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# Synergies and end-effector kinematics in upper limb movements

Tuitert, Inge

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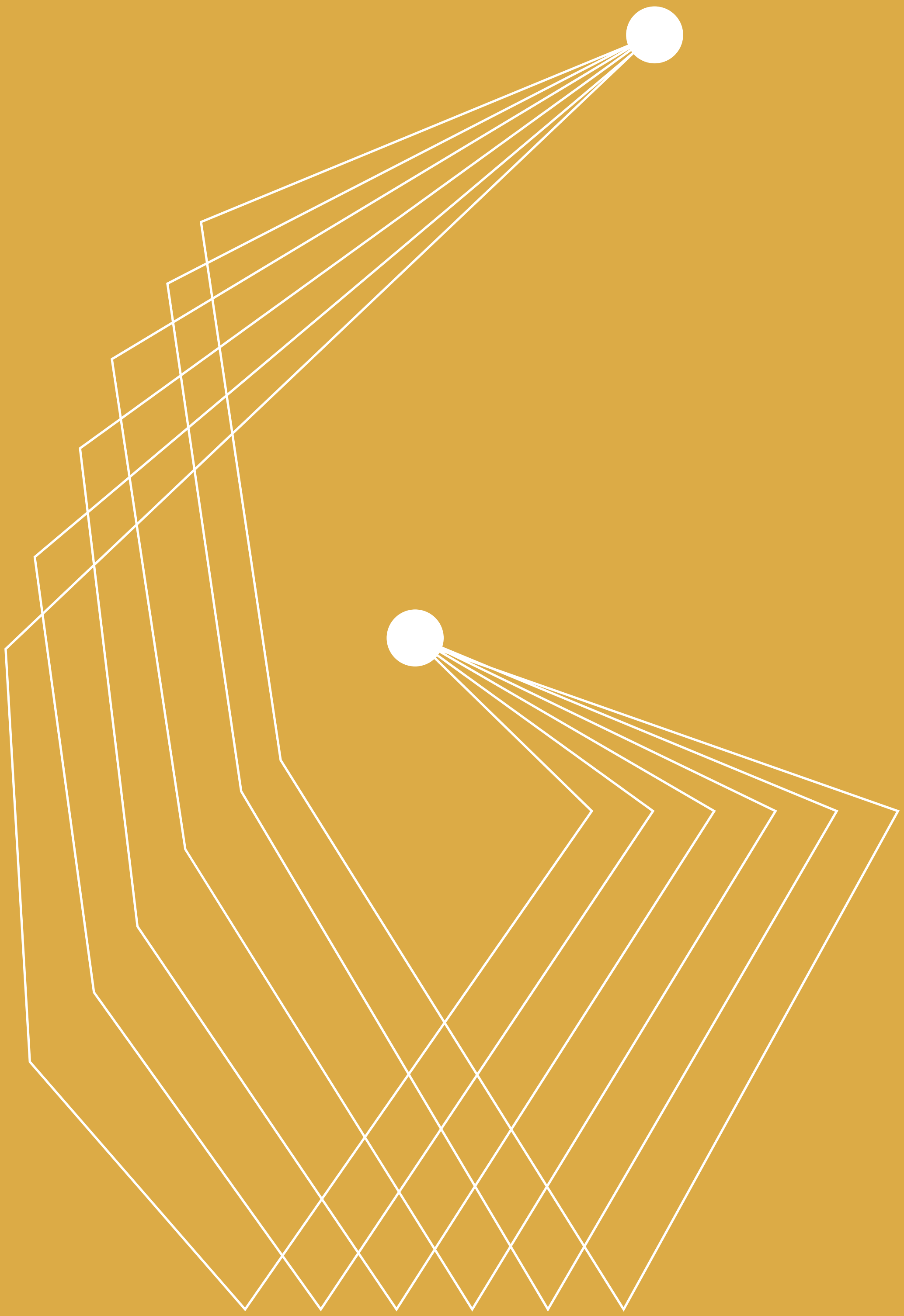

