Arm and Hand Movement Control

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Introduction

The control of arm and hand movements in human and nonhuman primates has fascinated researchers in psychology, neuroscience, robotics, and numerous related areas. Movement appears effortless to the uninitiated observer—only when trying to duplicate such skills with artificial systems or when examining the underlying neural substrate, one discovers a surprising complexity that, so far, has prevented us from understanding the biological implementation, how to repair neural damage, and how to create human-like robots with a human level of movement skills.

Research towards an understanding of motor control can be approached on different levels of abstraction, for instance, by examining the biochemical mechanisms of neuronal firing, the representational power of single and populations of neurons, neuroanatomical pathways, the biomechanics of the musculoskeletal system, the computational principles of biological feedback control and learning, or the interaction of perception and action. No matter which level of inquiry is chosen, however, ultimately we need to solve the "reverse engineering" problem of how the properties of each level correlate with the characteristics of skillful behavior. Motor control of arm and hand is an excellent example of the difficulties that arise in the reverse engineering problem. Behavioral research has discovered a variety of regularities in this movement domain, but it is hard to determine on which level they arise. Moreover, most of these regularities were examined in isolated arm or hand movement studies, while, as detailed later, the coordination of arm and hand is a coupled process where hand and arm movement influence each other. In this article, we will discuss some of the most prominent regularities of arm and hand control, and examine suggestions where they may come from, with a particular focus on computational and neural network models. It will become apparent that an interesting competition exists between explanations sought on a neural, biomechanical, perceptual, and computational level that has created a large amount of controversy in the research community over the years.

Behavioral Phenomena of Arm and Hand Control

For most movement skills, there are infinitely many ways of how they can be achieved. For instance, when reaching for an object, an arbitrary hand path can be taken between start and endpoint, and the path can be traversed at arbitrary speed profiles. Moreover, due to the excess of the number of degrees-of-freedom (DOF) in the primate movement systems, there is additionally an infinite number of ways of how a chosen hand path can be realized by postural configurations (see ROBOT ARM CONTROL). On the biomechanical level, one finds an even larger level of redundancy as there are many more muscles than DOFs in the human body, and this level of redundancy becomes even worse on the neuronal level. From this line of arguments, it is extremely unlikely that two different individuals would use similar movement strategies to accomplish the same movement goal. Surprisingly, however, behavioral research did find a large amount of regularities, not just across individuals of a given species, but also across different species (e.g., see Flash & Sejnowski, 2001). These regularities or invariants have become a hallmark towards the understanding of perceptuomotor control, as they seem to indicate some fundamental organizational principles in the central nervous system.

Bell-shaped Velocity Profiles and Curvature in Reaching Movements

About 20 years ago, Morasso (see OPTIMIZATION PRINCIPLES IN MOTOR CONTROL) discovered that in point-to-point reaching movements in humans, the hand path in Cartesian (external) space was approximately straight and the tangential velocity trajectory along the path could be characterized by a symmetric bell-shape, a result that was also duplicated in monkeys. In contrast, velocity profiles in joint space and muscle space were much more complex. These findings gave rise to the hypothesis that point-to-point reaching movements are planned in external coordinates and not in internal ones. Later, more detailed examinations of reaching movements revealed that, although *approximately* straight, reaching movement showed a characteristic amount of curvature as a function of where in the workspace the start and endpoint of the movement was chosen. Also the symmetry of the velocity profile can be shown to vary systematically as a function of movement speed (e.g., Bullock & Grossberg, 1988). These behavioral phenomena gave rise to variety of models for explanation.

Initial computational models of reaching focused on accounting for the bell-shaped velocity profile of hand movement, employing principles of optimal control based on a kinematic optimization criterion for movement planning that favors smooth acceleration profiles of the hand (see OPTIMIZATION PRINCIPLES IN MOTOR CONTROL). As this theory would create perfectly straight-line movements in Cartesian space and perfectly symmetric bell-shaped velocity profiles, the observed violation of these features in behavioral expression was explained by assuming that these movement plans were executed imperfectly by an equilibrium point controller (see EQUILIBRIUM POINT HYPOTHESIS). Thus, the behavioral fea-

tures of point-to-point movements were attributed to perfect motor planning and imperfect motor execution.

