Motor variability as a characteristic of the control of reaching movements: Influence of sensory input and task constraints

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Abstract

Reaching towards the cup of coffee in the morning will, under most circumstances, result in successful grasping of it. Although it seems as if this is a very simple movement, executed already a thousand times before, it is actually very complex, requiring the control of numerous degrees of freedom at different hierarchical levels of the motor system. Importantly, not two reaching movements towards the cup of coffee will be identical. Flexibility in movement execution in the presence of stable task performance represents an exceptional ability of the human motor system. A major interest of motor control research is to understand how the control of complex reaching movements is adjusted to constantly changing environmental conditions and how task performance is stabilized under such circumstances. In this thesis, the influence of sensory input and external task constraints on human movement control is investigated. Four studies were conducted to investigate the influence of (1) vision, (2) proprioception, (3) target shape, and (4) age on the control of movement variability in complex reaching movements. Analyzing movement variability was chosen as the approach to gain insight into the processes underlying stable movement execution. First, it is shown that the availability of visual information is of minor importance for the control of this kind of movements. In the second study it is shown that the human motor control system immediately adjusts movement control to the availability of proprioceptive information without changes in tasks performance. Further, the healthy human motor system is able to simultaneously account for multiple task constraints without performance decrements. Thereby, multiple task constraints are differently accounted for, with the more constraint task variable being more strongly stabilized. It is further shown that this pattern changes with age. In general, the outcome of this work provides evidence that the human motor system is purposefully exploiting motor redundancy, i.e. flexibly and synergistically coordinating the effector degrees of freedom, to keep task performance stable under changing sensory input and external task constraints.

Overview

This thesis is structured in three main chapters. The first chapter gives a general introduction into the topic with the special focus on the two theoretical columns of this thesis: first, the control of movement variability, and second the influence of sensory input and external task constraints on the control of reaching movements. Further, an excursus on the topic of optimal feedback control is made and a short overview about the methodological approaches applied in the current thesis is presented. At the end of the introduction the aim of this thesis is stated.

The second chapter presents four research projects in form of manuscripts. At the beginning of that chapter the title of each manuscript and the contribution of the author of this thesis to each project are stated. Following, the four manuscripts are included in the format they are published, will be published or are submitted.

The first article deals with the influence of the availability of visual information and an accuracy constraint on the control of complex reaching movements. Based on the results of this project, the second article addresses the question whether healthy subjects are able to adjust the control of complex reaching movements to the loss of proprioceptive information. The third article deals with the question of how the control of a complex reaching movement accounts for multiple external task constraints that are induced by the geometric properties of the reaching target. Finally, the last article included in this thesis targets age-related changes in the control of reaching movements.

The third chapter offers a general discussion on the findings of the four research projects in relation to the current state of knowledge. In addition, a critical discussion on the methods used in this thesis and a short outlook on possible further directions of research is given.

Contents

1 General Introduction

When swimming through open water, each arm stroke can be characterized by two seemingly opposing features: flexibility and stability in movement execution. Both, flexibility and stability refer to the existence of variability in repeated arm strokes. Thereby, flexibility reflects the variability in the coordination of the redundant degrees of freedom (DoF) of the arm. This is of importance for the adjustment of the swimming technique to the ever-changing environmental conditions as for example the height of the waves. In contrast, stability refers to the variability in the movement outcome. Ideally, each arm stroke is executed stable and nearly optimal to provide the greatest propulsion. Interestingly, flexibility and stability in movement execution are related to each other, as the first grants the second.

To better understand this seeming contradiction one has to think about the two different levels of analysis when talking about flexibility and stability in movement execution. While flexibility, as described above, refers to the effector space, which means for example joint angles for arm movements, stability refers to the task space, as for example final arm posture. The distinction between effector and task space is of special interest when investigating the influence of sensory input or external task constraints (e.g. visual input for estimating drift or wave height, respectively) on the control of well-trained movements, where task performance changes little in the presence of changing environmental conditions. Then, analyzing the effector space can bring out differences in the control of movements that did yield similar task performances. In recent times, the distinction between effector and task space became especially meaningful as the advantages of motor redundancy foregrounded (Latash, Scholz & Schöner, 2007; Todorov & Jordan, 2002). Motor redundancy describes the phenomenon that the number of DoF within the effector space is greater than the one within the task space, resulting in an infinite number of possible task solutions. How the healthy human motor system takes use of motor redundancy to account for different environmental conditions in movement control is a question still under debate.

In this thesis, experimental work on the control of complex reaching movements under different sensory inputs and different external task constraints will be presented. In that regard, analyzing movement variability served as an approach to be able to investigate movement control. Reaching movements were chosen as the experimental task as they represent an elemental part of human’s every-day motor behavior, as for example reach-to-grasp a cup of coffee or reach-to-grasp the door handle. Due to that, they are usually performed with high quality, even under changing sensory inputs or changing external constraints (Cisek, Grossberg & Bullock, 1998; Fitts, 1954). At the same time, reaching movements are complex as they are requiring the coordination of numerous DoF in 3D. The sum of these points makes reaching movements to a very interesting and suitable motor task to study.

In the following, I will introduce the two main theoretical columns on which my thesis is based. First, the existing knowledge about the control of movement variability will be presented. Within that context, the distinction between effector and task space will be introduced. This will clarify some of the observed inconsistencies in the existing empirical evidence on the control of reaching movements by assigning them to the analysis of either one of the two levels. Further, the "problem of redundancy" will be introduced. This subsection describes how the human motor control system can take advantage of the superior number of effector DoF in the control of complex movements. Representing the second theoretical column, empirical evidence about the ability of the human motor control system to adjust to changing internal and external conditions will be reviewed. Subsequently and before stating the aims of this thesis, a short excursion on optimal feedback control will be made and different methodological approaches in analyzing movement variability will be considered. Finally, the aim of this thesis will be defined.

1.1 About the control of movement variability

Movement variability is an inherent characteristic of human motor behavior. Within the last recent years it has attracted a lot of scientific attention and its examination has become much more nuanced since then. In the following, a short overview about the current state of empirical and theoretical knowledge will be given.

1.1.1 Movement variability in the effector and the task space

With respect to the frame of reference, movement variability can be considered as either a sign of healthy or impaired motor control (Berardelli, et al., 1996; Cirstea & Levin, 2000; Latash & Anson, 2006; Latash, Scholz & Schöner, 2007). It is important to note that the seemingly contrasting positive or negative attribution of movement variability is often due to an analysis of movement execution on different levels. In principal, two levels of analyzing movement variability have to be distinguished: effector space and task space (also termed as intrinsic and extrinsic space; see e.g. Desmurget, et al., 1995). Thereby, variability in the effector space is usually referred to as flexibility in movement execution (Latash, Scholz & Schöner, 2007; Scholz & Schöner, 1999) or as stereotype when variability is absent (Müller & Sternad, 2009). On the other hand, there is variability in the task space that defines the quality in movement execution. In motor control research, much of the theoretical and experimental work has focused on analyzing movement variability in the task space. Recently, the "minimum variance" model was supposed, assuming that in reaching movements the motor control system tries to minimize variability of e.g. final hand position (Harris & Wolpert, 1998; see also 1.3 below). This theory builds the frame within much of the existing empirical evidence about the control of reaching movements can be ranged (see for example Grea, Desmurget & Prablanc, 2000; Simmons & Demiris, 2006). Though, it seems as if for redundant effector systems minimizing movement variability at movement end explains only parts of the strategy underlying human movement control (Latash, Scholz & Schöner, 2002; see also 1.3).

1.1.2 The problem of redundancy

Motor redundancy is a long-known phenomenon in motor control research. It describes the fact that the number of DoF in the effector space is often superfluous to the number of DoF in the task space. As a result, there are an infinite number of possible solutions of the motor task. To exemplify this phenomenon let’s assume to reach towards an object. The location of the object in space can be described by three dimensions (dimensionality of the task space): position in horizontal and vertical direction and in depth. The posture of the arm when grasping this object can be described by seven joint angles (i.e. three shoulder angles, two angles of the elbow, and three wrist angles; dimensionality of the effector space). As the dimensionality of the effector space is greater than the one of the task space there are theoretically infinite possible combinations of joint angles that would all result in successful grasping of the object.

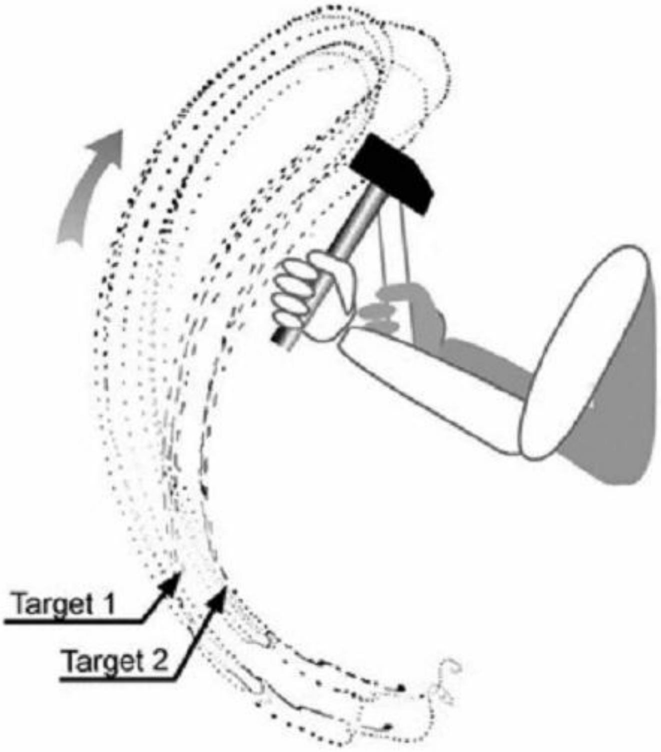


Fig. 1: Illustration of the Hammering-example of Bernstein (1967). The least variable points during the hammering trajectories were the locations of the two nails. The figure is obtained from Müller & Sternad, 2009.

For a long time, redundancy was considered as a problem for the motor control system, as it requires a complex strategy coordinating these DoF (Bernstein, 1967; Gielen, Vanbolhuis & Theeuwen, 1995). Though recently, the idea that the motor control system can take use of motor redundancy became of greater interest in motor control research (Latash, Scholz & Schöner, 2002; Müller & Sternad, 2009). In this context, the “blacksmith hammering a nail"-example of Bernstein (1967; see Fig. 1) is often cited. Bernstein noted that the least variable point during the hammering trajectory was the point when the hammer hit the nail. Looking at it the other way around, the variability observed in the movement trajectory would have led one to expect a greater variability at the target point as actually observed. Similar observations were made for many other tasks, like sit-to-stand (Scholz & Schöner, 1999), pointing (Domkin, et al., 2002; Verrel, Lövden & Lindenberger, 2012), or multi-finger force production (Shinohara, et al., 2004; Zhang, et al., 2008), too. What all these studies have in common is the observation that the variability within the effector space was correlated between the different effector DoF such that variability in the task space stayed relatively small. Based on that, movement variability in the effector space was further distinguished into task-relevant and task-irrelevant variability. Several methods have been developed to separate between the two kinds of movement variability (Cusumano & Cesari, 2006; Müller & Sternad, 2009; Scholz & Schöner, 1999; see also 1.4 for a more detailed description of the methods).

Different assumptions were put forward why motor redundancy could be advantageous. In line with the "minimum intervention principle" (Todorov & Jordan, 2002; Todorov, 2004), taking use of motor redundancy would allow to optimize the costs related to movement control, as it would then only be necessary to minimize variability in task-relevant directions, i.e. in directions which are of importance for successful movement execution. Alternatively, motor redundancy could be used to exploit the range of successful task solutions, potentially resulting in better task performance (Archambault, et al., 1999; van Beers, Brenner & Smeets, 2013). This explanation was suggested with regard to the improvement in motor performance during movement learning (Latash, Scholz & Schöner, 2007). As a third option, taking use of motor redundancy may allow to account for multiple task variables during the control of complex movements. This may become relevant when moving in natural environments, which are characterized by the varying availability of sensory inputs and varying external task constraints. Taking use of motor redundancy may be a way cope with these factors (Gera, et al., 2010; Zhang, et al., 2008). It is important to note that the three options are not mutually exclusive and may influence healthy human movement control concurrently.

1.2 Motor control under changing environmental conditions

When moving in natural environments, our behavior is influenced by multiple factors. The broadest differentiation one could possibly think of is between internal and external factors of influence. Thereby, internal factors are related to internal states such as general alertness, motivation, memory, etc. and to the characteristics of the sensorimotor system transforming e.g. visual or proprioceptive inputs into neural activity, and subsequently into motor actions. All these factors are subject to modification due to learning and aging. Opposed to that, external factors are induced by the environment.

External factors could be e.g. accuracy constraints or speed requirements in movement execution. Both internal and external factors have an influence on movement control (Desmurget et al., 1997a). In the following, a brief overview about the existing knowledge on the influence of internal and external factors on movement control will be given.

1.2.1 Sensory integration of vision and proprioception

Vision and proprioception build an important source of information used to plan and control reaching movements. Therefore, manipulating the availability or reliability of these two sources of information is a common approach in motor control research to gain information about the functioning of the human motor system in health and disease (see for example Bagesteiro, Sarlegna & Sainburg, 2006; Bays & Wolpert, 2007; Sober & Sabes, 2005).

As the availability and reliability of visual information are easily to perturb, affecting this source of sensory information is very common when investigating the planning and control of reaching movements (Ellenbürger et al., 2012; Goodale & Milner, 1992; van den Dobbelsteen, Brenner & Smeets, 2003). It was found that the availability of visual information about the target and the effector position prior to movement initiation is sufficient to plan a reaching movement, which can then be successfully executed without visual online-control (Desmurget et al, 1997b). Further, vision seems to be of particular importance for the planning of the movement distance, whereas proprioception seems to be of greater importance for movement online control (Bagesteiro, Sarlegna & Sainburg, 2006). There is ample empirical evidence that the healthy motor system is able to successfully plan and control reaching movements under changing visual conditions with respect to its movement outcome. However, so far, it is not equally well studied how the availability of visual information influences the control of movement variability *during* movement execution. This is the question to be targeted in the first study presented in this thesis.

A second important source of sensory information is proprioception. In contrast to vision, which is part of the exteroception of the sensory system, proprioception transmits information about the internal body-states, e.g. joint angles or muscle activity, through specialized organs (Bear, Connors & Paradiso, 2007). Due to that, it is assumed that proprioception plays a major role for the control of movements within the effector space (Desmurget & Prablanc, 1997; Gentilucci et al., 1994; Ghez & Sainburg, 1995). Thereby, proprioception is of special importance during online-control of the movement, when incoming information about the executed movement is compared to the efference copy, which contains information about the to-be-expected sensory consequences of the movement (von Holst & Mittelstaedt, 1950). Further, proprioceptive information are integrated in the internal representation of the movement during movement planning (Medina, Jax & Coslett, 2009). Because it is more difficult to manipulate the availability and reliability of proprioceptive than of visual information, its influence on the control of reaching movements is usually studied on patients with chronic proprioceptive impairments (see for example Medina, Jax & Coslett, 2009;

Nougier, et al., 1996; Sainburg et al., 1995; Sainburg, Poizner & Ghez, 1993). So far, it is not well-investigated how strong the motor system of healthy humans relies on proprioceptive information and whether it is able to immediately and effectively adjusts the control of complex reaching movements to the temporary loss of proprioception. This question will be targeted in the second study presented in this thesis.

1.2.2 Influence of external task constraints

External factors that are influencing the planning and control of reaching movements are versatile. A first factor is the difficulty of the task imposed by the target size, the reaching distance, or the required speed in movement execution. Task difficulty has a well-documented effect on movement speed and accuracy, described by Fitts' Law (Fitts, 1954; Fitts & Peterson, 1964): when aiming between two targets, increasing movement difficulty (by e.g. increasing the distance between the two targets), will lead to adaptive changes in movement planning so that movement duration and/or movement variability at the endpoint is increased. To put it in different words: when increasing movement speed in an aiming task, movement variability at the target will be increased. This so-called "speed-accuracy trade-off" is largely supported by empirical evidence (e.g. Adam, 1992; Buchanan, Park & Shea, 2006; Kovacs, Buchanan & Shea, 2008). Though, most studies focused on final task performance. How the adjustments of movement planning and control to increased movement difficulty due to an increased accuracy constraint are reflected in the time course of movement variability during movement execution is much less studied (for an example see Boyles, Panzer & Shea, 2012) and will be targeted in the first study of this thesis.

Another external task constraint, whose influence on movement control is documented by ample empirical evidence, is the shape and the orientation of the reaching target. David Rosenbaum proposed that reaching movements are planned and executed in a way that final arm posture at target location is most comfortable, even if that requires uncomfortable arm postures during movement execution, known as the "end-state comfort effect" (Rosenbaum et al., 1992). Hence, the end-state comfort is determined by the shape of the reaching target and its final location. Further, Desmurget and colleagues (1995) could show that final arm posture of a reaching movement is determined by the orientation of the target, independent of whether the reaching target was stationary or changed its orientation after movement onset. This suggests that the human motor system is able to adjust the online-control of a reaching movement to the changing target orientation. Altogether, this suggests that the reaching target itself has an influence on the control of the reaching movement in the bid to achieve a certain final arm posture. Though, so far it is not clear whether, when reaching towards different targets which do not enforce different final arm postures, but whose target shapes apply differently strong constraints on certain parameters of it, the healthy motor system accounts for these constraints by adjusting movement control. This question will be targeted in the third study presented in this thesis.

1.2.3 Age-related changes in movement planning and control

Aging leads to changes on multiple levels of the human motor system (Seidler et al., 2010). These changes are often related to a decrease in systems complexity, but can also be due to increased complexity (in a sense of less structure, see Vaillancourt & Newell, 2002, for a review). The age-related changes within the motor system are usually accompanied by a decrement in motor performance, becoming apparent for example in slowed movement execution, or less stable motor performance (Newell, Mayer-Kress & Liu, 2009; Verrel, Lövden & Lindenberger, 2012). In the context of motor redundancy, it was hypothesized, that older people are less able to flexibly coordinate the redundant effector DoF, leading to less stable task performance across repeated movement trials (Latash & Anson, 2006; Verrel, Lövden & Lindenberger, 2012). Though, the existing empirical evidence on the control of redundant motor systems in older people was established by using experimental tasks with only one, clearly defined task variable. Though, as mentioned already above, when moving in natural environments the motor system has to account for multiple task constraints simultaneously during movement planning and control. Whether aging generally leads to a decrease in stable movement execution or whether this decrease is just one manifestation of several adaptive changes in the control of complex reaching movements in the presence of multiple task constraints remains a question to be answered and will be targeted in the fourth study presented in this thesis.

1.3 Excurse: Optimal feedback control

Within the course of research on the control of human motor behavior, a number of models have been developed which were able to explain and predict some aspects of healthy human motor behavior. Usually, it was supposed that the human motor system follows a strategy that tries to minimize a certain parameter of movement execution to maximize task success. The minimization process could then be described by a cost function. Several different parameters have been brought up in that context, as for example “minimum jerk” (Flash & Hogan, 1985), reflecting the rate of change in acceleration with the goal to execute the smoothest movement possible, or “minimum torque change” (Uno, Kawato & Suzuki, 1989). A more recent model was the “minimum variance” model by Harris and Wolpert (1998). This model captures important features of saccadic eye movements and reaching behavior and states that the human motor control system tries to minimize variance at movement end. In this concept, variance in movement behavior arises from noise in the motor signal, which linearly increases with signal size.

Though, empirical evidence suggests that the motor system does not only account for the minimization of movement variability at movement end, but does also account for various other costs during movement planning and control. In natural environments multiple internal and external factors are simultaneously influencing movement control. Therefore, best movement behavior can only result from the weighting of all the cost factors such that they are optimally accounted for. The resulting cost function is a compromise attempting to minimize all costs related to the task constraints. A theoretical approach that takes this trade-off into consideration was supposed by Todorov and Jordan (2002), known as “optimal feedback control”. In this approach it is assumed that the motor system exploits motor redundancy to optimize motor behavior. This optimization is based on a cost function that takes into account minimum variance at movement end, as well as minimum energy consumption. To achieve this, the “minimum intervention principal” was proposed, stating that the human motor system is oriented towards minimizing movement variability only in task-relevant directions in order to minimize the costs for controlling the movement. Consequently, this approach captures both features of human motor behavior: flexibility and stability in movement execution. Variability in the effector space may or may not be detrimental for variability in the task space. It is assumed that only that portion of variability in the effector space that has an influence on the movement outcome in the task space is minimized by the motor system. In this way, the costs for controlling complex movements are optimized. This idea is in line with the concept of synergistic movement coordination and empirical evidence created by recent research on the topic of motor redundancy (Cusumano & Cesari, 2006; de Freitas, Scholz & Stehmann, 2007; Latash, Scholz & Schöner, 2002).

A special feature of the optimal feedback control theory is that it seems to be able to explain how the human motor system can account for changing environmental conditions to grant stable movement outcome, namely through optimal estimation. Recent empirical evidence suggests that this procedure can be well described by Bayesian decision theory (Green & Angelaki, 2010; Wolpert, 2007). It accounts for the flexible integration of multisensory feedback and is thereby able to explain the ability of the human motor system to successfully adjust human motor behavior on a trial-by-trial basis (Verstynen & Sabes, 2011).

The neural correlates of optimal feedback control are currently under debate, as the functional role of many cortical regions in complex tasks is unresolved, yet (Green & Angelaki, 2010). Two cortical regions which are commonly supposed to be of importance for the control of movement variability are the cerebellum and the posterior parietal cortex (PPC). In studies applying TMS to induce a “virtual lesion” in healthy subjects it was shown that functional deficits in these areas result in increased movement variability (Miall, et al., 2007; Vesia, et al., 2008; see Koch & Rothwell, 2009 for a review). Though currently, different, partially contrary functions have been assigned to the two areas: Shadmehr and Krakauer (2008), referring to human lesion studies, assign the creation of the estimate about the sensory consequences of the movement (termed “system identification”) to the cerebellum, whereas the parietal cortex is supposed to be responsible for the integration of the actual with the predicted sensory consequences (“state estimation”). In contrast, Scott (2012), based on the existing evidence in (non-) human primates, assigns the state estimation to the cerebellum. Independent of the reference base, Scott as well as Shadmehr and Krakauer emphasize the distributed nature of optimal feedback control, involving basal ganglia, cerebellum, parietal, as well as frontal cortical areas. This seems to be necessary to effectively integrate sensory information during the process of movement preparation and execution, as also supposed by Cisek (2007) in his model for action selection. Though, it becomes obvious that the identification of neural correlates to optimal movement control remains a challenging task for the future.

1.4 Methodological considerations

The analysis of movement variability was chosen as the methodological approach in this thesis, as movement variability is an inherent characteristic of human motor behavior. For a long time, variability observed in skilled motor performance was assigned to neural noise (Faisal, Selen & Wolpert, 2008; Harris & Wolpert, 1998; van Beers, Haggard & Wolpert, 2004). Only recently, it became generally accepted that variability inherent to skilled motor behavior might be of special meaning for movement learning and control (Latash, Scholz & Schöner, 2007; Müller & Sternad 2009). Since then, many different approaches have been developed to better describe the information content inherent in movement variability. Calculating the absolute amount of variability of a specific task variable can be considered as a first approach in that context (see for example Desmurget & Prablanc, 1997). This was also the first approach used in the current thesis. Thereby, not only variability at movement end, but also during movement execution was analyzed, as the time course of movement execution may reveal important insights about the *process* of movement control, not only its *effect*.

