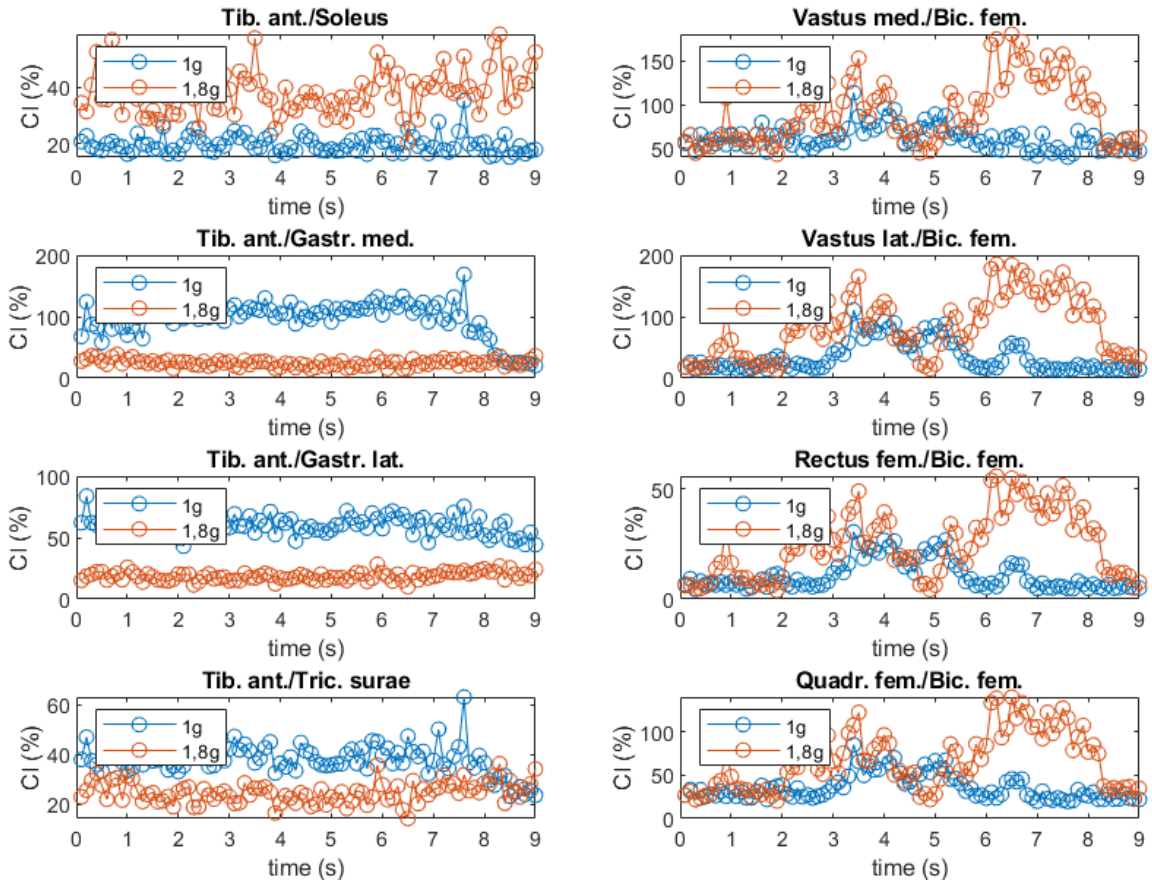

Fig. 13: Coactivation indices [CI] of EMG activity over 0,1-second time intervals computed for tibialis anterior and muscles comprising triceps surae, as well as for biceps femoris and muscles comprising quadriceps femoris.

be calculated as follows:

$$CI = \frac{EMG_{AG}}{EMG_{ANT}} \cdot 100\%.$$

Computations showed that the level of coactivation of tibialis anterior and soleus increased in overloading in comparison to normogravity [1g: 19,8±3,2, 1,8g: 38,3±7,8, $p < 0,001$], while coactivation of tibialis anterior and gastrocnemii decreased with the g level increase [1g: 97,0±29,4, 1,8g: 24,8±5,5, $p < 0,001$ for gastrocnemius medialis and 1g: 60,0±7,5, 1,8g: 18,7±3,4, $p < 0,001$ for gastrocnemius lateralis]. The index of coactivation of tibialis anterior and average activity of muscles comprising triceps surae also decreased in overloading [1g: 38,0±6,2, 1,8g: 24,7±4,3, $p < 0,001$]. Coactivation indices of biceps femoris and each of the thigh muscle, as well as their mean activity, increased with the increase of g level: 1g: 61,5±13,7, 1,8g: 90,7±36,7, $p < 0,001$ for vastus medialis; 1g: 34,6±24,8, 1,8g: 82,9±49,8, $p < 0,001$ for vastus lateralis; 1g: 10,9±6,8, 1,8g: 24,6±15,0, $p < 0,001$ for rectus femoris; 1g: 35,7±14,6, 1,8g: 66,1±33,6, $p < 0,001$ for average activity of quadriceps femoris. In all cases, mean

coactivation indices in 1g and 1,8g were compared using Wilcoxon rank sum test. Values of coactivation indices of the normalized EMG averaged on 0,1 s time intervals are shown in Fig. 13 [values exceeding 100% could be explained by imperfection of EMG normalization procedure].

As seen in Fig. 13, the level of coactivation of soleus and tibialis increased in overloading. At the same time, coactivation index of tibialis anterior and triceps surae [averaged activity] is higher in normogravity due to strong activation of gastrocnemii. This could indicate that the nervous system strives to increase stability in more challenging conditions of overloading, on the one hand, and to increase flexibility of control of the ankle joint, on the other hand. However, the real picture can possibly be hidden because other dorsiflexors were not considered in the experiment. One can also notice [Figs. 8 and 13 and the data above] that activity of particular muscles comprising quadriceps femoris as well as their average activity increased stronger with the increase in g level than activity of biceps femoris. This could point out that there is a tendency to keep the knee more extended in overloading and to allow more support to biceps femoris for its stronger activation and for keeping the hip extended.

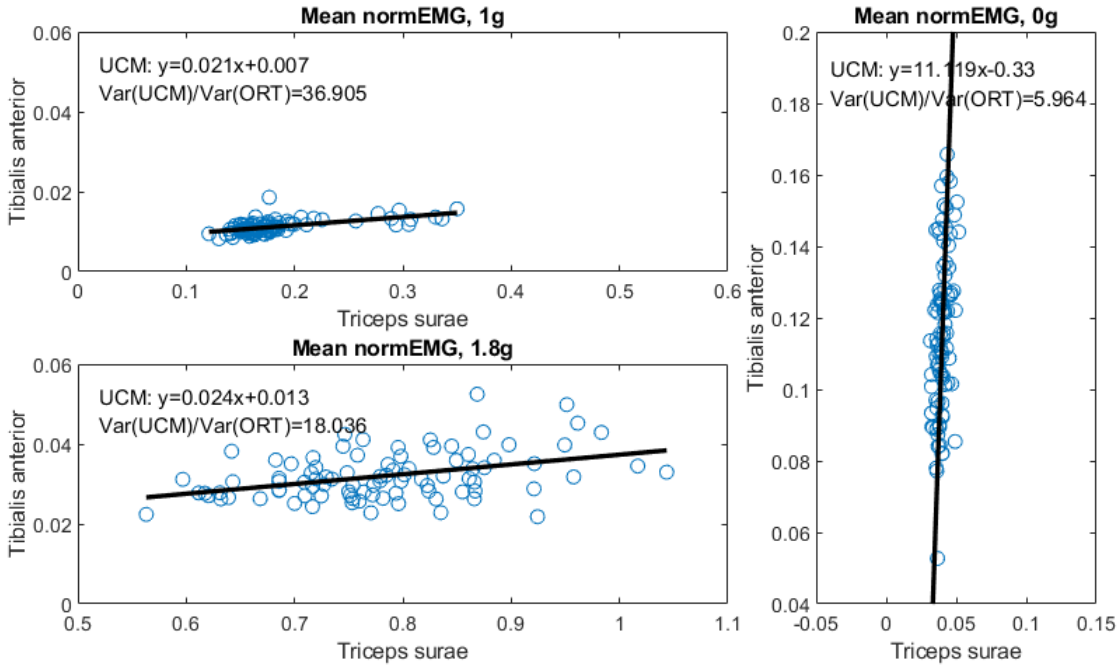

Fig. 14: Application of principal component analysis in order to identify the uncontrolled manifolds (black straight lines) of activity of tibialis anterior and sum activity of triceps surae in eyes open conditions.

The uncontrolled manifold analysis showed that the central nervous system seemingly preserves the same control strategies of the hip, knee and ankle joints in over-

loading as in normogravity, since uncontrolled manifolds (Latash et al., 2002, 2007) in these cases are the same or very similar [Figs. 14 and 15]. However, the index of the synergy [computed as a quotient of variances along the uncontrolled and orthogonal manifolds] (Latash et al., 2007) decreased for the ankle joint [Fig. 14] and increased for the knee and hip joints [Fig. 15]. This corroborates the suggestion made above that the nervous system strives for more stability in the hip and knee joints and allows more flexibility in control of the ankle joint. Such strategy of sway control in overloading resembles the ankle strategy of equilibrium control during translational perturbations observed in laboratory conditions on earth (Horak & Nashner, 1986; Horak et al., 1997; Horak, 2006). These findings also agree with the suggestion regarding the existence of two control subsystems in maintenance of body posture: conservative and operative (Lestienne & Gurfinkel, 1988b; Zatsiorsky & Duarte, 2000).

