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Preservation of motor flexibility in healthy aging

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General Introduction

1.1. MOTOR FLEXIBILITY IS A KEY FEATURE OF THE HEALTHY NEUROMUSCULAR SYSTEM

In daily life we reach and move objects of different size, shape and weight to different locations. While the gross appearance of reaching movements is the same, its' details are modified depending on the constraints to the movement (e.g., target location, shape, weight of objects) [1,2]. The gross shape of a prehension movement to a glass in an upright position as compared to it lying on a table is the same but the orientation of the hand slightly changes to grasp the glass. Similarly, when rising from a chair, the height of the chair and size of the support surface modify the trajectory of the lower and upper extremity joints but the global appearance of the sit-to-stand movement remains invariant. Even when we repeatedly reach to the same location small changes in initial body postures lead to different motions at the shoulder, elbow, and wrist joint but the trajectory of the hand is the same between repetitions. This ability to adapt to small changes in the constraints to movement and perform the same motor task with different motions at the joints reflects a key feature of human motor behavior: motor flexibility [3–7].

This flexibility in motor behavior is possible because the number of possible joint motions is usually more than actually needed to perform reaching, sit-to-stand and other tasks of our daily life [3]. Consider for example the task of pressing a button on a table. The goal of this task is to keep the finger on a pre-defined position on the table. There are two dimensional constraints to the task goal, the x and y coordinates of the fingertip position on the table. We can keep the fingertip on the button even if we flex or extend our elbow by adjusting the shoulder, wrist and finger angle. Imagine now that only elbow and wrist flexion-extension was possible during the same button-pressing task. In this case the number of possible joint motions equals the number of constraints to the task goal, that is, two. Any change in shoulder or elbow angle will move the fingertip away from the button. Hence there is only one possible combination in shoulder and elbow angle, which brings the fingertip on the button. If we add again a joint motion at the shoulder, different combinations in shoulder, elbow and wrist angles can be used for the same fingertip position. This example illustrates that if the number of possible joint motions exceeds the number of constraints to the task goal, different coordination patterns between joints can be used to perform that task. When we reach and move objects in daily life there are usually more than seven joints in the arm, determining the three-dimensional position of the hand in space. Hence the number of possible joint motions, the degrees of freedom, is more than absolutely necessary. Due to this redundancy in the available joints there is an infinite range of movement possibilities to perform the same reaching task. The question arises which coordination patterns are selected from the many possibilities during performance.

When humans perform voluntary movements, the goal of the task and rules of performance, the environment in which we move, and the characteristics of our body define how we can coordinate our joints to achieve the task goal [1,2]. When we reach for an object at a given location, the length of our arm segments in combination with the distance to the target, the initial body posture and any interference in the environment, define which joint coordination patterns can be used to bring the hand to the target. These constraints to movement can be categorized into task and intrinsic constraints (adapted from Hu and Newell, 2011; Newell, 1986). Task constraints are defined by the goal of the task, rules of performance and the environment in which we move. The movement distance, required time to reach the target and metabolic costs associated with the movement are examples of task constraints. Other task constraints are the weight of an object, the size of the target or any obstacle in the environment. Constraints associated with our body are defined as intrinsic constraints. The given segment length, available muscle strength, level of fatigue, joint range of motion and actual body posture are examples of intrinsic constraints. Importantly, the constraints to movement interact with each other and based on this interaction a given coordination pattern can be observed during performance [1,2,8].

Summarizing, redundant joint degrees of freedom characterize human voluntary movements, including daily tasks such as reaching and rising from a chair. Motor redundancy provides humans with flexibility to successfully perform upper and lower extremity voluntary movements under different intrinsic and task constraints. The main research question of this thesis was whether and if so how age-related changes in intrinsic constraints affect flexibility in joint coordination during reaching and sit-to-stand movements. The hypotheses are based on two motor control perspectives, the internal model approach and the principle of motor abundance. Based on these frameworks the thesis examines two competing hypotheses with regard to age-differences in motor flexibility. Based on the internal model approach, detailed in the third section, the central hypothesis posits that age-related declines in neuromuscular functions impair flexibility in joint coordination during reaching and sit-to-stand. Based on the principle of motor abundance, detailed in section 4, the alternative hypothesis states that age-related deficits in intrinsic constraints facilitate the emergence of alternative coordination patterns leading to an increase in motor flexibility during old adults' reaching and sit-to-stand performance.