Besides the analysis of the amount of movement variability, also the structure of movement variability is supposed to contain important information about the functioning of the human motor system (Müller & Sternad, 2009; Schöner & Scholz, 2007). Different approaches exist targeting that aspect. A common method in this context is the principal component analysis, revealing preferred directions within the multidimensional space of variability (Bortz & Schuster, 2010). This approach is usually used to reduce the dimensionality of high-dimensional data sets. In the context of reaching movements for example, it can be used to detect how many effector DoF (out of the seven DoF of the arm) are necessary to describe the majority of total effector variance. Usually, this leads to a reduction of the seven-dimensional effector space to a three- to four-dimensional space. The major disadvantage of this method is that, as this method is based on a transformation of the original data-set so that the resulting preferred directions are linear combinations of the initial dimensions, the resultant preferred directions of variance within the transformed data set have no physical meaning, which makes the findings difficult to interpret.

A way to circumvent this disadvantage was proposed by Scholz and Schöner (1999; “uncontrolled manifold hypothesis”) and similarly by Cusumano and Cesari (2006). In contrast to a principal component analysis, for these two approaches it is a prerequisite to have a specific hypothesis about the task variable that is controlled and to have a mathematically describable relationship between the effector variables and the task variable. Based on that control hypothesis, the high-dimensional space of effector variance is transformed in such a way that two orthogonal subspaces are obtained: (a) the “nullspace”, containing all effector combinations, whose variance has no effect on the variance of the task variable, and (b) the orthogonal space, containing all those effector combinations which have an influence on the task variable (Scholz & Schöner, 1999). Note that each obtained subspace may still be multi-dimensional. With this analysis it is possible to find out the relative size of the (a) task-irrelevant and (b) task-relevant components of the total effector variance. By calculating the ratio between the variance in task-irrelevant to task-relevant directions, one can infer about whether a task variable is of importance during movement control (Scholz & Schöner, 1999; Verrel, 2010). Though, as the control of complex movements in real world has to account for multiple task constraints, as mentioned already above, it is advisable to apply this method for multiple hypothetically important task variables. Only this allows getting an impression of the relative importance of each of these task variables. The interpretation of the outcome can be twofold. Initially, it was advised to take only the one task variable revealing the greatest ratio as the task variable that is controlled (Scholz & Schöner, 1999). Recently, the notion that multiple task variables can be controlled without interfering with each other has become more popularity (see for example Gera et al., 2010; Latash, Scholz & Schöner, 2002).

The uncontrolled manifold approach, which was used in the current thesis, allows relating variability in the effector space to variability in the task space at a specific point during movement execution or at movement end. Though, it does not allow inferring about the temporal transmission of effector variability with respect to the task variability at movement end. That means, by applying the uncontrolled manifold method it is not possible to get information about how much of the variability at movement end is explained by the variability at a certain time point during movement execution, or vice versa. This temporal transmission of movement variability, termed “redundancy” in mathematical contexts, can be investigated by use of a canonical correlation analysis (Bortz & Schuster, 2010).

As a general remark, it has to be noted that by analyzing movement variability, as for any other approach, it is appropriate to use several different methods, as each single one can explain special aspects, but not others. To get a comprehensive picture about the control of complex reaching movements, movement variability was analyzed by four methods in this thesis: the absolute amount of variability in effector and task space, the uncontrolled manifold method, the principal component analysis, and the canonical correlation.

1.5 Aim of the Thesis

When recapitulating what was presented above, it becomes obvious that the human motor system has the exceptional capability to perform complex movements stable in an environment where the sensory input and external constraints are constantly changing. The aim of this thesis was to investigate how the motor system accounts for these internal and external factors during the control of complex reaching movements, so that movement performance does not change. The approach used to study this capability was the analysis of movement variability. As it was shown above, by analyzing movement variability two features of healthy human motor behavior can be described: flexibility and stability in movement execution. These to features relate to movement variability in effector and task space, and are of special importance in the control of movements executed by a redundant effector system. Indeed, redundancy may not be a problem for the human motor system, but seems to be exploited to facilitate the control of complex movements. In the current thesis, complex reaching movements were chosen as experimental task, as they exhibit all important characteristics which signalize the exceptional capability of the human motor system: redundancy, skillfulness, and complexity.

Four main directions were pursued to develop a comprehensive picture about the ability of the healthy human motor system to adjust to permanent environmental changes: influence of (1) vision, (2) proprioception, (3) external task constraints, and (4) aging on the control of complex reaching movements. Thereby, the first study that will be presented in the following chapter studied the influence of vision and an accuracy constraint on the control of a complex reaching movement. Based on the outcome of this research, the second study investigated the ability of the healthy human motor system to adjust to the temporary loss of proprioceptive information. These two studies mainly dealt with the question of how the adjustments of the motor system to the availability of sensory information are reflected in the time course of movement variability. The third study investigates how the human motor system accounts for multiple task constraints which are applied in different strength by different reaching targets. Finally, the fourth study investigated age-related differences in the control of complex reaching movements.

2 Cumulative Thesis

This cumulative thesis consists of the two published research articles, one article accepted for publication, and one submitted article. Full papers are presented in the following. The complete list of publications, including those which are not included in this thesis, is indicated separately (see Contents). The research articles are presented in the following order:

1. Krüger, M., Eggert, T. & Straube, A. (2011). Joint angle variability in the time course of reaching movements. *Clinical Neurophysiology, 122*(4), 759-766.

The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript.

2. Krüger, M., Eggert, T. & Straube, A. (submitted). Rapid adjustment of human motor control strategies in reaching movements under temporal proprioceptive deafferentation.

The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript. The manuscript is submitted as a research article.

3. Krüger, M., Borbély, B., Eggert, T. & Straube, A. (2012). Synergistic control of joint angle variability: Influence of target shape. *Human Movement Science, 31*(5), 1071-1089.

The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript.

4. Krüger, M., Eggert, T. & Straube, A. (in press). Age-related differences in the stabilization of important task variables in reaching movements. *Motor Control.*

The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript. The manuscript was submitted as a research note, and is accepted for publication.

Clinical Neurophysiology (2011), 122(4), 759-766

Joint angle variability in the time course of reaching movements

Melanie Krüger, Thomas Eggert and Andreas Straube

Abstract

Investigating motor control processes is of primary interest in a number of scientific and practical fields. Movement variability is of increasing interest in this context. However, until now little has been known about the time course of variability during movement execution. The objective of this study was to investigate the influence of visual information and task specification on the variability of joint angle motion in reaching movements.

Subjects repetitively reached for a handle. Movement variability was quantified by the within-subjects standard deviation of mean joint angle. The analysis focused on the time course of variability during movement execution.

The availability of visual information did not influence the time course of joint angle variability whereas task specification on reaching accuracy did. Under high accuracy demand variability was reduced more strongly after reaching its maximum.

Results suggest that the availability of visual information plays a minor role in the control of well-trained reaching movements. This suggests that proprioceptive information is the main feedback source to control these movements.

The analysis of the time course of movement variability might be a valuable method to investigate the central or peripheral causes of movement disorders for diagnostic and rehabilitation purposes.

Introduction

Variability is a characteristic of human movements and has been the subject of increasing scientific interest in the last years (Schmidt et al., 1979; Haggard et al., 1995; Ma and Feldman, 1995; Harris and Wolpert, 1998; Eggert et al., 2003; Van Beers et al., 2004; Mutha & Sainburg, 2007). In general, movement variability is defined as the deviation from a specific target position across trials and it is supposed to be influenced by both, internal and external factors (for a review see Faisal et al., 2008).

There is empirical evidence that stresses movement difficulty as one important factor influencing the amount of movement variability (Fitts, 1954, Fitts and Peterson, 1964, Tseng et al., 2003). Fitts speed-accuracy trade-off highlighted the relationship between movement distance, target size and endpoint variability in pointing movements. Further empirical evidence highlights the importance of visual information for the control of upper limb movements (e.g. Van den Dobbelsteen et al., 2003; Saunders and Knill, 2004; Scheidt et al., 2005; Sober and Sabes, 2005). In particular, Desmurget and colleagues (1997) emphasize the importance of visual information about the hand prior to movement onset for the control of endpoint variability.

So far, it is not known how movement variability is specifically controlled and which brain areas are involved in that control process. Recently, it has been hypothesized that movement variability is corrected only to a certain extent to minimize overall costs of movement execution (Harris and Wolpert, 1998; Todorov and Jordan, 2002; Tanaka et al., 2006). One way to obtain this aim is to correct only that variability that interferes with the achievement of the movement goal (Scholz and Schöner, 1999; Todorov and Jordan, 2002). Therefore, variable movement execution by achieving the movement goal is regarded as a characteristic of an intact motor control system. Alternatively, increased variability is a typical sign of motor dysfunction, especially in the case of cerebellar dysfunction and ataxia. Similar problems can also be seen in patients with severe sensory deficits due to lesions of the dorsal columns of the spinal cord or the sensory fibres of the peripheral nerves. So far, it is not clear how to discriminate between intact and deficient control of movement variability. Consequently, enhanced knowledge about the control of movement variability is of special interest in a clinical context.

The literature already has a long history in the research of endpoint variability. There is empirical evidence showing that reaching movements of healthy subjects can be characterized by high endpoint accuracy and only small final posture variability (Gordon, 1994; Gréa et al., 2000). Furthermore, increased movement variability has been observed in patients with lesions in cerebral motor areas (Gréa et al., 2002; Eggert et al., 2003). However, by looking at endpoint variability one only gets information about the final result of a motor control process. As an alternative, the time course of variability may provide information about the motor control process itself and may offer a deeper insight into the origins of a deficient motor control process– e.g. a generally increase of variability versus a different time course of variability due to control deficits at a certain point in time during movement execution. So far, only a few studies exist that investigate the time course of variability during movement execution (for an example, see Morishige et al., 2006, Tseng et al., 2003).

Therefore, the aim of the present study was to investigate the time course of variability in joint angle during the execution of reaching movements. The main goal was to gain knowledge about the process of control of movement variability in an intact motor system. Special effort was spent to extract the variability due to internal processes of movement planning and control and to leave aside variability due to differences in the external conditions such as initial arm position or target position. Movement variability was quantified by the standard deviation of the joint angle. It was hypothesized that increased movement difficulty and decreased availability of visual information will result in different time courses of variability.

Methods

Participants

Thirty-four subjects (28 female, six male, mean 29 years) participated in this study. Subjects were paid for their participation. They had no previous experience with the experimental task and were not aware of the purpose of the study. Written consent was obtained prior to participation in the experiment. All subjects were right-hand dominant as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision.

Apparatus

The experimental apparatus (see Fig. 1A) consisted of a horizontal desk on which a linear table track was mounted. A cylindrical metal handle (9.5cm of width), driven by a 2-phase step motor with a resolution of 0.1 mm per step, was moveable on the table track in horizontal, fronto-parallel direction (position range: ± 19.5 cm). Subjects were comfortably seated on a chair in front of the desk with their body midline aligned to the center of the table track. The position of the subjects was adjusted so that they could easily reach both sides of the table track. The start position was defined by a handrail attached to the seat (Fig. 1B). White noise was presented through headphones to avoid anticipation of the handle position by the sound of the apparatus. Depending on the experimental condition, shutter glasses (Translucent Technologies, Toronto, Canada) were used to influence the availability of visual information.

Movement of the arm was recorded by an ultrasonic recording device (Zebris Medical, Isny, Germany) at 33Hz. Three microphones recorded the ultrasonic impulses of six sound-emitting markers in 3-D. Marker positions are described in Fig. 1B. From those positions the individual length of subjects' upper arm, lower arm, and hand could be determined. Data from the Zebris device were transferred online to a computer running a recording system (REX, Hays et al., 1982) and were used as real-time control signals to trigger the opening and closing of the shutter glasses and the positioning of the target handle between successive trials. The moment of contact between hand and handle was monitored by recording the electrical resistance between the subject and the handle (sampled at 1 kHz).

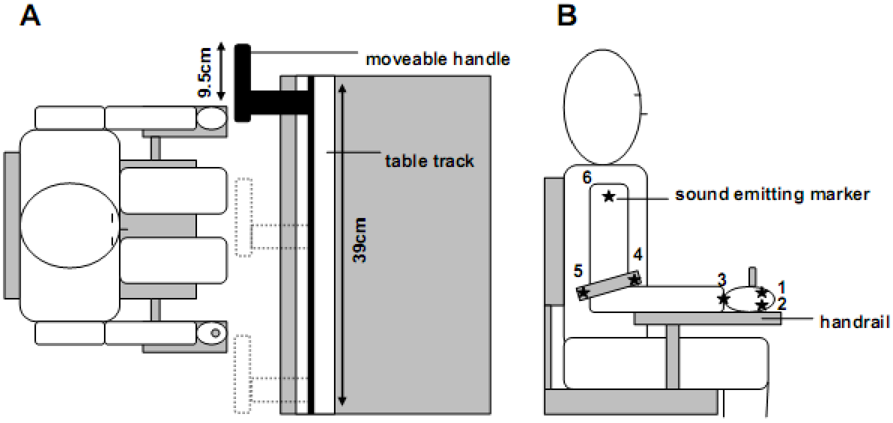


Fig. 1: Experimental Apparatus. A Schematic top view on the experimental set up. Subject's distance to the table track was adjustable with reference to subject's arm length. The handle could move along the table track. Possible positions of the handle are depicted (filled in black or unfilled, with dotted lines). B The side view shows the marker positions for the six ultra-sonic sound emitting markers. The markers were attached to following points: (1) basal joint of index finger, (2) basal joint of little finger, (3) center of wrist, (4) medial, above the elbow, (5) lateral, above the elbow, and (6) acromion. Sitting posture represents the start position, where subjects were grasping a wooden handrail. In the start position upper arm was adducted with the elbow flexed at approximately 90º. Fingers were moveable independent of each other during movement execution. In the start position, finger movement was restricted by the grasp of the handrail.

Procedure

At the beginning of each trial, subjects were asked to bring their dominant right arm into the start position (see Fig. 1B). To begin a trial subjects had to press a start button with their left hand that caused the handle to move to one of the three possible positions (left side of the table track, center, and right side). After a specific go-signal subjects had to reach for and grasp the handle in a natural manner. To provoke most natural reaching movements no particular demands were made concerning reaction time or movement speed. Subsequently, subjects moved their arm back to the start position. By pressing the start button again a new trial was initiated.

Availability of visual information was manipulated between experimental conditions so that the subjects in condition 1 (“initial vision”) were able to see the handle only before movement onset (as detected in real time by REX), which excluded visual control during movement execution. In a further experimental condition, subjects were able to see the handle only for 100 ms immediately before movement onset, so that movement planning and visual control were manipulated (condition 2, “flash”). Full vision during movement planning and execution was provided in experimental conditions 3 (“full vision”) and 4 (“accuracy demand”). Thus, the availability of visual information decreased from experimental condition 3 to condition 1 and condition 2. In condition 4 the experimental task was specified by instructing the subjects to grasp the handle in such a way that their right index finger was aligned with a visual marker affixed to the handle. With respect to the other experimental conditions, this led to an increase of the movement difficulty due to an increased accuracy demand. Whereas the marker had a width of 5 mm, the approximated accuracy demand in conditions 1-3 corresponded to about 1-2 cm, estimated as the difference between the handle width and the width of the subject’s hand (not counting the thumb). The experimental conditions were arranged in a between-groups-design. Thus, each subject performed only one of the experimental conditions. The resulting group sizes were n = 8, 9, 9, 8 for the “initial vision”, “flash”, “full vision”, and “accuracy demand” condition, respectively.

Before data recording, the subjects each performed five practice trails to familiarize themselves with the experimental task and apparatus. Afterwards, four blocks of 30 trials each block (120 trials in total) were recorded. Thus, each of the three possible handle positions was triggered 40 times per session in a pseudo-random order to avoid predictability and pre-planning of the movement. Between the experimental blocks a break of a maximum of 5min was offered to avoid fatigue.

Analysis

Data analysis

Data analysis was performed using Matlab 7.9.0 (Mathworks, Natick, USA). In a first step the seven joint angles of the arm were converted to Cardan angles as commonly used in the literature (Raikova, 1992; Riener and Straube 1997). This reduced the 18 (6 × 3) marker signals to the irreducibly necessary seven degrees of freedom, expressed as seven consecutive Cardan angles in the following order: two angles for the wrist (vertical, horizontal), two for the elbow (torsion, flexion), and three for the shoulder (torsion, horizontal, vertical). The zero position of all angles was defined by the arm pointing straight forward with extended elbow and wrist, the palm facing upward. Starting from that position, positive angles indicate the following directions: vertical upward, horizontal rightward and clockwise torsional motion. The vector containing these seven joint angles is hereafter referred to as “arm position”. Trials in which the reconstruction of joint angles was corrupted because of temporary occlusion of any marker were excluded from further data analysis. In addition, position of the hand in space (i.e. 3-D) was defined by the position of the centre between the two markers of the hand (see Fig. 1B) in world-fixed Cartesian coordinates.

Of primary interest for data analysis was the within-subject inter-trial variability of joint angles for the period of movement duration. Movement duration was defined as the time between movement initiation and the last position measurement immediately before the first contact with the handle (detected by the sudden decrease of the electrical resistance between subject and handle). In this way, any movements occurring under potential influence of tactile feedback were excluded from the analysis. Movement start was defined as the time when the hand velocity initially exceeded 10%

of its maximum velocity (v_{max}). Subsequently, movement initiation was defined by subtracting 10% of the acceleration time (the time between movement start and reaching v_{max}) from movement start. In this way, it was assured that the actual movement onset occurred always shortly after the time of movement initiation. The full temporal resolution of the joint angle trajectories was reduced to ten equidistant samples. Thus, each trial's movement duration was normalized to a time range between zero and one. Data of the first sample was not concerned in further analytical steps as it, by definition of movement initiation, refers to a time point immediately before movement onset.

Even though the initial hand position was roughly defined by the position of the handrail, the initial arm position differed slightly between trials. These differences, which are expected to affect the inter-trial variability of the movement, are not related to variability occurring on the level of movement planning and control, but are due to imperfections concerning the standardization of experimental border conditions. Likewise, the temporal normalization may not be sufficient to compensate for all inter-trial differences related to the differences in planned movement duration. For that reason, the within-subject deviations of the joint angles from their mean were submitted to a linear regression analysis with the predictor initial arm position and movement duration (i.e. 7+1=8 continuous predictor variables). This analysis was performed separately for each subject, experimental condition, handle position, and for each of the nine samples. Therefore, each of these regressions contained the data of 40 trials. Subsequently, the joint angle deviations from the mean that were predicted by this linear model were subtracted from the actual joint angles. Thereby, we corrected for within-subject variability due to differences in movement duration and initial arm position. In this way, we were able to extract the inter-trial variability of movements that were planned to reach the same goal, from the same start position, and within the same movement duration.

After this correction on the raw data the means and the standard deviations of the seven joint angles were calculated separately for each subject, each target position, and for each of the nine samples. Furthermore, a global measure of the standard deviation of the arm position was defined by the root mean square (RMS) of the standard deviation across all joint angles. This measure is called "standard deviation of arm position" hereafter. Note that all standard deviations reported in this study refer to within-subject standard deviations.

Statistical Analysis

The standard deviation of arm position and the standard deviations of the seven joint angles, as well as the standard deviation of the final hand position (in 3-D) were further analyzed with regard to the experimental conditions and handle positions. Since the distributions of the standard deviations of the joint angles, of the arm position, and that of the final hand position showed significant deviations from normal distributions, theses variables were logarithmically transformed prior to statistical analysis. The normality of the transformed standard deviations was checked using the

Lilliefors test. The logarithmically transformed standard deviations of each joint angle were submitted to a 4(experimental condition) × 3(handle position) × 9(time course) ANOVA with the experimental condition as a between-subjects factor and with handle position and time course as repeated factors. For further characterization of the effects of the factor time course an ANOVA with the single factor experimental condition was performed on the logarithmically transformed standard deviations of joint angles, separately for each of the nine samples. This analysis will be referred to as simple main effect analysis. Movement duration and the standard deviations of final hand position were submitted to a repeated measurement ANOVA with the experimental condition as between-subject factor and handle position as repeated, within-subject factor. The threshold for statistical significance was set at $p < .05$. Multivariate tests (Wilks' lambda) were calculated if the sphericity assumption was rejected by Mauchly's sphericity test. Statistical analysis was computed by using SPSS 9.0.

For the graphic representation of the data estimates of the median standard deviations and their 95% confidence limits across the population and handle positions or across the population and experimental conditions were computed by first estimating these parameters for the log-transformed standard deviations. Subsequently the reverse (exponential) transformation was applied on these parameters.

Results

Description of general characteristics

The subjects' age ranged from 18 to 51 years. Older subjects within the cohort did not show a different time course of joint angle variability than younger subjects. Figure 2 depicts the time course of the standard deviation of arm position of single subjects in each of the four conditions. The youngest and oldest subjects in each condition are highlighted. Beyond that, time course of the standard deviation of arm position showed an increase-decrease pattern with its maximum in the first half of the movement. Afterwards, joint angle variability slightly decreased or stabilized at that level.

The analysis of movement duration revealed that subjects with high accuracy demand needed significantly more time (~ 150ms) to reach for the handle than subjects in other experimental conditions, as indicated by a main effect of the factor experimental condition, $F(3,30) = 4.65$, $p < .01$ (see Fig. 3). The main effect of position also reached significance, $F(2,29) = 290.53$, $p < .01$. Post hoc analysis revealed that reaching for the handle at the left position took longer than for the center handle position and this again took significantly longer than reaching for the handle at the right position (see Fig. 3). The interaction between the factors experimental condition × handle position was not significant.

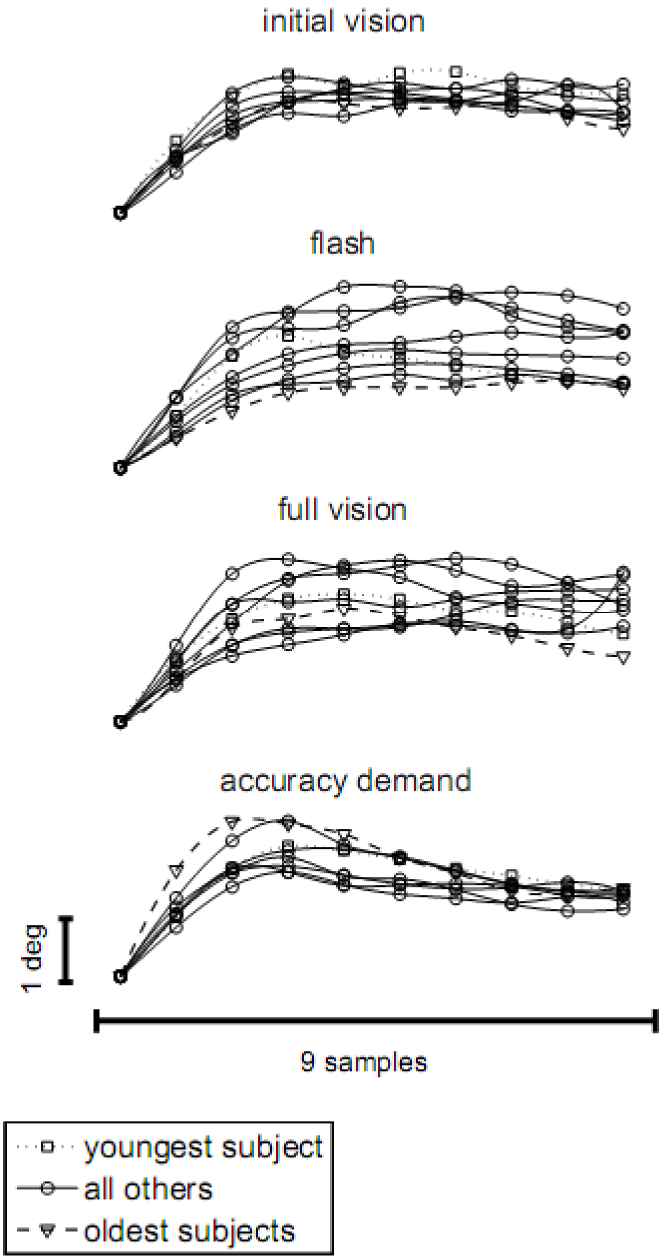


Fig. 2: Time courses of within-subject movement variability for each subject in each experimental condition are shown. Depicted are the standard deviations of the arm position (i.e. RMS of the standard deviation across joint angles) for each of the nine samples. Subjects in one group show similar time courses, independent of age. The youngest (triangles) and oldest (squares) subjects in each condition are highlighted.