An alternative viewpoint was suggested by Kawato and his coworkers (see OPTIMIZATION PRINCIPLES IN MOTOR CONTROL and EQUILIBRIUM POINT HYPOTHESIS). Their line of research emphasizes that the CNS takes the dynamical properties of the musculo-skeletal system into account and plans trajectories that minimize the "wear-and-tear" in the actuators, expressed as a minimum torque-change or minimum motor-command-change optimization criterion. According to this overall view, behavioral features of arm and hand control are an intentional outcome of an underlying computational principle that employs models of the entire movement system and its environment.

Recently, Harris and Wolpert (see OPTIMIZATION PRINCIPLES IN MOTOR CONTROL) suggested that the features of arm and hand movement could also be due to the noise characteristics of neural firing, i.e. the decreasing signal-to-noise ratio of motor neurons with increasing firing frequency. Thus, the neuronal level together with the behavioral goal of accurate reaching was held responsible for behavioral characteristics.

Several other suggestions were made to account for features of arm and hand control. Perceptual distortion could potentially contribute to the curvature features in reaching, and dynamical properties of feedback loops in motor planning could generate asymmetries of bell-shaped velocity profiles (Bullock & Grossberg, 1988). Moreover, imperfection of motor learning (see SENSORYMOTOR LEARNING) and delays in the control system could equally play into explaining behavior.

Movement Segmentation

For efficient motor learning, it seems mandatory that movement systems plan on a higher level of abstraction than individual motor commands as otherwise the search space for exploration during learning would become too large to find appropriate actions for a new movement task (LEARNING ROBOT CONTROL). Movement primitives (MOTOR PRIMITIVES), also called units of action, basis behaviors, or gestures (SPEECH PRODUCTION: MOTOR THEORIES OF PERCEPTION), could offer such an abstraction. Pattern generators in invertebrates and vertebrates (see MOTOR PATTERN GENERATION) and the few different behavioral modes of oculo-motor control (e.g., VOR, OKR, smooth pursuit, saccades, vergence) can be seen as examples of such movement primitives. For arm and hand control, however, it is a topic of ongoing research whether some form of units of actions exist (Sternad & Schaal, 1999). Finding behavioral evidence for movement segmentation can thus provide some first insights into the existence of movement primitives.

Since the 1980's, kinematic features of hand trajectories have been used as one major indicator to investigate movement segmentation. From the number of modes of the tangential velocity profile of the hand in linear and curvilinear drawing movements, it was concluded that arm movements may generally be

created based on discrete stokes between start points, via points, and end points, and, moreover, that these strokes were piecewise planar in three dimensional movement (for a review, see Sternad & Schaal, 1999). From these and subsequent studies, stroke-based movement generation and piecewise planarity of the hand movement in Cartesian space became one of the main hypotheses for movement segmentation (Flash & Sejnowski, 2001).

Recent work (Sternad & Schaal, 1999), however, reinterpreted these indicators of movement segmentation partially as an artifact, in particular for rhythmic movement, that, surprisingly, was also assumed to be segmented into planar stokes. Human and robot experiments demonstrated that features of apparent movement segmentation could also arise from principles of trajectory formation that use oscillatory movement primitives in joint space. When such oscillations are transformed by the nonlinear direct kinematics of an arm (see ROBOT ARM CONTROL) into hand movement, complex kinematic features of hand trajectories can arise that, nevertheless, are not due to movement segmentation. Sternad and Schaal (1999) hence suggested that movement primitives may better be sought in terms of dynamic systems theory, looking for dynamical regimes like point and limit cycle attractors (see also GEOMETRICAL PRINCIPLES IN MOTOR CONTROL), and using perturbation experiments to find principles of segmenting movements into these basic regimes.

