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Sensorimotor control of contact force

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Abstract

Interacting with objects in the environment introduces several new challenges for motor control: the potential for instability, external constraints on possible motions and novel dynamics. Grasping and manipulating objects provide the most elaborate examples of such motor tasks. We review each of these topics and suggest that when sensory feedback is reliable, it is used to adapt the motion to the requirements imposed by the object. When sensory feedback is unreliable, subjects adapt the stiffness of muscles and joints to the task's requirements. One of the simplifications introduced in the control of such movements is a reduction in the effective number of degrees of freedom (sensorimotor axes and muscle synergies) and recent findings and methodological considerations relevant to this topic are discussed.

Introduction

Perhaps the most interesting movements that we make are those in which we interact with various objects in our environment. These interactions introduce new challenges and problems for understanding the neural control of movement. One of these is the potential for instability. This arises especially in the use of tools. For example, if a screwdriver is not positioned properly and the force exerted by the hand is not directed correctly, the screw may topple or the screwdriver's blade may slip. Furthermore, in many cases, interaction with an object introduces a movement constraint. For example, when turning the handle on a door, the fingertips must follow the precise arc of the handle. Similarly, when inserting a cork into a bottle, the cork must be positioned properly, and the movement must be precisely vertical. Finally, interacting with an object can introduce novel and sometimes unpredictable forces. For example, when carrying a bucket of water, the natural back and forth motion of the hand can induce oscillations of the bucket. If the water is not to be spilled, these oscillations must be damped by compensatory arm movements.

Perhaps the most exquisite example of the control of contact forces arises in manipulatory movements of the hand and fingers. We use our hands to grasp a variety of objects; we can move these objects around freely in the hand, and we can use hand movements to explore the characteristics of the object, such as its size, shape and texture. In this review we will focus on the general topic of the motor control of contact forces and the sensory information that is utilized. Since the control of grasping has been the subject of several recent reviews (on tactile strategy [1], cortical control [2], and cognition [3]), we will refrain from duplicating topics covered in these reviews. However, since the issue of coordinate systems and degrees of freedom (synergies) has received less attention, we will review this topic in more depth.

Controlling potential instability

Intuitively, a posture or a movement is stable if, following a small perturbation, we can easily return to the same posture or the same path. This intuitive notion of stability conforms to its mathematical definition. Specifically, the criterion for stability is that positive work must be done to produce a deflection from the posture or path. Consequently, at a stable point, the potential energy is at a local minimum. Rancourt and Hogan [4] have provided several examples of motor tasks that are potentially unstable as well as a mathematical analysis of these tasks. Typically, one can define a domain of states that are stable; any state that is outside that domain is unstable. The extent of the domain depends on the limb configuration and impedance. An increase in impedance or stiffness in any particular direction (over the entire range of possible directions) can be actively produced by muscle co-contraction and/or stretch reflexes.

Recently, Valero-Cuevas *et al.* [5] have devised an interesting task that permits an assessment of human strength and manual dexterity. It requires subjects to compress a series of springs in a pinch, the springs varying in their stiffness and in their propensity to buckle. They subsequently provided a detailed analysis of the criterion for stability in this task [6••]; the task is stable provided that the endcap by which the spring is grasped does not rotate by more than a specified amount, the amount depending on the properties of the spring and on the amount of compressive force exerted. They assessed visual and tactile sensory contributions to the feedback control of this task and found that when available, tactile cues predominated, but that the sensory weights were adjusted [7] if tactile cues were unavailable (following digital anesthesia). The paradigm developed by this group is a promising one in that it offers the ability to study postural stabilization in a task that is relatively simple biomechanically. Stabilization of upright posture in standing humans has been the focus of numerous investigations in the last few decades, but that task is much more difficult to model mathematically because of the large number of degrees of freedom [8].

Kawato and his colleagues use a different task that also requires subjects to surmount a potentially unstable situation. They require subjects to make planar arm movements to a target using a robotic manipulandum. The manipulandum is programmed to produce elastic forces acting on the arm as the subject moves (see also [9]), the elastic forces moving the hand away from the intended path [10]. Thus, in contrast to the task just described [6••], there is no stable region; a deviation from a straight-line trajectory will not encounter a restoring force but will instead cause the hand to be pulled away. Subjects learned to compensate by selectively increasing the arm stiffness in the direction of instability, that is, in the direction perpendicular to the intended path. This was achieved by co-contraction of selective sets muscles [11]. Subjects required about six times as many trials to learn this task compared to movements in stable force fields [12], suggesting a different mode of learning. This was supported by a modeling study [13] showing that iterative learning rules that work for the learning of movements in stable force fields will not work in unstable force fields.

Most recently, Kawato and colleagues extended these results by testing how subjects compensate when they are exposed to three different unstable force fields, one perpendicular to the movement path, and the other two at oblique angles [14•]. In all three instances, subjects increased arm stiffness selectively so that it was always largest in the direction of instability. This study showed that subjects have selective control over the extent of co-contraction of shoulder, elbow and biarticular muscles.