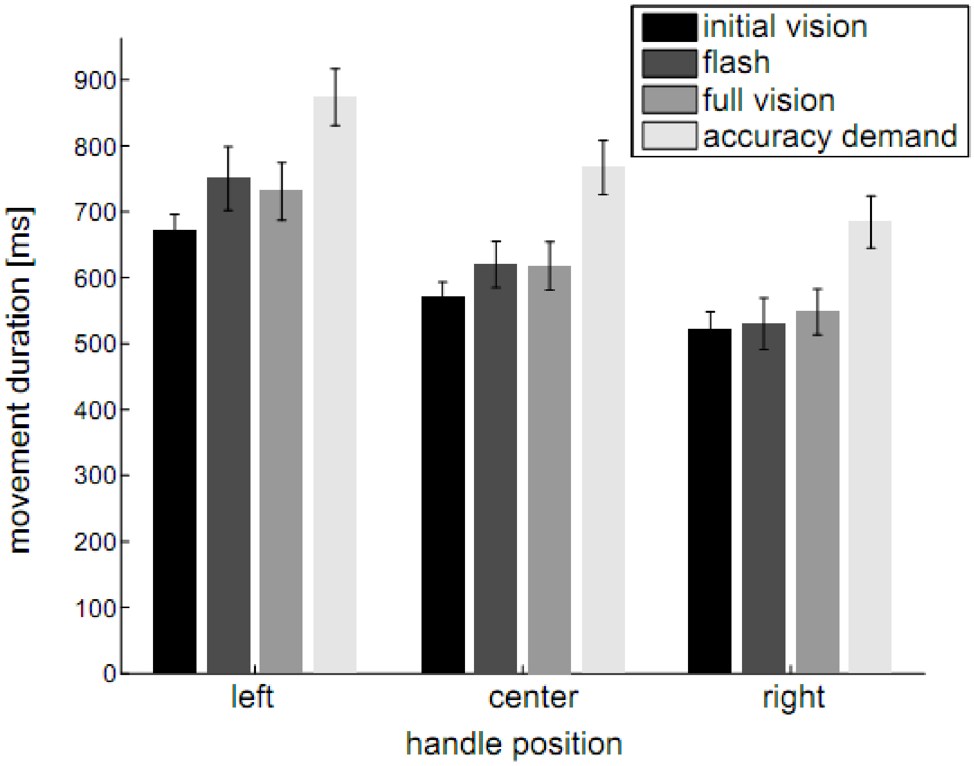


Fig. 3: Mean movement durations and corresponding standard deviations depending on experimental condition and handle position are presented. Under high accuracy demand, subjects needed significantly more time to reach for and grasp the handle (~ 150ms) compared to the other experimental conditions.

Analysis of endpoint variability

The variability of the final hand position, quantified by the standard deviations of the hand position at the ninth sample (in frontal, horizontal and vertical direction), was analyzed for further clarification of performance differences between experimental conditions (see Table 1). The results revealed increased endpoint variability (median ~ 6.5mm) of the hand when subjects were able to see the handle only for 100ms at movement onset (condition 2). In contrast, subjects with high accuracy demand (condition 4) showed least variability of final hand position (median ~2.5mm). These effects were significant in all three dimensions of the space. Handle position did influence endpoint variability of the hand only in the frontal direction.

Table 1: F-values and the corresponding p-values for analyzed within-subject standard deviations of final hand position are presented. In addition, median of within-subject standard deviations of final hand position (in 3-D) are shown for the four experimental conditions. Final hand position is determined by calculating the centre between the two hand markers at the ninth sample.

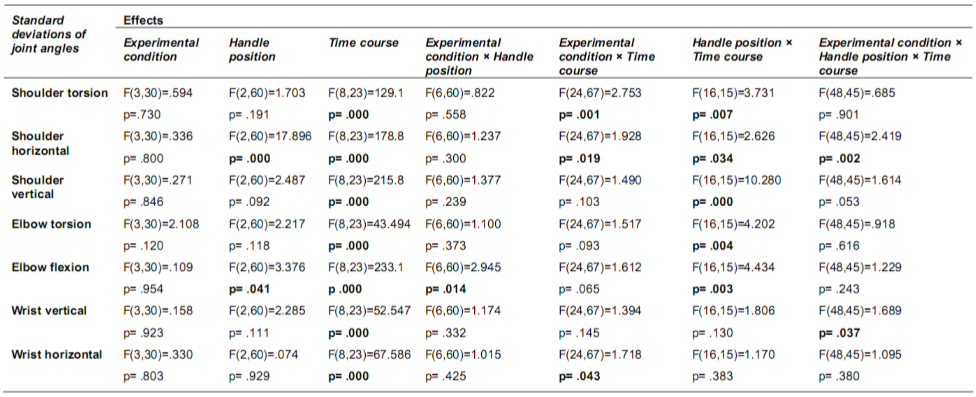
	Effects			**Median standard deviation [mm]**			
	Experimental condition	*Handle position*	*Experimental condition x Handle position*	*Initial vision*	*Flash*	*Full vision*	*Accuracy demand*
Frontal direction	F(3,30)= 9.605 **p= .000**	F(2,29)= 6.097 **p= .006**	F(6,58)= .513 p= .796	4.47	6.13	3.70	2.64
Horizontal direction	F(3,30)= 15.308 **p= .000**	F(2,60)= 2.476 p= .093	F(6,60)=0.067 p= .821	4.97	7.25	4.59	2.92
Vertical direction	F(3,30)= 11.742 **p= .000**	F(2,29)= .226 p= .799	F(6,58)= 1.058 p= .398	4.16	5.55	3.27	2.47

Time course of joint angle variability

Analysis across joint angles

The standard deviation of arm position (RMS of the standard deviation across joint angles) showed an increase-decrease pattern with stabilization around the fifth sample of the time course (see Fig. 4H) as indicated by a significant main effect of the factor time course, F(8,23) = 150.00, $p < .01$. Moreover, simple main effect analysis revealed differences between experimental conditions for the last three samples of time course. At the end of the reaching movement subjects with a high accuracy demand were less variable than subjects in the other experimental conditions. No further effects reached significance.

Table 2: F-values and the corresponding p-values for analyzed within-subject standard deviations of joint angles of the arm are presented. “Torsion”, “horizontal”, and “vertical”/“flexion” represent rotations around the respective spatial axis.



Standard deviations of joint angles	**Effects**						
	Experimental condition	***Handle position***	***Time course***	***Experimental condition × Handle position***	***Experimental condition × Time course***	***Handle position × Time course***	***Experimental condition × Handle position × Time course***
Shoulder torsion	F(3,30)=.594	F(2,60)=1.703	F(8,23)=129.1	F(6,60)=.822	F(24,67)=2.753	F(16,15)=3.731	F(48,45)=.685
	p=.730	p= .191	**p= .000**	p= .558	**p= .001**	**p= .007**	p= .901
Shoulder horizontal	F(3,30)=.336	F(2,60)=17.896	F(8,23)=178.8	F(6,60)=1.237	F(24,67)=1.928	F(16,15)=2.626	F(48,45)=2.419
	p= .800	**p= .000**	**p= .000**	p= .300	**p= .019**	**p= .034**	**p= .002**
Shoulder vertical	F(3,30)=.271	F(2,60)=2.487	F(8,23)=215.8	F(6,60)=1.377	F(24,67)=1.490	F(16,15)=10.280	F(48,45)=1.614
	p= .846	p= .092	**p= .000**	p= .239	p= .103	**p= .000**	p= .053
Elbow torsion	F(3,30)=2.108	F(2,60)=2.217	F(8,23)=43.494	F(6,60)=1.100	F(24,67)=1.517	F(16,15)=4.202	F(48,45)=.918
	p= .120	p= .118	**p= .000**	p= .373	p= .093	**p= .004**	p= .616
Elbow flexion	F(3,30)=.109	F(2,60)=3.376	F(8,23)=233.1	F(6,60)=2.945	F(24,67)=1.612	F(16,15)=4.434	F(48,45)=1.229
	p= .954	**p= .041**	**p .000**	**p= .014**	p= .065	**p= .003**	p= .243
Wrist vertical	F(3,30)=.158	F(2,60)=2.285	F(8,23)=52.547	F(6,60)=1.174	F(24,67)=1.394	F(16,15)=1.806	F(48,45)=1.689
	p= .923	p= .111	**p= .000**	p= .332	p= .145	p= .130	**p= .037**
Wrist horizontal	F(3,30)=.330	F(2,60)=.074	F(8,23)=67.586	F(6,60)=1.015	F(24,67)=1.718	F(16,15)=1.170	F(48,45)=1.095
	p= .803	p= .929	**p= .000**	p= .425	**p= .043**	p= .383	p= .380

Analysis of single joint angles

The standard deviations of the single joint angles showed a main effect of time course for each of the seven joint angles (see Table 2). For all joints standard deviation increased with time with a more or less pronounced decrease at the end of the reaching movement (see Fig. 4A-4G). Moreover, with high accuracy demand (condition 4) standard deviation of joint angles decreased much more strongly after reaching its maximum for shoulder torsion, and horizontal wrist angle as indicated by a significant interaction of experimental condition × time course. (see Fig. 4A, 4G). Simple main effect analysis revealed significantly less standard deviation with high accuracy demand from the seventh sample on. In addition, the interaction of experimental condition and time course reached significance for the horizontal shoulder angle but could not be clarified by further analysis.

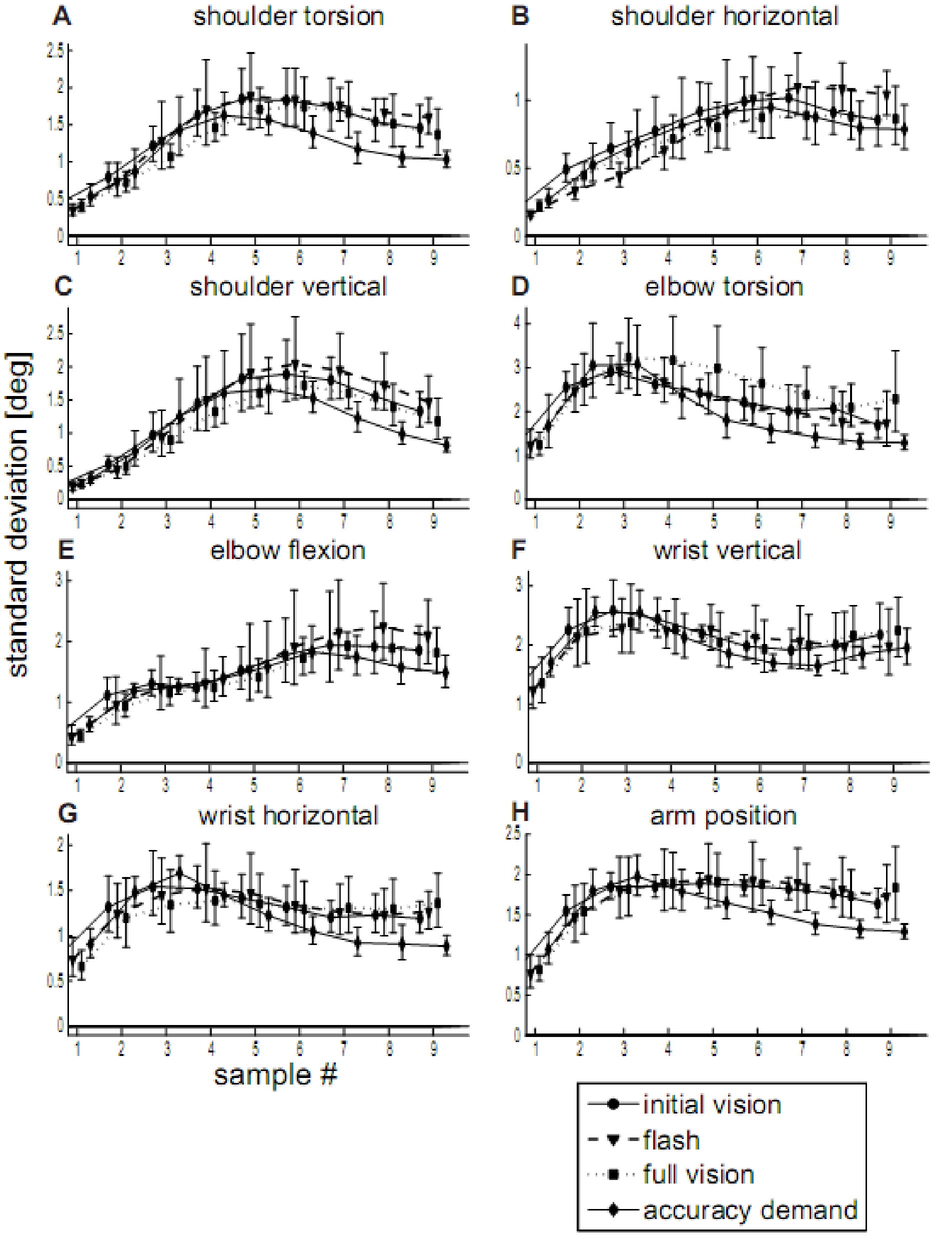


Fig. 4: Within-subjects standard deviations of joint angles (y-axis) for the different experimental conditions are shown for each of the nine samples (x-axis). Symbols represent the median of the within-subjects standard deviation across the population. Whiskers indicate the 95% confidence limits of this median. Data is depicted for each of the four experimental conditions and for each of the nine samples Panels 4A-4G present the standard deviations for each single joint angle. Panel 4H presents the median of the standard deviation of the arm position (i.e. RMS of the standard deviation across joint angles). The time courses show a similar pattern of increase-decrease over time, whereby each joint angle reaches its maximum at another sample. Task specification on final position accuracy (“accuracy demand”) influences the time course of standard deviation in shoulder torsion as well as in horizontal wrist motion.

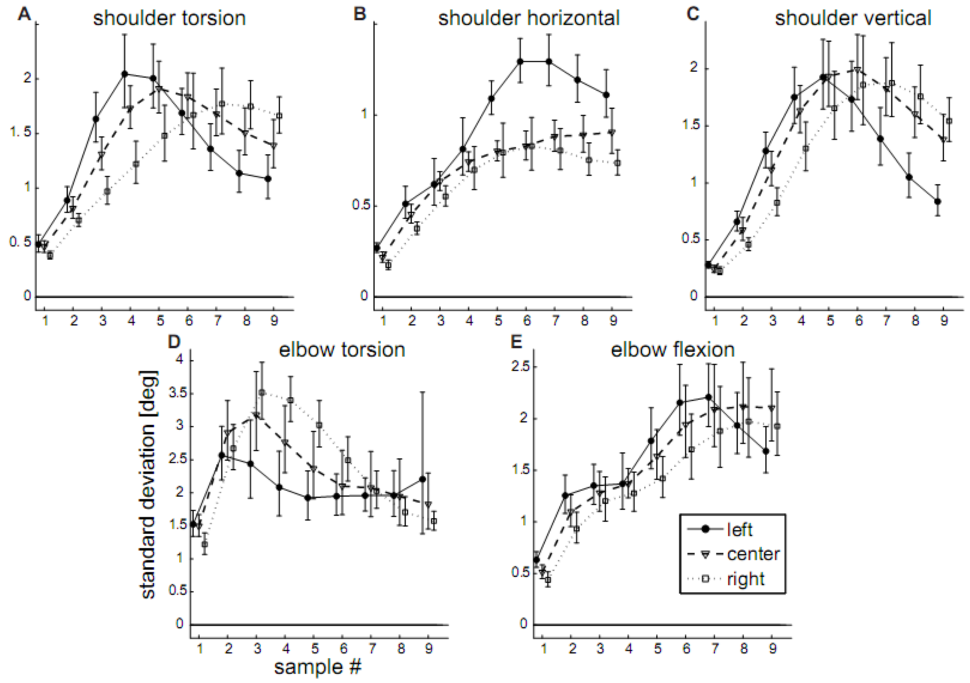


Fig. 5: Time courses of within-subjects standard deviations of joint angles for the three handle positions are depicted for shoulder torsion, (5A), horizontal shoulder angle (5B), vertical shoulder angle (5C), elbow torsion (5D), and elbow flexion (5E). Medians of the within-subject standard deviation (y-axis) are depicted. Whiskers indicate 95% of the confidence limits of this median for each of the nine samples (x-axis). Time courses differed mainly between the left handle position and the others. At the left handle position, standard deviation either decreased stronger after reaching its maximum (5A, 5C, 5E) or had a higher value at the end of the reaching movement (5B). Right handle position and centre position did not differ from each other in the time course.

Furthermore, analysis indicated that standard deviation of joint angles was greatest when reaching for the left handle position compared to the center and right handle position for horizontal shoulder motion, and elbow flexion (see Table 2) as indicated by a significant main effect of handle position. Finally, analysis revealed a different time course of standard deviation of joint angle when reaching for the left handle, where maximum was reached earlier with a more pronounced decrease afterwards, as indicated by a significant interaction of handle position × time course for shoulder torsion, shoulder horizontal motion, vertical shoulder motion, as well as for elbow torsion, and elbow flexion, (see Table 2 and Fig. 5A-5E). Finally, the interaction experimental condition × handle position reached significance for elbow flexion. Simple main effect analysis did not reveal any consistency in the amount of standard deviation of elbow flexion across experimental conditions and handle positions. No other effects reached significance.

Discussion

The purpose of the present study was to investigate the time course of movement variability in unconstrained reaching movements. Movement variability in this context was defined as the standard deviation of joint angle at different samples during movement execution. While considerable knowledge exists about movement endpoint variability in reaching movements, less is known about the time course of variability during movement execution. For that reason, we introduced a new analysis method with which we are able to describe the time course of joint angle variability in healthy subjects. The analysis was especially designed to extract the inter-trial variability of movements that were planned to reach the same goal, from the same start position, and within the same movement duration.

General characteristics

Analysis of the time course of joint angle variability during movement execution revealed an increase-decrease pattern with a maximum standard deviation in the middle of movement execution. This pattern was independent of age, handle position or joint. It applied for the standard deviations of single joints as well as for the global measure of the standard deviation of arm position and suggests that joint angle variability was limited by control mechanisms which became efficient during the second half of the movement. A similar pattern of variability during movement execution was found by Morishige and colleagues (2006). They analyzed the time course of variability in hand position, whereas we focused our analysis on the variability in the joint angle space of the arm. We did so because variability of hand position is determined by variability of all joints. Even if one supposes a hand-centered reference frame of motor control (Gordon et al., 1994; Haggard et al., 1995), it is not known how such control strategy is realized on the basis of the seven degrees of freedom of the arm. Our observation that joint angle variability saturates or even decreases in all joints suggests that motor control processes influence all seven degrees of freedom of the arm.

Movement duration was greatest for subjects with high accuracy demand (condition 4). It seems as if those subjects reached more slowly to the handle to be able to fulfill the task specification. This finding is in line with the assumptions of Fitts' Law (Fitts 1954; Fitts and Peterson 1964). In addition, movement duration was greatest for the left handle position. Reaching for the right handle position took least movement time. This is clearly due to the different distances from start position to handle position, with the longest distance to reach for the left handle position.

Endpoint variability of the hand

We found differences in endpoint variability of the hand as a function of the availability of visual information. Subjects with only limited visual information at movement onset (condition 2) were most variable in final hand position. This is in line with Desmurget and colleagues (1997) who could show that subjects are most variable, when they are not able to see the limb before movement onset. Faisal and Wolpert (2009) showed that subjects, who virtually had to catch a ball under a time constraint, choose an optimal compromise of balancing sensory and motor accuracy to minimize overall task variability. In the present study, manipulation of the availability of visual information before movement onset was not compensated by increased movement duration to improve accuracy of motor execution, but resulted in increased endpoint variability. This is similar to the results of the "Sensory variability experiment" of Faisal and Wolpert (2009) in which, as in our experiment, there was no restriction on movement duration. Hence, the balance of sensory and motor variability results most likely from a coupling induced by external constraints than from an internal control strategy. In addition, least endpoint variability of the hand was found in subjects with high accuracy demand (condition 4). This was to be expected, because those subjects were explicitly instructed to have as little variability as possible in the final hand position. It is important to reiterate that the final position accuracy was only achieved with longer movement duration.

Time course of joint angle variability

Influence of handle position

Analysis of the time course of joint angle variability for the different handle positions revealed significant differences for two of the seven joint angles. In the design of this study, we did not particularly control for differences in movement difficulty due to different target distances, because it was not the purpose of this study to compare handle positions. Nevertheless, apparent differences in the time course of joint angle variability depending on handle position need to be discussed.

The time course of standard deviations of joint angles showed a pronounced increase-decrease pattern for the left handle position, whereas variability increased continuously or showed less decrease at the end of the movement at the other two handle positions. Moreover, maximum joint angle variability was greatest for shulder torsion as well horizontal shoulder angle and was reached earlier in time when reaching to the left handle position. This may be due to the bigger movement amplitude necessary to reach for the left handle position. Conceivably, increasing movement amplitude correlates with increasing variability in proximal joint angle motion of the arm.

Influence of visual information and task specification

To test the influence of movement difficulty and visual information on the time course of variability, task specification (i.e. accuracy demand) and the availability of visual information were changed between experimental conditions. Under increased accuracy demand (condition 4) the standard deviations of shoulder torsion and horizontal wrist angle decreased to a greater degree after reaching its maximum. The instruction in this experimental condition forced subjects to bring their hand as close as possible to a specific marker on the handle. Probably, adjustments in those two angles were most promising to achieve that goal.

Additionally, results indicated less joint angle variability in some samples of the movement when task was specified by an accuracy demand (condition 4). Especially at the end of the reaching movement, joint angle variability was generally less variable. Since movement duration was longer in experimental condition 4, it seems as if decreased joint angle varaibility was achieved at the expense of longer movement duration. This is in line with Fitts' Law (Fitts 1954, Fitts and Peterson 1964).

Overall, joint angle variability seemed to be controlled more closely when the experimental task was specified on accuracy compared to the other experimental conditions. However, since we did not analyze covariances or built up on the theories of functional synergies (e.g. Scholz and Schöner, 1999; Todorov and Jordan, 2002) it is not possible to infer about the underlying control strategy (e.g. hand centered reference frame). This needs to be a subject of future exploration.

No other differences in the time course of joint angle variabilty between experimental conditions turned out to be significant. Surprisingly, standard deviations of joint angles during movement execution were not significantly greater when visual control was manipulated (as in condition 1 and 2). This suggests that the availability of visual information plays only a minor role in the control of these well-trained, everyday reaching movements. In contrast, the results suggest that this class of movements is predominantly controlled by proprioception or a low-level mechanism (e.g. at spinal cord level). This knowledge could potentially be used to apply the analysis method in diagnostic or rehabilitation contexts to shed light on and differentiate between the peripheral or central causes of movement disorders.

Altogether the analysis of the time course of movement variability offers the possibility for important insights into the mechanisms underlying human motor control and might be a valuable method for diagnostic and rehabilitation purposes. The described method is able to depict characteristic feature of movement variability over time and is sensitive to movement difficulty. This makes the investigation of the time course of movement variability an interesting and promising goal for the future.

