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Short review

Task-dependent reduction of the number of degrees of freedom in sensorimotor systems

C.C.A.M. Gielen *, B.M. van Bolhuis

Dept. of Medical Physics and Biophysics, University of Nijmegen, Geert Grooteplein 21, Nijmegen NL-6525 EZ, Netherlands

Abstract

In this paper we present a concise review of experiments on sensorimotor performance in man from the perspective of new opportunities provided by research in microgravity, which will contribute to our basic understanding of sensorimotor processes. In particular, we will discuss some new results on strategies for dealing with the large number of degrees of freedom in biological limbs with special emphasis on human motor control and on the specific role for mono- and bi-articular muscles. Finally, we propose some ideas for future experiments on motor function in microgravity, which will reveal new basic knowledge about the role of the CNS in motor control and which will contribute to a better performance of man in sensorimotor tasks in microgravity conditions. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Force; Position; Muscle; Microgravity; Sensorimotor

Contents

1. General introduction

Life science studies in microgravity were initially driven by the need to obtain a better understanding of how man could sustain the difficult conditions during space flights. Although this is still a major drive for studies in microgravity conditions on man, it has become clear that life science research in microgravity conditions can also provide unique opportunities to study fundamental processes in man with important results which are difficult to obtain, if at all possible, in normal conditions on earth. Realizing this dual benefit of studies in microgravity has also led to a shift in research topics. In the first studies, emphasis was particularly focused on medical aspects and on those aspects of human performance which are most vital for the survival of man in space. Typical research areas were the cardiovascular system, changes in bone density during flight and after landing, and space sickness of astronauts. With the insight that microgravity studies could shed light

* Corresponding author. Fax: +31-24-3541435; E-mail: stan@mbfys.kun.nl

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on other important issues in life science, new topics have been included in manned space flights, such as embryonic development, and adaptation and plasticity in the central nervous system. An excellent and rather complete overview of the present state of the art is presented in Ref. [14].

It is well known that astronauts have difficulty in walking after space flights. Although part of this disability originated from a reduction in muscle cross-sectional area (see Chapter 2 in Ref. [14]) this cannot explain all of it, since a reduction of muscle cross-sectional area leaves enough muscle force to walk. There is now increasing evidence, that there are major adaptive changes in the central nervous system (see, e.g., Ref. [17]) and that the deteriorated motor performance in space is due to changes both at the peripheral muscle level as well as at the level of the central nervous system. This hypothesis, which is supported by several experimental observations, demonstrates the importance of neuroscience research in microgravity conditions. Such research will be invaluable to understand the performance of astronauts during space flights and after return, and in addition provides unique opportunities to study adaptation and plasticity of the CNS. In this chapter we will focus on important issues in sensorimotor research and their impact for basic research and for space flights.

2. Short introduction to sensori-motor control

When growing up to adulthood, man has to learn a broad repertoire of movements in various conditions of complexity. Learning new movement skills requires full attention and the on-line use of multiple sensory signals (see Ref. [18]). When a particular movement skill has been mastered, that movement type can, after a while, be made more or less automatically. The ability to learn new movement skills and to store these movement skills as motor programs, which can be retrieved more or less automatically, provides a good opportunity to increase the number of movements, which can be made simultaneously. As a result of that man is able to do many things in parallel while paying attention only to perceptual or motor tasks, which are most important or most critical. The ability to make several movements in parallel is due to the increased capacity of information processing of man.

It is well known that complex action-perception tasks require a large information processing capacity since they require much attention and time-consuming computations. In agreement with this general observation several studies have shown an interaction between cognitive tasks and postural control [10,21]. Good performance in complex motor tasks does not go together with other complex, cognitive tasks. Astronauts in space will face similar situations, since they perceive their new environment really as very unusual. As an example, proprioception in space is disturbed, giving rise to a false percept of limb position [30]. This will require visual attention to control posture and will limit the use of visual information for other tasks. Also astronauts have difficulty in orienting [1,31] and in the use of proprioceptive information for position and force control [16]. It is without doubt that the unfamiliar conditions in space will give rise to degraded sensorimotor performance in astronauts and it is not known yet how long that will last and how to alleviate the consequences of it. In the following we will focus on the consequences for the coordination of multi-joint limb movements.