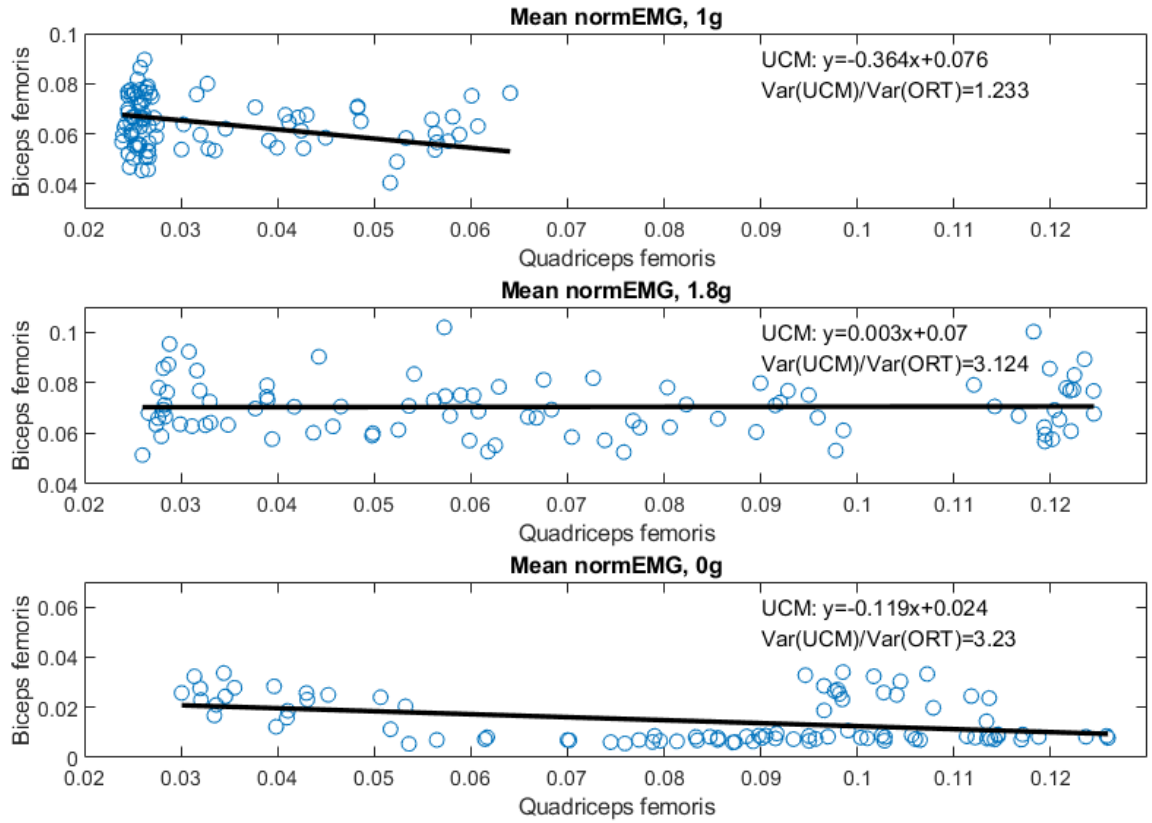

Fig. 15: Application of principal component analysis in order to identify the uncontrolled manifolds (black straight lines) of activity of biceps femoris and sum activity of quadriceps femoris in eyes open conditions.

Furthermore, a smaller index of the ankle synergy and a larger index of the knee/hip synergy could point out single-link-inverted-pendulum-like sway behavior around the ankle joints. Together with increased toppling torques, this could lead either to a larger

amplitude of involuntary sway in the anteroposterior direction or to accelerated sway, or both. [Unfortunately, recordings from the force platform in the horizontal plane were not provided to be able to prove or disprove this conjecture.] Increased body sway during bipedal upright stance while holding a considerable additional load placed at the level of the body center of mass can be observed (Costello, Matrangola, & Madigan, 2012; Wojciechowska-Maszkowska & Borzucka, 2020). Oscillations of the center of pressure were also shown to get faster even under more moderate additional loading (Qu & Nussbaum, 2009; Costello et al., 2012; Wojciechowska-Maszkowska & Borzucka, 2020). In both cases [increased amplitude or velocity of sway], changes in sway behavior could help the nervous system gain additional information about changes in the external force field. Although increases in sway amplitude and velocity can be of a purely mechanistic nature, the nervous system can allow increased values of sway variables. This sounds reasonable if one assumes that sway might represent a purposeful mechanism employed by the nervous system for posture control (Van Emmerik & Van Wegen, 2002). Decomposition of the trajectory of the center of pressure showed that the nervous system can possibly set a referent trajectory of the body center of mass with the vertical projection within the base of support (Zatsiorsky & Duarte, 2000). Setting a referent sway trajectory during standing could be useful for keeping muscles contracting and, by that, to attenuate Ib inhibition [see section 2.3] or/and to adjust muscle stiffness in an anticipatory manner (Loram et al., 2004). That is, combination of active control of a referent trajectory and passive control of smaller deviations from this trajectory might be more optimal/balanced than only active control of larger deviations occurring due to external forces and due to ”sloppiness” of sensory information and control of multiple motor units. Such features of upright posture control as increased amplitude or velocity of body sway could be allowed by the nervous system in order to involve proprioceptors and cutaneous and subcutaneous receptors of the sole of the foot more intensively. This gain in sensory information could lead, in its turn, to a stronger activation of postural muscles and could be hypothetically needed to modulate sub-threshold pre-activation of spinal networks participating in anticipatory postural adjustments and balance-maintaining motor actions.

It is also worth mentioning that observed changes in EMG in overloading are consistent with the findings described in section 2.3 and suggest that both Golgi tendon organs and foot receptors serve in this case as load receptors. So, increased toppling

torques might increase tension in plantarflexors (Masani et al., 2013) and in knee and hip extensors. Increased tension force in soleus might facilitate activity of tibialis anterior [and of extensor digitorum longus] (Nichols et al., 2016). Cutaneous receptors of the foot sole may also participate in facilitation of anti-gravity [extensor] muscles (Duysens et al., 2000; Fallon et al., 2005; Smith et al., 2020). One further indication thereof is single-link-pendulum-like sway behavior similar to that during small postural equilibrium perturbations (Horak & Nashner, 1986; Horak et al., 1990; Horak & Moore, 1993).

Weightlessness conditions

Transition from overloading to weightlessness in parabolic flight was accompanied by almost complete and immediate deactivation of plantarflexors and strong activation of tibialis anterior within a second after reaching the state of weightlessness. Activity of quadriceps femoris stayed increased, and activity of biceps femoris became lower. These observations are similar to those made by Clement and André-Deshays (1987) in parabolic flight and by Clement et al. (1984) during a space mission.

It is worth mentioning that the subject in the described experiment [section 3.1] was not firmly attached to the floor during the transition from overloading to weightlessness [can be seen on the video of the the experimenter]. Plantar- and knee flexion observed immediately after the transition [Fig. 6] could be explained by a stronger activation of triceps surae during the presiding 1,8g phase, and/or by passive forces of elastic components of the same muscle (Clement & André-Deshays, 1987). After the subject was pulled down by the experimenter, the ankle angle returned to the value close to that measured during normogravity and overloading and the knee angle was also partially restored [Fig. 6]. It is also important to note that in the given experiment the subject's pose was hold orthograde by a harness connecting the trunk to the cabin of the aircraft. If only feet were connected to the surface, the subject would probably first tilt backward (Clement & André-Deshays, 1987). In the same study, following forward tilt together with activation of tibialis anterior was also observed in weightlessness. Moreover, this forward tilt was consciously perceived by subjects as exaggerated. This percept served possibly as a stimulus for attenuated activity and earlier activation of tibialis anterior after some parabolas were flown (Clement & André-Deshays, 1987).

This happened perhaps due to a direct and stronger cortical modulation of this muscle (Brouwer & Ashby, 1992; Solopova et al., 2003; Lauber, Gollhofer, & Taube, 2018). This led to the restoration of upright posture in weightlessness (Clement & André-Deshays, 1987). The same tendency to acquire a new posture control strategy with weaker activation of tibialis anterior [and quadriceps femoris] can also be observed in space flight (Clement et al., 1984).

A strong increase in activity of tibialis anterior might point out its tonic stimulation and continuous control by supraspinal neural networks that could be especially beneficial for obstacle avoidance during locomotion and for locomotion stability (Grillner & El Manira, 2020). This could be also a result of a decrease in inhibition from active plantarflexors occurring during standing. A similar effect [an exaggerated ankle joint flexion] can be observed during locomotion after cutting the tibial nerve (Pearson, Misiaszek, & Fouad, 1998).

Different UCMs in weightlessness compared with normogravity and overloading can indicate that the nervous system is much more adapted to load increasing than to unloading and passes into a learning mode in order to acquire new control strategies in unusual conditions.

4 Foot receptors in equilibrium control

Based on the discussed in section 3.3, it would be reasonable to assume that cutaneous feedback serves the purpose of stabilization of upright posture and withstanding possible perturbations. Moreover, increased or accelerated sway can be considered as a purposeful mechanism (Zatsiorsky & Duarte, 2000; Van Emmerik & Van Wegen, 2002; Loram et al., 2004) aimed at gaining more information at least in the beginning phase of acquisition of a new control strategy in a new environmental context. Besides that, an increase in sway velocity could be the primary mechanism used to increase volume of sensory information from foot and to suppress Ib inhibition (Duysens et al., 2000). The last conjecture agrees with the observation of Fallon et al. (2005) that leg muscle activity is mainly modulated by stimulation of rapidly-adapting cutaneous receptors.

Below we take a closer look at some studies in which perturbations of standing balance and modulation of sensory signals from cutaneous foot receptors are used

in order to reveal neural principles of equilibrium control. We consider two types of studies: (i) with translational and rotational perturbations in the sagittal plane without stepping; (ii) with direct cutaneous stimulation or foot anesthetizing in healthy subjects. Studies described below were mainly taken from the reference lists in Rasman, Forbes, Tisserand, and Blouin (2018), Dietz and Duysens (2000) and Horak et al. (1997).