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Submitted

Rapid adjustment of human motor control strategies in reaching movements under temporal proprioceptive deafferentation

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Abstract

Proprioception is an important source of information for the control of movements. Patients with chronic deafferentation due to neuropathy show impaired motor control in reaching movements. In contrast, studies of temporary deafferentation of healthy humans producing simple motor tasks showed rapid adjustment to the loss of proprioception on a behavioral and cortical level. The goal of the current study was to investigate whether healthy subjects are able to immediately and efficiently change the control of a complex reaching movement to compensate for the experimentally induced loss of proprioceptive information. To this end, we induced an ischemic block to the upper arm of 15 healthy subjects and recorded reach-to-grasp movements towards a spherical target in the 7 degrees of freedom of the arm. In agreement with the findings in chronically deafferented patients, the results showed increased movement duration, decreased movement amplitude, as well as altered movement coordination under ischemia, which resulted in a reduced complexity of movement control. Movement endpoint variability was not increased under ischemia. This suggests that healthy subjects are able to immediately and efficiently adjust the control of complex reaching movements to compensate for the loss of proprioceptive information.

Introduction

When reaching towards a target, the integration of different sensory information during movement control provides the basis for stable movement execution. Therefore, the manipulation of the availability of sensory information is of interest for behavioral and clinical neuroscientists (Krüger et al. 2011; Grea et al. 2002; Prablanc et al. 2003; Keresztenyi et al. 2009; Schaefer et al. 2009) who want to gain insights into the control of healthy human motor behavior.

Empirical evidence suggests that the healthy motor system controls movements such that variability of a hypothesized task variable at movement end is minimized (Todorov 2004; Todorov and Jordan 2002; Harris and Wolpert 1998). In a redundant effector-system like the arm, one possibility to reduce variability in the task variable is to synergistically coordinate the effector variables (Latash et al. 2010; Latash et al. 2007). This coordination leads to a number of kinematic degrees of freedom (DoF) that is smaller than the number of mechanical DoF of the effector-system. Empirical evidence suggests that, in complex reaching movements, the joint angles of the arm are synergistically coordinated so that variability in hand position and hand orientation is reduced (Keresztenyi et al. 2009; Krüger et al., 2012).

Proprioception about joint positions is an important source of information for the control of complex reaching movements (Bagesteiro et al. 2006; Ghez and Sainburg 1995). In a recent study we could show that, for every-day reaching movements, the availability of visual information before or during movement execution was of minor importance for the control of movement variability (Krüger et al. 2011). This led us to the conclusion that proprioception plays a major role in guiding the planning and control of these reaching movements. Supporting this assumption, studies on chronically deafferented patients suffering from severe peripheral sensory neuropathy showed impaired motor control of arm movements, including slowed movement execution (Hepp-Reymond et al. 2009; Gentilucci et al. 1994), increased movement variability (Medina et al. 2010; Gentilucci et al. 1994) and deteriorated movement coordination (Ghez and Sainburg 1995; Sainburg et al. 1995; Sainburg et al. 1993). Studies of temporary peripheral deafferentation of healthy humans showed immediate adjustment to the loss of proprioception on a behavioral (Moisello et al. 2008, applying limb immobilization) and cortical level (Bjorkman et al. 2004b; Bjorkman et al. 2004a, applying a local anaesthetic cream; Ziemann et al. 1998, applying an ischemic nerve block). However, these studies mainly requested the production of simple motor tasks with a limited range of kinematic DoF. Studies on the production of complex motor behavior, such as reaching movements, are rare as it is difficult to experimentally induce an effective proprioceptive loss of larger body parts like the multi-joint effector system arm. One way to influence the flow of proprioceptive afference in larger body parts is the application of a complete ischemic block using a tourniquet (Fellows et al. 1993; Jacobson et al. 1994).

The aim of this study was to investigate whether healthy subjects are able to immediately and efficiently adjust the control of complex arm movements to temporary proprioceptive deafferentation due to an ischemic block.

Methods

Participants

Fifteen healthy subjects (mean age ± SD: 26 ± 5years; 8 female) voluntarily participated in the study. All subjects were right-hand dominant as determined by the Edinburgh Handedness Inventory (Oldfield 1971) and had normal or corrected-to-normal vision. None of the subjects had any record of neurological disorder. All participants were paid for their participation and had given written informed consent prior to participation. The experimental procedure was in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Medical Faculty of the Ludwig-Maximilians University Munich.

Experimental set-up

Subjects were seated on a chair in front of a table, with the trunk supported by a chair back. A linear table track was mounted on the table, with a spherical object (reaching target, diameter: 80mm) attached to it. Due to its geometric properties, the reaching target constrained final hand position but not final hand orientation. The size of the target forced the subjects to grasp it with the whole hand, and not just with two fingers, which is why single finger motion was not of interest in the current study. The reaching target could be freely moved horizontally (in the fronto-parallel plane) between the bounds of the table track. These bounds (distance: 39cm) were the two positions at which the reaching target could be located. The sitting position of the subjects was adjusted so that: (a) trunk movement was not necessary to reach the target, and (b) body midline was centered to the table track. To minimize within-subject between-trial variability due to differences in the initial position, the starting position was defined by a wooden lever, attached to the right side of the chair, which had to be grasped with the dominant right hand before each trial (see Fig. 1A).

Joint angle motion of the arm in its seven degrees of freedom was recorded by an ultrasonic sound-emitting system (Zebris Medical, Isny, Germany). Six sound-emitting markers were attached to the arm and hand of the subject; each marker recorded at a frequency of 33Hz (200Hz in total). The following marker positions were chosen and are also depicted in Fig. 1B: markers 1 and 2 were attached to the metacarpophalangeal joints of the index (1) and little finger (2). The third marker was at the center of the wrist. Markers 4 and 5 were attached to the medial (4) or lateral (5) end of a bracelet directly above the elbow. The sixth marker was attached at the acromion. From those marker positions the individual length of the subject’s upper arm, lower arm, and hand could be determined. Based on these lengths, a geometrical model of the arm was created, as described in more detail below (see Section 2.4.1). Further, the signal of the first marker was used to trigger the opening and closing of shutter glasses (Translucent Technologies, Toronto, Canada) that were used to prevent visual online control of the movement. The first contact with the reaching target was detected by changes in the electrical resistance between the subject and the target (sampled at 1 kHz).

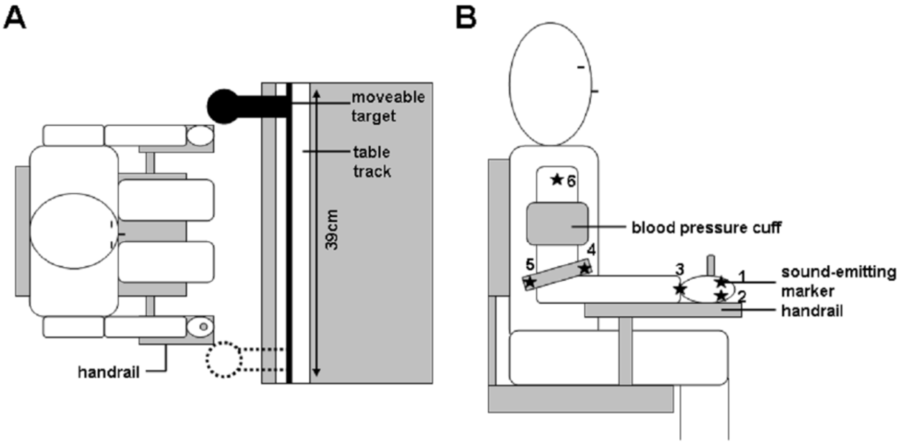

Fig. 1 Experimental set up **A** Overhead view of the experimental set up. Sitting position was individually adjusted so that the moveable target could be reached without trunk motion. The target could be located at the two bounds of the table track. Initial starting position was defined by grasping the handrail. **B** Positions of the six ultrasonic sound-emitting markers and the blood pressure cuff are depicted.

Procedure and design

Subjects repeatedly had to reach towards and grasp the reaching target with their dominant right hand. At the beginning of each trial, subjects had to adopt the starting position (see Fig. 1A). Subsequently, subjects were instructed to press a button with their non-dominant hand, after which the target changed its position. After an acoustic go-signal, subjects had to perform the reaching movement in a natural manner. To provoke the most natural movement behavior, subjects were informed before movement recording that movement speed and reaction time were not of interest in the study. Shutter glasses occluded as soon as the subjects started their movement, thus preventing visual online control of the movement. After the subjects had grasped the target, the shutter glasses opened again and the subjects returned to the starting position. A new trial was initiated by pressing the button again.

All subjects participated in two experimental conditions in separate sessions, the order of which was counterbalanced across subjects. Experimental sessions were separated by one to two days. In the first condition (“Ischemia”), a customary blood pressure cuff was applied to the upper arm of the subject and inflated up to 150-160mmHg (i.e. slightly above systolic blood pressure). The duration of inflation was in a range of 20-25min. This timeframe included 10min of preparation to guarantee impairment in the proprioceptive afference, and a subsequent 10-15min of movement recordings. The blood pressure cuff induced an ischemic block, which is known to first affect the large, fast conducting afferent fibers, especially Ia afferents arising from the muscle spindle afferents (Fellows et al. 1993). Other effects, such as changes in producible muscle force (Bjorkman et al. 2004a) can be disregarded in the current set-up because of the brevity of the ischemic block. Before movement recording started, the proprioceptive impairment was tested indirectly by testing subjects' touch sensitivity with von-Frey filaments (Marstock, Schriesheim, Germany, Rolke et al. 2006). On the back of the subjects' hands it was tested which of the 12 logarithmically scaled filaments subjects were at least able to perceive. Subjects' touch sensitivity had to be reduced by at least one filament from the time point at which the blood pressure cuff was applied before the experiment was continued. This procedure allowed us to be sure about the effectiveness of the ischemic block. At the same time, the duration of preparation was minimized, which was of importance to prevent unwanted side-effects of the ischemic block, as for example ischemic pain. The second experimental condition ("Control") served as a control condition, executed identically but without inflated blood pressure cuff.

Two blocks with 40 trials in each block were recorded in each session (i.e. 80 trials per session). Each experimental block consisted of 20 trials of each of the two target positions, arranged in a random order to avoid predictability of the target position. Between the blocks a break of maximally five minutes was offered to avoid fatigue. Before movement recording started, subjects were allowed to perform five trials to familiarize themselves with the experimental task and apparatus.

Analysis

Data analysis

Data analysis was calculated using Matlab 7.9.0 (Mathworks, Natick, USA) and was in line with earlier studies by our group (Krüger et al. 2012; Krüger et al. 2011). In a first step, the seven joint angles of the arm were computed from the marker position using a three-segment rigid body model, and expressed as seven consecutive Cardan angles. The order of the angles was as follows: two angles for the wrist (vertical, and horizontal), two angles for the elbow (torsion, and flexion), and three angles for the shoulder (torsion, horizontal, and vertical). The zero position of the arm was defined as the arm pointing straight forward with the elbow extended and the palm facing up. Based on that, positive joint angle indicated the following directions: vertical upward, horizontal rightward, and torsion clockwise. The vector containing the seven joint angles is hereafter referred to as arm posture. The position of the hand in space (i.e. 3D) was defined by the center of the two hand markers in world fixed Cartesian coordinates. In addition, the orientation of the hand in space was defined in Helmholtz coordinates relative to the external world.

Four aspects of movement execution were analyzed, separately for each condition, subject, target position and trial. The four aspects were chosen on the basis of the existing literature about deafferented patients and recent empirical findings about the planning and control of reach-to-grasp movements in healthy subjects: (1) movement duration, (2) movement amplitude, (3) movement variability, and (4) movement coordination.

First, overall movement duration was defined as the time between movement initiation and movement end. To determine movement initiation, movement start was defined as the time point at which the hand velocity first exceeded 10% of its peak velocity. Movement initiation was then determined by subtracting 10% of the acceleration time (i.e. the time between movement start and reaching peak velocity) from movement start. Movement end was defined as the last sample recorded before the first contact with the reaching target, as determined by the change in electrical resistance (see Section 2.2). Subsequently, duration of acceleration and duration of deceleration were calculated. In addition, peak velocity was analyzed. Thus, temporal characteristics of the reaching movements will be described by four measures: (1) overall movement duration, (2) duration of acceleration, (3) duration of deceleration, and (4) peak velocity.

Second, movement amplitudes were determined by calculating the absolute value of the difference between the maximum and minimum joint angle separately for each of the seven joint angles. Subsequently, mean movement amplitude was calculated as the average movement amplitude across the seven joint angles. In addition, to evaluate the curvature of the movement trajectory the total path length in the 7D-joint space was calculated.

Third, movement variability during movement execution and at movement end was analyzed. Prior to that, the full temporal resolution of the joint angle motion was reduced to ten equidistant sampling points between movement initiation and movement end. To account for small inter-trial variations in the actual starting position of the arm and in movement duration, a correction of the joint angle trajectories was calculated as described in Krüger et al. (2011). After this correction, the covariance matrix of the starting position (first sample) reduced to zero and was not considered in further analytical steps. Thus, the covariance matrix of the joint angles was analyzed at nine equidistant sampling points during the movement. Afterwards, movement variability was analyzed at two levels: the effector space and the task space. To examine the amount of variability during the time course of reaching movements in the effector space, the square-root of the mean within-subject variance, averaged across the seven joint angles of the arm (hereafter referred to as: “standard deviation of arm posture”), was calculated. In the task space, the square root of the mean within-subject variance, averaged across its three dimensions was calculated for the task variables (a) hand position (“standard deviation of hand position”) and (b) hand orientation (“standard deviation of hand orientation”).

Fourth, movement coordination was examined by two measures: (1) coupling between joint angles within the arm posture at a given sampling point, and (2) temporal coupling between the arm posture at a given sampling point and the final arm posture. To accomplish the first measure, a principal component analysis was calculated on the 7×7 covariance matrix of the arm posture separately for each subject, target position, and sampling point. Subsequently, the variances for each of the seven eigenvalues of the covariance matrix were averaged across sampling points, and the percentage of total variance explained by the first two eigenvalues was calculated. A relative increase of this percentage is closely related to a relative decrease of the number of kinematic DoF with respect to the mechanical DoF. To accomplish the second measure, the temporal coupling between the arm posture during the movement and the final arm posture was assessed by canonical correlation analysis evaluating the percentage of inter-trial variance of the final arm posture that could be explained by the variance of arm posture at a given sampling point. The redundancy, as returned by the canonical correlation analysis, equals the mean R^2 across the multiple regressions explaining the final arm posture as linear functions of the arm posture at a given sampling point. Note the difference in the meaning of the term “redundancy” in this mathematical context and “motor redundancy” (see e.g. Latash et al. 2007 for its definition).

Statistical analysis

Statistical analysis was calculated using SPSS 9.0. Pairwise comparisons were calculated for the measures of movement duration, movement amplitude, as well as for the two measures of movement coordination. A repeated measurement ANOVA with condition (Control vs. Ischemia) as the between-group factor, and sampling point as the repeated factor was calculated for the following dependent variables: (1) standard deviation of arm posture, (2) standard deviation of hand position, and (3) standard deviation of hand orientation. Bonferroni corrected pairwise comparisons were calculated for post-hoc analysis of significant interactions. A Greenhouse-Geisser adjustment was made if the sphericity assumption was rejected by Mauchly’s sphericity test. Variance data was tested for normal distribution with the Lilliefors-test. Data was normally distributed for both groups and for almost all sampling points. The critical value for significance was set at $p < 0.05$. Subjects were excluded from single analyses in case of data corruption.

Results

Since the influence of target position on complex reaching movements was not of interest in the current study, and was already discussed elsewhere (Krüger et al. 2012; Krüger et al. 2011), only the results for reaching towards the left target position will be presented here. Similar results were found for reaching movements towards the right target position, though in general the observed differences were smaller for the right target position as compared to the left target position.

Movement duration

Overall movement duration was 778 ± 167ms (mean ± SD) for the ischemia condition and 713 ± 142ms for the control condition (see Fig. 2). This difference was significant ($t_{14} = -3.55$, $P < 0.01$) and based on a significantly increased duration of the acceleration phase under ischemia (403 ± 83ms vs. 352 ± 84ms, $t_{14} = -3.08$, $P < 0.01$). Neither duration of the deceleration phase (375 ± 116ms vs. 360 ± 101ms), nor peak velocity (1068 ±

198.57mm/s vs. 1095 ± 195mm/s) differed between the ischemia and control condition.

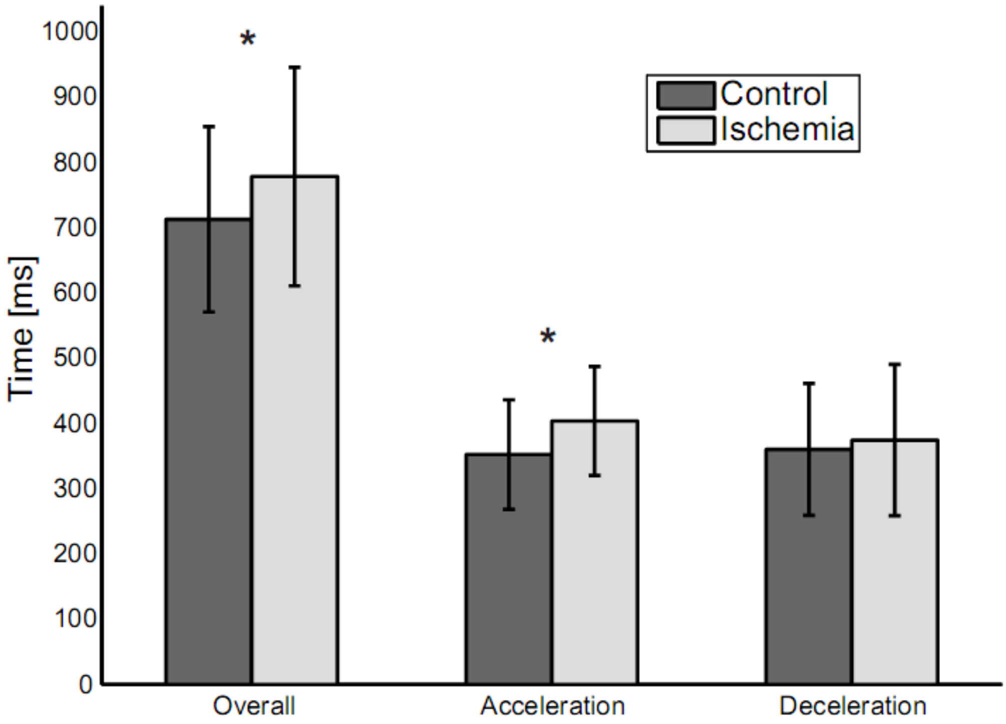

Fig. 2 Movement durations (means ± standard deviation) for the three analyzed parameters: Overall movement duration, duration of acceleration and duration of deceleration. Statistically significant differences between experimental conditions are indicated by an asterisk.

3.2 Movement amplitude

When reaching towards the target, trajectories for five out of the seven joint angles of the arm (shoulder torsion, shoulder horizontal, shoulder vertical, elbow torsion, and wrist horizontal) showed a continuous increase or decrease between movement initiation and movement end, with the trajectories slightly curved. For elbow flexion and wrist vertical, joint angle trajectories showed a reversal in movement direction during the movement. Under ischemia, total path length in the 7D-joint space was decreased by 15% (control: 40.8 ± 6.8deg vs. ischemia: 34.3 ± 5.4deg), indicating less curved joint angle trajectories in this condition. Associated with that, the subjects' mean movement amplitude was significantly decreased under ischemia as compared to the control condition (26.3 ± 4.1deg vs. 31.3 ± 4.7deg, $t_{14} = 5.32$, $P < 0.01$, see Fig. 3A). This difference was especially pronounced in four of the seven joint angles: shoulder torsion ($t_{14} = 2.46$, $P = 0.03$), shoulder vertical ($t_{14} = 2.95$, $P = 0.01$), elbow torsion ($t_{14} = 3.93$, $P < 0.01$) and elbow flexion ($t_{14} = 5.50$, $P < 0.01$, see Fig. 3B).

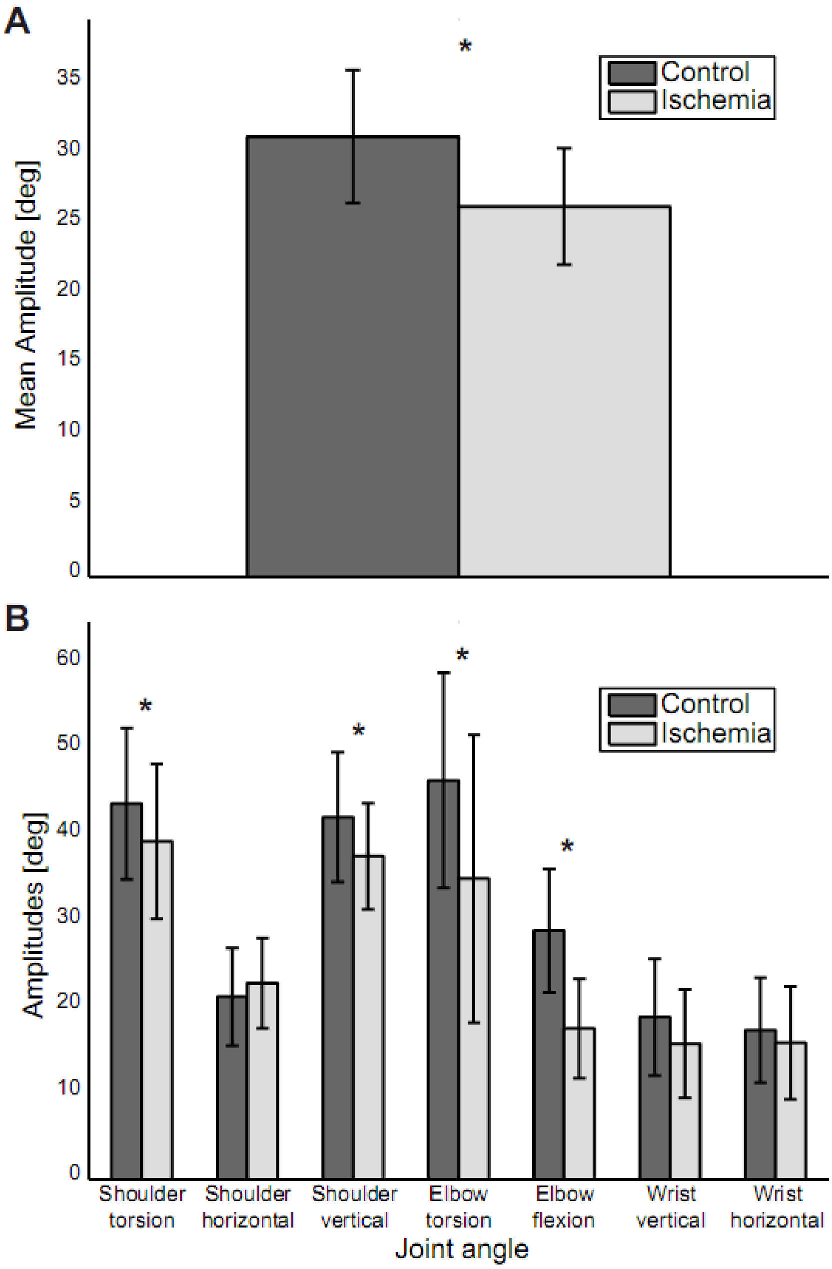

Fig. 3 Movement amplitudes **A** Mean movement amplitude (mean ± standard deviation) is depicted. Movement amplitude was significantly decreased under ischemia. **B** Movement amplitudes for each joint (mean ± standard deviation). Asterisks indicate significant differences between the two conditions. Movement amplitude was decreased in joints distal, as well as proximal to the blood pressure cuff.

Movement variability

Movement variability was analyzed with respect to three measures: (a) standard deviation of arm posture, (b) standard deviation of hand position, and (c) standard deviation of hand orientation. The amount of movement variability did not differ between the two experimental conditions (i.e. no significant main effect of experimental condition) for any of the three measures either across the nine sampling points or at movement end. However, for each of the three measures, a significant main effect of sampling point became evident: (a) $F_{2.39,23.92} = 21.21$, $P < 0.01$, (b)

$F_{2.36,23.62} = 53.35$, $P < 0.01$, and (c) $F_{2.48,24.83} = 22.93$, $P < 0.01$. In all cases, movement variability increased until the middle of the movement and decreased afterwards. Variability at movement initiation was smallest and on an intermediate level at movement end (see Fig. 4A-C).

