Synergies and end-effector kinematics in upper limb movements

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GENERAL INTRODUCTION

The degrees of freedom problem

When humans perform movements repeatedly, they are never completely the same. This is possible because many degrees of freedom (DOF) of the human motor system are involved when performing a motor action. In most cases, the number of DOF involved exceeds the minimum necessary to complete the motor task at hand. This results in many possible solutions for a given task, which is the so-called redundancy problem [1–3]. The latter appears at different levels of the human motor system. For example, at muscle level [1,4,5], where more than one muscle is available for a specific joint rotation, or at end-effector level, where there are ample 3D position solutions to move the end-effector from one place to another [6,7]. An important level that also depicts redundancy is the joint level. The Russian physiologist Nicolai Bernstein described redundancy at the joint level in his famous example investigating professional blacksmiths [1]. Using a motion analysis system, Bernstein captured blacksmiths hitting a chisel with a hammer and analyzed both the joint level and the end-effector (i.e., the hammer) level during the execution of the task. He revealed that each hitting repetition was slightly different, that is, the motions of all joints were different, while the hammer hit the chisel at almost the exact same location with each repetition [8]. Bernstein called this the 'repetition without repetition' phenomenon [1]. He was intrigued by this finding and one of his main questions was how the redundant DOF are coordinated to accomplish a motor task with high precision.

Motor coordination

Coordination of redundant DOF has been a major topic of research during the past decades (e.g., [1,9–13]). The questions studied concerning the redundant DOF (also called DOF problem; [1]) range from how and at what levels the DOF should be selected (e.g. [10]), and whether the redundancy should in fact be called abundancy (e.g. [2,11]), to ideas on how the DOF are coordinated, such as, muscle synergies (e.g. [12,14]), optimal control theory (e.g. [15–17]), or dynamical systems theory [10,13,18–20]. In the discussion about how the DOF are coordinated, variability in DOF has received a large amount of attention and has been studied from different perspectives. For example, from an optimal control perspective one could argue that variability is equivalent to noise because there is only one optimal solution to the DOF problem for a given task and all deviations from that solution are the result of sensorimotor noise [15]. In contrast, from a dynamical systems perspective, variability in motor behavior is considered to characterize a motor system [3,13,18,20,21]. The latter perspective will be followed in the present thesis and will be further introduced below.

The dynamical systems perspective on motor coordination

Motor coordination from a dynamical systems perspective can be described within a system not merely restricted to the DOF that need to be coordinated, but it includes the full perception action cycle [22,23]. This cycle comprises the environment and the agent, where interactions amongst environment, organism, and task constraints regulate the motor behavior that emerges [10,24,25]. These constraints can be exemplified by returning to the blacksmith example. Here, the ranges of motion in the joints of the arm are an example of organism constraints, the location of the chisel is one of the task constraints, and the gravity working upon the arm is one of many environmental constraints. Accordingly, the hitting behavior emerges from the interactions amongst the range of motion of the joints, the location of the chisel, the gravity working upon the arm, and many other constraints.

Within the dynamical systems perspective, it is suggested that due to these interacting constraints, synergies emerge that temporarily link the DOF into task-specific units [3,13,18,20]. Note that, synergies are closely related to the concept of coordinative structures (e.g. [18,20]). In such a task-specific unit, potentially independent DOF are temporarily linked [10,13,26] into a unit with respect to a certain function or task. That is, DOF co-vary to stabilize the specific task performance, which implies that variations in (one) DOF are compensated for in other DOF in such a way that the performance remains constant, this is the so-called flexibility of a synergy [18,26–28].

Kay [10] described the emergence of a synergy as the first step of a two-step constraining process (see also [26,29,30]). In the first step, the interactions amongst environment, organism, and task constraints temporarily link the independent DOF into a synergy (see Figure 1). In the second step, the constraints act on the synergy, resulting in the specific behavior (see Figure 1). This approach explicitly states that after the assembly of the synergy, a further constraining process must come into play, to produce one particular movement of the subset of solutions [10]. Kay [10] analyzed the outcome of both steps of the two-step constraining process at once using dimensionality analysis in a rhythmic task. In most other dynamical systems accounts on coordination by other authors, the differentiation into two steps has not often been described and examined as such. An example of an exception is a description of the two-step process in a perspective article on interpersonal coordination by Riley et al. [26], accompanied by an analysis of predominantly the first step of the process by Romero et al. [31]. However, to examine whether a two-step process occurs, I think that the interaction of the two steps of the process should be investigated. That is, to be able to grasp how the interactions of constraints lead to the emergence of behavior, both steps of the constraining process should be analyzed.