4.1 Translational and rotational perturbations

The analysis of perturbation studies shows that medium- and long-latency responses after equilibrium disturbances seem to be rather not task-specific [rotation vs. translation]. The type of perturbation influences the appearance of short-latency responses in triceps surae that occur about 40-60 ms after the onset of the external dorsiflexion (Diener, Bootz, Dichgans, & Bruzek, 1983; Allum, 1983; Keshner, Allum, & Pfaltz, 1987; Dietz et al., 1992; Allum & Honegger, 1998; Carpenter, Allum, & Honegger, 1999). Short-latency responses are absent after translational perturbations (Nashner, 1977; Horak & Nashner, 1986; Dietz et al., 1992; McIlroy & Maki, 1993; Horak & Moore, 1993; Torres-Oviedo & Ting, 2007). Irrespective of the perturbation type, tibialis anterior and thigh and trunk muscles activate at latencies from 60 to 130 ms depending on the muscle and foot pre-loading conditions. Plantar- and dorsiflexors also activate almost always at latencies 75-130 ms (Nashner, 1977; Diener et al., 1983; Allum, 1983; Horak & Nashner, 1986; Keshner et al., 1987; Dietz et al., 1992; McIlroy & Maki, 1993; Horak & Moore, 1993; Allum & Honegger, 1998; Carpenter et al., 1999) and typically simultaneously with leg and trunk muscles or 20-30 ms prior to them (Nashner, 1977; Horak & Nashner, 1986; Keshner et al., 1987; Horak & Moore, 1993; Allum & Honegger, 1998; Carpenter et al., 1999). Such latencies and activation time lags indicate that muscle activity is not caused by chain-wise stretch reflexes but rather by ”pre-programmed” balance-maintaining whole-body reactions. These reactions are triggered by a perturbation and seemingly depend on its characteristics such as amplitude, velocity and possibly acceleration (Horak & Nashner, 1986; Allum & Honegger, 1998) as well as on characteristics of the support surface (Horak & Nashner, 1986; Horak & Moore, 1993). This dependence must manifest itself in somewhat different patterns of activations of upper leg and truck muscles. This difference is also likely to be individual-specific.

Manipulations with muscle and foot pre-loading before the perturbation onset also influence activation patterns. Pre-loading typically shortens activation latencies and

changes EMG magnitude. Muscles of the dorsal side of the body show quicker and stronger responses after external toe-up rotations and backward translations with prior pre-loading by means of forward tilts (Diener et al., 1983; Horak & Moore, 1993) and after combinations of toe-up rotations and backward translations (Allum & Honegger, 1998). Backward leaning prior to the perturbation leads to quicker and stronger activations of ventral muscles (Allum, 1983; Horak & Moore, 1993; Allum & Honegger, 1998). Forward tilts [and combinations of rotational and translational perturbations] and backward tilts have typically the opposite effect on muscles of the ventral and dorsal side of the body, respectively (Diener et al., 1983; Allum, 1983; Horak & Moore, 1993; Allum & Honegger, 1998). This holds true for both short-latency responses and medium-/long-latency responses. However, when the pre-loading is too strong and when the subject reaches the boundaries of the base of support during leaning, the effects of pre-loading can be reversed (Horak & Moore, 1993).

Two ”polar” types of reaction strategies in response to translational perturbation were described: ankle and hip strategies [Fig. 16]. Ankle strategy is described as [medium-latency] activation of muscles of the dorsal or ventral part of the body in order to counteract forward or backward tilts, respectively. During that, posture stays erect. This strategy is observed during perturbations of moderate amplitudes and velocities (Horak & Nashner, 1986; Horak & Moore, 1993; Horak et al., 1997). Hip strategy is associated with [medium-latency] activation of abdominal muscles and hip flexors during backward platform translations and with activation of back muscles and hip extensors/knee flexors during forward platform translations. This strategy is observed during perturbations of large amplitudes and velocities and during perturbations on small surfaces (Horak & Nashner, 1986; Horak et al., 1997). In some cases, balance maintenance strategy can have characteristics of both ankle and hip strategies (Horak & Nashner, 1986; Horak & Moore, 1993; Horak et al., 1997; Allum & Honegger, 1998). Thus, triggered postural reactions form a spectrum between ”pure” ankle and ”pure” hip strategies and depend on perturbation characteristics (Horak et al., 1997).

In the majority of the articles cited, it is suggested that the stretch of ankle flexors and extensors or tension created therein or stimulation of foot receptors can elicit automatic postural responses described above. However, the absence or negligibility of stretch reflex in any muscles after translational perturbations indicates rather that ten-

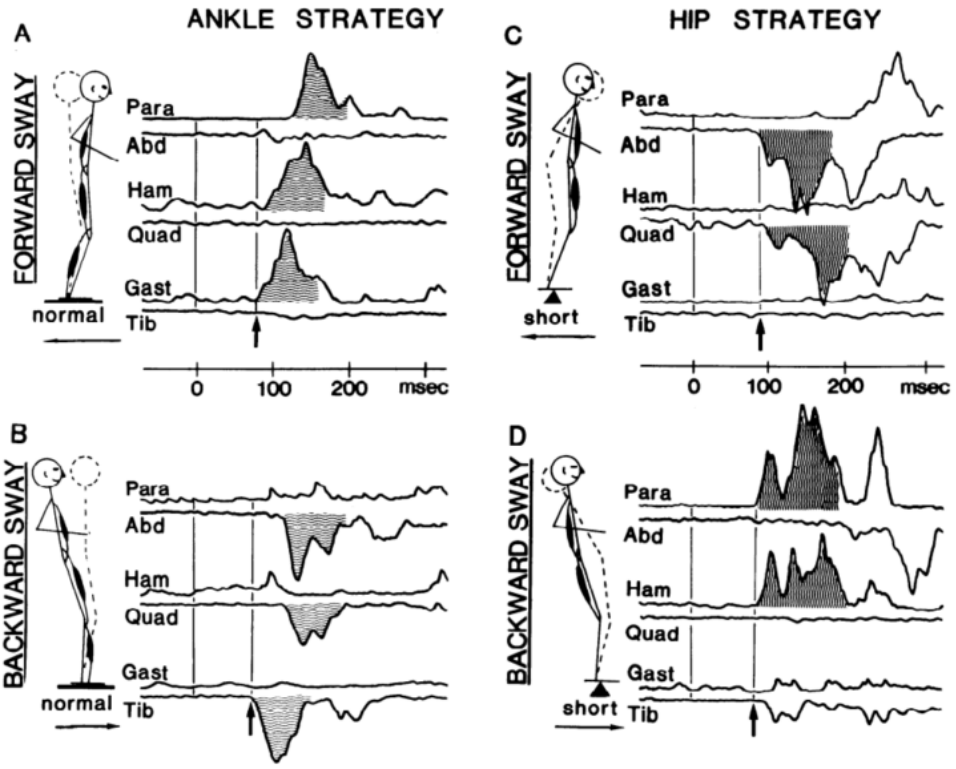

Fig. 16: A, B. Ankle strategy is elicited by backward [A] and forward [B] platform translations during standing on a large enough surface. This strategy is characterized by middle-latency activation of muscles of the dorsal or ventral side of the body. The body maintains balance by means of rotation around ankle joints while knee and hip joints stay extended. C, D. Hip strategy is elicited by backward [C] and forward [D] platform translations during standing on a narrow beam. In this case, abdominal and hip flexor muscles are activated after backward platform translation [C] and back and hip extensor muscles are activated after forward platform translations. Reprinted from Horak and Nashner (1986).

sion created at the muscle-tendon junction and pressure exerted to the plantar surface of the foot must play a dominant role in postural reactions than muscle stretch. This suggestion is corroborated by the observation that plantarflexors are shortened during swaying rather than stretched (Loram et al., 2004).

The results of the perturbation studies described in this section are also summarized and represented in Tables 2 and 3.

4.2 Modulation of cutaneous sensory feedback

As seen from sections 2.3 and 4.1, muscle spindles seem to play rather an auxiliary role in equilibrium control during standing. Thus, one can hypothesize that Golgi tendon organs and plantar foot receptors are in charge of balance maintenance. Let us now take a quick look at how modulation of sensory signals from foot receptors can influence muscle activity and body kinematics during standing.

Table 2: Overview of muscle activation latencies in perturbational studies described in section 4.1. Asterisk [*] denotes that a muscle/muscle head was not [exactly] specified. ”pre→” denotes changes in latencies if the muscle and the corresponding part of the feet were pre-loaded.

Study	Perturbation	Dorsiflexors	Plantarflexors	Knee flexors/ hip extensors	Knee extensors/ hip flexors	Back muscles	Abdominal muscles
Nashner (1977)		tibialis anterior:	gastr. medialis:	hamstring*:	quadriceps*:		
	backward translation	–	100 ms	113 ms	–		
	forward translation	100 ms	–	–	111 ms		
Diener et al. (1983)		tibialis anterior:	triceps surae*:				
	rotational dorsiflexion	128 ms	56 ms [pre→53 ms]				
	rotational plantarflexion	118 ms [pre→73 ms]	153 ms				
Allum (1983)		tibialis anterior:	soleus:				
	rotational dorsiflexion	95 ms [pre→83 ms] 137 ms [pre→128 ms]	48 ms [pre→47 ms] 144 ms [pre→138 ms]				
Horak and Nashner (1986)		tibialis anterior:	gastr. medialis:	biceps femoris:	rectus femoris	erector spinae	rectus abdominis
	backward translation	–	88 ms	111 ms	–	138 ms	–
	forward translation	91 ms	–	–	109 ms	–	138 ms
	backward translation (ss)	–	–	–	104 ms	–	85 ms
	forward translation (ss)	–	–	94 ms	–	94 ms	–
Keshner et al. (1987)		tibialis anterior:	soleus:			trapezius:	
	rotational dorsiflexion	84 ms 122 ms	59 ms 126 ms			117 ms	
McIlroy and Maki (1993)		tibialis anterior:	gastr. medialis:				
	forward translation	130 ms	–				

Table 3: Overview of muscle activation latencies in perturbational studies described in section 4.1. Asterisk [*] denotes that a muscle/muscle head was not [exactly] specified. ”ss” in brackets in the study of Horak and Nashner (1986) means ”small surface”. In the study of Torres-Oviedo and Ting (2007), all muscles that were active in the time window between 100 and 250 ms after the onset of perturbations are listed without specifying activation latency [muscles that were active the most are given in black and that were less active are given in gray].