There is considerable evidence from psychophysical and neurophysiological experiments that the control of volitional aiming movements such as reaching movements to a target involves a series of sensorimotor transformations proceeding from high-level spatiotemporal representations of movement to motor commands incorporating the detailed properties of the effector system, culminating in signals that generate the appropriate muscle activity patterns. These processes are usually described for heuristic purposes in terms of the convenient but arbitrary parameter spaces (hand path, joint angles, joint torques) and transformations (inverse kinematics, inverse dynamics). Many psychophysical studies have revealed the physiological parameters, reference frames, and transformations by which the motor system plans and implements movements [19,20]. In this contribution we will focus upon the transformations from representations related to hand trajectory or direction of force in 3-D (i.e., in extrinsic coordinate frames) to a representation related to the biomechanical properties of the effector system (i.e., in intrinsic coordinate frames).

3. Reduction of degrees of freedom

One of the major problems in motor control is related to the control of the large number of degrees of freedom (DOF), which provide a large flexibility to biological limbs. Yet, this large number of DOF's also creates some problems, for example due to the fact that rotations in 3 dimensions do not commute [24]. The latter means, that the orientation of an object after two rotations along noncolinear axes depends on the order of the rotations. As a consequence the orientation of the eye, head and upper arm would depend on movements in the past unless special neural control algorithms alleviate this problem. The large number of DOF's becomes also evident from the number of joints in a limb, each with multiple rotational degrees of freedom, and from the number of mono- and bi-articular muscles which is acting across each joint. The large number of joints and muscles involved in movements allow, for example, that the same position of the hand can be obtained by a large number of muscle activation patterns. Yet, recent studies have revealed that the normal repertoire of human movements is reproducible and characterised by a consistent reduction of the number of degrees of freedom.

3.1. Rotational degrees of freedom

Although the large number of joints and their rotational degrees of freedom allow many arm postures for most positions of the index finger, primates perform a particular motor task in a very stereotypic fashion from trial-to-trial and from day-to-day [6]. The reproducibility of limb postures is thought to be the result of a systematic reduction in the number of degrees of freedom. For many joints with three rotational degrees of freedom (like the eye, head, and shoulder) there is a reduction of the number of degrees of freedom from three to two [5,9,12,22]. This reduction of degrees of freedom becomes evident from the observation that the rotation vectors, which describe the orientation of the eye, head or upper arm as a rotation from a reference position (usually called ‘primary position’), are contained in a two-dimensional surface. As a consequence the orientation is uniquely specified for each direction of gaze (eye and head) or pointing direction (for the arm).

The reduction in the number of rotational degrees of freedom from three to two should not be interpreted in the sense that not all degrees of freedom of these joints are accessible to the CNS. Rather, it means that for postures of the human arm involved in normal pointing and grasping movements, only two out of three degrees of freedom are used. If all degrees of freedom are necessary for arm postures during a particular type of movement, they can be used very well, but only with special attention by the subject (unpublished observation) which, most likely, reduces the information processing capacity at that time.

