

Getting a Grasp on Coordination

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Motor coordination is realized by the nervous system at different levels. Concepts about the coordination within a limb define the controlled parameter in cartesian or joint space, whereas concepts about the coordination between limbs stress the temporal control of schemas. Motor deficits of neurological patients point to the role of the different motor areas in motor coordination.

Picking up a glass of beer in a pub does not seem to be a difficult task. Yet, the apparent ease with which we execute this action obscures the complex tasks our motor system has to solve when organizing this drinking action. In fact, the motor system has to organize the action at different levels. For the prehension movement to the glass, the reach has to be coordinated with the grasping component to bring the hand in the proper configuration to the right place (8). When one lifts the glass, the load and grip forces applied by the fingers have to be coordinated to account for the weight of the glass, its fragility, and possible slippage (9). Furthermore, when one fills the glass from a bottle, the actions of the two arms must be coordinated. For example, the holding of the glass with one hand has to be functionally synchronized with the pouring action of the other hand (14). The coordination of the drinking action within the sequence of actions that precede or follow it takes place at another organizational level. The action structure is different whether we want to simply drink, to clink glasses, or to give the glass to somebody else.

Many concepts have been used to describe the coordination of the upper limbs at these different organizational levels. Concepts about the coordination within a limb stressed the spatial aspects. The question of how the motor system controls the multiple degrees of freedom (DoF) within a limb, which allow for an infinite number of solutions for a particular motor task (the redundancy problem), was approached by looking for the variables that might be optimized by the motor system and thereby reduce its computational load. One subset of theories defined the limb posture at the end of the movement as the controlled variable, whereas others concentrated on the trajectory of the endpoint of the limb as the optimized parameter.

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The coordination between limbs was mainly described within the temporal domain. The idea of a higher-order coordinating mechanism that temporally organizes lower-level elements might explain not only the coordination between the reach and grasp components in prehension movements but also the synchronized activation of different body parts in pointing or the goal-directed temporal synchronization of the two hands in complex bimanual tasks. In this paper, we examine some of the concepts that have been proposed to understand the problem of coordination for movements of the upper limbs and relate these concepts to some of the relevant clinical findings on motor coordination.

Intralimb coordination: Cartesian space or joint space?

Planning trajectories in Cartesian space. One possibility for reducing the computational load implied by the number of DoFs is that the commands for each given movement are selected according to optimality rules and that these rules constrain the limb to act as a unit and not as a set of muscles and joints. This concept was originally inspired by the classical Bernstein idea of "muscle synergies" and the related concept of "coordinative structures," defined as a group of muscles that are temporarily constrained to act as a task-specific unit.

One of the variables that could be optimized by the motor system to the aim of reducing the number of DoFs is the limb endpoint trajectory in space. When a hand-held lever is displaced toward visual targets in a plane, the corresponding movements have bell-shaped velocity profiles and follow approximately straight spatial paths. These characteristics were adequately reproduced by the minimum-jerk model of Hogan and Flash (6), with jerk being the fourth time derivative of position. This model predicts that the parameter controlled by the central nervous system is the spatial path of the hand, which implies that movements would be planned in

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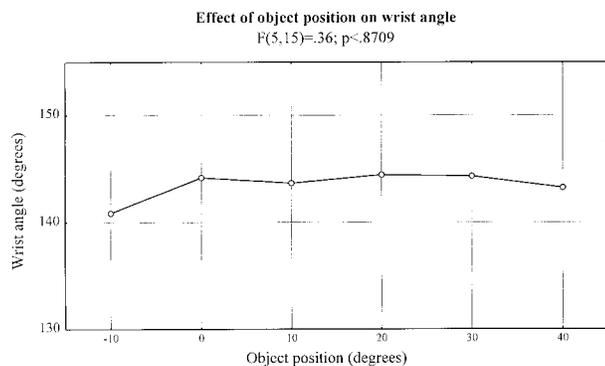
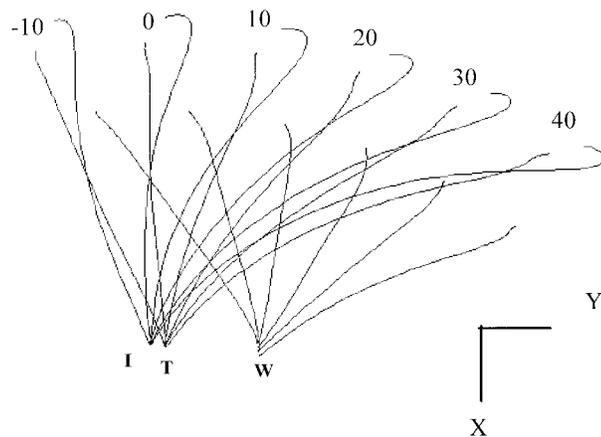


