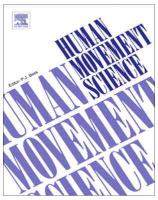
Human Movement Science 44 (2015) 225–233

Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov



Muscle fatigue as an investigative tool in motor control: A review with new insights on internal models and posture–movement coordination

Florian Monjo [a,*], Romain Terrier [a,b], Nicolas Forestier [a]

[a] *Laboratoire de Physiologie de l'Exercice (EA 4338), UFR-CISM/STAPS/Université de Savoie, 73376 Le Bourget du Lac, France*
[b] *Cevres Santé, Savoie Technolac, BP 322, 73377 Le Bourget du Lac, France*

ARTICLE INFO

Article history:
Received 1 April 2015
Revised 28 August 2015
Accepted 14 September 2015

Keywords:
Muscle fatigue
Motor control
Internal models
Posture–movement coordination

ABSTRACT

Muscle fatigue is a common phenomenon experienced in everyday life which affects both our force capacity and movement production. In this paper, we review works dealing with muscle fatigue and motor control and we attempt to demonstrate how the Central Nervous System deals with this particular state. We especially focus on how internal models – neural substrates which can estimate the current state as well as the future state of the body – face this internal perturbation. Moreover, we show that muscle fatigue is an interesting investigative tool in understanding the mechanisms involved in posture–movement coordination.

1. Introduction

A critical issue in motor control is the necessity to coordinate different moving effectors, such as the eyes and the hand during reaching/pointing movements, or different systems, such as the focal and the postural system during whole body movements. Over the past several decades, strong debates about the control of these complex motor acts have been discussed in the literature. One major concern was to determine (a) whether a unique motor command acts on both effectors/systems (single-process hypothesis) or (b) whether effectors/systems are independently controlled (dual-process hypothesis). Former experimental data supported the theory of a common neuromuscular command for gaze and hand during pointing movements (Biguer, Jeannerod, & Prablanc, 1982; Bizzi, Kalil, & Tagliasco, 1971) and for the postural and focal components during posture movement coordination tasks (Paulignan, Dufossé, Hugon, & Massion, 1989). However, more recent contributions challenged this theory by clearly demonstrating the independence of gaze and hand commands (Gribble, Everling, Ford, & Mattar, 2002). Indeed, while studies supporting the single process hypothesis only focused on the stability of the temporal pattern between gaze and arm kinematic data, Gribble and colleagues, by investigating the temporal characteristics of the neuromuscular commands, clearly evidenced that the two systems were independently controlled. The dissociated character of the postural and focal commands has also been widely documented (Ahmed & Wolpert, 2009; Benvenuti, Stanhope, Thomas, Panzer, & Hallett, 1997; Kurtzer, Herter, & Scott, 2005; Massion, Alexandrov, & Frolov, 2004). For instance, Ahmed and Wolpert (2009) observed different learning rates for the postural and focal components during arm movements performed in the presence of dynamic perturbations, demonstrating that two independent neural motor commands are involved in the control of posture and movement. Beside, at a neuronal level, it appears that some neuron

---

* Corresponding author.
E-mail address: flomonjo@gmail.com (F. Monjo).

http://dx.doi.org/10.1016/j.humov.2015.09.006
0167-9457/

populations specifically code for the execution of posture, while others are clearly intended to the control of the focal movement (Kurtzer et al., 2005). This parallel mode of control implies that some neural structures allow an accurate coordination of independent effectors through prediction of the sensory and mechanical consequences of an effector displacement relative to another. In this vein, a concept has emerged in the field of neuroscience and motor control and is particularly explicative of this control capacity. This is the concept of internal model (Kawato, 1999; Miall & Wolpert, 1996; Wolpert & Ghahramani, 2000). Internal models are the primary neural substrates of predictive motor control and can be divided into two categories, i.e. inverse and forward models. Inverse models allow computing motor commands as a function of the environment and of a desired state (Kawato, 1999; Wolpert & Kawato, 1998) while forward models, based on the current state of the body, and in response to a copy of motor commands (efference copy), can estimate the future state of the motor apparatus (Wolpert & Flanagan, 2001). Seen in this context, coordination tasks involve that forward models, in response to an efference copy and depending on the current configuration of an effector/system, can predict and organize the behavior of another effector accordingly. Given that humans are exposed to a high environmental variability, internal models need be both flexible enough to predict a wide range of motor situations and easily updatable. This is particularly the case when confronted with muscle fatigue, which is a transient and highly fluctuating sensorimotor phenomenon commonly experienced in everyday life. Muscle fatigue is a complex state comprising both objective and subjective components and is defined as a loss of force associated with an increase in the perceived effort necessary to exert a desired force (Enoka & Stuart, 1992). From a neurophysiological perspective, during local muscle fatigue, thin chemosensitive sensory fibers, namely group III and IV afferents, are activated by the thermal, metabolic and mechanical changes occurring in the working muscles (Sinoway, Hill, Pickar, & Kaufman, 1993). This represents the peripheral origin of muscle fatigue. The spinal and supraspinal integration of these afferents result in the implementation of inhibitory reflex, leading to a modulation of the mechanical outputs (Gandevia, 2001). This represents the central component of fatigue. From a practical view and given that muscle fatigue is potentially deleterious and increases the risk of injuries (Côté, Raymond, Mathieu, Feldman, & Levin, 2005), it is of great interest to investigate the features of predictive motor control in the presence of muscle fatigue.