Therefore, I aimed to gather more understanding on how the redundant DOF are coordinated by focusing on synergies and their role in specific behavior. To do so, I focused on the influence of task constraints on the two steps of the process of emergent behavior and the interaction of these two steps. That is, I examined the influence of task constraints on synergies and specific behavior in discrete upper extremity movements. Investigating this in discrete upper extremity movements, such as goal-directed reaching and interception, is of major importance because these actions are involved in many activities in daily life. Because in previous research on discrete upper extremity movements the level of synergy and the level of specific behavior have not been analyzed as separate steps, a different methodology is needed in the present thesis, which can be outlined as follows. I assessed the synergies that are hypothesized to emerge in the first step of the two-step process in discrete upper extremity movements by examining structure in variability of DOF, using the uncontrolled manifold (UCM) analysis which will be explained below [4,32,33]. The specific behavior that is hypothesized to emerge from this synergy is quantified by means of end-effector kinematics in the present thesis. The outlined innovative methodology is tested separately for each level, before looking at the interactions of the two levels. The present thesis assessed the influence of task constraints on the following aspects of goal-directed actions: 1) synergies, 2) end-effector kinematics, and 3) the interaction of synergies and end-effector kinematics. In the subsequent section, I will discuss the influence of constraints on the separate levels of synergies and end-effector kinematics, because, to my knowledge, the interactions of the two have not received much attention in the past.

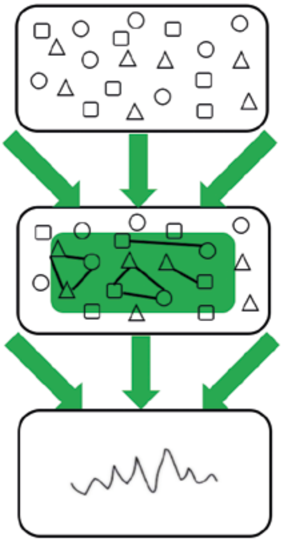

Figure 1. Two-step constraining process where the DOF (squares, triangles, and circles at upper panels) are linked into a synergy at the upper arrows and the synergy is constrained to specific behavior at the lower arrows. The green arrows represent environment, organism, and task constraints.

The influence of constraints on emergent behavior

In the present thesis, the two-step constraining process of, first, the emergence of synergy and, second, the emergence of specific behavior will be assessed by looking at the influence of task constraints on synergy and end-effector kinematics. A selection of previous research on these topics will be outlined below.

Before addressing synergies, I will explain the method of analysis applied in the present thesis. The UCM analysis will be used to quantify the structure in variability of individual DOF across repetitions of trials [4,32,33]. To explain this analysis, I use manual pointing as an example. In pointing, the DOF selected at the joint level (i.e. elemental variables) are the shoulder, elbow, wrist, and finger joint angles, and the DOF at the end-effector level it is the 3D fingertip position. All different joint angle configurations which maintain the fingertip position compose the solution space for the task. Using this solution space, the variability observed in joint angles over repetitions can be parsed into two types of variability: V_{ucm} and V_{ort}. The former is the variability within the solution space that does not affect the position of the fingertip (see the green stick figures in Figure 2), and the latter is the variability outside the solution space, which does affect the position of the fingertip (see the red stick figures in Figure 2; [4,32,33]). These two types are used to examine the structure of variability of the

DOF. Variability within the solution space should be larger than outside the solution space such that the performance remains close to constant. In the present thesis, this structure in variability of DOF is interpreted as the consequence of a synergy and previous research will be presented as such. The UCM method also allows for the quantification of flexibility. This is quantified by the ratio of V_{ucm} and V_{ort}, where a larger V_{ucm} with respect to V_{ort} reflects a larger flexibility. Additionally, I also aim to take the UCM analysis to a higher level by making it more suitable for multi-joint tasks (chapter 2) and obtaining different measures (chapter 5) from this analysis that enables direct comparisons between synergies. These measures will also be applied in the present thesis.