FIGURE 1. Effect of object location on arm posture in prehension movements to objects at different positions in the work space. *Top:* trajectories of the index finger (I), thumb (T), and wrist (W) are plotted for prehension movements to 6 identical cylindrical objects placed in the same distance at different angular positions with respect to the subject's midline (-10, 0, 10, 20, 30, and 40°). The final position of the fingertips on the object was not invariant but depended on the object's position in the workspace. However, wrist angle did not vary with object position (as shown in *bottom*), indicating that the forearm and hand were displaced as a whole, representing freezing of degrees of freedom in the upper limb.

Cartesian coordinates. This view is in conflict with other models that postulate that the motor system plans movements in joint coordinates, in which the controlled parameter is the position of each of the joints contributing to the movement. In contrast with the minimum-jerk model, the joint-space model predicts curved movement trajectories. This apparent discrepancy was recently resolved by Desmurget et al. (3). They measured pointing movements in two conditions: in the "compliant" condition, the subjects held a cursor in the hand that they displaced toward the target; in the "unrestrained" condition, they moved their hand freely to the target. Whereas, in the first condition, movements had a straight spatial path, in the second condition, the trajectory was curved. This result demonstrates that control strategies for goal-directed movements (and the resulting coordination between joints) differ according to the task in which the subject is involved. Finally, other optimization models (the minimum-change-in-torque model, for example) are also able to reproduce some of the characteristics of goal-directed arm movements, such as the bell-shaped velocity profile.

Postural coding. Synergies result in "freezing"

some of the DoFs in natural movements. Consider, for example, the action of grasping cylindrical objects (e.g., a glass) placed at different locations in the workspace. Paulignan et al. (Ref. 11, see Fig. 1) showed that the position of the fingertips on the object was determined by the selection of an invariant final posture of the arm, not an invariant visual landmark on the object. This was achieved by combined rotations at the shoulder and the elbow joints, whereas the other DoFs of the upper limb were frozen: the forearm and the hand were displaced as a whole, irrespective of object location, and, consequently, the wrist angle did not vary for different object locations. This result indicates that, whenever possible, the final arm posture tends to remain invariant, and it is only when required by object shape that new DoFs are recruited.

A similar behavior is observed during corrective movements generated as a result of perturbations of the goal. Desmurget et al. (4) recorded the final arm posture when a subject reached to grasp a bar placed at different orientations. On some occasions, the orientation of the bar was changed at the onset of the reaching movement. The configuration of the arm was rapidly altered

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so as to match the new orientation; that is, the arm moved to the final posture that was assumed during unperturbed movements directed at a bar with this orientation. In other words, each orientation of the bar determined a unique final posture of the whole limb.

These results fit into the general framework of the "equilibrium-point" hypothesis, which assumes that the motor system specifies goal positions for the limbs, not movements between positions. Accordingly, the command system would specify a final posture for the limb by pre-setting the stiffness of the acting muscles and movement would occur as a consequence of the springlike properties of the muscles, until the actual position of the limb would correspond with the equilibrium position. This hypothesis has its own limitations, however. Gomi and Kawato (5), for example, showed that the velocity of the observed limb trajectory during a pointing movement does not correspond to that estimated from the measured stiffness and the generated torque. Instead, they believe that the actual trajectory depends on commands issued from an internal "model" or representation of the final posture of the limb. Such a representation can be perceived as a memory structure combining information about the limb from various sensory sources derived from the experience of interacting with the environment. Observations on grasping behavior, showing that spontaneous hand position (e.g., overhand vs. underhand) tends to tolerate initial discomfort for the sake of final comfort, provide a rationale for the existence of such a representation. This "end-state" comfort effect reflects planning of future task demands.

Localizing the internal representation. The assumption that actions are planned in advance raises two questions: 1) what is the nature of the representation generated by the motor system, and 2) how is the achievement of the goal state signaled to the motor system? Pathological conditions provide some hints to these questions.