To test these hypotheses, we established age-differences in motor flexibility during repeated performance of challenging reaching and sit-to-stand tasks in four experimental studies (Chapter 2 – 5). We chose reaching and sit-to-stand tasks because these are fundamental activities of daily living, performed frequently under different task constraints.

1.2. HEALTHY AGING IMPAIRS NEUROMUSCULAR FUNCTIONS AND MOTOR PERFORMANCE

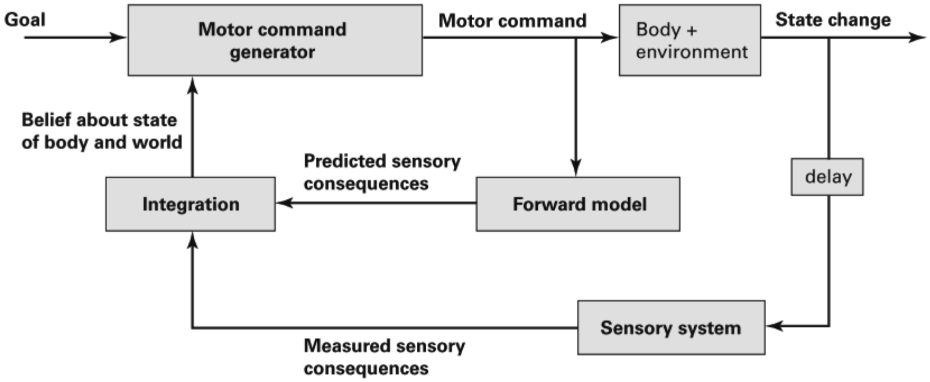
Healthy aging, the disease-free progression of life, affects functions of the central and peripheral neuromuscular system. Healthy old as compared to young adults have fewer and smaller muscle fibers resulting in 10% per decade decline in maximal voluntary force and power [9–15]. Age-related degradation in connective tissue and articular cartilage leads to joint stiffening and limitations in the available joint range of motion in which old adults can move [16,17]. Age-related remodeling of motor units leads to an increased number of muscle fibers per motor unit impairing the old adults force coordination abilities [18–21]. Furthermore old adults have fewer and smaller afferent fibers[22], a reduced motor cortical inhibition [23–26], more white matter lesions[27–30] and impaired central nervous system connectivity [31–33]. This loss in functional and physiological degrees of freedom with aging has been associated with a general decline in old adults' motor performance. Healthy old as compared to young adults perform reaching and sit-to-stand tasks slower and less smoothly, execute gross postural and fine finger movements less accurately, show impaired performance of bimanual motor tasks and are less able to adapt to systematic errors in new motor tasks [30,34–49]. The age-related deficits in intrinsic constraints and the decline in kinematic performance measures with aging motivates the idea that healthy aging also impairs flexibility in joint coordination.

1.3. HEALTHY AGING IMPAIRS FLEXIBILITY IN JOINT COORDINATION. AN INTERNAL MODEL APPROACH

The idea of a direct link between age-related deficits in neuromuscular functions and flexibility in joint coordination is in line with motor control theories such as the internal model approach [50–53] (Figure 1). The idea is that the neuromuscular system restricts the available degrees of freedom and chooses a specific coordination pattern for a given motor task. This unique coordination pattern is chosen to minimize the required effort associated with the task (e.g. metabolic costs) [50–54]. During movement inverse and forward models are used to minimize deviations from the desired joint trajectories in space. Internal models are neurophysiological structures which reside in distinct areas of the central nervous system such as the cerebellum [50,55–59].

Based on the internal model approach humans define a desired, optimal trajectory of consecutive shoulder, elbow and wrist positions before they start and move the hand in space [50] (Goal in Figure 1). Given the actual and desired joint positions inverse models are used to calculate the required inputs into the alpha-moto-neuronal pools at a given point along the movement path to achieve the desired muscle activity and joint trajectories in space. Based on these computations, motor commands are generated by the central nervous system (motor command generator) to activate the corresponding motor units. To generate adequate motor commands the central nervous system requires an estimate of the actual length, velocity and force of the muscles in the shoulder, elbow and wrist joint. This sensory information provides an estimate of the actual joint positions and state of our body in the environment ("belief about the state of our body" in Figure 1). Two distinct sources provide the central nervous system with this sensory information. First, central and peripheral feedback loops (e.g. muscle spindles and the cerebellum) measure the actual level of muscle activity, muscle length and joint positions. However, measured sensory information is delayed in time and corrupted by noise. To compensate for the delayed and noisy feedback signals feedforward models are used. Feedforward models use information from the generated motor commands to predict the sensory consequences and expected change in muscle length and joint positions. The predicted sensory information is combined with the actually measured sensory information to provide an estimate about the actual state of our body and joint positions in space. Age-related changes in the neuromuscular system would impair the accuracy of the actual state of our body through feedforward models leading to an inaccurate estimate of the actual joint positions.