# GENERAL DISCUSSION

Motor actions involve numerous degrees of freedom (DOF), which usually outnumber the minimum necessary to accomplish the task at hand. Consequently, there are many possible solutions for a task, which is the so-called redundancy problem [1–3]. To coordinate the redundant DOF, they have been proposed to be temporarily linked into task specific units, named synergies [3,13,25,26,110,112,113]. In the present thesis, I focused on synergies and their role in specific behaviors in the coordination of the arm, to gather more understanding on how the redundant DOF are coordinated. I followed a dynamical systems approach where the emergence of synergies and their specific behaviors are hypothesized to be part of a two-step process of emergent behavior [10,26,29]. First, interactions amongst environment, organism, and task constraints are hypothesized to temporarily link the individual DOF into a synergy. Second, the synergy is further constrained giving rise to the specific behavior (i.e., the specific movement pattern of the end-effector). In the present thesis, I tested the influence of task constraints on the two-step process by studying whether different constraints are involved in different steps of the process (i.e., synergies and end-effector kinematics), aiming to gain more insight into how the redundant DOF are coordinated.

To analyze the separate steps of the process, a different methodology than before was applied in the present thesis. This methodology is outlined in the following. The first step of the two-step process, the emergence of synergies, was assessed using the uncontrolled manifold (UCM) analysis [4,33,79]. This method partitions variability in DOF across multiple trials into two types of variability: variability that does not affect the end-effector position ($V_{ucm}$) and variability that does affect the end-effector position ($V_{ort}$). The variability in DOF should be structured such that $V_{ucm}$ is larger than $V_{ort}$ to accomplish a given task. This structure has often been found in manual pointing tasks ([37,43,44,115,116,119] see also chapter 2, 3, and 5). In the present thesis, a larger $V_{ucm}$ than $V_{ort}$ is interpreted as the consequence of the emergence of a synergy (cf. [112]), which corresponds to the first step of the two-step process. Moreover, the second step, the emergence of the specific behavior, was assessed using end-effector kinematics. Various different variables have been used to assess end-effector kinematics, such as features of the end-effector velocity patterns or curvature of the end-effector path ([6,7,53–57,59] see also chapters 4 and 5).

The current chapter will start with discussing the main findings on the coordination of the redundant DOF and their relation to the two-step process of emergent behavior. Next, emergent synergies will be placed in a broader context. Subsequently, I will address a different perspective on emergent synergies and methodological considerations regarding the UCM analysis. Finally, future directions for studying the two-step process and some concluding remarks on the coordination of the redundant DOF are given.

## Main findings of the present thesis

The UCM analysis was used to examine the first step of the two-step process. One important step in this analysis is the creation of the linear model, which is evaluated in chapter 2. A linear model relates changes in elemental variables, e.g., joint angles, to changes in performance variables, e.g., 3D end-effector position. Linear models are usually created by means of an analytical method, however, a multiple regression analysis can also be used.

To examine which method is most suitable, I compared both methods using a multi-joint reaching data set. The results suggest that the regression method gives a better description of the data. First, the results revealed that the relation between measured and estimated (i.e., based on the model) fingertip-position deviation from the mean of individual trials was stronger if the model was created using the regression method compared to the analytical method. Second, the relation between measured fingertip variability and $V_{ort}$ was also stronger if the linear model was created using the regression method. Third, the values of $V_{ucm}$ and $V_{ort}$ indicated that the linear model created with the regression method gives a more accurate description of the data. Therefore, I recommend using the regression method to create the linear model in multi-joint UCM analysis. In chapter 2, I established this methodological aspect regarding the assessment of synergies, which is exploited in chapter 3 and 5 to examine the first step of the two-step process of emergent behavior.