Study	Perturbation	Dorsiflexors	Plantarflexors	Knee flexors/ hip extensors	Knee extensors/ hip flexors	Back muscles	Abdominal muscles
Dietz et al. (1992)			gastr. medialis:				
	rotational dorsiflexion		40 ms				
	backward translation		83 ms				
Horak and Moore (1993)		tibialis anterior:	gastr. medialis:	biceps femoris:	rectus femoris	erector spinae	rectus abdominis
	backward translation	–	92 ms [pre→91]	–	130 ms	190 ms	–
	forward translation	104 ms [pre→93]	–	120 ms	120 ms	–	155 ms
Allum and Honegger (1998)		tibialis anterior:	soleus/gastr.*:		quadriceps*:	trap./paraspin.*:	
	rot. plantarfl.+ backw. transl.	–	–/100 ms		60 ms 160 ms	120 ms/120 ms	
	rotational dorsiflexion	120 ms	50 ms/50 ms 130 ms/–		80-100 ms	100 ms/80-100 ms	
	rot. dorsiflex.+ backw. transl.	120 ms	50 ms/90 ms		80 ms 120 ms	100 ms/120 ms	
Carpenter et al. (1999)		tibialis anterior:	soleus:		vast. lateralis:	paraspinalis*:	
	rotational dorsiflexion	120 ms	44 ms 100 ms		100 ms	68 ms	
	rotational plantarflexion	73 ms	100 ms		85 ms	100 ms	
Torres-Oviedo and Ting (2007)	backward translation		gastr. medialis gastr. lateralis soleus peroneus	semitend. semimemb.			rectus abdominis obliquus ext. abd.
	forward translation	tibialis anterior	gastr. lateralis	biceps femoris semitend. semimenb.	rectus femoris vast. lateralis vast. medialis	erector spinae	obliquus ext. abd.

In a series of studies by Kavounoudias et al. (1998, 1999, 2001) and Thompson et al. (2011), forefoot and heel regions of the foot were stimulated by means of vibration. It was shown that stimulation of the forefoot regions usually elicits whole-body backward tilts whereas stimulation of the heel region provokes forward inclination. This could mean that pressure exerted onto the forefeet may activate muscles of the dorsal side of the body and activation of heel receptors may lead to activation of the muscles of the ventral side of the body. These observations agree with the suggestion that backward translations provoking increase in forefeet pressure trigger activation of calf, hamstring and back muscles. Similarly, it is quite likely that pressure applied to the heels during forward platform translations excites cutaneous receptors and, by that, provokes activation of ventral body muscles in the ankle-strategy-like manner.

The possibility that foot receptors are the receptors that regulate sway and postural responses after small and moderate perturbations is corroborated by the study of Horak et al. (1990). In this study, peripheral somatosensory loss was simulated by means of anesthesia of foot receptors [via hypoxic ischemia]. The function of receptors of lower leg muscles was likely unaffected. Simulated somatosensory loss led to the inability of subjects to keep balance by means of ankle strategy. These subjects demonstrated instead hip strategy that is based on veridical vestibular information. The ability to counteract external disturbances by means of ankle strategy was restored after removal of the pneumatic cuffs from the ankle joints (Horak et al., 1990).

In general, anesthesia of foot receptors and other manipulations lead to diverse effects on motor control and presumably to a malfunction of automatic postural responses. For example, muscle activation latencies increase in case of reduction of underfoot surface density (Wu & Chiang, 1997; Chiang & Wu, 1997). Attenuation of plantar cutaneous feedback can lead to a temporal facilitation of muscle activity (Billot, Handrigan, Simoneau, Corbeil, & Teasdale, 2013) and to an increase in velocity of oscillations of the center of pressure (Magnusson, Enbom, Johansson, & Pyykkö, 1990; Meyer, Oddsson, & De Luca, 2004; Billot et al., 2013) that can be, however, at least partly compensated by vision (Magnusson et al., 1990; Meyer et al., 2004).

4.3 Summary of experimental findings

Before passing to the computational musculoskeletal model and to suggestions regarding enhancements of its control architecture, it makes sense to summarize all

findings made and discussed in sections 3, 4.1 and 4.2 in one place.

Analysis of the data derived in parabolic flight shows that activity of almost all muscles rises with increasing weight. However, EMG activity stays far below its maximum. Electromyographic activity depends on the presence and absence of vision and is typically larger in eyes open conditions. However, the most exceptions from this rule emerge in weightlessness. Weightlessness is presumably a much more unusual condition for the nervous system and perhaps stimulates active re-weighting of sensory information in order to adapt motor output to a new environment. Such adaptations typically arise after some trials (Clement & André-Deshays, 1987) or within few days if subjects are exposed to prolonged weightlessness (Clement et al., 1984; Lestienne & Gurfinkel, 1988b).

Under additional loading the nervous system seemingly tends to exploit postural strategies resembling those appearing in normogravity. However, some modifications can be observed. Besides an increase in EMG magnitude, variability of EMG activity also increases, especially in ankle and knee extensors. Mutual activity of knee flexors and extensors becomes ”less antagonistic”, which, together with increased muscle activity, can indicate increased joint stiffness. Hip extension is controlled by a more or less constant activity of biceps femoris, while activity of quadriceps femoris significantly varies depending presumably on the direction of body sway. Variability of EMG activity of tibialis anterior rises stronger than that of triceps surae [more exactly: variability along the orthogonal manifold increases stronger than along the uncontrolled manifold]. Such changes in mutual variability may indicate stronger interference of supraspinal control in adjustments of activity of tibialis anterior (Brouwer & Ashby, 1992; Solopova et al., 2003; Lauber et al., 2018). In general, acute adaptations just mentioned indicate a shift to single-link-inverted-pendulum-like sway behavior with stiffened knee and hip joints and oscillations around the ankle.

Changes in sway behavior could lead to an increase in oscillation amplitude and velocity of the center of pressure as shown earlier in studies with additional weightings (Qu & Nussbaum, 2009; Costello et al., 2012; Wojciechowska-Maszkowska & Borzucka, 2020). These sway alterations can be due to increased toppling torques acting on the body center of mass. However, it is possible that the nervous system does not strive to reduce sway amplitude and velocity and allows or even encourages

their increases. As suggested earlier (Zatsiorsky & Duarte, 2000; Loram et al., 2004), it is possible that the nervous system controls sway in an anticipatory manner, and increased sway characteristics are beneficial for exploratory behavior (Van Emmerik & Van Wegen, 2002). Rapidly-adapting plantar foot receptors could build the basis for this (Fallon et al., 2005). By means of an exploration of environmental changes, the nervous system could modify activation thresholds of α-motoneurons and modulate activity of γ-motoneurons and, therefore, sensitivity of muscle spindles. This can be of the highest importance for adaptation of anticipatory postural adjustments and for more optimal and adequate muscle activation and coordination during possible perturbations or for desired voluntary motor actions in a new environment.

Regarding equilibrium control during upright standing, correct pre-activation of spinal circuits seems to be needed in order to elicit a particular strategy of balance maintenance. Simulations of peripheral somatosensory loss and investigations on subjects with vestibular loss showed that their postural reactions to translational perturbations are different from those in healthy subjects (Horak et al., 1990). Pre-loading of plantar foot receptors and pre-stretch of leg muscles also lead to modifications in muscle responses. Under such modifications are typically shortened muscle activation latencies (Diener et al., 1983; Allum, 1983; Horak & Moore, 1993) and increased magnitudes of EMG activity (Diener et al., 1983; Allum, 1983; Horak & Moore, 1993; Dietz et al., 1989, 1992). However, when pre-loading is created by means of extreme body tilts the response can be the opposite (Horak & Moore, 1993).

Although manipulations with sensory information allow to modify reactions during balance maintenance, these reactions seem to be quite stereotypical. Moreover, perturbations elicited by means of surface rotations around the ankle joint (Diener et al., 1983; Allum, 1983; Keshner et al., 1987; Allum & Honegger, 1998; Carpenter et al., 1999) and translational perturbations (Nashner, 1977; Horak & Nashner, 1986; McIlroy & Maki, 1993; Horak & Moore, 1993) lead to similar muscle responses of medium- and long-latency. Short-latency responses are observed 40-60 ms after toe-up rotations in soleus (Diener et al., 1983; Allum, 1983; Keshner et al., 1987; Allum & Honegger, 1998; Carpenter et al., 1999), in gastrocnemii (Diener et al., 1983; Dietz et al., 1992; Allum & Honegger, 1998) and in quadriceps (Allum & Honegger, 1998). These responses are explained by phasic stretch reflex and are absent if joint rotation is abol-

ished (Allum & Honegger, 1998). Medium- and long-latency responses are normally observed 80-140 ms after the perturbation onset. They occur in multiple muscles including leg, trunk and neck muscles almost simultaneously or at short mutual latencies [see Tables 2 and 3]. It was suggested that these coordinated responses have a ”pre-programmed” nature (Horak & Nashner, 1986; Horak et al., 1997) and are triggered by specific sensory signals (Horak et al., 1990; Horak & Moore, 1993). Two main motor strategies for balance maintenance were proposed: ankle strategy and hip strategy (Horak & Nashner, 1986; Horak et al., 1997). Ankle strategy can be described as activation of muscles of the dorsal or ventral part of the body in order to counteract forward or backward tilts, respectively. During that, posture stays erect. This strategy is observed during perturbations of moderate amplitudes and velocities (Horak & Nashner, 1986; Horak et al., 1990; Horak & Moore, 1993) and is thought to be triggered by foot receptors (Horak et al., 1990). A distoproximal muscle activation pattern is observed in this case (Horak & Nashner, 1986; Horak et al., 1990; Horak & Moore, 1993). Hip strategy is associated with activation of abdominal muscles and hip flexors during backward platform translations and with activation of back muscles and hip extensors/knee flexors during forward platform translations. Muscle activation pattern has a proximodistal character (Horak & Nashner, 1986; Horak et al., 1990). This strategy is observed during perturbations of large amplitudes and velocities and during perturbations on small surfaces (Horak & Nashner, 1986; Horak et al., 1990). Since hip strategy is absent in subjects with vestibular loss, its elicitation probably requires veridical vestibular information (Horak et al., 1990). These two strategies can be presumably combined and lead to complex muscle activation, as it was the case for Carpenter et al. (1999); Torres-Oviedo and Ting (2007), when both somatosensory receptors and receptors of the inner ear were likely activated. Moreover, muscles stabilizing pelvis in the mediolateral direction are also activated during forward and backward perturbations (Torres-Oviedo & Ting, 2007).