Figure 1. The internal model approach to movement control [50].



The age-related change in intrinsic constraints affects the relation between the generated motor commands and the sensory consequences. This change in input-output relation results in an increased discrepancy between expected and actually measured sensory consequences [33,59,60]. For example, old as compared to young adults have fewer motor units and the available motor units innervate a larger number of muscle fibers [18–21]. Activating an old, remodeled motor unit as compared to a healthy young motor unit at the same frequency would lead to a higher level of muscle activity and faster change in muscle length. This age-related change between generated motor commands and actual sensory consequences leads to inaccurate forward model predictions and inaccurate estimations about the actual state of the body.

There might be two adaptation mechanisms which old adults could use to compensate for inaccurate estimations in the actual body positions through feedforward models. First, old adults might rely more on the measured sensory information [35,36,61,62]. However, measured sensory information is delayed in time and corrupted by noise. Therefore, more reliance on delayed and noisy feedback signals seems undesirable to improve accuracy in the estimation of the actual body positions during fast reaching movements. Alternatively, old adults might update existing forward models based on the age-related change in the relation between motor commands and sensory consequences. However, this adaptation process is probably impaired as well by age-related dysfunctions in the cerebellum and a loss of central nervous system connectivity [22,26,32,33,55]. Hence, based on the internal model framework, we hypothesized that age-related deficits in neuromuscular functions impair the control of individual degrees of freedom and therefore flexibility in joint coordination during reaching, sit-to-stand and other motor tasks. Age-related deficits in motor flexibility impair reaching accuracy and sit-to-stand stability in daily life possibly leading to task failure and falls.

Following this line of reasoning, recent studies comparing old and young adults' motor flexibility during reaching, sit-to-stand, standing balance, walking and multi-finger force coordination tasks provide somewhat unexpected results [38,63–75]. Overall these studies report inconclusive findings on whether and if so how the age-related reductions in neuromuscular function might affect motor flexibility. Even for similar reaching tasks, studies reported opposing results. For example, Verrel et al. (2012) and Dutta et al (2013) reported less whereas Krüger et al (2013) reported greater and Xu et al. (2013) similar motor flexibility in old and young adults' reaching behavior [38,63–65]. These studies imply that there is not a general decline in motor flexibility with aging. Instead, the inconclusiveness in previous studies might suggest that individual differences in the characteristics of the young and old adults' neuromuscular system interacted with the details of the reaching tasks leading to individual and task specific age-differences in joint coordination patterns.

The following paragraph will introduce the principle of motor abundance as an alternative to the internal model approach and provide a framework to predict how age-related changes in intrinsic constraints affect flexibility in joint coordination during reaching, sit-to-stand and possibly other motor tasks.

1.4. THE PRINCIPLE OF MOTOR ABUNDANCE

The principle of motor abundance assumes that having more degrees of freedom than absolutely necessary to perform a given motor task is an advantage [4,76]. Abundance means that there is something extra but that this extra is actually nice to have rather than needless (or redundant). The idea is that our neuromuscular system does not restrict a certain range of the available degrees of freedom by selecting a single coordination pattern. Instead, the neuromuscular system makes use of the many degrees of freedom to use a range of different but equivalent coordination patterns for the same movement [4,6,7,77]. Hence there are abundant rather than redundant degrees of freedom.

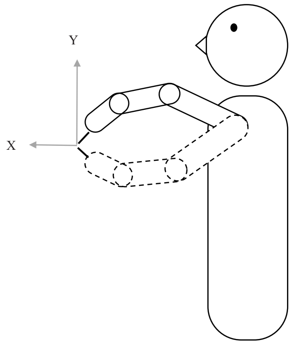
Having a range of movement possibilities for the same task is an advantage because it improves the neuromuscular systems' capacity to maintain task success in case of an unexpected change in the actual constraints to movement or internal (e.g. noise) and external perturbations.