The reduction of the number of DOF’s from three to two is the reason why the rotation vectors, which describe the orientation of the eye, upper arm, or head, are contained in a two-dimensional surface. This surface appears to be a flat plane for the eye [24] and a curved surface for the head and upper arm [4,22]. The orientation and curvature of the surface is somewhat different for the head and upper arm. The data in the literature [9,12,22,24] suggest that for each system (i.e., for the eye, head, arm) the reduction in the number of DOF’s is the same for static postures and for movements such that joint postures are reproducible. The particular orientation of the surface with rotation vectors is not understood yet, since it has been remarked frequently (see, e.g., Ref. [22]), that a reduction of the number of DOF’s from three to two could be obtained with different orientations and curvatures of the two-dimensional surface with rotation vectors. Hence, the origin of the different curvature of the surfaces for eye, head and shoulder has been questioned, having either a sensory or motor origin. The definite answer is not clear. It could be related to the specific neuromuscular properties of the effector system, or even to perceptual aspects (see Ref. [29]). Also, it has been shown that the orientation of the surface, describing the rotation vectors for the head, changes when the orientation of the body relative to the gravity vector changes [13]. Presumably, this is due to the fact that the output signals of the otolith system, which are known to affect eye- and head-positions, are changed by the different orientation of gravity relative to the otoliths. This observation suggests a change of the frame of reference for the control of head movements in conditions of micro-gravity. At least the latter finding illustrates that microgravity affects the strategies used for the reduction of the number of DOF’s and movement coordination. This observation might provide a nice model for studying recalibration of head movements by otolith signals in microgravity.

Important questions, which can now be stated are: why is the frame of reference for head movements (as expressed by the different rotation vectors under different gravity conditions) different for different orientations of the body relative to gravity? Does the frame of reference (and the corresponding muscle activation patterns) for arm movements relative to the shoulder also change for different gravity conditions? Related to this possible change of the reference frame for the coordination of movements, the transformations from sensory representation of target position to head and limb movement commands should change concomitantly. If these coordinate transformations change in microgravity, what is the time constant for the rate of change and any other (re)calibrations of the sensori-motor system involved? All these questions can be studied relatively easily by presenting visual and/or auditory targets and by measuring eye, head and arm movements in 3 dimensions at regular time intervals after onset of microgravity conditions.

3.2. Number of muscles acting across a joint

With regard to the number of DOF’s related to the number of mono- and bi-articular muscles acting across a joint, a similar reduction of the number of DOF’s is present since the relative activation of muscles is stereotypical across trials and across subjects for each motor task (see, e.g., Ref. [23]). Several authors have speculated about the underlying mechanisms to reduce the number of DOF’s related to muscle activation. One of the hypotheses, which have been proposed, is that mono- and bi-articular muscles have a different functional role. Evidence for this hypothesis comes from experimental observations and model simulations which, among other things, have shown that small differences in the timing of onset of activation of bi-articular muscles, but not that of monoarticular muscles, during vertical jumping have a large effect on the height achieved [28]. The explanation is that bi-articular muscles are able to transport rotational energy from one joint to another and thereby can provide an optimal set of joint angle rotations with maximal efficiency. Bi-articular muscles also contribute to the efficiency of multijoint movements. In Gielen and van Ingen Schenau [3] it was pointed out that many movements of a multi-joint limb (like the arm or leg) require that joint torque and change of joint angle have opposite sign (see Fig. 1). This implies that work (defined as the product of joint torque and change in joint angle) done at such a joint is negative. Therefore, if only mono-articular muscles would have been available, a muscle in such a case would dissipate work, rather than contribute positive work. As a consequence other muscles should produce much more work in order to be able to make the movement and to generate the work which is dissipated at other muscles. The availability of bi-articular muscles does not make lengthening of activated mono-articular muscles necessary and thereby contribute to a higher efficiency of the motor system in cases when mono-articular muscles would be lengthening while being activated.

Later experiments have revealed a simple hypothesis to explain the specific activation patterns of mono- and bi-articular muscles [27]. This hypothesis implies that the activation of bi-articular muscles is completely determined by the amplitude and direction of the force at the end effector. The activation of the mono-articular muscles depends on movement direction in a way that mono-articular muscles tend to be activated during normal aiming movements more for movements in directions corresponding to shortening of that muscle.