It is, however, problematic to distinguish whether foot or muscle receptors, or both, are responsible for elicitation of balance-maintaining responses from perturbational studies alone. Horak et al. (1990) anesthetized foot receptors with hypoxic ischemia prior to translational perturbations leaving ankle muscle receptors seemingly unaffected by anesthesia. After that, subjects switched from the ankle to hip strategy for balance maintenance. In studies of Kavounoudias et al. (1998, 1999, 2001); Thomp-

son et al. (2011) forefoot and heel regions were mechanically stimulated. Vibration applied to the forefeet elicited backward whole-body tilts (Kavounoudias et al., 1998, 1999, 2001) while stimulation of the heel area of both legs simultaneously provoked forward whole-body leaning (Kavounoudias et al., 1998, 1999) with some knee and hip flexion (Thompson et al., 2011). So, foot receptors seem to spatially encode application of external loads and to give rise to balance-maintaining reactions.

Studies in which influences of load attenuation and foot anesthesia on postural reactions and muscle activity were investigated seem to deliver controversial results. On one hand, a decrease in surface density can lead to longer muscle activation latencies (Wu & Chiang, 1997; Chiang & Wu, 1997), and gradual load increase can magnify muscle responses (Dietz et al., 1989, 1992). Complete functional deafferentation of load receptors provoked by weightlessness leads to almost complete inhibition of ankle extensors (Clement et al., 1984; Clement & André-Deshays, 1987). In the latter case however, it is hard to distinguish between influences of foot receptors, Golgi tendon organs and muscle spindles on muscle activity. On the other hand, cooling of the feet either has no influence on muscle activity or increase it during upright standing (Billot et al., 2013). Anesthesia of the foot can have either an inhibitory (Cruz-Montecinos, Maas, Pellegrin-Friedmann, & Tapia, 2017) or a facilitatory (Halder, Gao, & Miller, 2014) effect on force production during a maximal voluntary contraction. Thus, one can with caution conclude that, unlike additional loading, unloading and anesthesia of foot receptors have ambiguous effects on muscle activity, and corresponding reactions are likely individual- and task-specific and experience-dependent.

Based only on studies described above, there could be at least two plausible explanations of neuronal mechanisms underlying the observed reactions. The first one is that forefoot receptors directly [oligosynaptically] facilitate excitation of α-motoneurons innervating plantar- and knee flexors and hip extensors, as well as back muscles, while heel receptors directly facilitate excitation of α-motoneurons innervating dorsiflexors, knee extensors, hip flexors and abdominal muscles. The second explanation is that foot and muscle receptors have inhibitory effects on one or both muscle ”chains”. In the study of Clement and André-Deshays (1987), the transition from overloading to weightlessness led to backward tilt and, since subjects' feet were attached to the floor, this tilt could stimulate heel receptors that could perhaps, in their turn, activate tibialis

anterior. However in the experiment described and discussed in section 3, the subject was neither tightly attached to the floor nor held by the experimenter at the beginning of the weightlessness phase of the parabolic flight in eyes open conditions. Despite of that, strong activation of tibialis anterior was observed. The same happens also in space flight (Clement et al., 1984), and exaggerated dorsiflexion can be also observed after cutting the tibial nerve (Pearson et al., 1998). Furthermore, it is known that tibialis anterior is more actively controlled by supraspinal circuits than soleus [and maybe also gastrocnemii] (Brouwer & Ashby, 1992; Solopova et al., 2003; Lauber et al., 2018). So, one can assume that motoneurons innervating dorsiflexors are tonically stimulated supraspinally and can be inhibited by forefoot and plantarflexor receptors. In overloading, activity of biceps femoris is nearly constant and is hardly modulated by activity of quadriceps femoris [Fig. 15].

Thus, based on previous studies and our observations, the following neural scheme can be suggested to explain ankle strategy for equilibrium maintenance in healthy subjects. In case of forward sway or tilt, forefoot receptors activate plantarflexors [mainly gastrocnemii] at latency 80-100 ms. After a ”reconsilation” of an anticipatory descending command for standing, pre-activated hip and back extensors are typically stronger activated within following 10-20 ms [activity of biceps femoris does not change drastically in overloading]. At the same time, tonically stimulated α-motoneurons of dorsiflexors are inhibited [but corresponding γ-motoneurons could be hypothetically excited in order to adjust sensitivity of muscle spindles]. During backward swaying or leaning, heels receptors inhibit motoneurons of plantarflexors which leads to suppression of their inhibitory effect on motoneurons of dorsiflexors and, therefore, to their excitation [activation latency of tibialis anterior is normally slightly longer that that of triceps surae what could indicate involvement of fewer additional synapses]. The same signal from heel receptors increases activity in hip flexors and abdominal muscles.

5 Neuromusculoskeletal model

5.1 Description of the model

In previous sections, some experimental findings regarding neural principles of postural control are described and analyzed. Classically, suggestions on how the motor nervous system functions were made based on experiments on animal preparations

and observations of neurologically atypical people or patients with severe neural malfunction. These studies are indisputably essential in unraveling how humans and other animals perform motor actions. However, when interpreting and generalizing their results, one has to keep in mind some important things. First of all, it is worth mentioning that findings made on a damaged nervous system can be extended to an intact one with great caution due to immediate and delayed compensatory effects in the nervous system. Based on the concept of synergies (Gelfand & Latash, 1998; Latash, 2008), one can assume that the nervous system continues to operate optimally [with regard to some sensorimotor constrains] even after lesions and such manipulations as decerebration, spinalization or deafferentation, and only the amount of ”resourses” available for stable and, at same time, flexible control is reduced. Observed motor deficits, for example after a lesion, can predominantly reflect neuromuscular compensatory mechanisms (Dietz, 2002). Besides that, experiments are usually conducted under restricted laboratory conditions and deal with particular types of motor behavior. In order to verify experimental findings, to explore boundaries of drawn conclusions and to be able to confirm cause-effect relations in motor control, a look from another perspective could be very helpful. In this case, modeling of the neuromuscular system can be an important tool for developing and testing different hypothesises on how neural mechanisms separately identified in experimental studies interact within the nervous system. One particular question which is already implicitly formulated in section 4 is what neural mechanism in reality underlies the ability to maintain balance during unexpected external perturbations. Two possible circuits are suggested in the end of section 4.3. To prove or disprove them, these pathways could be implemented in a complex neuromusculoskeletal model which must be then tested and results must be compared with experimental data.

Historically, posture and locomotion were studied separately in the framework of the modeling approach. Moreover, locomotion models of different complexity usually aimed to unravel what mechanical and energetic principles play a key role in motion maintenance and what is the contribution of passive structures and their properties in it. Modeling of posture, on the contrary, was concentrated on control principles, for example, what role sensory feedback plays in controlling of the center of mass (Allen & Ting, 2016).

One general model of functional organisation of the nervous system was proposed a long time ago by Gelfand et al. (1966). According to that proposal, functional construction of any automatic or voluntary biological motor action must firstly include generation of a set of commands by supraspinal levels of the nervous systems. However, these commands cannot be too complicated and must take into account initial conditions [e.g. the initial posture or ongoing movement]. Afferent signals must help to simplify the set of commands from higher neural levels to the lower ones [pools of α-motoneurons and interneurons] and help to maintain a relative autonomy of the lower level subsystems. Thanks to direct afferent information from muscle-tendon units [homonymous feedback] and some information exchange between lower level neural networks [heteronymous feedback and interneuronal connections], these neural networks can maintain a goal specified by the higher neural centers and minimize interaction with them until significant corrections are required. Besides that, other mechanisms for simplification of control such as muscle synergies [or muscle modes] were also proposed (Gelfand et al., 1966). Such a hierarchical-modular [synergistic] organisation of the nervous system must allow motor control to be both stable and flexible (Gelfand et al., 1966; Gelfand & Latash, 1998). A corresponding scheme of this organisation is shown in Fig. 17.