Imagine to place a full cup of coffee on a table. During this task, the horizontal position of the cup needs to be stabilized to prevent spilling content (content which is so relevant to finish a PhD). Imagine now that at a given point along the movement path an external perturbation leads to an undesired change in shoulder, elbow or wrist position (e.g. by another person). If we would have only one possible combination in joint positions to stabilize the horizontal position of the cup we could not adapt to the perturbation and spill the coffee. However, if we allow different coordination patterns to emerge while moving, the horizontal position of the cup can be stabilized against the perturbation through small coordinated adjustments among the shoulder, elbow and wrist joint. Hence, motor abundance allows us to safely and successfully perform reaching and sit-to-stand movements in daily life environments where the actual constraints to movement are unpredictable and frequently change. This idea of performance stability through flexibility might be interpreted in the context of a dynamical systems approach [1,2,8,78–81].

During fast reaching movements, the constraints of the task (e.g. target location) and our body (e.g. segment length) define the desired trajectory of the hand in space [1,2]. At each point along this movement path is a given joint range within which small changes in the shoulder, elbow and wrist positions do not affect the position of the hand in space (Figure 2). Within this solution space the shoulder, elbow and wrist joint co-vary and all possible joint combinations form equivalent motor solutions for the same task. During performance, the individual degrees of freedom converge to this solution space leading to joint coordination patterns which best satisfy the actual constraints to movement [1,2,8,78,79,82,83]. The details of the solution spaces evolve during performance based on the actual state of the moving body (e.g. level of muscle activity) and the constraints to movement. A fluent, goal-directed movement might be described as the transition between consecutive solution spaces [83]. This form of performance stability through flexibility allows the neuromuscular system to adjust individual joint positions in response to unexpected changes in movement constraints or small perturbations without compromising task success.

Based on this framework, the idea emerges that age-related deficits in intrinsic constraints (e.g., muscle strength) change the interaction between the actual constraints to movement leading to age-differences in motor flexibility. We hypothesized, that if age-related deficits in intrinsic constraints compromise stability of task important variables old as compared to young adults increase co-variation among the involved joints and employ a larger range of the available coordination patterns. Using a larger range of different coordination patterns for the same task would allow old adults to guarantee reaching and sit-to-stand stability in daily life environments despite deficits in neuromuscular functions.

Figure 2. Goal equivalent coordination patterns.



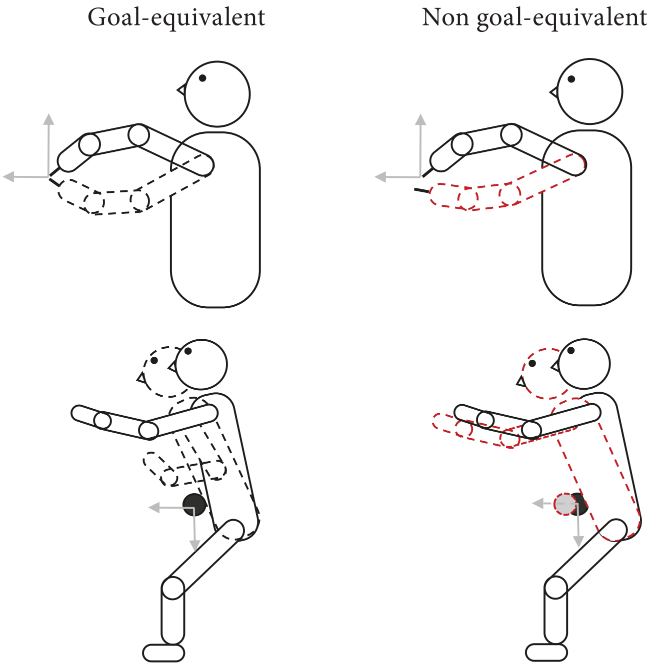
Within this pointing task there are three possible joint motions and two dimensional constraints to the task goal (x and y coordinates of the target). The same pointertip position can be achieved with different joint configurations (solid vs dashed segments). The solution space contains all joint configurations leading to the same pointertip position [6].