To generalize from the results described above, we make the following suggestion. If there is a bounded stable domain, such as in the task studied in [5,6••], subjects rely on sensory feedback to maintain stability. However, if the task is inherently unstable [10–13,14•] and sensory

feedback is ineffective, subjects can learn to selectively increase the impedance of the limb in specific directions and to overcome the instability by this means.

Constrained movements

As mentioned in Section 'Introduction', in a large class of movements the motion is constrained by the characteristics of the object with which we interact, as in turning a door handle. If the motion of the hand does not conform precisely to this constraint, large, potentially destructive, off-axis torques could be exerted on the hand as well as the handle. For this reason, such tasks are notoriously difficult to execute with robots, which are intrinsically stiff. To our knowledge, the control of constrained motion has not been studied in detail. However, following from the results described above, one can hypothesize that their control would also involve the modulation of limb impedance, namely a lowering of the off-axis impedance to allow for deflections from the constrained path.

Constrained movements also involve sensory feedback control, and may involve adaptive variation of finger, hand and arm posture. Imagine the process of running a fingertip along a curved surface to explore its shape. Initial studies of haptic exploration have focused on distortions in perceived shapes [15–17]; fewer studies have investigated the processes of using somatosensory feedback during the movement (see also [1]). Adaptive variation in arm posture has been documented in a task which involved interacting with a hand-held object with novel (but stable) dynamics [18]. Subjects held a spinning gyroscope while they reached to targets in three-dimensional space. Over the first few trials, the subjects went through a process of learning the mechanics of this unusual tool by gradually changing the arm posture. Analysis showed that the observed changes in arm posture were well-suited to learning the dimensions of mechanical resistance provided by the gyroscope.

Novel object dynamics

Interacting with objects can alter the dynamics of the arm in sometimes unpredictable ways. For example, when walking while carrying a pail of water, the motion of the arm can induce oscillations of the pail, resulting in reactive forces on the arm and in turn altering its motion. Furthermore, if the pail is to be stabilized, the motion of the arm has to be modified to damp out the oscillations. Subjects can learn this task as shown by Dingwell *et al.* [19]. In their task subjects had to move a mass coupled to the hand by a spring. To succeed in stabilizing the final location of the mass, subjects had to produce hand trajectories that consisted of two alterations of acceleration and deceleration, that is, the hand had to be decelerated in the middle of the movement. Their results showed that subjects constructed internal models even for these non-rigid objects with unusual dynamics; the learning did not involve merely an increase in limb stiffness. As discussed by Kawato [20], internal models can take two forms: an inverse model maps a desired trajectory into the appropriate forces to produce it, and a forward model predicts the motion resulting from a particular force command. By contrast, in a study of the transport of an object held in a tripod grasp [21••], intrinsic finger stiffness was sufficient to damp the somewhat unpredictable oscillations provided by a pendulum hanging from the object.

A standard question in motor learning paradigms concerns the extent to which skills learned in one locus can be generalized to other spatial configurations [22]. This approach was recently applied to a task in which dynamic interactions between the two hands were produced by connecting them with a (virtual) spring [23•]. Subjects pulled with the right hand and had to resist the force with the left hand. Using a standard design, the investigators interspersed catch trials where the right hand force was not transmitted, and they measured the reactive force generated by the left hand. They then changed the subjects' posture so that the left arm was rotated by 30° but the force direction was unchanged, and determined whether generalization occurred in a frame of reference tied to the arm or to the object. The results depended on the

complexity of the dynamical object (the spring). When the spring configuration was simple, the force was defined in an object-centered frame of reference, but this was not the case when the complexity of the configuration was increased by altering the force direction by means of a pulley arrangement.

Grasping and manipulating objects

Object grasp and manipulation provides the most exquisite example of the sensorimotor control of contact forces and it has been studied extensively. The criteria for a stable grasp are well understood and have been formulated by roboticists [24]. The coefficient of friction of the surface to be grasped requires that the ratio of components of the force tangential and perpendicular to the surface be less than a critical value, limiting permissible contact forces to be within a friction cone (Figure 1a). Experimental evidence shows that subjects regulate this ratio quite precisely [25]. When an object is grasped with several digits (such as in a tripod grasp), additional constraints are provided by the requirements for equilibrium [24,26]. The vertical components of the contact forces (the load forces) equal the object's weight, and the horizontal force components must intersect at a common point (force focus, Figure 1b). This force focus must lie within the intersection of the three friction cones; the larger this area is, the more stable is the grasp (see also Figure 1c). This consideration affects the choice of contact points for grasping [24], but other factors are also likely to be influential. For example, a contact point at a region of high surface curvature would be undesirable, because the direction perpendicular to the surface, and hence the friction cone, could change appreciably if the contact point changes only slightly (Figure 1d).