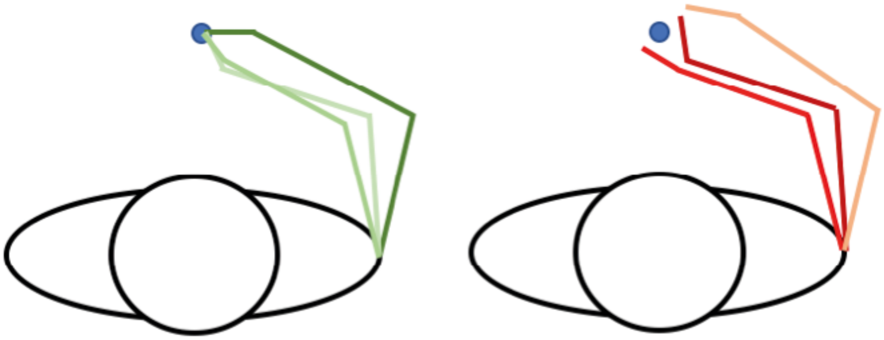

Figure 2. The UCM analysis partitions variability in V_{ucm} and V_{ort}. V_{ucm} is depicted by the stick figure at the left and V_{ort} at the right.

In manual pointing, sit-to-stance, or finger-force production, it is revealed that V_{ucm} is larger than V_{ort}, indicating that there is structure in variability [31,32,34–43]. We interpreted this as the emergence of a synergy, which organizes the DOF to perform those tasks. Additionally, synergies' hallmark flexibility has received much attention in previous research. Several studies suggest that if task constraints are more demanding, flexibility is exploited [39,40,44–46]. For example, when participants perform a pointing task in the context of a potential change of target location, flexibility increases. Moreover, the flexibility of a synergy is also influenced by organism constraints [47,48]. For example, flexibility is reduced in particular groups, such as in patients with Parkinson's disease [47,49], which probably makes it more difficult for those groups to maintain task performance in more demanding task conditions. Also, in a visuomotor adaptation paradigm, it has been shown that participants with high flexibility at baseline have higher learning rates [50].

Synergies are hypothesized to be constrained to specific behavior in the second step of the process, which is quantified by end-effector kinematics in the present thesis (cf. [10]). I outline previous research portraying the influence of task constraints on end-effector kinematics in the upper extremity tasks selected in the present thesis: manual reaching and manual lateral interception. Generally, the differences in task constraints between manual reaching and manual lateral interception seem to lead to different velocity patterns. That is, in manual reaching velocity patterns are bell-shaped [51,52], while in manual lateral interception the patterns are often skewed to the right [53] and expose an angle of approach effect [53–56]. This latter effect indicates that the angle of approach of the goal target influences the velocity profile of the end-effector during the interception movement in a systematic way. Additionally, a generally known kinematic feature in manual reaching is the slightly curved trajectory of the end-effector in the horizontal plane (the so-called horizontal curvature; see [6,7,57–59]). This feature has also been shown to be affected by task constraints [6,7,57–59]. More precisely, horizontal curvature has been shown to be larger for unconstrained reaching movements, where the fingertip is lifted from the table top, compared to constrained reaching movements, where the fingertip is constrained to the table top [6,7,57–59].

Aim and outline of the thesis

In the present thesis, I aimed to gather more understanding on motor coordination by focusing on synergies and their role in specific behavior. To do so, I examined the influence of task constraints on synergies and on end-effector-kinematics. Finally, I studied the relation between these levels and the two-step process of emergent behavior.

Before doing so, I evaluated the UCM analysis in chapter 2. This chapter focused on how the linear model is created for UCM analysis and aimed to make the analysis more suitable for multi-joint tasks. Then I turned to the two-step process approach, where an innovative methodology is applied to analyze both steps of the two-step process approach of emergent behavior in discrete movements. In chapter 3, I assessed the influence of task constraints on synergies that are hypothesized to emerge in the first step of the two-step process by examining structure in variability of DOF. More specifically, it is examined whether changes in a task constraint during practice enhance the flexibility of a synergy in reaching. In chapter 4, I examined the influence of task constraints on end-effector kinematics that is hypothesized to emerge from the second step of the process. That is, I examined the relation between lifted height of the end-effector and horizontal curvature of the end-effector in both unconstrained and constrained reaching. If both the level of synergies and the levels of end-effector kinematics can separately be influenced by task constraints using the current methodology, I can test the influence of task constraints on both synergies and kinematic level concurrently. This is done in chapter 5, where I examined whether different constraints are involved in different steps of the process in manual reaching and manual lateral interception, by asking whether different synergies were used when task constraints are varied. When I find that some task constraints can be involved in the first step, while others can be involved in the second step, this would concur with the two-step process approach. Finally, chapter 6 summarizes and discusses the main findings of this thesis.