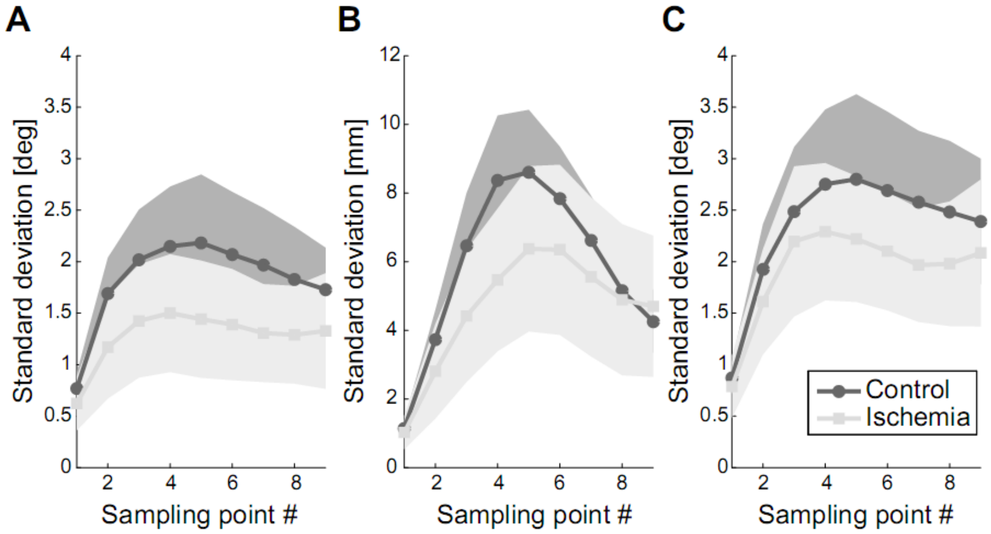

Fig. 4 Movement variability **A** Standard deviation of arm posture and the respective confidence interval is shown. It represents the mean across subjects. **B** Standard deviation of mean hand position (+ confidence interval) is depicted. Hand position variability was less modulated under ischemia. **C** Standard deviation of mean hand orientation and the respective confidence interval is shown.

Table 1: Post-hoc analysis for the significant interaction Condition × Sampling point for the measure: Standard deviation of hand position. Data in the upper right half of the table represents p-values of significant pairwise comparisons of single sampling points for the Ischemia-condition. Data in the lower left half of the table represents p-values of significant pairwise comparisons of single sampling points for the control condition. Bonferroni correction for multiple comparisons was applied to all calculations.

		Ischemia								
	Sampling point #	1	2	3	4	5	6	7	8	9
Control	1		p = 0.05	p = 0.01	p < 0.01	p < 0.01	p < 0.01	p = 0.02	p = 0.03	p = 0.02
	2	p < 0.01		p < 0.01	p < 0.01	p = 0.01	p = 0.03	n.s.	n.s.	p = 0.07*
	3	p < 0.01	p < 0.01		n.s.	p = 0.04	n.s.	n.s.	n.s.	n.s.
	4	p < 0.01	p < 0.01	p = 0.03		p = 0.06*	n.s.	n.s.	n.s.	n.s.
	5	p < 0.01	p < 0.01	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.
	6	p < 0.01	p < 0.01	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.
	7	p < 0.01	p = 0.02	n.s.	n.s.	p = 0.01	p < 0.01		n.s.	n.s.
	8	p < 0.01	n.s.	n.s.	p = 0.4	p < 0.01	p < 0.01	p < 0.01		n.s.
	9	p < 0.01	n.s.	n.s.	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p = 0.06*	

The interaction of experimental condition × sampling point was significant for standard deviation of hand position. Qualitatively, this effect became evident as a weaker modulation of hand position variability across the nine sampling points in the ischemia condition (see Fig. 4B). Post hoc analysis revealed that, under ischemia, only the first two sampling points differed largely from the other sampling points, whereas under control conditions almost all sampling points differed significantly from each other (see Table

1). In addition, there was a trend towards a significant difference of hand position variability between the two experimental conditions at the fourth sampling point, when the difference in the standard deviation of hand position was greatest ($t_{14} = 2.04$, $P = 0.07$, see Fig. 4B). No other effects reached the level of significance.

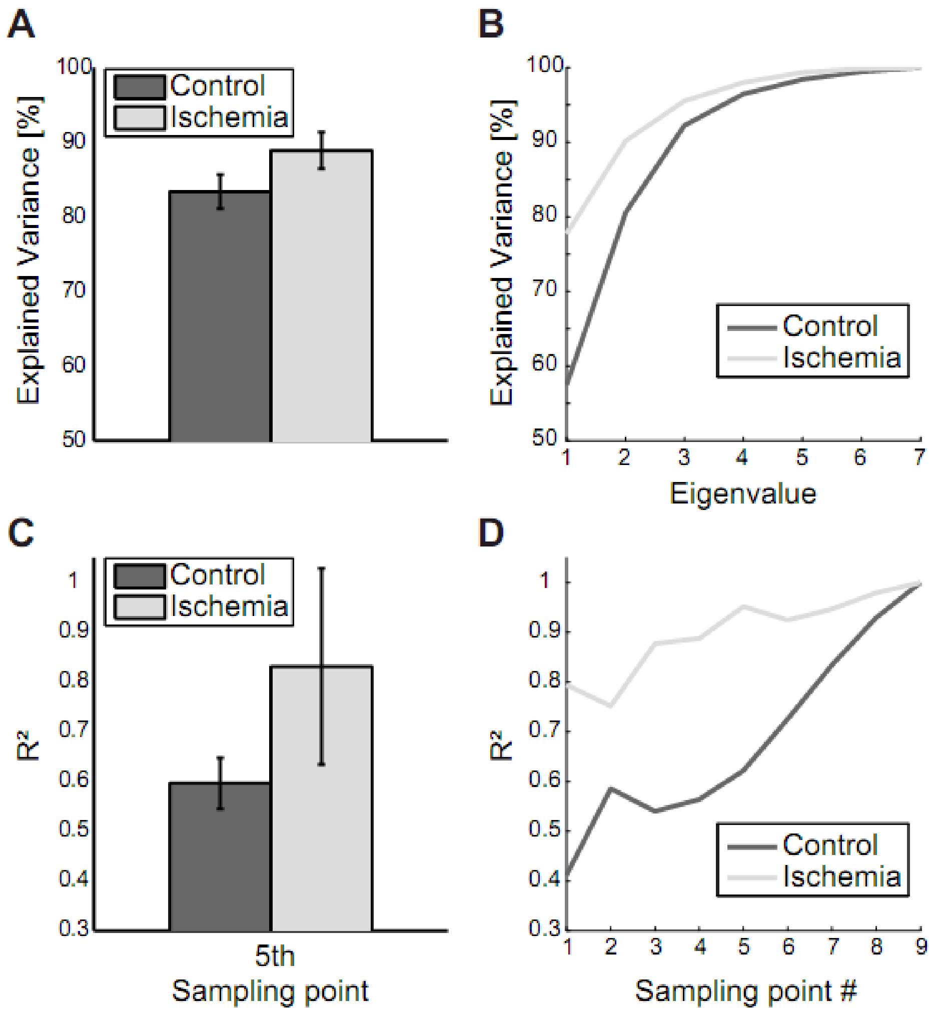

Fig. 5 Movement coordination **A** Group mean (± standard deviation) of the variance explained by the two biggest eigenvalues, averaged across the nine sampling points, is shown. Under ischemia significantly more variance was explained by the first two eigenvalues as compared to the control condition. **B** Explained variance by the seven eigenvalues, averaged across the nine sampling points, is shown for one representative subject. **C** Redundancy (R^2) of final arm posture variance with respect to arm posture variance at the fifth sampling point. Error bars represent standard deviations. Under ischemia redundancy was higher than in the control condition. **D** Redundancy (R^2) of final arm posture variance with respect to arm posture variance for each sampling point is shown for a representative subject for both conditions.

Movement coordination

As a first measure of movement coordination, the coupling of joint angles within the arm posture at a specific sampling point was analyzed using a principal component analysis applied to the inter-trial 7×7 covariance matrix of the arm posture at the specific sampling point. Under ischemia, the first two eigenvalues explained 88.90 ± 2.44% of total joint angle variance compared with 83.40 ± 2.27% in the control condition (see Fig. 5A for group mean and Fig. 5B for a representative subject). This difference was significant ($t_8 = -18.43$, $P < 0.01$).

Secondly, the temporal coupling of the arm posture was analyzed using the redundancy of final arm posture with respect to the arm posture during movement execution (see Section 3.3). As a matter of course, the redundancy increased towards movement end and finally reached the level of 1 (see Fig. 5D for a representative subject). The redundancy of final arm posture with respect to the variance of the arm posture at the first sampling point was smaller in the control condition ($R^2 \sim 0.4$) than under ischemia ($R^2 \sim 0.7$). Consequently, the subsequent increase in redundancy up to the value 1 at movement end was steeper in the control condition than under ischemia. For group comparison, only the redundancy with respect to the fifth sampling point, when the standard deviation of arm posture was maximal, was analyzed. Under ischemia the redundancy was significantly higher than in the control condition (R^2: 0.83 ± 0.20 vs. 0.60 ± 0.05, $t_4 = -3.248$, $P = 0.03$, see Fig. 5C).

Discussion

In the current study we investigated the influence of temporary proprioceptive deafferentation on the control of a complex reaching movement. We found increased movement duration due to increased acceleration duration, decreased movement amplitude, as well as changes in movement coordination under reduced proprioceptive afference due to ischemia. The changes in movement coordination became evident as an increased coupling of joint angles within a specific arm posture, as well as an increased temporal coupling between arm postures during movement execution with final arm posture, resulting in a decreased number of kinematic DoF of the effector-system. Movement endpoint variability was not influenced by the ischemia. Overall, the results suggest that healthy subjects are able to immediately and efficiently adjust to the impaired flow of proprioceptive information. These ischemia-induced adjustments may concern different levels of the motor system such as muscle functions (Jacobsen et al. 1994), spinal reflexes (Fellows et al. 1993), cerebellar feedback-control, or movement planning.

It can be speculated why the ability to compensate for the impaired flow of proprioceptive information is different in healthy subjects as compared to patients with chronic deafferentation. One possible explanation could be that the proprioceptive deafferentation applied in our study is qualitatively different to the one induced by chronic peripheral sensory neuropathy. Both processes may involve different sensory processing mechanisms. Another possible explanation could lie in the duration of the impairment of deafferented patients. Whether the ability to flexibly and efficiently integrate available sensory information in healthy subjects would decrease with the duration of the proprioceptive deafferentation, when the proprioceptive input to the feed-forward and feedback signals becomes increasingly less informative and less precise, can be speculated. If this holds true one would expect increasingly deteriorated movement performance, similar to that observed in chronically deafferented patients (Sainburg et al. 1995; Medina et al. 2010; Gentilucci et al. 1994).

In this study, the flow of proprioceptive afference was incompletely blocked by a blood-pressure cuff which was applied to the subjects' upper arm and inflated slightly above systolic blood pressure. Consequently, partial proprioceptive information was still accessible during movement execution. Though, the observed strength of the changes in movement control under ischemia proved this procedure to be effective for studying effects of proprioceptive deafferentation. Ischemic pain and muscle weakness were not observed in our study, due to the relatively short duration of the experiment (Harriman 1977; see also 2.3 in the Methods section for a more detailed description on the effects of an ischemic block).

Adjustment of movement duration

Movement duration was increased by the ischemia as a result of increased acceleration duration. The influence of proprioception on the duration of acceleration was already recognized by Bagesteiro and colleagues (2006) and associated with sensory-based online-correction of the movement. Movement's peak velocity was not increased under ischemia. Increased duration of acceleration without increased peak velocity indicates decreased peak acceleration and, consequently, decreased peak force. A reduction in total force applied during movement execution is accompanied by a reduction in signal-dependent noise (Harris and Wolpert 1998). This may be advantageous under ischemia, as the precision of movement planning is of greater importance when movement online-control based on proprioceptive feedback is impaired. Our results suggest that healthy subjects are able to immediately and efficiently adjust the precision of movement planning to the lack of proprioceptive information.

Adjustment of movement amplitude

Movement amplitude was decreased under ischemia, due to less curved joint angle trajectories. Importantly, this was not only true for joints distal to the applied blood pressure cuff (i.e. elbow torsion and elbow flexion), which were directly affected by the ischemic block, but also for two joint angles proximal to the cuff (i.e. shoulder torsion and shoulder vertical), which were not directly affected by the ischemia. In combination with the finding of stronger inter-joint coupling under ischemia, this suggests a more global change in the strategy of joint angle coordination involving all joints of the arm, to compensate for the ischemia. A reason for planning a reaching movement with decreased mean movement amplitude may be the associated decrease in the signal-to-noise ratio (Harris and Wolpert 1998), facilitating the control of movement endpoint variability. This assumption is also supported by Fitts' Law (Fitts 1954), which describes the relationship between movement amplitude, movement duration and movement accuracy. According to this law, in order to keep movement endpoint variability constant in a task with increased task difficulty, movement duration and/or movement amplitude must be adjusted. Assuming that the ischemia may have increased task difficulty, as an important source of sensory information was disabled, planning a movement with decreased movement amplitude and increased movement duration may have allowed the subjects to keep movement endpoint variability constant, as observed in our study.

Changes in movement control, involving movement duration and movement amplitude, were also reported in a study by Medina and colleagues (2009), where a patient with chronic, peripheral deafferentation had to point to targets of different size (implying different movement difficulties) and at different distances from the starting point (implying different movement amplitudes). Increased movement difficulty and increased movement amplitude were both accompanied by increased movement duration and resulted in decreased endpoint accuracy. Although similar results were found for the healthy control subjects in this study, the trade-off was much steeper for the deafferented patient than for the control subjects. In contrast to Medina and colleagues, who found decreased endpoint accuracy in the deafferented patient, endpoint variability was not increased under proprioceptive deafferentation in our study. This may be explained by differences in the experimental task (grasping versus pointing), and more probably by the fact that the deafferentation in our study was only incomplete and temporary, whereas the patient in the study by Medina and colleagues was chronically deafferented for more than 20 years. However, as a common conclusion, it can be inferred that proprioceptive deafferentation leads to a strategic change in the control of the reaching movements. Importantly, healthy subjects are able to efficiently and immediately compensate for the temporary loss of proprioceptive information by increasing movement duration and decreasing movement amplitude so that movement endpoint variability is not increased.

Adjustment of movement variability

Another important finding of our study was that the modulation of hand position variability during movement execution was altered under ischemia, in such a way that the initial increase and subsequent decrease of hand position variability was less pronounced. The increase-decrease pattern of movement variability was already described in earlier studies by our group (Krüger et al. 2012; Krüger et al. 2011) and is a sign of successful minimization of variance at movement end. It indicates that signal-dependent noise (Harris and Wolpert 1998), introduced by forces during the acceleration period, is successfully compensated by feedback control acting primarily during the deceleration phase (Elliott et al. 2010; Elliott et al. 2001). The fact that this increase-decrease pattern of hand position variability is less pronounced under ischemia (see Fig. 4) is probably related to both reduced acceleration forces, resulting in a reduced increase of variability, and impaired proprioceptive feedback, resulting in a reduced decrease of variability. Interestingly, both of these changes compensated for each other in such a way that endpoint variability was almost identical in the control condition and under ischemia. This is in contrast to findings of studies with chronically deafferented patients (Gentilucci et al. 1994; Nougier et al. 1996; Gordon et al. 1995; Medina et al. 2009) and reflects the ability of the motor control system of healthy subjects to immediately and efficiently adjust to the loss of proprioceptive information.

Adjustment of movement coordination

Movement coordination was altered under ischemia, a finding similar to that observed in studies on deafferented patients (Ghez and Sainburg 1995; Sainburg et al. 1993; Sarlegna et al. 2006). In the current study, the alterations in movement coordination became evident for the coupling between single joints of a specific arm posture as well as for the temporal coupling of arm posture during movement execution with that at movement end. For both parameters, the coupling was stronger under ischemia, which can be interpreted as a reduction of the number of kinematic DoF of the redundant effector-system arm and consequently as a facilitation of its online-control. The “problem” of redundancy is well-known (Bernstein 1967) and of recent interest in motor control research (Eggert et al. 2003; Gielen et al. 1995; Prablanc et al. 2003; Krüger et al. 2012). Recently, the benefits of redundancy came to the fore (de Freitas et al. 2007; Gera et al. 2010; Latash et al. 2010). Associated with that, the effort and the costs of controlling movement variability are reduced as only variability that counteracts successful movement execution needs to be minimized (Todorov 2004; Todorov and Jordan 2002). Increasing the strength of joint angle coupling under ischemia, i.e. increasing the synergistic coordination of the redundant DoF, may reflect a change in the control strategy concerning the way motor redundancy is used.

Conclusions

The results suggest that healthy subjects are able to immediately and efficiently adjust the control of complex reaching movements to the loss of proprioceptive information. Qualitatively similar to the findings in studies on chronically deafferented patients, movement duration was longer, movement amplitude was decreased and movement coordination was altered. This led to a reduction in movement complexity, which, generally speaking, results in facilitated movement control. As a result, variability at movement end was not increased, which seemed to be an important goal of the task.

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Synergistic control of joint angle variability: Influence of target shape

Melanie Krüger, Bence Borbély, Thomas Eggert, and Andreas Straube

Abstract

Reaching movements are often used to study the effectiveness of motor control processes with respect to the final position of arm and hand. Empirical evidence exists, showing that different targets can be grasped with similar final position accuracy. However, even equally effective controlled movements towards different targets can be based on different control strategies. In particular, control strategies may differ in the control of the abundant degrees of freedom with respect to the task specific costs. The objective of the present study was to investigate whether the applied control strategy is influenced by the shape of the target to be grasped. It was investigated whether differently strong pronounced constraints, which are imposed by the shape of the targets, are leading to different synergistic coordination of the degrees of freedom of the arm. For that purpose, subjects were asked to either grasp a cylindrical or spherical target, which imposed differently strong constraints on final hand orientation and position. Variability of joint angles of the arm, as well as variability of hand orientation and hand position was analyzed over the whole time course of movement execution, using the uncontrolled manifold method. Analysis revealed that the degrees of freedom of the arm were synergistically coordinated to stabilize both, hand orientation and hand position, when grasping to either the spherical or cylindrical target. This suggests that multiple task constraints can be simultaneously controlled. The analysis further revealed that joint angle variability of the arm was more closely controlled to stabilize hand orientation when reaching towards a cylindrical target as compared to the spherical target. In contrast, hand position was more strongly stabilized in the spherical target condition. This suggests that different target shapes do influence the control strategy of reaching movements even though variability at movement end was not affected.

Introduction

Reaching and grasping movements represent an elemental part of the human movement repertoire. Because of this, this class of movements is often used to investigate motor control processes (Bagesteiro, Sarlegna, & Sainburg, 2006; Boulinguez, Nougier, & Velay, 2001; Desmurget et al., 1995; Haaland, Prestopnik, Knight, & Lee, 2004; Ohta, Svinin, Luo, Hosoe, & Laboissiere, 2004; Sainburg & Kalakanis, 2000; Scheidt, Conditt, Secco, & Mussa-Ivaldi, 2005; Simmons & Demiris, 2006). Two main approaches that are used in this context can be found in the literature: (1) the investigation of the amount of movement variability (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget & Prablanc, 1997; Eggert, Tihanyi, & Straube, 2003; Grea, Desmurget, & Prablanc, 2000; Kruger, Eggert, & Straube, 2011; Magescas, Urquizar, & Prablanc, 2009), and (2) the investigation of the structure of movement variability (de Freitas, Scholz, & Stehman, 2007; Eggert, et al., 2003; Gera et al., 2010; Latash, Scholz, & Schoner, 2002, 2007; Scholz, Danion, Latash, & Schoner, 2002; Scholz, Schoner, & Latash, 2000; Y. W. Tseng, Scholz, & Galloway, 2009; Zhang, Scholz, Zatsiorsky, & Latash, 2008).

As a representative of the first group, Desmurget and Prablanc (1997), for example, found empirical evidence that the mean final arm posture of reaching movements is invariant to perturbations. In their study, Desmurget and colleagues showed that, when reaching towards a cylindrical target, final arm posture was neither different nor more variable when the target was stationary or changed its orientation after movement onset. This result was interpreted as a hint for the postural control hypothesis, which states that the strategy used to control reaching movements is constructed to stabilize final arm posture. This hypothesis was further confirmed by the finding that the invariance of final arm posture to perturbations did not depend on the particular orientation constraints induced by the cylindrical handle but can also observed with spherical handle (Grea, et al., 2000). These studies even though they proved the importance of final arm posture for cylindrical and for spherical targets, did not investigate how the control of final arm posture was affected by target shape. In addition, looking at the variability of final arm posture provides only information about the consequence of the motor control process. In contrast, investigating the time course of variability during movement execution reveals characteristic features of the underlying control strategy (Kruger, et al., 2011).

In the past years, the investigation of the structure of movement variability during movement execution became of increasing interest in that context. (Domkin, Laczko, Djupsjobacka, Jaric, & Latash, 2005; Domkin, Laczko, Jaric, Johansson, & Latash, 2002; Y. Tseng, Scholz, & Schoner, 2002; Y. W. Tseng & Scholz, 2005; Y. W. Tseng, Scholz, Schoner, & Hotchkiss, 2003; van der Steen & Bongers, 2011). The notion of a synergistic control of abundant degrees of freedom (DoF) was introduced (Latash, et al., 2007). Latash and colleagues (2007) defined synergistic control of the multi-element system in a way that: the task is shared across different elemental variables of the system, and that those elemental variables are able to covary with each other to ensure stability of the multi-element system. By doing so, the system is supposed to become more resistant against perturbations (Latash, et al., 2007). Synergistic neural control of movements therefore ensures flexibility and stability of the multi-element system.

Scholz and Schoner (1999) proposed the uncontrolled manifold method through which it is possible to examine whether inter-trial variability in movement execution is structured to synergistically stabilize particular task variables. By applying this method, movement variability (e.g. variance of joint angle positions) is partitioned into two independent components – one leaving a proposed task variable (e.g. hand position) unchanged (“uncontrolled variance” - V_{ucm}), whereas the other, orthogonal component contains that part of the movement variability which has an influence on the proposed task variable (V_{orth}). While the first component gives hint about the flexibility of the system in coordinating specific joint configurations, the ratio of these two components (V_{ucm}/V_{orth}) reflects the stability of the system (Latash, et al., 2007). This method was further elaborated by Latash and colleagues (Latash, Levin, Scholz, & Schoner, 2010; Latash, et al., 2002, 2007; Zhang, et al., 2008) and associated with other concepts of motor control (Freitas & Scholz, 2009; Latash, 2008, 2010).

The aim of the present study was to investigate the influence of target shape on the amount and structure of joint angle variability during reaching movements by directly contrasting spherical and cylindrical target shape, using the uncontrolled manifold method (Scholz & Schoner, 1999). Grasping the sphere leaves three rotatory degrees of freedom (DoF) unrestraint, whereas grasping the cylindrical target leaves one rotatory and one translational DoF unrestraint. Hence, we hypothesized that stabilization of hand orientation is less important when grasping the sphere than the cylinder. In contrast, we hypothesized that the stabilization of hand position is less important when grasping the cylinder than the sphere. To test this hypothesis, we investigated the structure of joint angle variance by evaluating V_{ucm} and V_{orth} with respect to the task variables hand orientation and hand position. Furthermore, we investigated the effectiveness of the control process by directly quantifying the variances within the two task spaces (hand orientation, hand position).

Methods

Participants

Ten healthy subjects (6 female, 4 male, age: 29.4 ± 7.9 years) participated in the study. Subjects had given written informed consent prior to participation. All subjects were right-hand dominant as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. The experimental procedure was in accordance with the Declaration of Helsinki and approved by the local Ethical Committee.