This is illustrated in Fig. 2, which shows a polar representation of the amount of EMG activity as a function of movement direction for a mono-articular elbow flexor muscle (m. brachioradialis) and a bi-articular muscle (m. biceps brachii, caput breve) for various force directions. Clearly, the mono-articular muscle has a preferred movement direction, for which the EMG activity is maximal. This preferred movement direction is in the middle of the

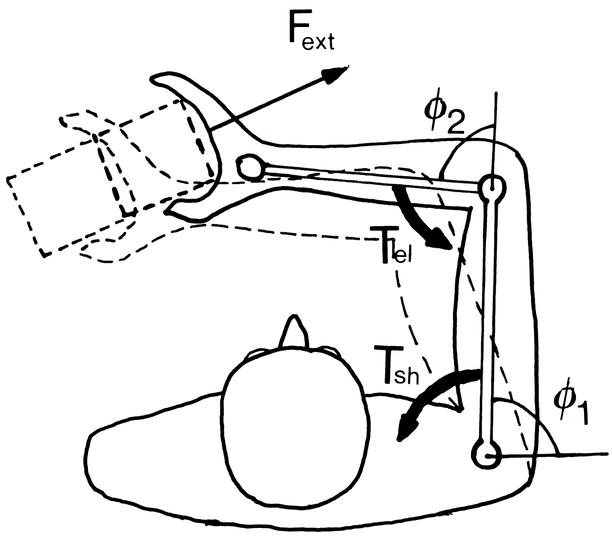

Fig. 1. Schematic drawing of a subject exerting a force against an external force F_{ext}. Such a force requires a flexion torque in elbow and shoulder joints. However, a movement opposite to the external force F_{ext} requires extension of the elbow, which means that the change in elbow joint angle and the elbow (flexion) torque are opposite in sign. As a consequence, the work done at the elbow has negative sign.

range of movement directions for which m. brachioradialis is shortening. The amount of EMG activity decreases gradually for movement directions away from the preferred movement direction. Changing the direction of force results in a simple scaling of the shape of the EMG activation pattern for all movement directions. At the contrary, no such preferred movement direction is obvious for the activation of the bi-articular m. biceps. The EMG activity of the bi-articular muscle is more or less the same for all movement directions. However, there is a 'preferred' direction for the force at the wrist (in a world coordinate system), for which the biceps receives the largest activation. In Ref. [27] it is shown that the activation gradually decreases for other force directions. The observation that the relative activation of muscles is task dependent is in agreement with earlier observations by van Bolhuis and Gielen [26] and by Theeuwen et al. [23].

Another hypothesis, which predicts a specific role for bi-articular muscles, is based on stiffness regulation. A stable posture of the hand requires that the hand generates forces opposite to small external loads. The amount of stiffness determines the amplitude of the hand displacement to changes in external load. This stiffness is the result of muscle mechanical properties and of reflex actions. It can be shown [8] that stiffness in work space requires a specific stiffness in joint space which cannot be obtained with mono-articular muscles. Recent experiments [11] have shown that a constant joint stiffness does not guarantee a stable posture of the hand. At the contrary, it is essential that subjects vary stiffness at the joints for different arm postures in order to maintain a stable limb posture in the presence of applied external forces at the hand. The proper control of stiffness attributes a special role to the bi-articular muscles providing a coupling between the stiffness in neighbouring joints [8]. This coupling determines the orientation of the stiffness field, as was shown by Flash and Mussa-Ivaldi [2]. These results were obtained in conditions in which random force perturbations were applied to the hand while subjects were instructed to not consciously intervene. This observation, which predicts a special role for bi-articular muscles, is not in contradiction to other results on muscle activation. Rather it is compatible with the observation that muscle activation is task-dependent (see Ref. [23]). The results of McIntyre et al. [11], which show that a constant joint stiffness does not guarantee stability for all postures of the arm, suggest that the relative activation of mono- and bi-articular muscles should be changed in order to meet different stability requirements for different motor tasks. Such a different relative activation is in agreement with theoretical and experimental results of Gielen and van Ingen Schenau [3] and van Bolhuis et al. [27].

