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Muscle force compensation among synergistic muscles after fatigue of a single muscle

Norman Stutzig *, Tobias Siebert

Exercise Science, Institute of Sport- and Movement Science, University of Stuttgart, Germany

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ABSTRACT

Purpose: The aim of this study was to examine control strategies among synergistic muscles after fatigue of a single muscle. It was hypothesized that the compensating mechanism is specific for each fatigued muscle.
Methods: The soleus (SOL), gastrocnemius lateralis (GL) and medialis (GM) were fatigued in separate sessions on different days. In each experiment, subjects ($n = 11$) performed maximal voluntary contractions prior to and after fatiguing a single muscle (SOL, GL or GM) while the voluntary muscle activity and torque were measured. Additionally, the maximal single twitch torque of the plantarflexors and the maximal spinal reflex activity (H-reflex) of the SOL, GL and GM were determined. Fatigue was evoked using neuromuscular stimulation.
Results: Following fatigue the single twitch torque decreased by −20.1%, −19.5%, and −23.0% when the SOL, GL, or GM, have been fatigued. The maximal voluntary torque did not decrease in any session but the synergistic voluntary muscle activity increased significantly. Moreover, we found no alterations in spinal reflex activity.
Conclusions: It is concluded that synergistic muscles compensate each other. Furthermore, it seems that self-compensating mechanism of the fatigued muscles occurred additionally. The force compensation does not depend on the function of the fatigued muscle.

* Corresponding author at: Institute of Sport- and Movement Science, Allmandring 28, 70569 Stuttgart, Germany. Tel.: +49 711 685 63 108; fax: +49 711 685 63 165.
E-mail address: norman.stutzig@inspo.uni-stuttgart.de (N. Stutzig).

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1. Introduction

Human movements are based on coordinated activity of different muscles. Single muscles (e.g., the plantarflexors), which act across the same joint (Buchanan, Almdale, Lewis, & Rymer, 1986) and in the same direction are defined as synergistic muscles. For a given task, muscle synergies provide higher forces in the same direction than a single muscle. Both single muscles and movement tasks (e.g., coordination of different synergistic muscles) are represented in the primary motor cortex (Kakei, Hoffman, & Strick, 1999). Thus, functional interaction of several synergistic muscles is controlled by descending central commands from the motor cortex (supraspinal level). However, synergistic muscles are also controlled at the spinal level. It has been reported in the literature that synergistic muscles are linked via Ia afferents (primary afferent fiber) (Eccles, Eccles, & Lundberg, 1957; Nichols, 1989). Spindle afferents of a single muscle connected to α-motoneurons of synergistic muscles and have an excitatory effect on the α-motoneurons of synergistic muscles (Pierrot-Deseilligny & Burke, 2012). At present, the control mechanism for synergistic muscles is not well known. Examination of synergistic muscle control strategies may help to get a deeper understanding about synergistic muscle function and their neuromuscular connectivity.

Synergistic muscles are able to compensate each other in terms of higher muscle activity to maintain a given movement task (Ciubotariu, Arendt-Nielsen, & Graven-Nielsen, 2004; Cronin, Peltonen, Sinkjaer, & Avela, 2011; Hellsing & Lindstrom, 1983; Kinugasa, Yoshida, & Horii, 2005). For example, it was observed that fatigue of a single muscle can be compensated for by synergistic muscles resulting in unchanged synergistic muscle forces (Akima, Foley, Prior, Dudley, & Meyer, 2002; Stutzig & Siebert, 2015; Stutzig, Siebert, Granacher, & Blickhan, 2012). Stutzig et al. (2012) and Stutzig and Siebert (2015) fatigued the *gastrocnemius lateralis* (GL) solely and observed increased synergistic (*soleus*, *gastrocnemius medialis*) muscle activities (about 10%) during isometric maximum voluntary contractions (MVC: maximal contraction that a subject accepts as maximal and that is produced with appropriate continuous feedback of achievement (Gandevia, 2001)). Similar results have been reported by Akima et al. (2002) who fatigued the *vastus lateralis*. Performing dynamic knee extensions at 50% MVC, they found increased muscle activities of the synergistic *rectus femoris*, *vastus medialis* and *vastus intermedius*. It is known that force compensating strategies depend on a variety of conditions such as muscle length (Stutzig & Siebert, 2015) and blood supply (Sacco, Newberry, McFadden, Brown, & McComas, 1997).

With regard to muscle synergies the triceps surae is a frequently examined muscle (Ciubotariu et al., 2004; Cronin et al., 2011; Sacco et al., 1997), because (1) compensating effects at MVC have been reported (Stutzig & Siebert, 2015), (2) it is an appropriate muscle group for measuring electrically evoked contractions and (3) the cross linkages between Ia fibers and α-motoneurons among the muscles of the triceps surae are known from experiments with decerebrated cats (Nichols, 1999). Approximately 80% of the force during plantar flexions originates from the triceps surae muscle (calculations are based on the cross-sectional area and the moment arms of the triceps surae) (Arndt, Komi, Bruggemann, & Lukkariniemi, 1998; Gregor, Komi, Browning, & Jarvinen, 1991). The triceps surae muscle consists of the mono-articular *soleus* (SOL) and the bi-articular GL and *medialis* (GM). Mono- and bi-articular muscles differ in muscle architecture, e.g., pennation angle, mean fiber length, muscle thickness, fiber type (Chow et al., 2000; Saltin & Gollnick, 1983), and function (Mueller, Siebert, & Blickhan, 2012). However, at the spinal level the synergistic muscles are not equally connected via Ia afferents. It has been reported that strong connections exist from SOL to GL and from GM to GL but weak connections exist from GL to GM and from GM to SOL (Nichols, 1999). Further, increased spinal reflex activity was found after high frequency stimulation (Collins, Davis, & Mendell, 1988; Lagerquist, Mang, & Collins, 2012; Nordlund, Thorstensson, & Cresswell, 2004). If compensation mechanisms were triggered based on different Ia connections between synergistic muscles it could be hypothesized that synergistic muscle compensation depends on the specific muscle that has been fatigued. We would expect that muscles with strong Ia connection to synergistic α-motoneurons (e.g., from SOL to GL) can be compensated for but muscles with weak connections to synergistic muscles cannot. Additionally, if muscle compensations depend on muscle function and architecture then we would expect different results for SOL than for the gastrocnemii.