The existence of all these neural mechanisms was since then experimentally confirmed. For locomotion, it was shown that commands from higher to lower control levels can be indeed relatively simple. Modulation of strength or frequency of electrical stimulation applied to two locomotor regions in the midbrain allows to control gait types and velocity (Grillner & El Manira, 2020). Spinal neural networks seem to be indeed structurally organized in a modular way (Bizzi et al., 2008; Kiehn, 2016; Grillner & El Manira, 2020). Muscle modes [structural units of synergistic muscle activity] during balance tasks (Ting & Macpherson, 2005; Torres-Oviedo & Ting, 2007; Allen & Ting, 2016) and different types of locomotion were also identified (Bizzi, d'Avella, Saltiel, & Tresch, 2002; Ivanenko, Poppele, & Lacquaniti, 2004), along with various degrees of their independence from afferent signals (Cheung, d'Avella, Tresch, & Bizzi, 2005). Excitatory and inhibitory pathways between different muscles needed for synergistic control of limbs were also found (Duysens et al., 2000; Nichols et al., 2016), as well as compensatory effects and redistribution of activity within different muscles groups during force production tasks (Stutzig, Siebert, Blickhan, & Thorhauer, 2010). All said

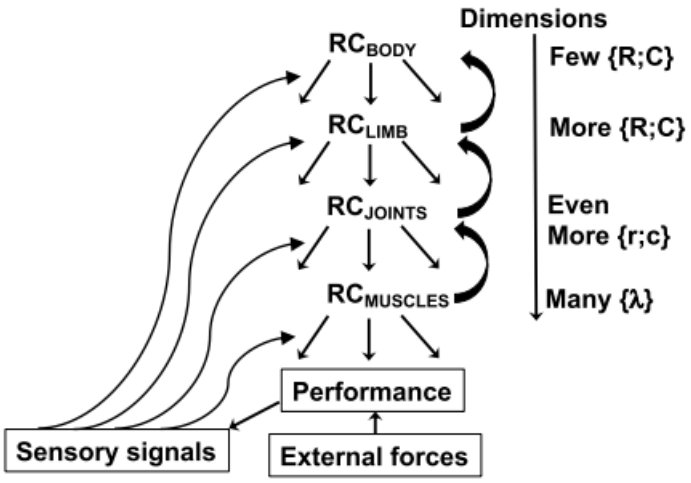

Fig. 17: A general scheme of a hierarchical-modular [synergistic] organisation of motor control with reference to the equilibrium-point hypothesis (Feldman, 2015). According to this scheme, the nervous system generates only few task-specific commands [level of the whole body]. These commands are then distributed between neural networks actuating particular limbs, joints and muscles. Activity within these networks can be modified by peripheral sensory signals. This functional organisation allows these networks to control the ongoing motor action as specified on the higher control level. Reprinted from Latash (2021).

above suggests that a control architecture of all biological motor actions must have similar functional principles and possibly be modeled uniformly.

The control scheme described above (Gelfand et al., 1966) considers main possible neural mechanisms involved in motor control and its simplification. However, some physical [structural and dynamical] properties of the body can also potentially lessen the complexity of a set of central neural commands needed for feasible neuromuscular control. One control architecture testing this hypothesis is proposed by Walter et al. (2021). The developed architecture controls a full-body musculoskeletal model consisting of 36 Hill-type muscle-tendon units and 20 angular degrees of freedom. Each [hinge] joint is assumed to be actuated in the sagittal plane by a singe-joint pair of flexors and extensors. The proposed control architecture [Fig. 18] takes into account the hierarchicity of neural control [as described above and in sections 2.2 and 2.3] and has three hierarchical layers: conceptual, transformational and structural, and includes a feedforward and feedback control mechanisms. The first, conceptual layer sets joint torques that the musculoskeletal model must exert in order to reach and maintain a particular desired body orientation. Herein the difference between current and desired joint torques defines the time evolution of joint angles and their end state

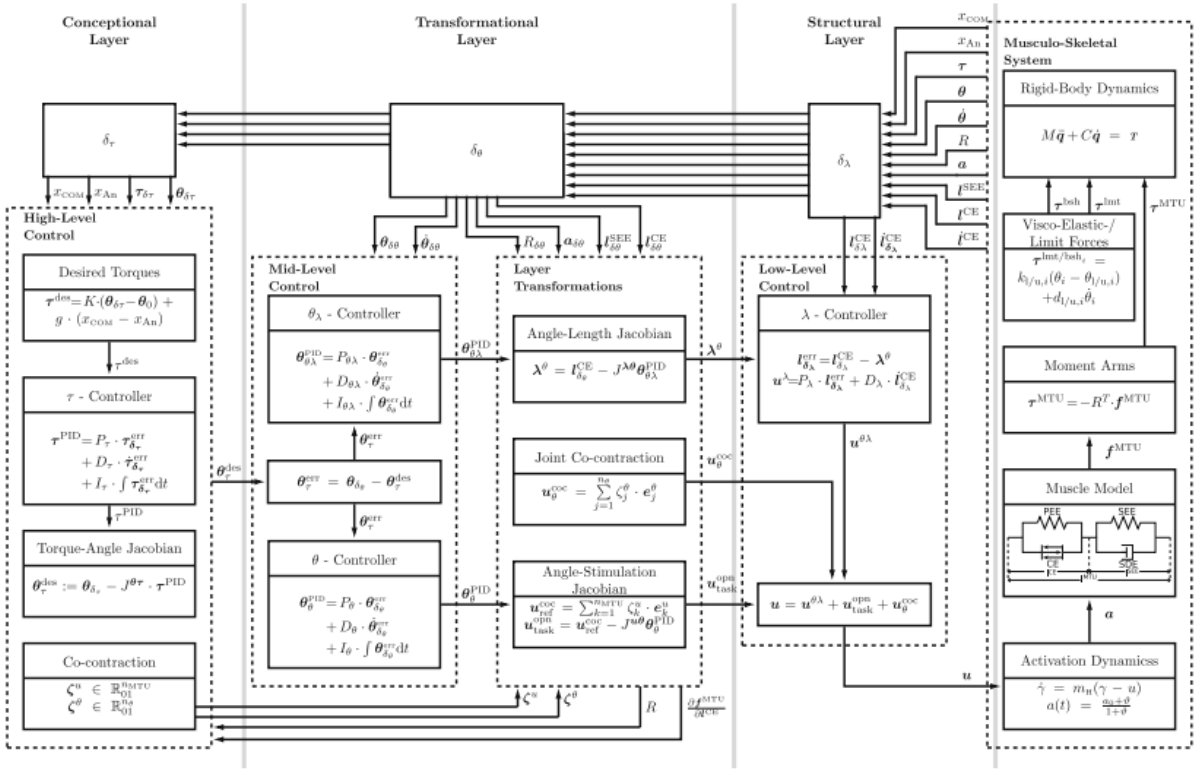

Fig. 18: The scheme of the control architecture. The plan of a motor action is formulated in terms of joint torques in the conceptual layer. A corresponding joint angle configuration is computed in this layer based on the specified torque values. In the transformational layer, a set of desired muscle lengths is determined based on the computed joint torques. Muscle stimulation commands are determined in the structural layer based on the actual muscle lengths and the lengths computed in the transformational layer. Reprinted from Walter et al. (2021).

[desired] value based on the proportional–integral–derivative control law. In the second, transformational layer, the time evolution of muscle lengths and their end state [desired] values are analogously found based on the difference between the current and desired joint angles. In the third, structural layer, muscle stimulation commands are defined based on the difference between the current and desired muscle lengths and sent after that to the musculoskeletal model. The generation of the stimulation command based on the difference between the current and desired muscle lengths represents exactly the function of muscle spindles. Changes in the state of the system are reported back to the structural and transformational layers representing spinal feedback loop, and to the conceptual layer representing supraspinal feedback loop [see section 2]. Control of muscle lengths is performed in this architecture by shifting the current muscle length to the desired one by changing torque values in the conceptual layer. This control principle is based on the principles of referent control [equilibrium-

point hypothesis] (Feldman, 2015).

The proposed architecture allows to transform the motor plan formulated in terms of only few joint torques into a higher number of muscle stimulation commands [i.e. the dimension of the space of stimulation commands is much bigger than the dimension of the space of torques]. These transformations are based on morphological features of the musculoskeletal model such as muscle moment arms, the stiffness relations of muscle-tendon units and length-dependant muscle activation dynamics. That is, the functionality of these control architecture allows to assume that not only organisational features of the nervous system, but also properties of the musculoskeletal system contribute to the simplification of motor control (Walter et al., 2021).

5.2 Model's responses to altered gravity

In order to identify how the neuromusculoskeletal model responds to altered gravity, it was tested for different gravity levels during simulation of upright standing with a small squat movement. Gravity level [g level] was varied in the range from 0g to 2g with the 0,1g step. It was found that the model can successfully hold stable upright posture, squat, stand up and stand again for g level values from 0,5g up to 1,2g. For tested g level values lower than 0,5g, the model cannot keep a contact with a underfoot surface and ”flies away”. Further testing showed that the model falls just immediately or few seconds after the beginning of simulation for g level values exceeding 1,4g [i.e. 1,5g and more]. For g level values equal 1,3g and 1,4g, the model can stand until the onset of the squat movement but falls during performing this movement. The position of the center of mass of the model in some simulations is shown in Figs. 19-21. It was also found that during standing and squatting, ankle, knee and hip extensor muscles are always maximally activated irrespective of the g level value.

Further, the model was tested while the maximal force parameters of ankle, knee and hip flexors and extensors were gradually reduced down to 50% [with the 10% step]. The model was able to stand after 10% maximal force reduction for 1,4g, after 20% reduction - for 1,3g, after 30% reduction - for 1,2g, after 40% reduction - for 1,1g, and was not able to stand after 50% reduction for 1g and 0,9g. The position of the center of mass of the model in some of these simulations is shown in Figs. 22-24.