In the absence of gravity, the role of position and force control will be different in normal and microgravity conditions. This predicts that the differences found in the relative activation of muscles in force and position control

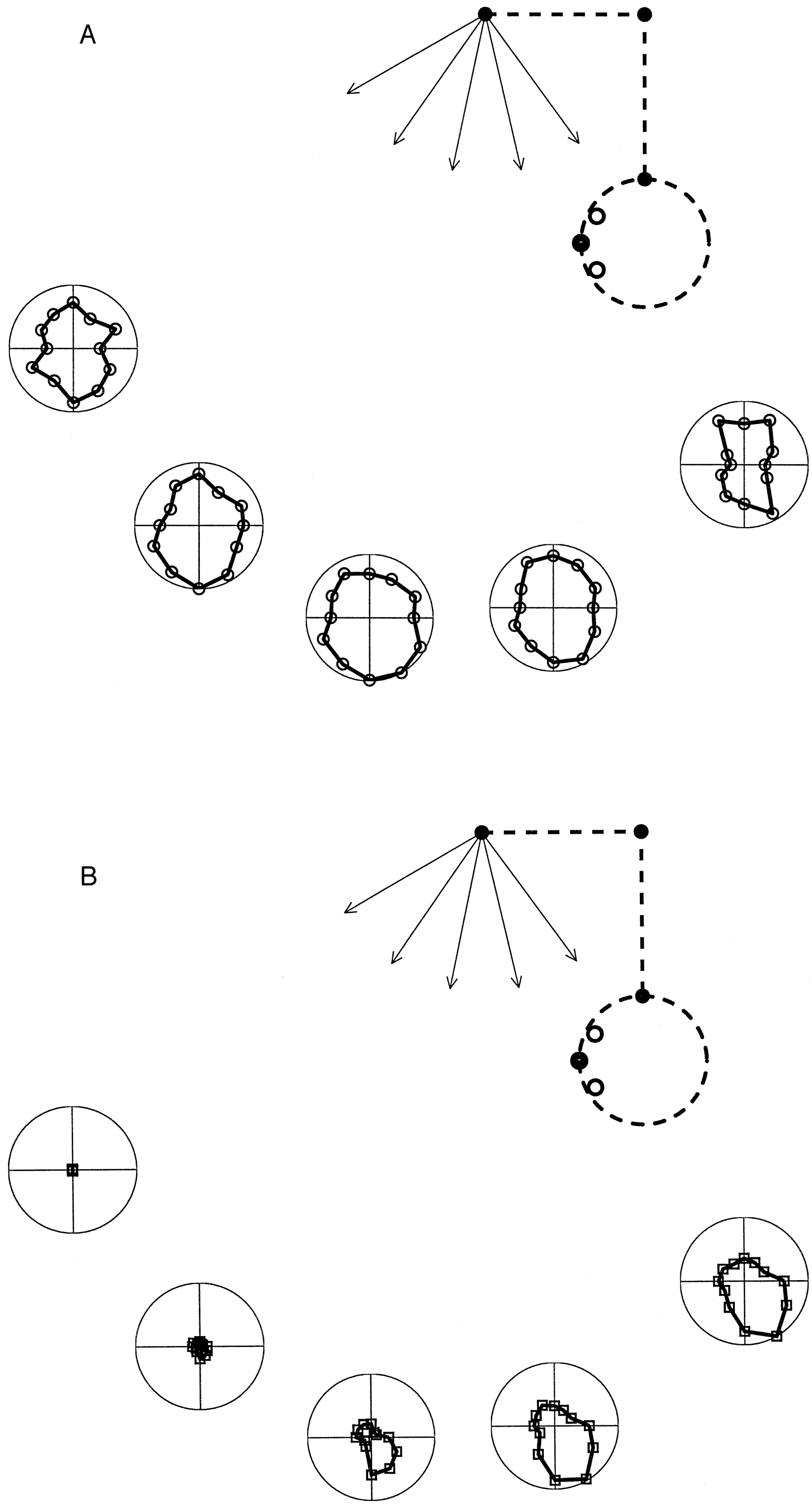

Fig. 2. EMG activity of m. brachioradialis (mono-articular muscle) (A) and m. biceps (caput breve) (bi-articular muscle) (B) for forces in various directions and for movements in various directions. Each plot shows a polar plot of the EMG activity as a function of movement direction for a constant force vector (amplitude 30 N) at the hand indicated by the arrows pointing to each of the plots. All data points represent the mean EMG activity in 2 repeated trials. The subject was sitting in a chair with the arm in a horizontal plane, as shown by the schematic drawing. For a more detailed overview of EMG activation as a function of force and position and the experimental procedures, see van Bolhuis et al. [27].

tasks, will be reflected in different muscle activation patterns for identical movement tasks in normal and microgravity conditions.

The task-dependent activation of muscles becomes evident not only at the level of muscles, but also at the level of motor unit populations. One of the cornerstones in our understanding of motor control is the size principle, which states that motor units of a muscle are recruited in a fixed order corresponding to the size of the motoneuron soma [7]. This principle was based on the assumption of a homogeneous activation of the pool of motoneurons. However, several studies have presented evidence for deviations of a homogeneous activation in various conditions. As a consequence, deviations from a fixed recruitment order can be observed. Nardone et al. [15] demonstrated reversal of motor unit recruitment during lengthening contractions in gastrocnemius in man. Later, van Bolhuis et al. [25] showed that very systematic differences in recruitment are observed for sinusoidally modulated isometric contractions and rhythmic movements of the forearm. Clearly their results demonstrate that some motor units are preferably activated for isometric contractions while other motor units give larger contributions to muscle force during movements. These results provide another illustration of the task-dependent activation of muscles. Since microgravity changes the amount of force for limb movements and posture, the question arises how this will effect the activation of muscles in motor tasks, which on earth require more or less independent control of force or position.