Ample evidence points to an important role of the cerebellum in such a feedforward control mechanism. Miall et al. (10) conceive the cerebellum as a "Smith predictor," i.e., it generates a prediction of the sensory consequences of a movement and keeps this prediction in memory to compare it with the actual sensory feedback. As a result of this comparison, corrections are issued and adaptation of the predictive representation occurs. In addition, Miall et al. (10) hypothesize that there might be two separate Smith predictors working in the cerebellum: one, in the lateral cerebellum, works in a visual, peripersonal coordinate system, whereas the

other, in the intermediate cerebellum, uses intrinsic, motor coordinates.

The importance of the cerebellum in motor coordination is supported by the frequent clinical observation that patients with cerebellar lesions show more pronounced deficits for movements involving multiple joints than for simple movements. However, experiments examining this phenomenon quantitatively with the help of kinematic analysis are rare. When throwing, cerebellar patients are unable to temporally control their relative muscle activations, especially those of the antagonist muscles, resulting in more variable limb trajectories. Similar variable trajectories were also observed by Bastian et al. (1) when cerebellar patients pointed in the sagittal plane. In addition, these authors noted slowness of movement, undershooting of the target, and decomposition of the multijoint movement into single joint movements. These abnormalities were viewed as the patients' strategic compensations for their inability to control the dynamic interaction of torques produced at different joints during the movement. Therefore, these findings suggest that lesions in the cerebellum may lead to a loss of an internal representation of the limb, rendering the patients unable to predict the consequences of their own movements.

Proprioceptive input provides the motor system with information about the current position of the limb in relation to the predictions based on the internal representation and thus may signal the achievement of the limb's goal state. By analyzing kinematically and dynamically reaching movements in patients suffering deafferentation from peripheral neuropathies, Ghez's group (13) elucidated the role of proprioception in multijoint movement. Their prominent finding was that, similar to patients with cerebellar lesions, deafferented patients exhibited more variable movement trajectories, in addition to a temporal decoupling of the elbow and shoulder joints. Providing these patients with visual feedback improved their movement trajectories but not their deficits in coordinating muscle activation patterns with interaction torques, leading to disturbed joint coordination. Ghez and colleagues (13) thus inferred that proprioceptive information is essential for updating an internal representation of the limb's inertial properties. With the help of this updated internal representation, the consequences of motor commands can be predicted by feedforward control mechanisms. Such a control mode enables more efficient responses to perturbations than when the motor system can only rely on proprioceptive feedback to issue corrective commands.

"Providing these patients with visual feedback improved their movement trajectories..."

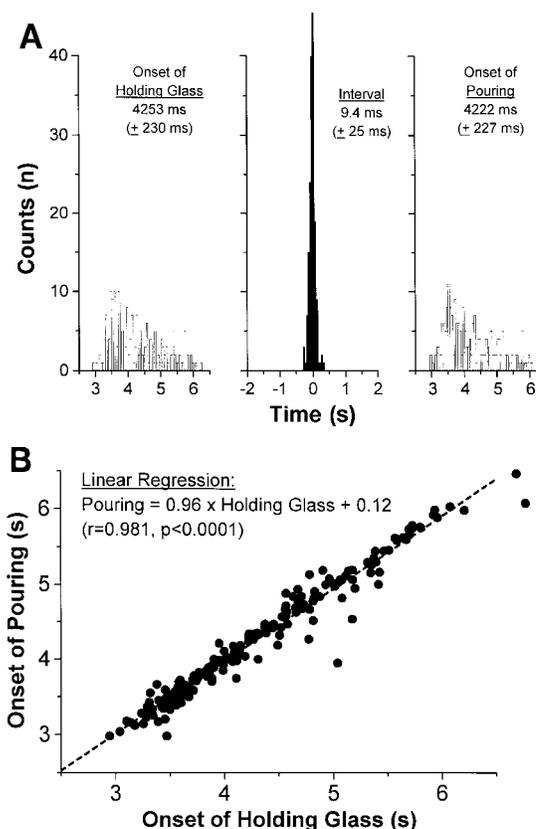


FIGURE 2. Functional bimanual synchronization within the complex action of pouring from a bottle into a glass. *A:* to quantify bimanual coordination, onset of holding a glass with one hand (*left*) is related to the movement onset of pouring fluid from a bottle into a glass with the other hand (*right*). For each action, the interval between these 2 functionally related events is calculated (*middle*). Successful bimanual synchronization is represented by the narrow distribution of the interval compared with scattered distributions of either event. Means and SE are given. *B:* this bimanual coordination is also indicated by the highly significant linear regression function between the 2 functionally related events.