The 2/3 Power Law

Another related behavioral feature of primate hand movements trajectories, the 2/3 power law, was discovered by Lacquaniti et al. (in Flash & Sejnowski, 2001). In rhythmic drawing movements, the authors noted a power law relationship with proportionality constant k between the angular velocity $a(t)$ of the hand and the curvature of the trajectory path $c(t)$:

$$a(t) = k \ c(t)^{2/3} \tag{1}$$

There is no physical necessity for movement systems to satisfy this relation between kinematic (i.e., velocity) and geometric (i.e., curvature) properties of hand movements. Since the power law has been reproduced in numerous behavioral experiments (Viviani & Flash 1995, in Flash & Sejnowski, 2001) and even population code activity in motor cortices (Schwartz & Moran 1999, in Flash & Sejnowski, 2001), it may reflect an important principle of movement generation in the CNS.

The origins of the power law, however, remain controversial. Schaal and Sternad (2001) reported strong violations of the power law in large scale drawing patterns and, in accordance with other studies, interpreted it as an epiphenomenon of smooth movement generation (Flash & Sejnowski, 2001). Nevertheless, the power law remains at an interesting descriptive feature of regularities of human motor control and has proven to be useful even in modeling the perception of movement (see MOTOR THEORIES OF PERCEPTION).

The Speed Accuracy Tradeoff

In rapid reaching for a target, the movement time MT of reaching the target was empirically found to depended on the distance A of the start point of movement from the target and the target width W—equivalent to the required accuracy of reaching—in a logarithmic relationship $MT = a + b \log2(2A/W)$, where a and b are proportionality constants in this so called Fitts' Law or speed-accuracy trade-off. Since Fitts' Law is a robust phenomenon of human arm and hand movement, many computational models used it as a way to verify their validity. Unfortunately, Fitts' Law could be modeled in many different ways so far, including models from dynamics system theory, noise properties of neuronal firing, and computational constraints in movement planning (for a review see Mottet & Bootsma, 2001,Bullock & Grossberg, 1988). Thus it seems that the constraints provided by Fitts' Law are too unspecific to give clear hints into the organization of the nervous system. Nevertheless, the empirical phenomenon of Fitts' Law remains a behavioral landmark.

Resolution of Redundancy

As mentioned above, when reaching for a target in external space, the excess number of degrees-of-freedom in the human body's kinematic structure usually allows an infinite number of postures for each hand position attained during the reaching trajectory. An active area of research in motor control is thus concerned with how redundancy is resolved, whether there is within and/or across subject consistency of the resolution of redundancy, and whether it is possible to deduce constraints on motor planning and execution from the resolution of redundancy.

Early studies by Cruse et al. (in Bullock, Grossberg, & Guenther, 1993) demonstrated that redundancy resolution was well described by a multi-term optimization criterion that primarily tries to keep joint angular position as far as possible away from the extreme positions of each joint and also minimizes some physiological cost. When starting a reaching movement in a rather unnatural posture, the movement slowly converged to the optimal posture on the way to the goal rather than trying to achieve optimality in an immediate way. This strategy resembles the method of resolved motion rate control in control theory, suggested as a neural network model of human motor planning by Bullock et al. (Bullock et al., 1993). Grea, Desmurget, and Prablanc (2000) observed similar behavior in reach and grasp movements. Given that the final posture at a grasp target was highly repeatable even if the target changed its position and orientation during the course of the reaching movement, the authors concluded that the CNS plans the final *joint space* position for reach and grasp, not just the final hand position. However, the optimization methods by Bullock et al. (1993) could result in similar behavior, without explicitly planning the final joint space posture. An elegant alternative view to optimization methods is suggested in GEOMETRICAL PRINCIPLES IN MOTOR CONTROL, where motor control and planning based on force fields is emphasized. Thus, some more work will be needed before a final conclusion is reached on the issue of redundancy resolution.