4. Summary and discussion

This mini-overview presents a summary of relevant results on the planning and the coordination of multi-joint movements in various task-conditions. The results in the literature demonstrate that there is a consistent reduction of the number of degrees of freedom depending on the task (position control, force control, accuracy). Most of these results are related to relatively simple motor tasks, which presumably are made based on afferent activity from various sensory modalities. In microgravity, the sensory input will be disturbed. Dealing with this unfamiliar situation will require a recalibration process of bottom-up sensory signals as well as a recalibration of top-down driven intentional/cognitive aspects of motor control. It might also lead to a different role of feedforward and feedback mechanisms in movement control. How (re)calibration of sensory feed-back takes place and with what time constants is unknown. Yet, it is extremely important information, both from a purely scientific point of view as well as for understanding and improving the degraded performance of astronauts in space.

Research in microgravity conditions will provide many important new basic insights which will contribute to the benefit of sensorimotor performance of man in microgravity conditions. These results will provide insight in the adaptation processes of sensori-motor behaviour as a function of time, will alleviate many adaptation problems to microgravity, and will contribute to a better performance of man in space.

For this purpose, dedicated hardware will be necessary which will allow measurement and control of human limbs and posture (e.g., two 6-DOF robot manipulators to study and manipulate bi-manual arm movements) and advanced equipment for stimulation (e.g., Transcranial Magnetic Stimulation (TMS)) and recording (quantitative EEG and EMG) of neuronal activity. TMS is a relatively new technique, which is gaining popularity both for clinical and basic research. TMS, if used properly, induces action potentials of neurons, which are already near threshold. Since the effect of TMS on motor control functions can be studied relatively easily by recording EMG activity in response to TMS, the role of various cortical structures can be investigated in motor control in space, in particular during the recalibration process after launch.

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