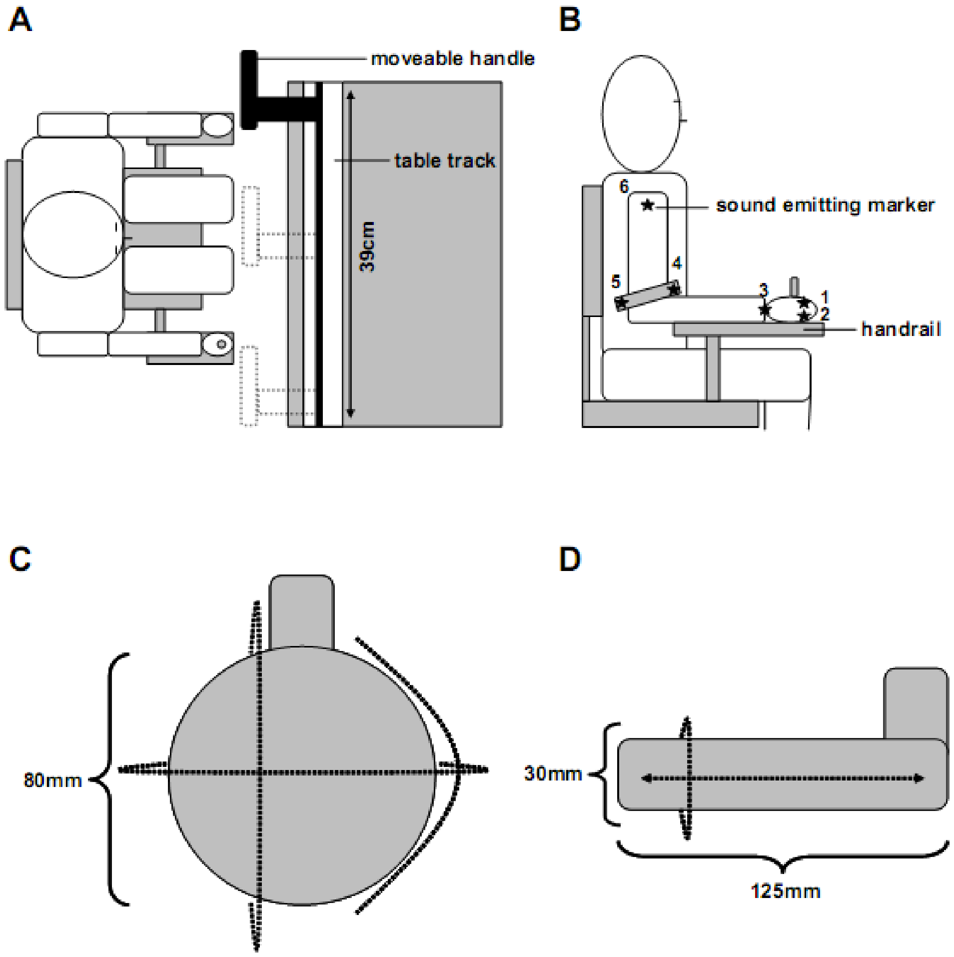

Fig.1 Experimental set-up and apparatus. **A** Top view on the experimental set-up. Sitting distance of the subject could be adjusted to individuals arm length. The black, solid bars represent one of the three possible positions of the moveable handle. Dashed bars show the other two possible handle positions. The moveable handle was mounted on a horizontal table track, which moved the handle in a horizontal, frontal-parallel plane. **B** Starting position of the dominant right arm was defined by grasping a wooden lever attached to the handrail. Positions of the six ultra-sonic sound emitting markers are depicted. **C** The spherical target to be grasped is depicted. The small bar represents the link with the table track. In addition, the three (rotational) dimensions, which do not constrain the grasping movement, are drawn (dashed lines). **D** The cylindrical target with its respective length and depth is depicted. Again, the two dimensions, which are not constrained by the target shape, are drawn (dashed lines). Parts A and B are reprinted from Clinical Neurophysiology, 122/4, Kruger, M., Eggert, T., & Straube, A., Joint angle variability in the time course of reaching movements, 759-766, Copyright (2011), with permission from Elsevier

Experimental set-up

Subjects were comfortably seated in front of a table on which a linear table track was mounted. The grasping object was moveable on the table track in a horizontal, frontal-parallel direction (position range: ± 19.5cm) to three equidistant positions within the boundaries of the table track (i.e. left side – center – right side). The object was driven by a 2-phase step motor with a resolution of 0.1mm per step. The sitting position of the subjects was individually adjusted as follows: (a) body midline had to be aligned to the centre handle position, (b) the handle positions were within the anatomical range of motion of the subjects arm, and (c) trunk motion was not necessary to fulfil the reaching movement. The subject's individual starting position was defined by a wooden lever, which was attached to the right side of the chair, and that had to be grasped with the dominant right hand before each trial (see Fig. 1A). Thereby, within-subject between-trial variability due to differences in the starting position was tried to minimize.

Procedure

Two experimental conditions were set up to investigate the influence of target shape on the control of joint angle variability. In the first condition, subjects had to reach towards a spherical target (Ø 80 mm), whereas a cylindrical target (length: 125 mm, Ø 30 mm) had to be grasped in the second condition. The size of the objects forced the subjects to grasp the targets with the whole hand, and not just with two fingers. Due to its geometric properties, the cylindrical target imposed more constraints on the final hand orientation than the spherical target did. In contrast, the spherical target imposed more constraints on the final hand position (see Fig. 1C & 1D). However, it has to be noted that position and orientation of the hand are not absolutely independent from each other in this task, as for example vertical hand rotation also leads to a change of hand position in depth. All subjects participated in both conditions in separate experimental sessions. The order of sessions was counterbalanced across subjects.

At the beginning of each trial, subjects had to take in the starting position. Each trial started with the subjects pressing a start button, after which the handle position changed. Subsequently, a specific go-signal sounded and subjects had to reach towards and grasp the target with their dominant right arm in a natural manner. To provoke the most natural movement, no demands concerning movement speed or reaction time were made. As soon as the subjects started their movement, the shutter glasses occluded and thereby prevented visual online control of the movement. Subjects were instructed to go back to the starting position after having grasped the target and to initiate a new trial by pressing the start button again.

Before data acquisition, subjects performed five trials to familiarize themselves with the experimental task and apparatus. Subsequently, four blocks with 30 trials in each block were recorded in each session (120 trials per session). Each experimental block consisted of 10 trials of each handle position, arranged in a pseudo-random order to avoid predictability of the handle position and pre-planning of the reaching movement. Between the blocks a break of maximum five minutes was offered to avoid fatigue.

Analysis

Data analysis

The joint angles of the arm were deducted from the marker signals using Matlab 7.9.0 (Mathworks, Natick, USA) to create a geometrical model of the arm and hand. Those joint angles were converted to seven consecutive Cardan angles, expressed in the following order: two angles for the wrist (vertical, horizontal), two for the elbow (torsion, flexion), and three for the shoulder (torsion, horizontal, vertical). The vector containing these seven joint angles is hereafter referred to as arm posture (Kruger, et al., 2011). In addition, orientation of the hand in space (i.e. 3D) was defined by the orientation of the plane defined by the three markers on the hand and wrist. The orientation was specified in Helmholtz coordinates (Haslwanter, 1995) relative to the external world. Furthermore, hand position in space (i.e. 3D) was determined by the position of the center between the two markers of the hand in world-fixed Cartesian coordinates. Trials were excluded from further data analysis, if one of the markers was temporary occluded. In general, this affected not more than 10 trials per subject. The full temporal resolution of the joint angle motion was reduced to ten equidistant sampling points between movements initiation (i.e. immediately before the first increase in movement velocity of marker (1) was detected) and movement end (i.e. last positional signal before the first contact with the handle).

Before estimating the 7x7 covariance matrix of the arm posture for reaching movements between fixed starting position and fixed target position, a correction of the joint angle trajectories for small inter-trial variations of movement duration and of the actual starting position of the arm was calculated. This was necessary because, although subjects' individual starting position was predetermined by the experimental set-up (see point 2.2), small variations were still possible. In the same way, variations in movement duration were possible due to the fact that the reaching movements were not restricted to specific movement duration. This correction was calculated by submitting each joint angle to a linear regression analysis with the predictors starting position (7 joint angles) and movement duration. This regression analysis was calculated independently for each subject, handle position and sampling point. For each trial, the joint angles were corrected by subtracting the difference between the predicted and the average joint angle. After this correction, the covariance matrix of the starting position (first sample) reduced to zero and was not considered in further analytical steps. Thus, the covariance matrix of the joint angles was analyzed at nine equidistant sampling points during the movement.

Three overall measures were computed to examine the amount of variability of the reaching movements on joint angle level during the time course and at the endpoint: (1) square-root of the mean within-subject variance, averaged across the seven joint angles of the arm ("standard deviation of arm posture"), (2) square root of the mean within-subject variance of hand orientation in Helmholtz angles, averaged across the three rotational dimensions ("standard deviation of hand orientation"), and (3) square root of the mean within-subject variance of hand position in Cartesian coordinates, averaged across the three directional dimensions ("standard deviation of hand position"). These overall standard deviations were calculated separately for each subject and sampling point.

Analysis based on the Uncontrolled Manifold method

In addition to the analysis of the amount of joint angle variability, the question about the underlying structure of this variability was of interest in this study. Therefore, in a first step, hypothetical task variables were defined. It was hypothesized that the central nervous system synergistically stabilizes the value of: (1) hand orientation, and (2) hand position during movement execution. We wanted to test whether the actual control strategy differed between the spherical and cylindrical target shape condition. Following that initial step, the total variance of the specific mean arm posture, (i.e. the sum of variances of all joint angles) was calculated for each of the nine sampling points.

To examine the covariation structure between joint angles of the arm with respect to the different hypothesized task variables, the uncontrolled manifold method (Latash, et al., 2002, 2007; Scholz & Schoner, 1999) was applied, based on the geometrical model of the arm as described above (see 2.4.1). The structure of variance in the frame of the uncontrolled manifold method is defined by the amount of variance that does not lead to changes in the task variable in comparison to the amount of variance that does change the task variable. The Jacobian matrix (J), obtained through the geometrical model of the arm, expresses the differential changes of the 3-dimensional task variable (Δv; either hand position or hand orientation) as a linear function of the differential changes of the 7 joint angles ($\Delta\varphi$): $\Delta v = J \times \Delta\varphi$. The subspace of joint configurations, in which differential joint angle changes do not influence the task variable, builds the uncontrolled manifold. Variance within the uncontrolled manifold (V_{ucm}) was defined as the variance of the projection of all deviations of the joint angles from their mean on the null space of the Jacobian matrix: $V_{ucm} = trace(B_{ucm}T \times \sum \times B_{ucm})$. Where $\sum$ denotes the covariance matrix of the joint angles and B_{ucm} the basis matrix of the null-space obtained from the last 4 columns of the orthogonal matrix Q computed by the QR-decomposition (performed with the Matlab-function qr) of the transposed Jacobian matrix: $Q = [B_{orth} , B_{ucm}]$ with $[Q,R] = qr(J\ T)$.

The amount of variance within the uncontrolled manifold may be interpreted as the flexibility of covariation between the joint configurations (Latash, et al., 2007). The orthogonal subspace contains those joint configurations, whose differential joint angle changes do lead to changes in the task variable. The amount of variance within this orthogonal subspace (V_{orth}) is determining the success of the motor performance: $V_{ucm} = trace(B_{orth}T \times \sum \times B_{orth})$. The total variance of the arm posture was partitioned into the two components (V_{ucm} and V_{orth}) for each task variable, each subject and each of the nine sampling points.

Variance in each subspace was normalized to the number of its DoF within that subspace to allow comparisons between the two orthogonal subspaces. When (1) hand orientation or (2) hand position was the task variable, the subspace of V_{orth} consisted of three DoF. The number of DoF within the V_{ucm} consisted of the difference between the total number of DoF (seven) and the number of DoF within the subspace of V_{orth}. In addition, the ratio between normalized V_{ucm} and V_{orth} was calculated. When this ratio was greater than one, V_{orth} was smaller than V_{ucm}, suggesting that stabilizing the task variable was part of the control strategy. The size of this ratio is interpreted as a measure for the stability of the synergistic control of the hypothesized task variable (Latash, et al., 2007).

Statistical analysis

Statistical analysis was calculated using SPSS 9.0. A repeated measurement ANOVA was calculated on the last sampling point, with target shape as repeated factor, for the standard deviation of arm posture, the standard deviation of hand orientation and standard deviation of hand position, as well as for the variance ratios, V_{ucm} and V_{orth} of the assumed task variables: hand orientation, and hand position. This procedure should allow cross-experimental comparisons with the studies of Prablanc and colleagues (Desmurget & Prablanc, 1997; Grea, et al., 2000) as well as Gera and colleagues (Gera, et al., 2010). In addition, a 2 (target shape) × 9 (sampling point) repeated measurement ANOVA was calculated for each of the above mentioned dependent variables. The threshold of statistical significance was set at $p < 0.05$. Greenhouse-Geisser adjustment was made, if the sphericity assumption was rejected by Mauchly’s sphericity test.

Results

Amount of joint angle variability of arm and hand

Standard deviation of arm posture did not differ between target shapes, neither for the last sampling point nor across the whole time course of movement execution. The interaction target shape × sampling point also did not reach significance. However, standard deviation of arm posture differed across the time course of movement execution; increasing until the fourth sampling point and slightly decreasing again afterwards, as indicated by the main effect of sampling point (see Table 1 and Fig. 2A).

Standard deviation of hand orientation also did not differ between the target shapes, again neither for the last sampling point nor across the time course of movement execution. The main effect of sampling point was significant (see Table 1 and Fig. 2B). The time course of standard deviation of hand orientation showed a similar increasing-decreasing pattern as the standard deviation of arm posture. Other effects did not reach the level of significance.

Standard deviation of hand position also did not differ significantly between the target shapes at the last sampling point. However, there was a marginal effect of target shape with respect to joint angle variability (see Table 1). The standard deviation of hand position tended to be less for the spherical target than for the cylindrical target during the time course of movement execution, but did not differ at movement start and movement end (see Fig. 2C). Furthermore, the interaction of target shape × sampling point was significant (see Table 1). Again, standard deviation differed across the time course of movement execution, as illustrated by a main effect of sampling point. Standard deviation increased until the middle of the movement and decreased afterwards.

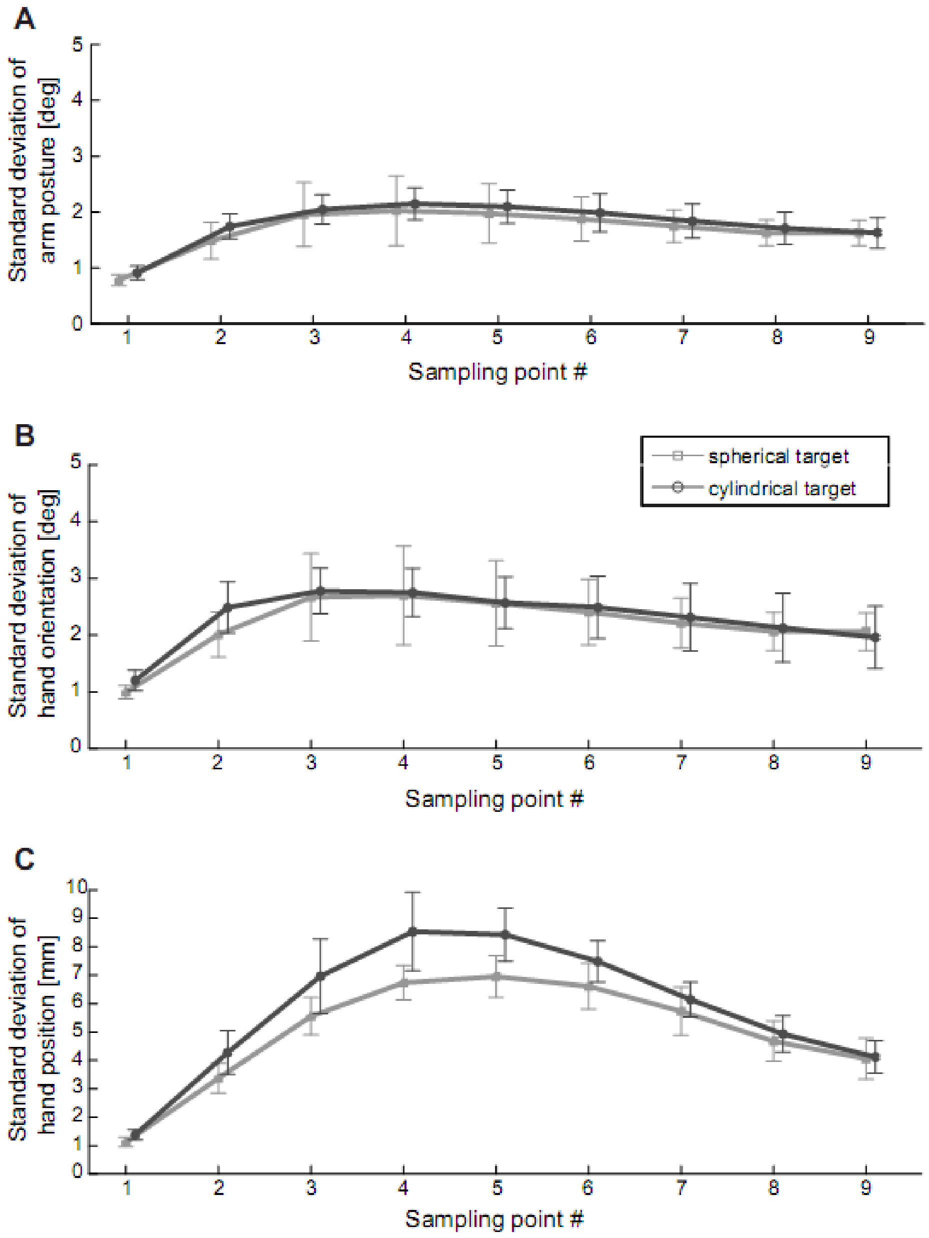

Fig.2 The time courses of joint angle variability are depicted for the two target shape conditions at the nine sampling points. **A** Time course of standard deviation of arm posture. Target shape does not influence the variability of arm posture, neither at the end point nor during the time course of movement execution. Error bars represent the confidence intervals. **B** Time course of standard deviation of hand orientation. Again, target shape did not influence variability of hand orientation. Variability was quantified as the within-subject standard deviation of hand orientation averaged across subjects. **C** Time course of standard deviation of hand position. Subjects showed less variability in hand position when reaching towards the spherical target as compared to the cylindrical target, but only during the middle of the movement, and not movement start or movement end. Symbols show the group mean of root mean square of the standard deviations across all angles (A: 7, B: 3) or Cartesian directions (C: 3). Error bars represent the confidence intervals of the group mean (N = 10).

Table 1 Summary of statistically significant effects for standard deviation of arm posture, standard deviation of hand orientation and standard deviation of hand position. F-values and the respective p-values are listed for the analysis of endpoint variability and for the time course of movement execution (i.e. across the nine sampling points). The asterisks mark effects, which show a trend towards significance

	Effects			
	Endpoint variability	***Time course of variability***		
	Target shape	***Target shape***	***Sampling point***	***Target shape × Sampling point***
Standard deviation of arm posture	n.s.	n.s.	F(1.597,14.374) = 24.241, p = 0.000	n.s.
Standard deviation of hand orientation	n.s.	n.s.	F(1.969,17.723) = 24.242, p = 0.000	n.s.
Standard deviation of hand position	n.s.	F(1,9) = 3.661, p = 0.088*	F(1.470,13.231) = 120.125, p = 0.000	F(2.315,20.837) = 5.035, p = 0.013

Structure of joint angle variability of arm and hand

The structure of joint angle variability of the arm during movement execution was investigated with regard to the task variables: hand orientation, and hand position. Statistical characteristic values are reported in Table 2.

Table 2 Summary of the effects of the analysis of the structure of arm posture variability with regard to the two task variables (uncontrolled manifold method): hand orientation, and hand position. F-values and the respective p-values are listed for the significant effects for the analysis of endpoint variability and for the time course of movement execution (i.e. across the nine sampling points). The asterisks mark effects, which show a trend towards significance

Task variable	**Effect**	**V_{ucm} / V_{orth}**	**V_{ucm}**	**V_{orth}**
		End point variability		
Hand orientation	**target shape**	F(1,9) = 18.524, p = 0.002	n.s.	n.s.
Hand position	**target shape**	F(1,9) = 6.683, p = 0.029	n.s.	F(1,9) = 4389, p = 0.066*
		Time course of variability		
Hand orientation	**target shape**	F(1,9) = 10.007, p = 0.011	n.s.	n.s.
	sampling point	F(1.491,13.420) = 9.779, p = 0.004	F(1.443,12.990) = 9.291, p = 0.005	F(1.582,14.239) = 9.271, p = 0.004
	target shape × sampling point	F(2.332,20.989) = 10.449, p = 0.000	n.s.	n.s.
Hand position	**target shape**	F(1,9) = 5.664, p = 0.041	n.s.	F(1,9) = 7.079, p = 0.026
	sampling point	F(1.878,16.899) = 61.962, p = 0.000	F(1.607,14.461) = 9.248, p = 0.004	F(1.438,12.943) = 31.623, p = 0.000
	target shape × sampling point	n.s.	n.s.	F(1.978,17.801) = 2.790, p = 0.089*

Control of hand orientation

The ratio of V_{ucm}/V_{orth} was greater than one at all sampling points for both target shapes. In addition, the analysis of the variance ratio revealed a main effect of target shape for the last sampling point (see Table 2). Subjects showed a bigger variance ratio when reaching towards the cylindrical target (see Fig. 3A). This was apparent during the whole time course of movement execution, but was stronger during the second half than during the first half of the movement, as indicated by a significant main effect of target shape across all sampling points, together with a significant interaction effect of target shape x sampling point (see Table 2). The interaction was due to the continuous increase of the variance ratio when subjects had to reach towards the cylindrical target, whereas no clear trend was visible for the spherical target condition (see Fig. 3A).

The analysis of V_{ucm} and V_{orth} did not reveal any significant differences between the two target shapes, indicating that the significant difference in the variance ratio was due to small differences in both subspaces of variance. The main effect of sampling point reached significance for both, V_{ucm} and V_{orth} (see Table 2). Variance increased in both subspaces until the middle of the movement and decreased again afterwards (see Fig. 3B). Other effects did not reach the level of significance.