Reach and Grasp

The coordination of reach and grasp has been offering at least three important windows into the understanding of motor control. First, reach and grasp require a resolution of redundancy, as outlined in the previous section. However, small changes in target orientation can lead to the need for a drastic change of arm and hand posture at the target, such that movement planning requires carefully chosen strategies for successful control. Second, reach and grasp are two separate motor behaviors, which may or not be executed independently of each other. This issue allows examining the superposition and sequencing of movement primitives. Third, grasping has a more interesting perceptual component than reaching since appropriate grasp points, grasp strategies, and grasp forces need to be selected as a function of target shape, size, and weight. Principles of perceptuomotor coordination can thus be examined in well-controlled experiments, including grasping objects that induce visual illusions.

Among the key feature of reach and grasp are that there is a fast initial arm movement to bring the hand close to the target, a slow approach movement when the hand is near the target, and a preshaping phase of the hand with initial progressive opening of the grip, followed by a closure of the grip until the object size is matched and the object is finally grasped (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995, Arbib and Hoff 1993 in Jeannerod et al., 1995). While early models of reach and grasp assumed independence of these different phases and just executed them in a programmatic way, behavioral perturbation studies, which changed the target size, orientation, or distance, revealed a coupling between the phases (for a review, see Jeannerod et al., 1995), e.g., such that the preshaping partially reversed when the target distance was suddenly increased. Using optimization principles, Hoff and Arbib (in Jeannerod et al., 1995) developed a model of these interactions by structuring the reach-and-grasp system in appropriate perceptual and motor schemas (see SCHEMA THEORY), including abstraction of the multi-fingered hand in terms of two or more virtual fingers to simultaneously model different grip types (e.g., precision grip, power grip) and their opposition spaces for contact selection. This model can also be mapped onto the known functional cortical anatomy in primates. Grip force selection and the anticipation of object properties was studied by a number of authors (e.g.,Flanagan & Beltzner, 2000) who consented that the CNS seems to use internal models to adjust grip force. From studies of the resolution of redundancy, it was concluded that the entire arm posture at the target seem to be planned in advance (Grea et al., 2000), but this result may need differentiation as outlined in the previous section. In general, there seems to be consensus that behavioral features of reach-and-grasp are carefully planned by the CNS and not accidental.

Motor Learning

Due to the continuous change of body size and biomechanical properties throughout development, the ability to learn motor control is of fundamental importance in biological movement systems. Moreover, when it comes to arm

and hand control, primates show an unusual flexibility of how to devise new motor skills to solve novel tasks. Learning must therefore play a pivotal role in computational models of motor control.

One of the most visible research impacts of motor learning was the controversy between equilibrium point control (see EQUILIBRIUM POINT HYPOTHESIS) and internal model control (see SENSORIMOTOR LEARNING and CEREBELLUM AND MOTOR CONTROL). Proponents of equilibrium point control believed that learning of internal models is too complicated to be plausible for biological information processing, while proponents of internal model control accumulated evidence that various, in particular fast, movement behaviors cannot be accounted for by equilibrium point control. At present, there seems to be increasing consensus that internal model control is a viable concept for biological motor learning, and that the equilibrium point control strategy in its original and appealing simplicity is not tenable. Behavioral learning experiments that were created in the wake of the equilibrium point control discussion sparked a new branch of research on motor learning (see SENSORIMOTOR LEARNING and GEOMETRICAL PRINCIPLES IN MOTOR CONTROL). Adaptation to virtual force fields, to altered perceptual environments, or to virtual objects are among the main behavioral paradigms to investigate motor learning with the goal to better understand the time course, representations, control circuits, retention, and functional anatomy of motor learning (see SENSORIMOTOR LEARNING).