Motor coordination in the temporal domain

Interlimb coordination. Successful goal achievement in complex action involving different limbs requires precise temporal coordination. One of the basic principles that seems to operate at this organizational level is that of simultaneous onset. For free-pointing movements involving eye, head, and arm movements directed at the same target, it was found that the motor commands for all effectors were released (almost) simultaneously. For complex bimanual tasks, the functional synchronization of movement segments executed by either hand seems to be more important than the synchronization of movement onsets. Wiesendanger et al. (15) measured the degree of synchronization of the two hands during the action of pulling a drawer with one hand and grasping a small object in it with the other. They found that, despite large variations in the occurrence of the segment

onsets of either hand, functionally related segments of the two hands were tightly synchronized. This represents a good example of a goal-related coordination whereby the temporal invariance of the whole system is achieved despite the variability of its components. An extensive study of the action of pouring from a bottle into a glass (14) provides further examples of this behavior (see Fig. 2).

A model proposed by Hoff and Arbib (7), originally designed for the coordination of reach and grasp components during the action of unimanual grasping, (see Fig. 3), seems to account for the observed terminal invariance in bimanual actions. The general idea is that there is a two-way interaction between the motor “schemas” involved in the action. Hoff and Arbib (7) postulated the existence of a hierarchically higher “coordinating schema” that receives from each of the constituent schemas an estimate of the time it needs to move from its current state to the desired final state. Whichever schema is going to take longer is given the full time it needs, whereas the others will be slowed down. The time needed by each schema is regulated by optimality criteria which are embedded in feedback controllers. This model accounts for the rapid corrections generated in response to sudden displacement of the target object at the onset of a reaching movement. In addition, it unifies within the same framework the concepts of goal-directed coordination, hierarchical control, and terminal invariance that seem to govern complex movements.

Cortical motor areas and (bimanual) coordination. The focus of the clinical research on interlimb coordination concentrated on finding structures within the brain that might subserve this function (15). Many cortical areas like the premotor cortex, the parietal cortex, and the mesial motor cortices, including the supplementary motor area (SMA), were found to contribute to the temporal coordination of the limbs in bimanual tasks.

Consistent with the finding of bilateral projections from premotor cortex to the motoneurons controlling proximal musculature, the decomposition of proximal bilateral movements, like windmill movements of the arms or bicycling movements, is described as sequela of lesions in the lateral premotor areas. A breakdown of coordinated motor patterns in prehension movements was quantitatively described after lesions of the parietal association areas. A patient with an hemianesthesia due to a parietal lesion was unable to coordinate the reaching and grasping components in prehension movements with the impaired arm. Similarly, parietal lesions disrupt finger movements during exploration of objects.

“Many cortical areas... contribute to the temporal coordination of the limbs in bimanual tasks.”