In chapters 3, 4, and 5 I examined the influence of task constraints on the following aspects of goal-directed actions: 1) synergies, 2) end-effector kinematics, and 3) both synergies and end-effector kinematics, respectively. In chapter 3, I focused on the first step of the constraining process, the emergence of a synergy. Here, I examined whether changes in task constraints during practice in pointing enhance a characteristic of a synergy, the so-called flexibility, which is defined as the variations in (one) DOF which are compensated for in other DOF such that the performance remains close to constant. Flexibility was quantified using the ratio of $V_{ucm}$ and $V_{ort}$, where a larger ratio implies a higher flexibility. A high flexibility implies much variation in DOF while the performance remains constant, which is particularly useful when the task context changes, for instance, due to a potential change in target location, or in the presence of a secondary task, or new constraints [39,44–46]. The task constraint manipulation during practice was obstacle height, that is, while pointing the participant had to move the hand over an obstacle that varied in height. The goal of this practice phase was an enlargement of the exploited joint angle range. The results revealed that practicing movements over obstacles of different heights indeed led to the use of an enlarged range of joint angles. The effects of practice on flexibility were tested by comparing the pretest and the posttest that comprised one obstacle of intermediate height, not included in the practice phase. The comparison of pre and post practice revealed that the ratio of $V_{ucm}$ and $V_{ort}$ did not change, implying that flexibility was not affected by the practice phase. Importantly, $V_{ucm}$ decreased from pretest to posttest, which suggests a decrease in the employment of joint angle configurations after practice. That is, the task constraint manipulation led to the usage of less different joint angle configurations within the synergy after practice, implying a slight change in the first step of the two-step process. In sum, the results of chapter 3 indicated that changes in task constraints during practice lead to changes in the first step of the two step process, the synergy.

In chapter 4, the second step of the constraining process, the further constraining of the synergy resulting in end-effector kinematics, was examined. In this chapter on reaching movements, the task constraint of interest was the constraining of the fingertip to the surface, where the fingertip can be either constrained to the surface (i.e., constrained) or not (i.e., unconstrained). It has been repeatedly reported that constrained movements show a smaller horizontal curvature, i.e., the curvature of the end-effector trajectory in the horizontal plane, than unconstrained movements (e.g., [6,7,57,59]). In unconstrained movements, the hand is lifted to a certain height, which suggests a relation between the height to which the hand is lifted and horizontal curvature (cf. [6]). In chapter 4, I examined the task constraint lifted height by focusing on two questions: 1) does a systematic increase in the height of the surface over which the end-effector has to move lead to a gradual increase in horizontal curvature in constrained movements, and 2) does a relation exist between the height to which the end-effector was lifted and horizontal curvature in unconstrained movements. This was done using three experimental conditions: constrained movements over vertically curved surfaces that differed in height, constrained movements over a flat surface, and unconstrained movements. In constrained movements, a strong linear relation between height of the curved surface and horizontal curvature was found. However, the relation between lifted height of the end-effector and horizontal curvature was weak for unconstrained movements. These results indicated that the task constraint lifted height in the constrained condition systematically affected the second step of the two-step constraining process: the end-effector kinematics.

The results of chapters 3 and 4 indicated that at the separate levels, a change of task constraints had an effect on the step of the process acting at that level. The next step is to analyze both steps of the two-step process concurrently, to examine whether different task constraints affect different levels of the process. This was done in chapter 5, where I tested whether the task constraint differences between manual reaching and manual lateral interception with three angles of approach, such as timing and guidance, affected synergies, end-effector kinematics, or both. I chose these conditions based on the results of earlier studies [51–56], suggesting that the end-effector kinematics of all conditions would be different. More specifically, earlier studies revealed bell-shaped velocity patterns in manual reaching [51,52], whereas in manual interception, asymmetric velocity patterns were found with a prolonged declarative tail of which the characteristics differed for different angles of approach [53–56]. The results of chapter 5 statistically confirmed these expected differences in end-effector kinematics between tasks and amongst conditions.

This offered the possibility to examine whether these different kinematic end-effector patterns emerged from the constraining at the first or the second step of the two-step process. That is, I examined whether the differences in kinematics followed from different synergies, or that similar synergies were constrained differently. Here, a variation on an adapted version of the UCM method ([114] see also [87]) was used to compare the synergies between conditions, i.e., comparing the clusters of joint angle configurations. The results of chapter 5 revealed that in reaching and interception toward the same target (arrival) position different synergies were used, whereas interception conditions that differed in angle of approach, were performed with similar synergies. Importantly, interception movements to the same target arrival position where objects approached with different angles of approach were performed with similar synergies but different end-effector kinematics. These results suggest that some constraints, such as timing and guidance, creating the differences between reaching and interception, are mainly involved in the first step of the process, that is, the emergence of a synergy. Whereas other constraints, such as angle of approach, mainly influence the second step of the process. Taken together, these findings suggest that different task constraints are involved in each step of the two-step constraining process, suggesting that a two-step process is at play to coordinate the redundant DOF of the arm.