Interlimb Coordination

In robotics, the control of two limbs can be accomplished as if the two systems were completely independent, thus simply reducing the control problem to that of controlling two robots instead of one. In biological motor control, such independence does not exist, and a rich area of behavioral investigation examines the computational principles and constraints that arise from the coordination of multiple limbs. In arm and hand control, the approach of dynamic pattern formation (e.g., Kelso, 1995) has been a prominent methodology to account for interlimb coordination. In this approach, motor control in general and interlimb coordination in particular is viewed as an assembly of the required degrees-of-freedom of the motor system into a task-oriented attractor landscape (Saltzman & Kelso, 1987, in Kelso, 1995). Interlimb coordination is thus conceived of as the result of coupling terms in nonlinear differential equations. An important question thus arises as to what kind of equations models the control of movement, and what kind of variables causes the coupling. A variety of models of movement generation with nonlinear dynamics approaches were suggested either based on differential equations that generate movement plans (Kelso, 1995; Sternad, Dean, & Schaal, 2000a) or that directly generate forces (see GEOMETRICAL PRINCIPLES IN MOTOR CONTROL). The origin of coupling between limbs, however, remains an issue of controversy. Possible sources could be perceptual, proprioceptive, purely planning-based, interaction force-based, a preference for homologous muscle activation, or also neural cross talk. By demonstrating that the orientation of limbs in external space can explain a certain class of interlimb coordi-

nation, recent behavioral results (Mechsner, Kerzel, Knoblich, & Prinz, 2001) emphasized that perceptual coupling may be much more dominant than previously suspected. In general, however, there seems to be strong need of detailed computational modeling to elucidate the computational and neuronal principles of interlimb coordination.

Intralimb Coordination

Intralimb coordination is concerned with the question whether there are specific principles of how the individual segments of a limb move relative to each other. The models of arm and hand control that are based on optimal control (see OPTIMIZATION PRINCIPLES IN MOTOR CONTROL) or optimal resolution of redundancy automatically solve the intralimb coordination problem by means of their optimization framework—any kind of special behavioral features would be considered accidental. However, there have also been various pieces of research that examined whether some special rules of information processing of the CNS can be deduced from regularities of intralimb coordination. For reaching movements, simple mechanism of joint interpolation can account of a large set of behavioral features when onset times of the movements in individual degrees of freedom are staggered, an older observation that has been confirmed in the more recent literature (Desmurget, Prablanc, Rossetti, Arzi, Paulignan, Urquizar, & Mignot, 1995). For rhythmic movement, it is interesting how the oscillations in individual DOFs remain phase-locked to each other, and whether there are preferred phase-locked modes (Schaal, Sternad, Dean, Kotoska, Osu, & Kawato, 2000). As in interlimb coordination, models of nonlinear differential equations seem the most suitable to capture effects of rhythmic intralimb dynamics.

Perception-Action Coupling

Most of the behavioral studies outlined in the previous sections were primarily concerned with rather specific aspects of the *motor control*, but not so much issues that involve *perceptuomotor control*. It is, however, the interaction of perception and action that reveals many constraints that the nervous system is based upon. In the behavioral literature, there is a large body of research that examines particular perceptuomotor skills, for instance the rhythmic coordination of arm movement with juggling objects or the interaction of external forces and limb dynamics with the generation of movement (e.g., Sternad, Duarte, Katsumata, & Schaal, 2000b). Unfortunately, it is impossible to expand this topic in this article to its deserved length.

Concluding Remarks

Behavioral phenomena of arm and hand movement have sparked a rich variety of computational models on various level of abstraction. While some topics like internal model control have gained rather solid ground in recent years (Flash & Sejnowski, 2001), there are many other issues that remain controversial and de-

serve more detailed and computational investigations. For instance, the importance of the dynamic properties of the musculo-skeletal system in facilitating motor control, the role of real-time perceptual modulation of motor control, dynamic systems models versus optimal control-based models, etc., offer most interesting topics for the future.

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