1.5. THE UNCONTROLLED MANIFOLD METHOD

Bernstein (1967) provided the first experimental evidence for the principle of motor abundance [3]. During his experiment Bernstein asked professional blacksmiths to repeatedly hit a chisel with their hammer. The idea was that if the neuromuscular system employs a unique optimal motor solution, these highly trained blacksmiths would have discovered this solution and use it during actual performance. However, Bernstein observed that trial-to-trial variability in the joints was relatively large while the trajectory of the hammer tip position was kept fairly constant between repetitions. The main conclusion of this observation was that the neuromuscular system does not employ unique optimal coordination patterns. Instead, individual joints co-varied to stabilize the hammer tip at the desired trajectory in space.

Based on the findings from Bernstein in 1967 many experimental studies with more sophisticated experiments and analytical techniques followed and provided further evidence for the principle of motor abundance [5–7,82]. In 1995 the concept of the uncontrolled manifold (UCM) method was introduced to study flexibility in joint coordination during functional motor tasks [81]. When repeatedly performing the same reaching task, the UCM method makes it possible to decompose trial-to-trial variability in joint motions into those coordination patterns stabilizing the trajectory of the hand in space (coordination patterns within the solution space (V_{UCM}) or goal equivalent variability (GEV)) and coordination patterns causing a deviation of the hand position away from the mean value (variability orthogonal to the solution space (V_{ORT}) or non-goal equivalent variability (NGEV); Figure 3). Recall the button pressing example from the second paragraph. All combinations in joint positions not affecting the position of the fingertip would be attributed to GEV. Those joint configurations moving the fingertip away from the button would be attributed to NGEV. The amount of GEV reflects the extent to what our neuromuscular system makes use of the available range of possible motor solutions to stabilize task important variables at the mean. NGEV reflects the extent to what the neuromuscular system employs coordination patterns leading to a change in task important variables from the mean value. Based on these definitions large values of GEV imply that the neuromuscular system has a larger capacity to stabilize task important variables in case of unexpected changes in the actual constraints to movement [5–7,82].

Figure 3. Variability components GEV and NGEV in UCM analyses.



Examples of goal equivalent (dashed black lines) and non-goal equivalent variability (dashed red lines) during reaching and sit-to-stand movements with the end-effector and whole body center of mass position (dark filled dot and grey dot) as performance variable of primary importance.

The UCM method has been tested and elaborated in various methodological and experimental studies involving sit-to-stand, reaching, jumping, balance and multi-finger force coordination tasks [5,69,84–97]. For example, Scholz and Schöner (1999) showed that when healthy young adults repeatedly performed sit-to-stand tasks the lower and upper extremity joints co-varied to stabilize the whole-body center of mass position within the base of support (large GEV, low NGEV) [5]. The whole body center of mass position is the key variable, which needs to be controlled to during sit-to-stand movements [98]. Furthermore, UCM measures have been shown to be sensitive to changes in task constraints and external perturbations [99–103]. For example, when healthy young adults performed a bi-manual coordination task in addition to a standing balance task GEV increased more than NGEV to guarantee COM stability [99]. Hence, the additional coordination constraint interacted with the actual constraints to movement leading to a compensatory increase in motor flexibility.

In the current thesis we used the UCM method to establish whether and if so how age-related changes in the constraints to movement affect flexibility in joint coordination during reaching and sit-to-stand. We proposed that age-related deficits in task relevant neuromuscular functions lead to a compensatory increase in GEV during reaching and sit-to-stand tasks. There have been previous attempts to establish whether healthy old as compared to young adults differently employ flexibility in joint coordination [38,63–74]. However, these studies revealed inconclusive findings during even similar motor tasks and used rather simple motor tasks without changes in task constraints. We tested the hypothesis that healthy old adults employ larger motor flexibility when the actual constraints to movement challenge stability of task performance. During daily life, reaching and sit-to-stand tasks are performed under various accuracy, force and balance constraints. Therefore we manipulated accuracy, force and balance constraints during repeated sit-to-stand and reaching performance to establish age-differences in motor flexibility.

1.6. OUTLINE OF THE THESIS

The first experiment in chapter 2 established how healthy young as compared to old adults made use of flexibility in joint coordination to stabilize the whole body center of mass position during repeated chair rises. Based on the acquired results we established whether healthy old as compared to young adults differently adapt flexibility in joint coordination to guarantee a) reaching accuracy under high accuracy and force demands (chapter 3 and 4) and b) center of mass stability during repeated chair rises under high force and balance demands (chapter 5). Chapter 6 provides a general discussion and conclusion of our findings.

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