## Emergent synergies: the wider view

In the following section I will elaborate on the dynamical systems perspective on synergies. Moreover, I relate synergies to interpersonal coordination within the context of dynamical systems theory.

Following the perspective of the present thesis, the interactions amongst task, environmental, and organism constraints are thought to give rise to the synergy. More specifically, in a complex dynamical system, the bottom-up constraining process gives rise to the synergy pattern that then again links the DOF from the top down (e.g., [3,26]). That is, in the emergent processes the interacting constraints deny or allow certain states of the system, but these constraints do not prescribe the specific state the system emerges into. Such organization into a synergy is an example of self-organization, where the system organizes itself and there is no supervisor in the system doing the organizing [124,139]. An important characteristic of such a self-organizing system is that a small change in one of the constraints can lead to a change in the stability of behaviors [129]. Mapping these ideas onto an action system, synergies can be described as stable states in a system that can change due to the interaction of (task) constraints. Importantly, the current results are in line with the important characteristic of a self-organizing system. The results of chapter 5 revealed that synergies differ between reaching and interception, whereas no differences among synergies were found in the interception conditions. That is, as a function of some changes in constraints the self-organizing process results in a similar synergy while other changes lead to different synergies. Taken together, the findings of the present thesis seem to be in line with the idea that self-organizing synergies emerge as first step of the two-step constraining process.

The two-step constraining process is also studied in the related field of interpersonal coordination [26,31,128,140], which focuses on how individuals coordinate their movements with others. Interpersonal coordination can be approached using the framework of interpersonal synergies [26,31], which suggests that individuals do not interact at the level of end-effector kinematics, but at the level of synergies. That is, it is hypothesized that the DOF of both individuals are linked into one synergy through interactions of constraints, which is then again constrained to produce end-effector kinematics [26]. This hypothesis was investigated by Romero and colleagues [31] in an interpersonal manual pointing task. In this task, pairs of participants sat next to each other and each used one arm to complete a pointer-to-target task, where one person moved the pointer while the other person moved the target. Their results revealed that the stabilization of the interpersonal synergy, i.e., the strength of the linking of DOFs across participants, was stronger than the intrapersonal synergy, i.e., the strength of the linking of DOF within a participant (also quantified using the UCM analysis). These results suggest that one interpersonal synergy, and not two intrapersonal personal synergies are at play in this interpersonal manual pointing task. This interpersonal synergy brings about the interpersonal end-effector kinematics in the second step of the two-step process. Taken together, the results of this experiment support the interpersonal synergies hypothesis and also suggest that a two-step process is at play in emergent interpersonal behavior.

## A different perspective on emergent synergies

To quantify a consequence of the emergence of a synergy (i.e., structure in variability of DOF), I applied UCM analysis. The current conceptual framing of this analysis differs from the interpretation of a principal proponent of UCM research in the field of motor coordination: Mark Latash (e.g., [4,11]). His interpretation of the analysis also relates the findings of the UCM analysis to synergies from a dynamical systems perspective, however, according to his approach the central nervous system is of particular importance in the system [11]. Latash defined a synergy as a neural mechanism that ensures task-specific co-variation of DOF providing for desired stability properties of an important performance variable ($V_{ucm}$; e.g., [4,11]). Latash relates his notion of synergies to the equilibrium point hypothesis [11,141,142]. According to this hypothesis, commands from the central nervous system change the thresholds of the tonic stretch reflexes (lambda), which leads to muscle forces. These muscle forces interact with external loads on the limbs leading to the emergence of an equilibrium point, that is, a joint angle configuration [11]. While the equilibrium emerges from the interactions of the muscle forces, resulting from lambda, and external loads, lambda is controlled by higher neural structures. This highlights the particular importance of the central nervous system in Latash's notion of synergies. Thus, where Latash's view suggests that a dynamical neural organization is central in synergistic organization, the perspective of the present thesis advocates that synergies emerge within a dynamical system where all elements are of equal importance.