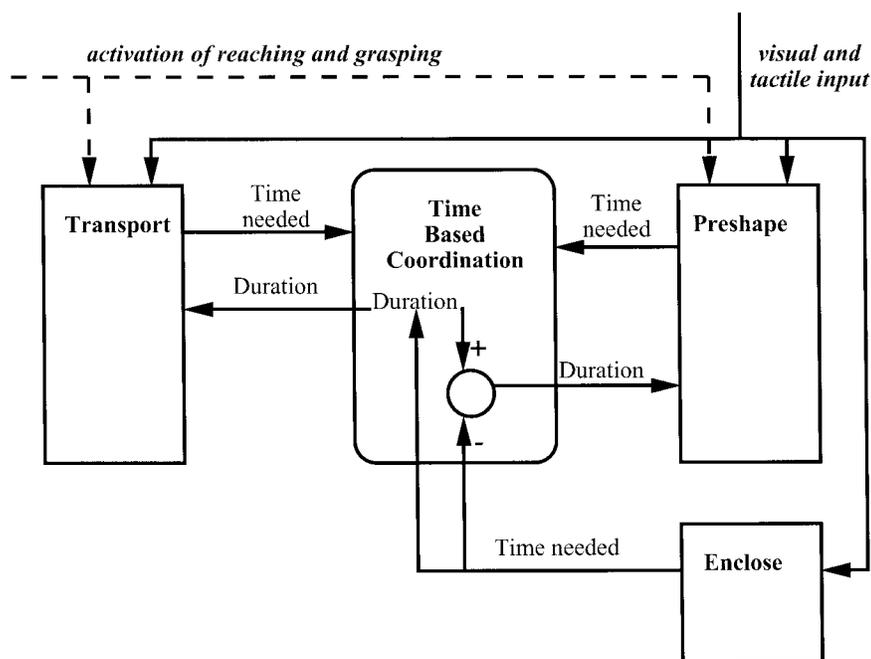


FIGURE 3. A model for the interaction of the reach and grasp components in prehension. Diagram symbolizes temporal coordination of the involved motor schemata by a higher time-based coordination schema. The 3 motor schemata represent transport of the hand to the object (Transport), preshaping of fingers according to properties of the object (Preshape), and closure of fingers around the object, starting from their maximal aperture (Enclose). This model can also be applied to temporal coordination of bimanual action by conceptualizing movements of the 2 hands as motor schemata that are synchronized by a time-based coordination schema. [Modified and reproduced with permission from Hoff and Arbib (7).]

Parietal patients are unable to precisely synchronize their manipulatory movements to allow for the appropriate contact between the object and skin receptors, rendering the hand useless for exploration even in the absence of paresis (12). In addition, the coordination of lift and load forces during grasping was deficient in these patients. Because the breakdown of coordination patterns rather than the disruption of elementary motor and sensory function compromised the utility of the hand for the patient, Pause et al. (12) termed the patient's deficit "tactile apraxia." The more common forms of apraxia, ideomotor and ideational apraxia, characterized by an impaired conceptual organization of movement after lesions in the parietal association cortex of the dominant hemisphere, usually affect both limbs and consequently disturb bimanual coordination at a high level.

Classically, the SMA is thought of as a bilaterally organized structure with bilateral projections to the spinal cord and dense callosal interconnections, as also evidenced by cell recording studies in monkeys and activation studies in humans. Patients with vascular lesions of the SMA, which often include parts of other mesial motor areas and parts of the corpus callosum, can present with the disabling symptom of "intermanual conflict" (or "diagonistic dyspraxia") as part of the "alien hand syndrome." These patients perceive their nondominant hand as alien, since it performs purposeful movements that they are

unable to control voluntarily. The intermanual conflict occurs when this alien behavior interferes with the actions of the other hand, e.g. turning back a book page that the other hand has just turned or holding down an object that the other hand wants to pick up. The intermanual conflict and other problems in bimanual coordination, especially deficits in learning new bimanual tasks, are also reported after surgical section of the corpus callosum (2). Thus different neural structures contribute to bimanual coordination, depending on the particular task requirements. Further research is needed to clarify the respective roles of the different structures in the cortical network subserving motor coordination. For this purpose, quantitative studies of goal-related invariances in complex bimanual tasks in neurological patients would nicely complement the careful studies in monkey of the Wiesendanger group (15).

Concluding remarks

In this review, we tried to relate some of the concepts about motor coordination at the intra- and interlimb level to clinical observations. In both areas, the notion emerges that the context in which a motor task is executed strongly influences its organization. Motor coordination seems to result when the intended goal of the action is translated into movement execution. The goal of an action is represented in higher coordinative

...impaired conceptual organization of movement after lesions in the parietal association cortex...."

structures or schemas, which coordinate interactions at the lower executional levels in the spatial and temporal domain. Consequently, the observed goal-related spatial and temporal invariances can be viewed as reflecting "motor equivalence." Therefore, motor coordination is not the goal but a means to achieve the goal of an action.

The reported clinical findings on deficits in motor coordination are not sufficiently explained by assuming a strict hierarchical structure of the motor system. However, promising new concepts postulate that many different, especially cortical, structures are recruited in a neural network subserving motor coordination depending on the goal of the action. Each structure contributes a certain function, and it is likely that only the interplay of many structures forms the coordinative schemas necessary for organizing an action. This would fit the clinical observations that different high-level aspects of motor coordination are disturbed when certain parts of the network are lesioned. To adequately approach the complexity of the coordination network, the trend to qualitatively and quantitatively study more complex, goal-directed actions should be reinforced.

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