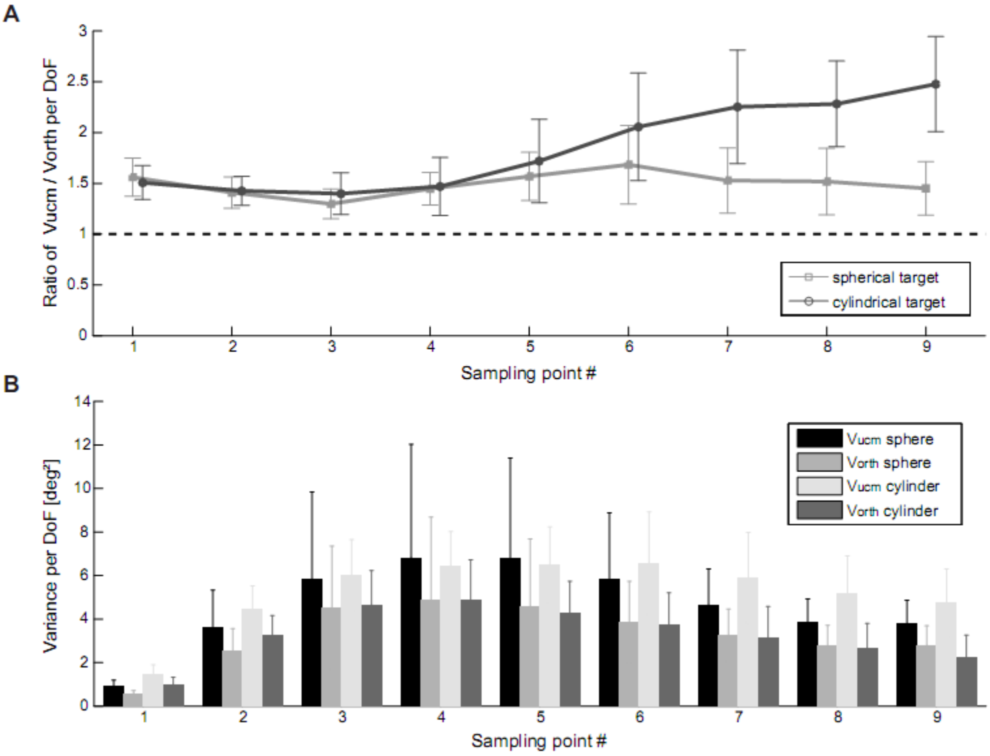

Fig.3 The time course of arm posture variance structured with regard to hand orientation calculated by means of the uncontrolled manifold method is depicted. **A** Ratio of V_{ucm}/V_{orth} per DoF and the respective confidence intervals are shown for each of the nine sampling points. The dotted line represents the critical value, above which it can be assumed that minimization of arm posture variance relevant for hand orientation was part of the underlying control strategy. The variance ratio of the cylindrical target condition was greater than that of the spherical target condition for the whole time course of movement execution. **B** V_{ucm} and V_{orth} and the respective confidence intervals are shown for each sampling point. Each bar represents the variance per DoF for one of the two orthogonal subspaces at the specific sampling point. No differences were evident between the two target shapes

Control of hand position

The ratio of V_{ucm}/V_{orth} of arm posture variance with regard to hand position variability differed between the target shapes for the last sampling point as well as across the time course of movement execution (see Figure 4 and Table 2: V_{ucm}/V_{orth}). Hand position was more strongly stabilized when reaching towards the spherical target. However, for both target shape conditions the variance ratio was greater than one at all sampling points. Moreover, data analysis revealed a significant main effect of sampling point. The ratio between V_{ucm} and V_{orth} was greatest at the beginning of the movement, decreased towards the middle of the movement and slightly increased again afterwards. The effect of highest variance ratio at the beginning of the movement can be related to the very small amount of V_{orth} at early sampling points.

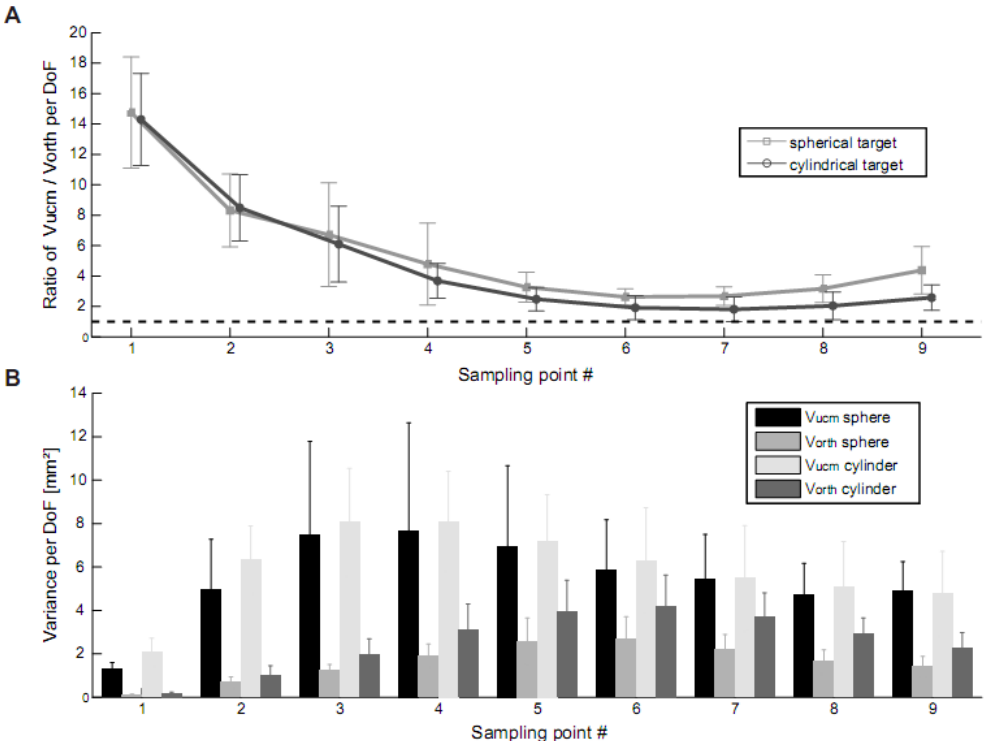

Fig.4 The time course of arm posture variance structured with regard to hand position. For this task variable, the variance ratios (A) and the two variances V_{ucm}/V_{orth} per DoF (B) are shown in the same way as in Fig. 3 for hand orientation. The variance ratio of the spherical target condition was greater than that of the spherical target condition, especially at the end of the movement. The ratio decreased and slightly increased again towards the end of the movement. Both target shape conditions showed the same time course. During the whole time course of movement execution, variance relevant for hand position (V_{orth}) was significantly smaller when reaching towards the spherical target shape as compared to the cylindrical target

Variance in the uncontrolled manifold (V_{ucm}) did not differ between the target shapes, neither at the last sampling point, nor across all sampling points. The interaction of target shape × sampling point did also not reach level of significance. However, the amount of V_{ucm}, as well as the amount of V_{orth} showed significant variations across the time course of movement execution (main effect of factor sampling point, see Table 2). In both cases, variance showed an increase-decrease pattern over time. Furthermore, analysis revealed a main effect of target shape for V_{orth} across all sampling points and a trend towards a significant main effect at the last sampling point (see Table 2). Variance was greater when reaching towards a cylindrical target, compared to reaching movements towards the spherical target (see Fig. 4B). In addition, the decrease of V_{orth} towards movement end tended to be slightly more pronounced on the sphere than on the cylinder as indicated by a marginal interaction of target shape × sampling point for the subspace of V_{orth}, which could not be further clarified (see Table 2 and Fig. 4B).

Discussion

The purpose of the present study was to investigate the influence of target shape on the control strategy underlying reaching movements. We asked subjects to reach towards either a cylindrical or spherical target, whereby different constraints on final hand orientation and position were imposed by the shape of the targets. We analyzed joint angle variability of the arm at the end point and during movement execution, by looking at its amount and structure.

In agreement with Grea and colleagues (2000), we found that target shape had no influence on arm posture variability at the end of the movement. Also, end point variability of hand orientation and hand position did not differ when reaching either towards a spherical or cylindrical target. Grea and colleagues (2000) reasoned that final arm posture is an essential part of movement planning, even if this posture is not enforced by target shape. We expanded on that by also investigating the time course of variability of arm posture, hand orientation, and hand position during reaching movements towards targets with different constraints on hand orientation and hand position.

Variability of arm posture or hand orientation during movement execution was not different for the spherical and cylindrical target shape. However, during the time course of movement execution hand position variability differed between the two target shape conditions, showing less variability when reaching towards the spherical target. This suggests that reaching trajectories are differently controlled with respect to the constraints in final hand orientation and position imposed by the grasping object. Though, the fact that this difference became evident only during movement execution, but not at movement end, shows that the endpoint variance of the hand position was kept invariant, despite different control of hand position during the movement execution. This points towards an endpoint control of reaching movements. Furthermore, the invariance of endpoint variability extends previous observations that endpoint variability is rather invariant against perturbations of target position (Grea, et al., 2000).

The analysis of the structure of joint angle variability also provides support for a dependence of the control strategy on target shape. By means of the uncontrolled manifold method (Latash, et al., 2002, 2007; Scholz & Schoner, 1999), total variance of joint angles during movement execution was partitioned into two components – a subspace of arm configurations, whose variance (V_{ucm}) did not influence either hand orientation or hand position, and an orthogonal subspace of arm configuration, whose variance (V_{orth}) had an unwanted effect on the variability of hand orientation or hand position. We found that for both target shape condition, and throughout the whole time course of movement execution, V_{ucm} was greater than V_{orth}. This suggests that the joints of the arm were synergistically coordinated to stabilize hand orientation as well as hand position throughout the whole movement, supporting the notion of a trajectory control of reaching movements (Domkin, et al., 2005; Y. Tseng, et al., 2002). This is also confirmed by other studies using the uncontrolled manifold method (Gera, et al., 2010; Y. Tseng, et al., 2002; Y. W. Tseng, et al., 2003).

In line with our hypothesis, constraints of final hand orientation and hand position imposed by the target shape did influence the stability of the synergistic coordination of joint angle variability. When reaching towards a spherical target, which imposed more constraints on final hand position than the cylindrical target, hand position was more strongly stabilized as when reaching towards a cylindrical target. In contrast, hand orientation was more strongly stabilized for the cylindrical target. Those effects became evident not only at the end of the reaching movement, but during the whole time course of movement execution, further supporting the notion of a trajectory control. However, this does not imply that the desired hand orientation and hand position are explicitly represented task variables at each point in time. A control strategy that compromises between functionally different task variables may be fully compatible with the presented results, and also in line with further studies (Freitas & Scholz, 2009; Ma & Feldman, 1995).

As another aspect, the results speak in favor of a flexible coordination of redundant degrees of freedom to stabilize differently constrained task variables. Gera and colleagues (2010) could show that multiple task constraints do not interfere with each other, i.e. the synergistic control of one task variable was not negatively influenced by the stabilization of another task variable. In line with those results, we found that hand orientation and hand position can be simultaneously stabilized throughout the whole time course of movement execution (i.e. $V_{ucm}/V_{orth} > 1$ at all sampling points). However, although multiple task constraints do not interfere with each other, flexible control strategies seem to be applied for reaching towards both target shapes to better cope with the differently strong task constraints. In the current study, subjects more strongly stabilized hand orientation when reaching towards a target that imposed stronger constraints in hand orientation (i.e. the cylindrical target). The same was true for the stabilization of hand position. It may well be that this flexibility in stabilizing particular task variables may help to take into account other task constraints, not considered in the current study. This relates to a notion of Gera and colleagues (Gera, et al., 2010), who state that, although the motor control system takes advantage of motor abundance in the control of movement variability, it also narrows the space of actually used joint configurations to be able to also take other task constraints into account.

The stronger stabilization of the hand position in the spherical target condition seemed to be achieved by a stronger decrease of that amount of variance that is relevant for hand position variability, which was evident during the whole time course of movement execution. Thereby, the total amount of movement variability was kept low in an optimal way, by reducing variability only in task relevant dimensions. This is in line with the "minimum intervention principle" (Todorov & Jordan, 2002), which suggests that movement variability is restricted only when it interferes with the performance of the task. By doing so, control processes can be organized in a cost-optimal way. However, the same pattern of control could not be found with respect to the control of hand orientation, suggesting that the stabilization of important task variables can be achieved in a flexible manner. This may allow the motor control system to adequately react and adapt to different situations and environments, as also suggested by Freitas and Scholz (2009).

Conclusion

In summary, the results suggest that in reaching movements target shape affects the strategy used to control task variables that are especially constrained, e.g. hand orientation or hand position, but not its effectiveness. This becomes evident in the way the single joints are coordinated to minimize variability in the constrained dimension, i.e. in the way joint angle variability is structured. The stronger the imposed constraint, the stronger is the stabilization of the respective task variable. In addition, the stabilization of the task variables (i.e. hand orientation or hand position) seems to be part of the control strategy during the whole time course of movement execution.

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Age-related differences in the stabilization of important task variables in reaching movements

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Abstract

Empirical evidence suggests that the ability to stabilize important task variables of every day movements by synergistically coordinating redundant degrees of freedom decreases with aging. The aim of the present study was to investigate whether this decrease may be regarded as a characteristic that also applies for the control of multiple task variables. We asked younger and older subjects to repeatedly reach towards and grasp a handle, while joint angle movement of the arm was recorded. The handle constrained final hand position and final hand orientation. Movement variability was analyzed during movement execution by using the uncontrolled manifold method. Results showed that hand orientation was less stabilized in younger than in older subjects. We conclude that aging changes the stability of important task variables. These changes may lead to decreased stability in some task variables, as reported in the literature, but also to increased stability in other task variables.

Introduction

In a recent study by Verrel and colleagues (Verrel, Lövden & Lindenberger, 2012) it was found that, in pointing movements, older subjects stabilize hand position less than younger subjects. Decreased stabilization of a hypothetically important task variable with age was also found in other studies (Olafsdottir, Zhang, Zatsiorsky & Latash, 2007; Shinohara, Scholz, Zatsiorsky & Latash, 2004), which could show that in multi-finger force production tasks, the decline in motor performance with aging was accompanied by a decrease in the stability of hypothetically important task variables. These authors used the uncontrolled manifold hypothesis (Latash, Scholz & Schöner, 2007; Scholz & Schöner 1999) for their analysis. In the concept of the uncontrolled manifold hypothesis, the amount of movement variability, which is not related to a hypothesized task variable (V_{ucm}), represents the flexibility in the synergistic coordination of the degrees of freedom (DoF; Latash et al., 2007, Latash, Levin, Scholz & Schöner, 2010). On the other hand, variability in task-relevant directions (V_{orth}) directly influences the performance outcome. The flexibility in the synergistic coordination (V_{ucm}) in relation to the variability in task-relevant directions (V_{orth}) gives an index about the stability of the motor system against perturbations (Latash et al., 2007). In the literature, a synergy index (i.e. V_{ucm}/V_{orth}) greater than one is interpreted as the motor system is stabilizing a respective task variable (Latash, et al., 2007). Latash and colleagues (Latash & Anson, 2006; Latash et al., 2010) highlighted the importance of this synergy index to describe accurate motor performance in older people. Verrel and colleagues (2012), for example, found that, towards the end of the movement, this synergy index was decreased in older people, whereas endpoint variability was not influenced. However, it is not clear, whether, in the presence of multiple, hypothetically important task variables, the decrease in the synergy index with ageing is a general characteristic that can be seen for all task variables, or whether, some of the task variables may be even more strongly stabilized. Gera and colleagues (2010) could show that younger people were able to synergistically stabilize multiple task variables without interfering between them. The question arises, whether the strategy to stabilize multiple task variables differs between age groups.

The aim of the present study was to investigate the stability of hypothetically important task variables in a reach-to-grasp movement, in younger and older people. For this purpose we investigated the variability of hand orientation and hand position in younger and older subjects, when reaching towards a cylindrical target. Variability of the task variables, as well as variability of the effector system (i.e. joint angle variability of the arm) was analyzed. A general decrease in the synergy indices would support previous findings (Olafsdottir et al., 2007; Shinohara, et al., 2004; Verrel et al., 2012), suggesting a decreased ability of older subjects to stabilize important task variables. An increase in the stability of one task variable with age, however, would suggest that aging may also lead to increased stabilization of hypothetically important task variables. This would imply different control strategies to stabilize multiple important task variables between younger and older people.

Subjects and Methods

Eleven younger (mean age: 25.5 ± 3.4 years) and eleven older (mean age: 66.3 ± 3.1 years) subjects participated in the study. They were paid for participation and gave written informed consent prior to participation. The subjects were not aware of the purpose of the study. All subjects were right hand dominant as determined by the Edinburgh Handedness Inventory (Oldfield, 1971).

A detailed description of the experimental set-up can be found in Krüger, Eggert and Straube (2011). Briefly, subjects repeatedly had to reach towards and grasp a cylindrical target, which was positioned within reaching distance in front of them (see Fig. 1A). To provoke the most natural movement, no demands concerning movement speed or reaction time were made. The target could be placed at three possible positions and changed its location between every reaching movement (trial). To minimize within-subject between-trial variability due to differences in the initial position, starting position was carefully defined by the set-up. The size of the target forced the subjects to grasp it with the whole hand, and not just with two fingers (see Fig. 1B). Due to its geometric properties, the cylindrical target constrained final hand orientation and hand position in two out of three possible axes, each. Four blocks with 30 trials in each block were recorded (120 trials). Each experimental block consisted of 10 trials of each handle position, arranged in a pseudo-random order to avoid predictability of the handle position. Between the blocks a break of a maximum of five minutes was offered to avoid fatigue.

Arm movement was recorded by an ultra-sonic sound emitting system (Zebris Medical, Isny, Germany). Recording frequency was 33 Hz for each of the six markers, which were attached to the subject’s arm to record joint angle motion in the seven DoF of the arm (see Fig. 1C). Shutter glasses (Translucent Technologies, Toronto, Canada) were used to prevent visual online control of the reaching movement. The opening and closing of the shutter glasses was triggered by the movement onset of the first marker (i.e. at the basal joint of the index finger). As soon as the subjects started their movement, the shutter glasses occluded and thereby prevented visual online control of the movement. The first contact with the handle was monitored by recording the electrical resistance between the subject and the handle (sampled at 1 kHz).

The data analysis is described in detail in a recent article by our group (Krüger, Borbély, Eggert & Straube, 2012). Briefly, the joint angles of the arm were computed from the marker position using a three segment rigid body model. Joint angles were expressed as seven consecutive Cardan angles in the following order: two angles for the wrist (vertical, horizontal), two for the elbow (torsion, flexion), and three for the shoulder (torsion, horizontal, vertical). The vector containing these seven joint angles is hereafter referred to as arm posture. In addition, orientation of the hand in space (i.e. 3D) was defined by the orientation of the plane defined by the three markers on the hand and wrist. The orientation was specified in Helmholtz coordinates relative to the external world. The hand position in space was defined by the centre of the two markers of the hand in world fixed Cartesian coordinates. The full temporal resolution of the joint angle motion was reduced to ten equidistant sampling points between movement initiation and movement end. Before estimating the 7x7 covariance matrix of the arm posture for reaching movements between fixed starting position and fixed target position, a correction of the joint angle trajectories for small inter-trial variations of movement duration and of the actual starting position of the arm was calculated. After this correction, the covariance matrix of the starting position (first sample) reduced to zero and was not considered in further analytical steps. Thus, the covariance matrix of the joint angles was analyzed at nine equidistant sampling points during the movement.

Two overall measures were computed to examine the amount of variability of the reaching movements on joint angle level during the time course of movement execution: (1) square-root of the mean within-subject variance, averaged across the seven joint angles of the arm (in the following referred to as: “standard deviation of arm posture”), and (2) square root of the mean within-subject variance of the task variable averaged across its three dimensions (“standard deviation of the task variable”). These overall standard deviations were calculated separately for each subject, and sampling point. Hand orientation, and hand position were considered as the two task variables in the current study. Target position was not considered as a factor in the further analysis, since recent work (Krüger, et al., 2012) showed that the overall standard deviations of both the task variables, and the effector variables (i.e. joint angle variability) did not differ across handle positions.

The uncontrolled manifold analysis was calculated as described in detail in Krüger et al. (2012). At each sampling point total joint angle variance was partitioned into two subspaces, with respect to the task variables: (1) the subspace of differential joint angle changes that did not affect task variables (irrelevant variance, normalized to the number of DoF in that subspace: V_{ucm}), and the orthogonal subspace (relevant variance, normalized to the number of DoF in that subspace: V_{orth}). Subsequently, the synergy index was calculated as the ratio between V_{ucm}/V_{orth}. All computations were performed using Matlab 7.9.0 (Mathworks, Natick, USA).

Statistical analysis was calculated using SPSS 9.0. A repeated measurement ANOVA was calculated with age-group (younger and older subjects) as the between factor, and sampling point as the repeated factor for the following dependent variables: (1) standard deviation of arm posture, and: (2) standard deviation of the task variable (for hand position, and hand orientation, each), (3) V_{ucm}, (4) V_{orth}, and (5) V_{ucm}/V_{orth}. The critical value for significance was set at $p < 0.05$. Greenhouse-Geisser adjustment was made, if the sphericity assumption was rejected by Mauchly’s sphericity test. Variance data was tested for normal distribution with the Lilliefors-test. Data was normally distributed for all of the above mentioned factors at almost all sampling points.

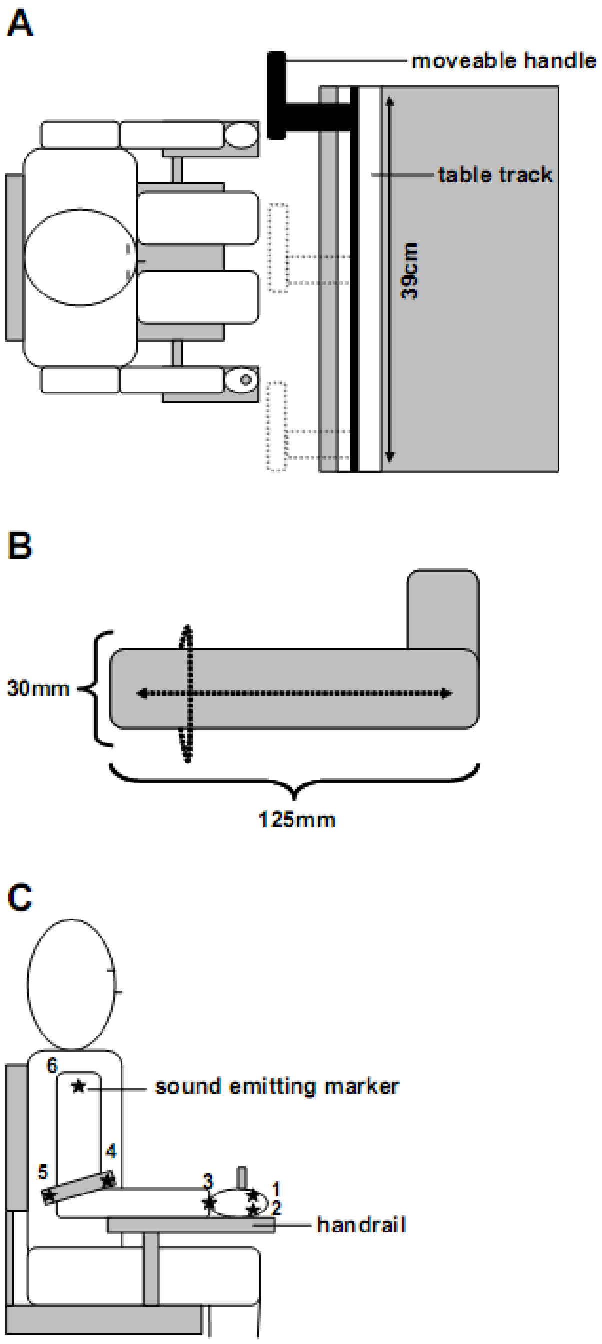

Fig.1 Experimental set-up and apparatus. **A** View of the experimental set-up from above. The black solid bars represent one of the three possible positions of the moveable target. Dashed bars show the other two possible target positions. **B** The positions of the six ultra-sonic sound-emitting markers are depicted. The starting position of the dominant right arm was defined by grasping a wooden lever attached to the handrail. **C** The cylindrical target is depicted with its length and depth. Parts A and C are reprinted from Clinical Neurophysiology, 122/4, Krüger, M., Eggert, T., & Straube, A., Joint angle variability in the time course of reaching movemetns, 759-766, Copyright (2011), with permission from Elsevier

Results

Neither standard deviation of arm posture, nor standard deviation of hand position or hand orientation differed between younger and older subjects, neither at movement end, nor across the time course of movement execution. The uncontrolled manifold analysis of joint angle variability with respect to the task variable hand position did not show any significant main effect or interaction involving the factor age group. Both age groups stabilized hand position throughout the whole time course of movement execution (i.e. $V_{ucm}/V_{orth} > 1$). The synergy index (V_{ucm}/V_{orth}) was greatest at movement start and decreased until the midst of the movement. Afterwards the index was stable at a level of 2.