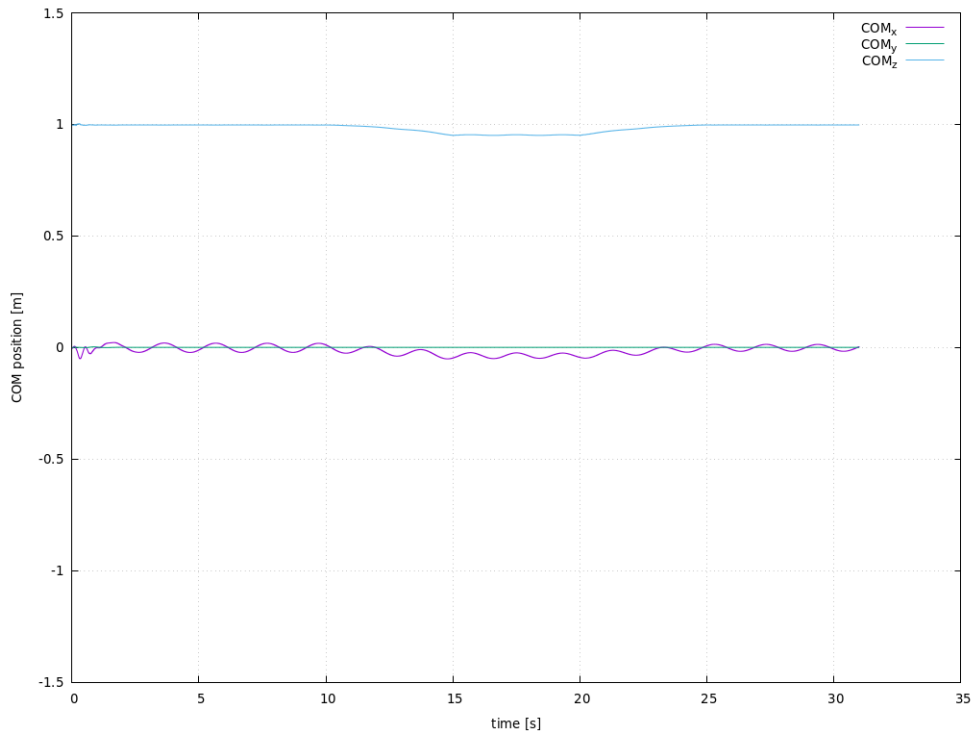

Fig. 19: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 0,5g, default muscle forces]. The model can successfully keep balance and perform a squat movement.

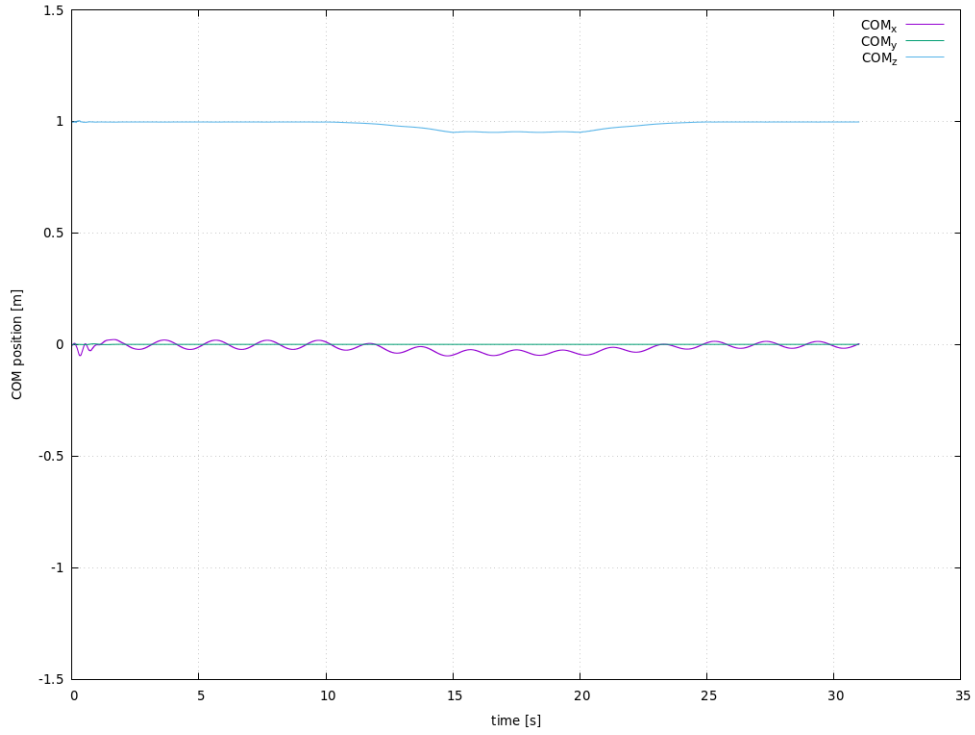

Fig. 20: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 1g, default muscle forces]. The model can keep balance and squat.

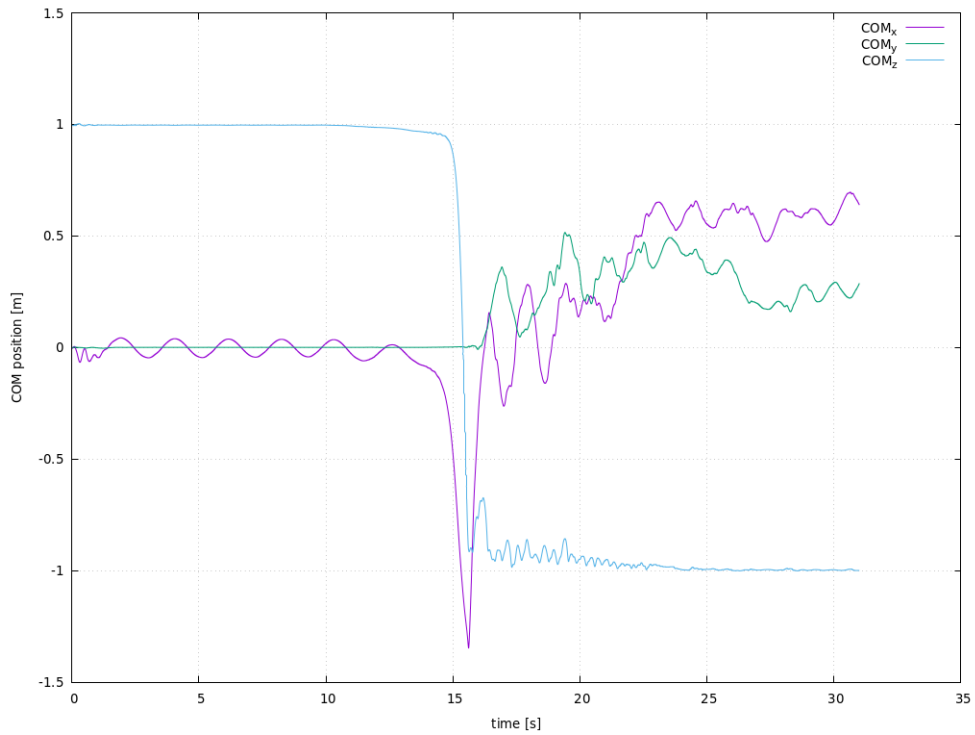

Fig. 21: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 1,4g, default muscle forces]. The model can keep balance during standing but falls during the squat movement.

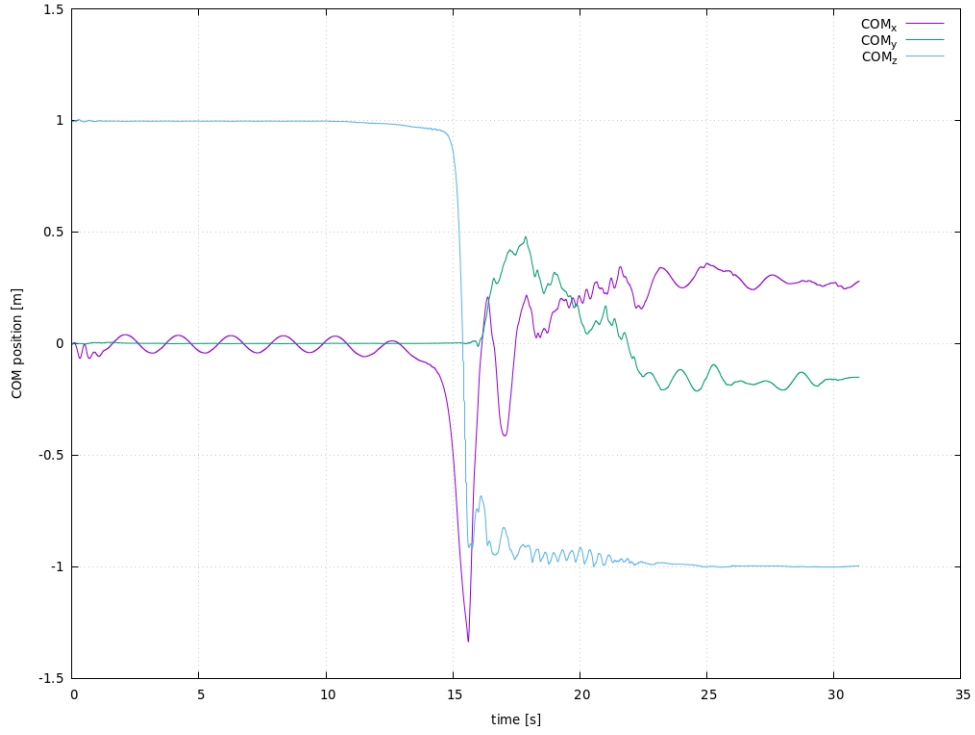

Fig. 22: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 1,4g, leg muscle force is reduced by 10%]. The model can stand but falls during the squat movement.