In the aim of understanding the motor control rules and functioning, humans are usually submitted to various constraints allowing investigation of their capacity for adaptation and learning. For instance, some studies introduced disturbances in the visual environment (Prablanc & Martin, 1992) or used mechanical disturbances by generating force fields on moving limbs (Shadmehr & Mussa-Ivaldi, 1994). Other works consist in transiently exposing subjects to microgravity environment (Papaxanthis, Pozzo, & McIntyre, 2005). However, such experimental paradigms exhibit some limitations as the disturbances are artificial and never experienced by the Central Nervous System (CNS) in daily life. This is not the case of muscle fatigue, which can act as an internal disturbance that is unavoidable.

In this review, we will show that muscle fatigue is an interesting experimental tool for provoking disturbances and has the ability to provide insights into the mechanisms of motor control. In order to clarify how the CNS deals with this particular disturbance, we will attempt to unify recent results of motor adaptations following muscle fatigue in a common theoretical frame of motor control, i.e. the internal model theory (Kawato, 1999). Such an approach could lead to consider the study of motor control in the presence of fatigue from a different and new perspective and could also bring new insights supporting the dual process hypothesis.

2. Basic historical evidence of the existence of internal models to explain predictive motor capacity and their neural substrates

The concept of internal models arose from the need to explain the predictive features of human movement and several lines of evidence support their existence. Historically, understanding the predictive capacity of humans in the field of motor control came from the observation that our visual environment remains stable when we voluntarily move despite the constant image displacements caused by eye, head and body movements. Indeed, this apparently naive issue implies that humans are able to overcome feedback delays and thus to anticipate motion-related disturbance to predictively move their eyes in a way that enable to maintain the gaze on a particular point. The first theoretical proposition accounting for this behavior was offered early in the 20th century by Ernst Mach and Jacob Von Uexkuell following the initial work of Bell and Purkinje (Bubic, Von Cramon, & Schubotz, 2010) and relies on the concept of efference copy (Von Holst & Mittelstaedt, 1950) which proposes that when we move, a copy of the outgoing motor commands is processed by some neural networks to simulate action and predict their consequences ahead of movement execution (Shadmehr, Smith, & Krakauer, 2010). This concept accounts for several observed "anticipatory" and "predictive" motor behaviors such as the fact that during gaze-hand tracking motions, eyes can follow hand trajectory with no delay (Miall & Reckess, 2002) and the fact that when we lift an object up, grip forces increase in parallel to the evolution of load forces (Flanagan & Wing, 1997). In this latter case, if the system only relied on sensory feedbacks to lift the object, it would slip because of the sensorimotor loop-related delays. Altogether, these examples are evidence that the motor commands sent to the muscles are known by the CNS before movement onset. The internal models responsible for such predictions have been proposed to be located in the cerebellum (Bastian, 2006; Bhanpuri, Okamura, & Bastian, 2013; Cerminara, Apps, & Marple-Horvat, 2009; Diedrichsen, Verstynen, Lehman, & Ivry, 2005; Wolpert, Miall, & Kawato, 1998) and in the parietal cortex (Desmurget & Sirigu, 2009; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; Wolpert, Goodbody, & Husain, 1998) (For reviews tackling these two views, see Desmurget & Grafton, 2000 as well as Blakemore & Sirigu, 2003). Regarding cerebellar internal