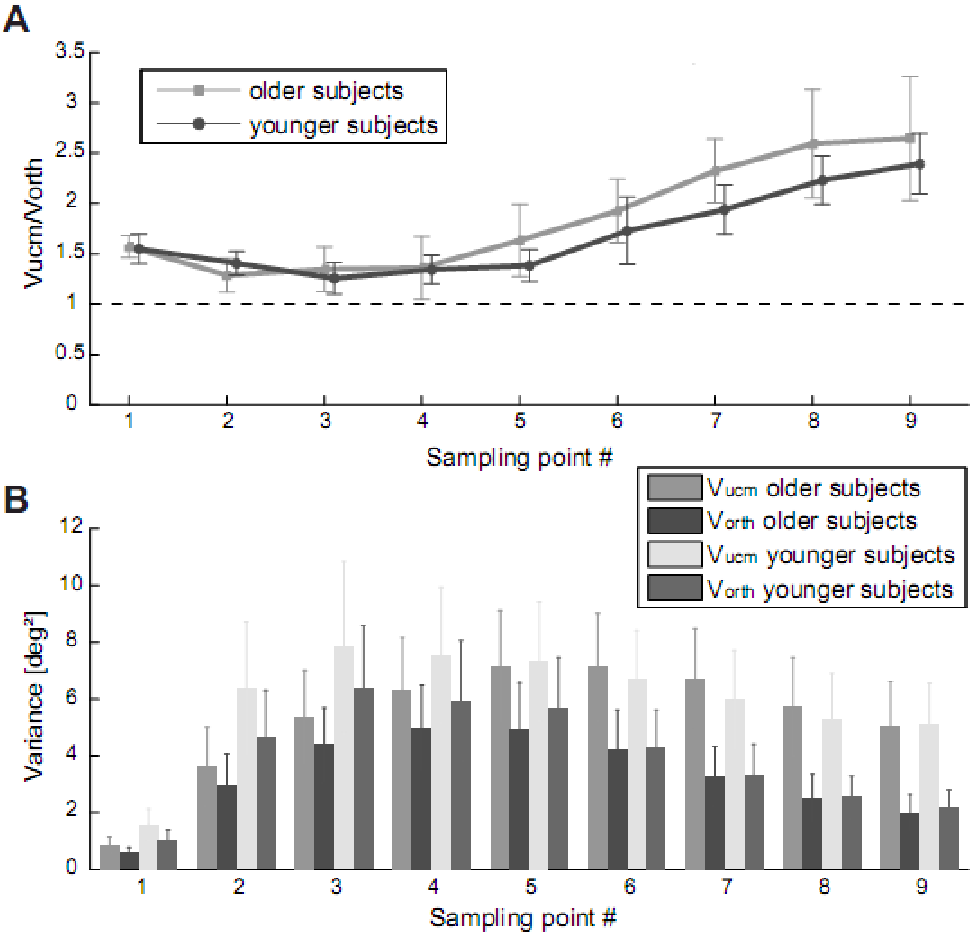

Fig.2 The time courses of variances analyzed by means of the uncontrolled manifold approach and respective confidence intervals, computed with respect to the task variable hand orientation. **A** V_{ucm}/V_{ort}h for younger and older subjects. Both age groups stabilize hand orientation during the time course of movement execution. The ratio is significantly smaller for younger subjects than for older subjects. **B** V_{ucm} and V_{orth} for both age groups.

The uncontrolled manifold analysis with respect to the task variable hand orientation revealed that hand orientation, too, was stabilized by both age groups throughout the whole time course of movement execution. The ratio of V_{ucm}/V_{orth} was stable at the beginning of the movement and increased continuously in the second half of the movement (see Fig. 2A). However, older subjects stabilized hand orientation more strongly than younger subjects, as indicated by a significant main effect of age group (F(1,19) = 4.885, p = 0.040). No other effects reached the level of significance.

Older subjects showed less variance than younger subjects within the subspace of the uncontrolled manifold (V_{ucm}) in the first half of the movement and more variance than younger subjects in the second half of the reaching movements. This qualitative observation was supported by a significant interaction of age group × sampling point (F(2.515,47.823) = 3.502, p = 0.029; see Fig. 2B). Pairwise comparison showed significant differences between the two age groups for the first two sampling points (#1: F(1,19) = 5.507, p = 0.030; #2: F(1,19) = 4.861, p = 0.040). For the task-relevant variance (V_{orth}), neither the main effect of the factor age group nor the interaction effect age group × sampling point reached significance.

The main effects of sampling point were significant for each dependent variable and were in line with recent observations by our group (Krüger et al., 2011; Krüger et al., 2012).

Discussion

The objective of the present study was to investigate the stability of hypothetically important task variables in a reach-to-grasp movement in younger and older people. Similar to the findings of Verrel and colleagues (2012) joint angle variability of the arm, as well as variability of hand position, and also hand orientation were not increased in older subjects. Hence, younger and older subjects performed the reaching movements with the same quality of performance. No age-related differences were found for the stabilization of hand position in our experiment. However, younger and older subjects differed in the strength of stabilizing hand orientation during movement execution, with older subjects stabilizing hand orientation more strongly than younger subjects. Leaving aside the sign of this difference, the observed change of synergy index was similar to other observations in so far that it was caused by a change of the task irrelevant variance. Verrel et al. (2002) found a decreased synergy index for stabilizing hand position in older people caused by decreased task-irrelevant variance. Domkin and colleagues (2002), who investigated the changes in the structure of movement variability with practice, also found a decreased synergy index due to decreased task-irrelevant variance. In general, a change of the synergy index without strong changes in the task-relevant variance may indicate a switch in the control strategy concerning the minimization of task-irrelevant variance.

The differences to the findings of Verrel and colleagues (2012), who found decreased stabilization of hand position in older subjects, may be due to the fact that the reaching task used in our experiment forced subjects to control multiple task variables. In contrast, the pointing movement used in the study by Verrel and colleagues constrained only one task variable, namely final hand position. Empirical evidence suggests that the motor control system is able to simultaneously stabilize multiple, hypothetically important task variables (Gera, et al., 2010). In a recent study (Krüger, et al., 2012) we could show that the motor control strategy differs in the stabilization of multiple, hypothetically important task variables, depending on the constraints applied by the movement task. The finding that younger and older subjects differ in the strength of stabilizing hand orientation, but not hand position, suggests that younger and older subjects adapt their motor control strategy differently to multiple task constraints. This suggests that the decreased ability of older subjects to stabilize important task variables, as reported in the literature (Olafsdottir et al., 2007; Shinohara et al., 2004; Verrel et al., 2012), is not a general characteristic associated with normal aging, but is influenced by the movement task. In the presence of multiple task constraints, older people may show different strategies in controlling important task variables, as when the movement task requires the control of one task variable, only.

We conclude that aging changes the stability in the control of hypothetically important task variables. These changes may lead to decreased stability in some task variables, but also to increased stability in other task variables.

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3 General Discussion

In this thesis it was investigated how the human motor system adjusts the control of a complex reaching movement to changing sensory input and external task constraints. Analyzing movement variability in the effector and task space was chosen as the methodological approach, because variability in movement execution is an inherent characteristic of the human motor system, reflected simultaneously as flexibility and as stability in movement execution. The influence of a range of different internal and external factors on the control of reaching movements was tested to gain a comprehensive view on the research topic.

In the first study presented in this thesis, it was shown that the availability of visual information is of minor importance for the control of complex reaching movements. Further, the influence of an accuracy constraint on the time course of joint angle variability was investigated. We found decreased joint angle variability in the time course of movement execution as well as decreased variability of final hand position. In the second study, it was shown that the healthy human motor system immediately adjusts movement control to the availability of proprioceptive information with the goal to keep movement endpoint variability constant. In the third study of this thesis, we investigated the influence of the target shape on the control of movement variability in complex reaching movements. The main outcome of this study was that the healthy human motor system is able to simultaneously account for multiple task constraints. Thereby, the more the task variable was constraint the more strongly it was stabilized. The fourth study of this thesis investigated age-related changes in the control of movement variability. We could show that older people are also able to simultaneously control multiple task variables without performance decrements. Importantly, we were able to show that aging leads to multi-faceted changes in the control of important task variables which became evident in an increased stabilization of an important task variable. In sum, the four studies presented as part of this thesis provide empirical evidence that the human motor system is able to effectively adjust the control of complex reaching movements to changing internal and external environmental conditions.

The observed adjustments of movement control were reflected mainly by changes in the structure of effector variability, and only minimally in the amount of task variability. The coordination of the effector DoF was adjusted to different sensory input (study 2) and external ask constraints (study 3), taking use of motor redundancy. As a consequence, movement endpoint variability was kept constant, reflecting stable task performance. As a benefit of the flexible coordination of the effector DoF multiple, simultaneously occurring task constraints could be accounted for without recognizable changes in task performance, as shown in the third and fourth study of this thesis. Importantly, the ability to simultaneously account for multiple task constraints seems to be influenced by aging, reflected by differences in the coordination of the redundant effector DoF between younger and older people (study 4).

In the following, certain aspects of the results will be discussed in more detail and will be integrated in the context of already existing knowledge on the topic. Further, the methods used to analyze movement variability will be critically discussed. At the end of the chapter an outlook to possible further research directions and a short conclusion will be given.

3.1 Flexibility in movement control

The most general outcome of the four studies presented in this thesis is that the human motor system flexibly adjusts the control of complex reaching movements to changing environmental conditions to ensure stable task performance. On that account, different sensory information is flexibly integrated with regard to their availability and reliability, as also suggested by Green and Angelaki (2010). In addition, external task constraints are flexibly accounted for, in dependence of the strength of the constraints they apply. Both cases will be discussed separately in the following. Thereafter, the influence of ageing on the control of complex reaching movements will be shortly discussed. Afterwards, it is carefully tried to differentiate how the processes of movement planning and control are reflected in the observed patterns of movement variability.

3.1.1 Integration of sensory information

Independent of whether the availability of visual or proprioceptive information was experimentally manipulated, subjects were well able to reach the target in a repeated and successful manner, as shown in the first two studies that were presented in this thesis. Under these conditions, general task performance was good, meaning that the movement goal, i.e. the grasping of the target, was repeatedly achieved with a mean standard deviation in final hand position of only 4-5mm. This suggests that the motor system was able to effectively compensate for the decreased availability of each source of sensory information by decreasing the reliance on it. This is in line with existing empirical evidence, which suggests that healthy subjects flexibly integrate visual and proprioceptive information to guide movement planning and control (Green & Angelaki, 2010; Sober & Sabes, 2005; Verstynen & Sabes, 2011). Importantly, the results of the first two studies of this thesis suggest that this flexibility in the integration of sensory information is very effective in so that task performance is kept stable.

It is generally assumed that visual and proprioceptive information are of different importance for different aspects of movement control (Bagesteiro, Sarlegna & Sainburg, 2006, Brown, Rosenbaum & Sainburg, 2003). Thereby, visual information seems to be primarily used for the control of the final position of the effector, whereas proprioceptive information is supposed to guide control during movement execution. Based on that, one would expect differences in the amount of movement variability either at movement end (for different visual conditions) or during movement execution (for proprioceptive information) when manipulating the availability of sensory information. Indeed, in the first study of this thesis the time course of joint angle variability was not influenced by the availability of visual information. Though, final hand position was more variable when visual information about the reaching target was available only shortly at movement onset (“vision flash”-condition in the first study) as compared to the full vision or initial vision conditions, which can be interpreted as support for the importance of visual information for final position control. In contrast, in the second study of this thesis, when the availability of proprioceptive information was experimentally manipulated, variability of final hand position was not influenced. However, the time course of hand position variability during movement execution was different from that of the control condition, providing support for an involvement of proprioceptive information in trajectory control. The two findings together provide empirical support for the importance of both kind of sensory information for different aspects in the control of reaching movements.

3.1.2 Adjustment to external task constraints

The influence of two different external task constraints on the control of complex reaching movements was investigated in the current thesis. First, the influence of an accuracy constraint in final hand position on the movement variability was investigated. As had to be expected, final hand position was less variable when subjects were instructed on final position accuracy. In association with that, movement duration was increased. The relationship of movement duration and accuracy is empirically profound and described as either linear (“impulse-variability” model; see Meyer, Smith & Wright, 1982) or logarithmic (“Fitts law”; see Fitts, 1954; see Fitts & Peterson, 1964 for discrete aiming movements). Importantly, the decrease in final hand position variability was preceded by a decrease in joint angle variability during the time course of movement execution, i.e. differences in task performance were already reflected in differences in the amount of variability in the effector space during movement execution. This effect became evident during the second half of the movement, when online-control processes are supposed to take effect (Elliott, et al., 2010; Woodworth, 1899). This suggests that the decreased variability in final hand position under accuracy constraint relates to a stricter control of movement variability in this condition as compared to the other experimental conditions, rather than to differences in movement planning.

The second external task constraint, whose influence on movement control was investigated, was the shape of the reaching target. In the third study presented, subjects had to reach to two different targets, either a sphere or a cylinder. Due to their geometric properties, both targets applied constraints on final hand position and final hand orientation. Importantly, when grasping the sphere, final hand position was more constraint than when grasping the cylinder. The opposite was true for final hand orientation. Analyzing movement variability in the task space did not reveal any differences between the two target shape conditions. That means, neither final hand position nor final hand orientation were more variable in one of the two conditions. Though, analyzing movement variability in the effector space did reveal significant differences. The stabilization of each of the two task variables (hand position or hand orientation) was stronger when reaching towards the target which applied the stronger constraint on it, as revealed by the analysis of the joint angle variability by use of the uncontrolled manifold method. Similar to the accuracy constraint, this effect became evident in the second half of the movement, when online-control processes are supposed to come into operation. Importantly, both task constraints were accounted for during movement execution, meaning that the effector DoF were synergistically coordinated such that hand position and hand orientation were stabilized at each sampling point between movement start and movement end. This suggests that the healthy human motor system is able to simultaneously account for multiple task constraints, as also suggested by other existing evidence (Gera, et al., 2010, Zhang, et al, 2008). The important new insight resulting from the third study of this thesis is that the healthy human motor system flexibly adjusts the control of complex movements such that, the more constraint a task variable is, the greater is also its stabilization. Interestingly, task performance itself was not influenced by these different control strategies. This, again, is an evidence for the suitability of analyzing the time course of movement variability in the effector and task space when trying to investigate the adjustment of human movement control to changing environmental conditions

3.1.3 Age-related changes in movement control

It is generally assumed that aging leads to changes in complex motor behavior, often reflected in decreased task performance (Darling, Cook & Brown, 1989; Newell, Mayer-Kress & Liu, 2009; Vaillancourt & Newell, 2002; Verrel, Lövden & Lindenberger, 2012). Studies investigating the synergistic coordination of redundant DoF with respect to specific task variables showed that aging leads to a decrease in the stability of these task variables, usually accompanied by increased task variability (see for example Olafsdottir, et al., 2007; Verrel, Lövden & Lindenberger, 2012). In contrast to these findings, we were able to show that older people are able to simultaneously stabilize multiple task variables without decrements in task performance. Importantly, for one of the task variables in our study, namely hand orientation, older people showed a stronger stabilization through synergistic coordination of the effector DoF than younger control subjects. This is a finding which has not been reported before, but is in line with the idea that aging leads to multifaceted changes in systems complexity (Vaillancourt & Newell, 2002). The above mentioned studies investigated movement control with respect to only one hypothetically important task variable. Though, in natural environments multiple task constraints are present and have to be accounted for. By investigating more complex behavior as we did, that means by trying to request reaching behavior that is as natural as possible, it seems to be possible to reveal the complexity in age-related changes in motor behavior.

3.1.4 Differentiation between movement planning and control

During movement execution, planning and control processes affect movements to different proportions. Generally, two phases are distinguished: an initial ballistic phase, when only feed-forward control takes effect and subsequently an online-controlled phase, when also feedback processes come into operation (Elliott, et al, 2010; Woodworth, 1899). In our studies, differences in movement execution became apparent during the second half of the movement, i.e. when feedback mechanisms are supposed to take effect. At the first glance, this seems to suggest that the human motor system mainly adjust the feedback control of complex reaching movements to changing internal and external conditions, whereas movement planning is not influenced. Though, information of the previous movement outcome is integrated during the formation of the internal representation, which is used to guide the planning of the next movement (Medina, Jax & Coslett, 2009; Shadmehr & Krakauer, 2008; Verstynen & Sabes, 2011). Therefore, it is reasonable to assume that adjustments of the feedback components of the movement also influence the planning of subsequent movements. Taken as a whole, the results of the studies presented in this thesis suggest that the healthy human motor system adjusts the planning *and* control of reaching movements to changing internal and external task constraints. Though, more research is needed to be able to better differentiate between the two processes (see also next section for some additional remarks).

3.2 Critical Discussion on the Method

Analyzing movement variability in effector and task space served as the approach in the current thesis to investigate the adjustments of human movement control under changing sensory input and external task constraints. For that, a number of analytical tools were used, which will be critically discussed in the following.

3.2.1 Analysis of the amount of movement variability

First, the amount of movement variability was analyzed during the time course of movement execution and at movement end in both effector and task space. Through this we were able to detect differences in the control of the reaching movements that did not become obvious in the task performance, itself. Based on this, we concluded that analyzing the time course of movement variability is a valuable method to investigate underlying mechanisms of movement control (see study 1).

3.2.2 The uncontrolled manifold method

Second, we analyzed the structure of effector variability with respect to hypothetically important task variables by use of the uncontrolled manifold method (Scholz & Schöner, 1999). This method was applied in two of the presented studies (see study 3 and 4). Through this we were able to investigate, first, whether a hypothetically important task variable of the reaching movement was indeed controlled, second, whether different task constraints influence the synergistic control of such a task variable, and third, how the human motor control system accounts for multiple task constraints.

The use of the uncontrolled manifold method was helpful in many aspects. It was chosen because it allows alleging and testing a clearly defined hypothesis about what the human motor system is taking care of during movement control. Further, the concept underlying this method is in line with current theoretical knowledge about human motor control (see Shadmehr & Krakauer, 2008; Todorov & Jordan, 2002). In the concept of the uncontrolled manifold approach, total effector variance is partitioned into two independent components with respect to a hypothetically important task variable: task-irrelevant and task-relevant variance. By calculating the proportion of these two components to each other (different possibilities are propagated in that context: see Latash, et al., 2010 for an overview) one is able to infer about the strength with which a task variable is stabilized through synergistic coordination of the effector DoF. Though, during the work on the different studies of this thesis, several problems were faced by applying this method.

First, a prerequisite of this method is that one has a hypothesis about the task variable that is controlled by the motor system during movement execution. In some tasks, as for example grasping an object, it is not difficult to find such task variables, as it is clearly defined. But in natural environments multiple task variables may be of importance for task success and have to be accounted for, which may not be that obvious and easy to define as in laboratory environments. Then the questions arise: (1) which are the task variables controlled by the motor system, (2) how many task variables are accounted for, and (3) how many task variables can be meaningfully controlled by the human motor system. Currently, it is still under debate, how the stabilization of multiple task variables has to be interpreted.

Second, we were able to show that the human motor system can account for multiple important task variables and that the task variable which is more constraint is also stabilized more strongly (see study 3). Though, this was only possible by separately partitioning total effector variance with respect to either one of the two task variables, hand orientation or hand position. At the current state it is not possible to calculate how the effector system accounts for multiple task variables, simultaneously. A further development of the method or the development of a more advanced method will be necessary to overcome that problem.

Third, with the uncontrolled manifold method one is only able to partition total effector variance with respect to the task variable at the same, specific sampling point during movement execution. Though in general, it would be of interest to see how the effector variance at each sampling point during movement execution propagates with respect to the variance of the task variable at movement end. In the second study presented in this thesis, this problem was approached by use of a canonical correlation analysis (see study 2). Trying to align the uncontrolled manifold method and the canonical correlation analysis may be a relevant goal for the future.

The fourth problem faced during the work on this thesis was that the uncontrolled manifold method does not allow inferring about whether the movement variability observed is already part of the movement plan or only a problem of movement control. A recent publication by van Beers and colleagues (van Beers, Brenner & Smeets, 2013) targeted this question and could show that at least some part of the observed movement variability was part of the movement plan. This problem also relates to the question what the task irrelevant variability, which constitutes an elemental part of the uncontrolled manifold concept, is caused by. The complementary use of the Tolerance-Noise-Covariance-model (Müller & Sternad, 2009) may prove itself as useful in answering this question.

3.2.3 Further approaches in analyzing movement variability

In addition to the analysis of the amount of movement variability and the uncontrolled manifold method, two different methods were applied in parts of this thesis. One method was the calculation of a canonical correlation, displaying the (mathematical) redundancy, i.e. the how much variability of the final arm posture can be explained by the variability of the arm posture at a certain point during movement execution. Besides the canonical correlation analysis, a principal component analysis was calculated in the second study presented. Both methods served as approaches to show how the human motor system copes with the temporary loss of proprioception in the control of complex reaching movements. They both revealed different aspects of the same compensatory mechanisms, namely the reduction of the task complexity by a stronger coupling of the effector DoF across the time course of movement execution (canonical correlation) and within one arm posture (principal component analysis). Although the results of the two methods are not straightforward to interpret in terms of the physiological substrates of movement control, they proved themselves to be helpful in the investigation of human movement control.

3.4 Prospective future research directions

As a matter of course, each question answered during the experimental work of this thesis raised many new questions for future experimental work. So far, the neural correlates underlying synergistic control of reaching movements are not well understood. One possibility to target this problem could be to introduce a temporary lesion in healthy subjects and to study the changes in movement control in comparison to normal conditions. The second study presented in this thesis can be seen as a first step in that direction. As the next step, it will now be necessary to study patients with chronic proprioceptive deafferentation and to compare the results with each other and range it into the existing models of motor control. Another possibility to introduce a temporal “virtual lesion” in healthy humans is TMS which allows studying the involvement of a specific cortical area in different phases of movement execution. The PPC, for example, is a cortical area, supposed to be involved in the integration of sensory information during movement preparation. It can be studied how the time course of movement variability changes with a virtual PPC lesion applied at different time points during movement preparation and execution. The results could then be compared to studies with patients with local PPC lesion.

The acquired knowledge in this thesis may influence the advances in some other fields of research. One field of interest could be the application in the context of sports. So far, the differentiation of effector variability in “task-relevant” and “task-irrelevant” has been successfully applied in laboratory experimental tasks, where the effector and task variables could be clearly defined and closely controlled by the experimental set-up. In sports, many different task variables influence task performance in a complex manner. The importance of these task variables may change during movement execution and they may be related to different effector variables. If and how the uncontrolled manifold method can be applied in that context and if it could prove itself useful as an analytical tool to describe different levels of skill performance in sports is an interesting question to be targeted in the future.

3.5 Concluding remarks

Within this thesis a comprehensive picture was developed about how the human motor system adjusts the control of complex reaching movements to changing environmental conditions. It was shown that the human motor system purposefully exploits motor redundancy to adjust to changes in the availability of sensory information and to the simultaneous existence of multiple task constraints. Thereby, the flexible reliance on sensory information proved itself to be not only a consequence of experimental manipulation, but a prerequisite of stable task performance. Further, this thesis demonstrates that the analysis of movement variability constitutes a valuable approach for quantifying adjustments in human movement control, not only at movement end but also during movement execution, and not only in the task space but also in the effector space.

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List of Publications

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Eidesstattliche Versicherung

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation

„Motor variability as a characteristic of the control of reaching movements: Influence of sensory input and task constraints“

selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

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„Motor variability as a characteristic of the control of reaching movements: Influence of sensory input and task constraints“

is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München, 21.05.2013

Melanie Krüger

Author's contribution to each publication

"Joint angle variability in the time course of reaching movements"
The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript.

"Rapid adjustment of human motor control strategies in reaching movements under temporal proprioceptive deafferentation"
The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript. The manuscript was submitted as a research article and is currently under review.

"Synergistic control of joint angle variability: Influence of target shape"
The author of this thesis designed and ran the experiment, analyzed the data and wrote the manuscript.

"Age-related differences in the stabilization of important task variables in reaching movements"
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