## Methodological considerations on UCM analysis

In the present thesis, synergies were assessed using the UCM analysis. In this analysis many computational and methodological choices have to be made, such as, how the linear model should be approximated. This computational consideration was examined in chapter 2, where the results indicated that it is recommended to create the linear model using regression analysis in multi-joint movements. Here, I address two additional points of consideration when applying UCM analysis, in particular when trying to understand motor learning. It is important to note that in early motor learning a lot of variation across trials is expected and the task is not always accomplished, whereas in late learning more consistency across trials and a better performance is likely. This should be considered when applying the UCM analysis in motor learning experiments. One should think about using the adapted version of the motor equivalence analysis presented in chapter 5 where a 'base' linear model is computed with a selection of trials. To approximate this 'base' in learning, the last trials of the learning experiment, where little learning can be expected to take place (i.e., more consistency over trials), should be used. If trials in early learning are included, the approximated linear model will show systematic deviations, whereas if the last learning trials are selected for the approximation, it is likely to be more representative for the task. This analysis can be accompanied by the trial by trial analysis put forward by Scholz et al. [102], if quantifying trial by trial improvements over learning is the aim of the analysis. This trial by trial analysis computes $V_{ucm}$ and $V_{ort}$ separately for each trial, instead of applying the compound measure (i.e., the variance over a set of trials within a condition), which is used in the present thesis and in most other studies [32,37,43,44,61,116]. If both the adapted version of the motor equivalence analysis and the trial by trial analyses would be combined, it could be analyzed how solutions are explored to form a synergy.

## Future directions for studying the two-step process approach

The present thesis focused on the influence of task constraints on the two-step process. To gain further insight into this process, future studies should examine how other task constraints and how environmental and organism constraints affect the two-step process. This would give insight into why certain constraints influence synergies and other constraint affect end-effector kinematics. In the upper extremity tasks used in the present thesis, organism and task constraints could, for instance, be manipulated by applying a learning paradigm using a visuomotor transformation [35,143] or blocking a joint using a brace. In addition, apart from the joint level and end-effector level there are many more redundant levels involved in the execution of movements [144], such as the muscle level or the neural level. How these other levels relate to the levels examined in the present thesis in light of the two-step process goes beyond the scope of this thesis and is a topic for future research.

The former proposal for future research should, in addition to the analyses put forward in the present thesis, also be assessed using other analyses that quantify the two-step process to further strengthen the conclusions. At synergy level this could, for example, be principal component analysis [145]. This analysis gives insight into how the DOF are reduced in dimensions across a block of trials. Quantifying how the DOF are reduced in dimensions can give insight into how the DOF are coupled in the synergies, which is a different characteristic of a synergy than analyzed using the UCM analysis. Additionally, at end-effector level 1/f scaling analysis [146] could be performed. This analysis would provide information on how the variability in end-effector movements is structured, which would add to the current analysis on end-effector level. That is, the 1/f scaling analysis would give insight into the structure of variability at end-effector level, instead of only looking at the mean. This could, for instance, be informative about the structure of variability of movement time of the end-effector during motor learning, which has been shown to become more patterned with learning (e.g., [146]).

## Concluding remarks

The aim of the present thesis was to gather more understanding on how the redundant DOF of the arm are coordinated by focusing on synergies and their role in specific behaviors. The latter two were hypothesized to be part of a two-step process, where first, the interactions amongst organism, environment, and task constraints link the independent DOF into a synergy, and second, the constraints act on the synergy, resulting in the specific behavior (i.e., end-effector kinematics). This two-step process was examined by looking at the influence of task constraints on synergies, on end-effector kinematics, and on both levels. The results revealed that task constraints influenced synergies (i.e., the first step of the process) and end-effector kinematics (i.e., the second step of the process) independently. More importantly, the results of both synergy and end-effector level demonstrated that some constraints are mainly involved in the first step of the process, whereas other constraints mainly influence the second step of the process. That is, different task constraints are involved in each step of the two-step constraining process, suggesting that a two-step process is at play to coordinate the redundant DOF. Future research should further unravel this two-step constraining process to gain more understanding on the coordination of the redundant DOF.