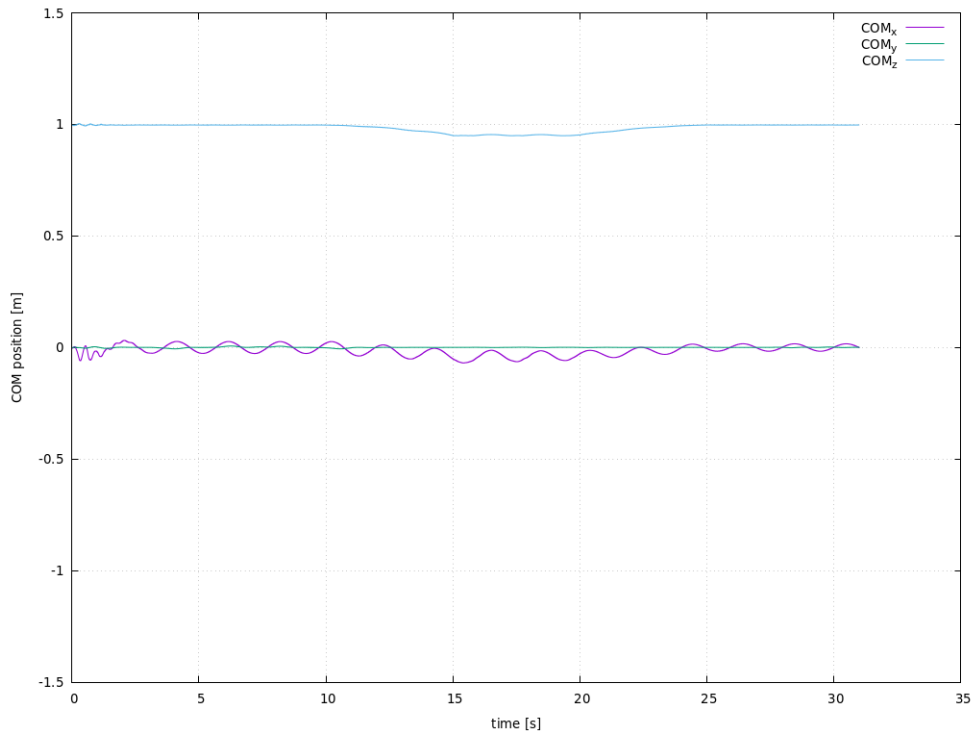

Fig. 23: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 1,1g, leg muscle force is reduced by 40%]. The model can both stand and squat.

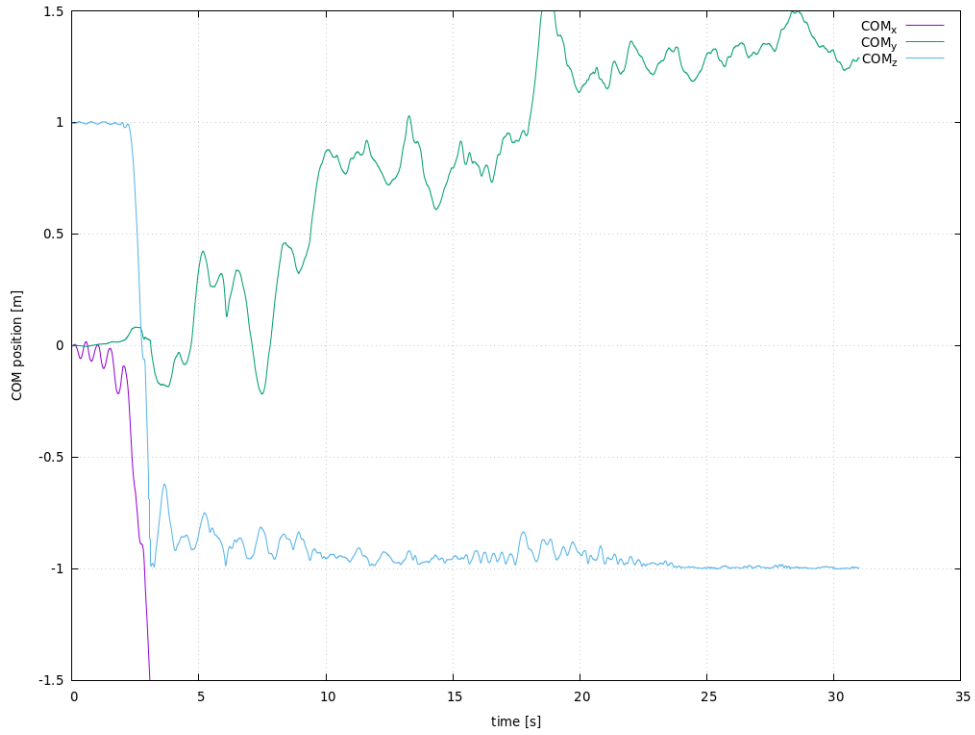

Fig. 24: Coordinates of model's body center of mass during a simulation of standing with a small squat movement in the middle [g level = 1g, leg muscle force is reduced by 50%]. The model cannot keep balance.

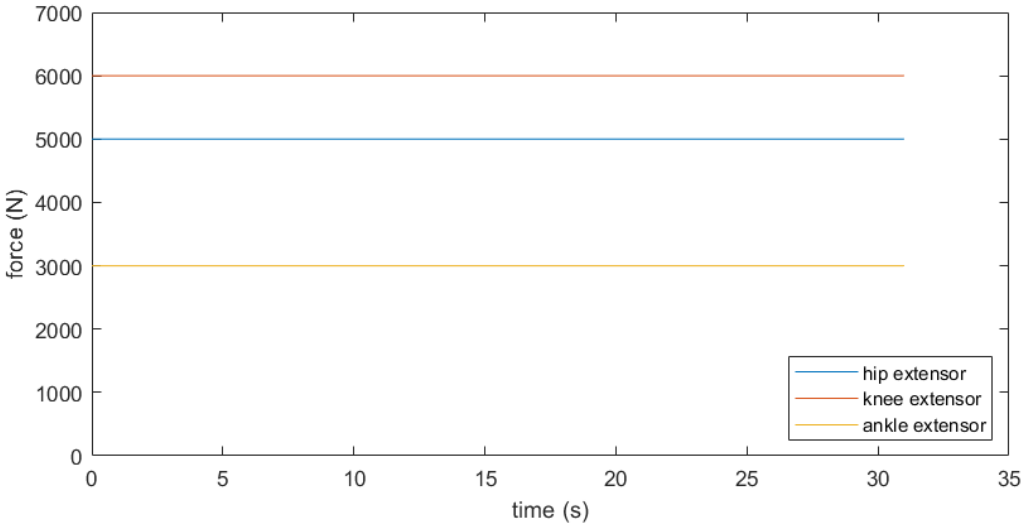

Fig. 25: Forces in anti-gravity muscles during a simulation of upright standing with a small squat movement in the middle [g level = 1g, default muscle forces].

One can notice the discrepancy in the ability to stand in overloading between the studied subject [section 3] and the model. This discrepancy can be explained at least by two possible phenomena or by their combination. First, additional stiffening of knee and hip joints and sway behavior in manner similar to the single-link inverted pendulum employed by the subject could provide more stability in overloading. Second, swaying like the single-link inverted pendulum could allow the subject to transfer the load induced by the increased weight force from muscles onto passive [bone] structures. In parabolic flight experiments, it was also observed that subjects were able to successfully squat and raise up to the standing position in overloading conditions though lowering the body was perceived as more rapid and upright position after raising up was perceived as ”too raised up” in comparison to normogravity (Lackner & Graybiel, 1981). This could mean that some changes in intermuscular coordination also appear during squatting, possibly due to alterations in sensory inflow.

5.3 Suggestions to the model

Based on the experimental studies described above and model testing, the following suggestions can be made.

- As model testing showed, muscle forces generated by model’s anti-gravity muscles do not depend on g level and are always maximal. This could point out a too large value of the muscle stimulation command. Since the model can maintain standing balance in normogravity with the 40% decrease in muscle force,

muscle stimulation can be potentially reduced. A too large value of the muscle stimulation command could be, for example, due to a too large chosen value of the co-contraction stimulation. Another assumption would be that stretch reflex implemented into the model is only one of the mechanisms of equilibrium control [see section 2.3]. Thus, parameters used for generation of the closed-loop stimulation command could be adjusted in order to lower its value. At the same time, these parameters can be potentially made g level-dependant in order to simulate gravitational sensitivity of muscle spindles as proposed by some researchers (Lackner & Graybiel, 1981; Lackner et al., 1992; Fisk et al., 1993).

- One of the further equilibrium control mechanisms can be ”pre-programmed” postural responses [see section 4]. Regarding sway control and small equilibrium disturbances, these reactions could be implemented based on the detection of changes in pressure in forefoot and heel regions or based on ankle joint torques. In a simpler form, an increase in forefoot pressure could lead to additional stimulation of dorsal muscles [plantar- and knee flexors, hip extensors, back muscles]. An increase in heel pressure could lead to additional stimulation of ventral muscles [dorsiflexors, knee extensors, hip flexors, abdominal muscles]. In case of strong equilibrium disturbances, head movements could be also taken into account. These movements could be detected directly by a otolith-like sensor or by means of stretch of neck muscles [or corresponding neck joint torques]. In case of large perturbations, ankle strategy can be suppressed and substituted by hip strategy. The implementation of more complex behavior of postural responses spanning from ”pure” ankle strategy to ”pure” hip strategy [i.e. mixed strategies] can also be considered.

- As discussed in section 4, it seems that muscle activation latencies also depend on foot pressure. Forefoot pressure might shorten latencies in plantarflexors and increase them in dorsiflexors [or correspondingly in dorsal and ventral muscles in general]. Heel pressure might shorten latencies in dorsiflexors and increase them in plantarflexors [or correspondingly in ventral and dorsal muscles in general]. That is, muscle activation latencies in the model could be made dependant on foot pressure.

- A pre-planned [referent] sway trajectory (Zatsiorsky & Duarte, 2000) near a fixed

point could be implemented and tested. This will presumably allow to formulate a postural plan in kinematic terms making it possible to describe standing and locomotion in the same manner.

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Statement of independence

I hereby confirm that I have written the present thesis by myself, without contributions from any sources other than those cited in the text. This applies to all figures and tables.

Place and date

Signature