In fact, subjects are very consistent in their choice of contact points [27] and results from a recent experiment demonstrate that subjects adjust the location of contact points to optimize contact forces. The task involved a five-digit grasp (the thumb opposing the four fingers) of an object with an eccentric weight that tended to rotate the object in the roll direction. If the location of the contact points of the digits is fixed, subjects adjust the contact forces at individual digits to counteract the external torque [28,29]. However, if they are free to do so, subjects alter the location of the contact points, primarily at the thumb and the index finger to minimize the effort required to grasp the object [30].

A concept that has been developed in the field of robotics also shows much promise for the study of the neural control of grasping. This approach characterizes the extent to which force and motion in each of the digits can be transmitted to the grasped object by means of matrix transformations [31]. The result of such an analysis yields velocity and force transmission ellipsoids for displacement and rotation. A similar analysis defines the effective stiffness of the hand plus the object. Thus, this approach provides a computational framework for analyzing grasp and manipulation. The analysis was applied for several different tasks, and showed that the orientations of the ellipsoids varied for objects (e.g. cup, jar, and teaspoon) as well as for tasks (grasping a jar to unscrew the lid versus lifting the jar). The analysis suggests that even when subjects choose identical contact points, they may adjust the posture of the hand in light of the intended manipulation of the object [32].

Hand impedance has been estimated [33] by asking subjects to grasp a handle (the thumb opposing the four fingers) whose aperture gradually increased and by measuring the resultant changes in grasp force. These authors reported values of 150–250 N/m, which is comparable to the reported stiffness of the arm [10,34].

Finally, we should note that the velocity transmission ellipsoid based strictly on finger kinematics may substantially underestimate the extent to which an object can be maneuvered, since it neglects motion of the wrist and of the proximal arm. In fact, it is quite likely that in

rotating a grasped object, much of the imparted motion results from motion at the wrist [35•, 36].

Muscle synergies in grasp and manipulation

The skeletal hand has a large number of degrees of freedom and the number of motor units innervating the hand is even larger. Nevertheless, there is substantial evidence that the effective number of the degrees of freedom, that is to say, the number of degrees of freedom that can be controlled independently, is considerably smaller. For example, the digits of the hand cannot be moved independently of each other [37,38]. Such constraints are commonly referred to as the expression of synergies [8] and a popular approach to define them has been to use principal components analysis (PCA, but see [39,40] for a different approach).

This analysis results in a set of functions that express the pattern of covariation among the mechanical degrees of freedom. Since this analysis has been applied in several different ways, a more detailed discussion of the method as applied to time-varying patterns such as EMG or finger movements is warranted. Consider a set of parameters $\mathbf{p}(t)$, where we define \mathbf{p} to be an n -dimensional vector and define $p_i(t)$ and $p_j(t)$ to refer to two of the degrees of freedom. Also assume that we have recorded m different movements. The usual PCA begins by computing the covariance matrix C_{ij}

$$C_{ij} = \sum_q \sum_m p_{im}(t_q) p_{jm}(t_q) \quad (1)$$

and the subscripts m and q refer to a particular trial and a particular point in time. Each principal component, determined from this covariance matrix, then defines a particular posture [41] or a particular combination (across muscles) of EMG levels. During movement, these patterns are then scaled in time.

A recent example is provided by an analysis of finger motion during haptic exploration and grasping tasks [42•]. This study found that as many as seven principal components were needed to account for 90% of the variance. Remarkably, the same synergies could account for grasping as well as haptic exploration and many were similar to those described previously [41,43].

The synergies as defined above require all of the values of all of the degrees of freedom (e.g. the activity in various muscles) to change together across time. However, this criterion is overly restrictive because it does not coincide with physiological observations. For example, during reaching movements in three-dimensional space, various arm muscles exhibit bursts that are staggered in time [44] (Figure 2a). Computing the covariance matrix in a different manner yields a result that relaxes the criterion of strict temporal covariation of the degrees of freedom.

Specifically, the subscripts i and j in Eq. (1) now refer to trials, while the subscript m now refers to a degree of freedom. This approach has been applied to characterize the kinematics of finger movements during grasping [45] as well as patterning of finger muscle activity during fingerspelling in the American Sign Language [46•]. Figure 2b shows the primary pattern (the first principal component) in the activity of finger muscles as subjects make a wide variety of abrupt (point-to-point) transitions from one static hand shape to another. In this analysis, each principal component was composed of EMG bursts that had a certain fixed phase relation across muscles, that is, a physiological pattern. Note that since the relative timing of bursts in different muscles is fixed (but not necessarily identical), there is a reduction in the number of effective degrees of freedom and a simplification of the control signals required to generate this pattern.

Thus an alternative approach to defining synergies, that is more physiological, has been developed by d'Avella *et al.* [47]. They use an iterative approach to identify the temporal waveforms that correspond to each synergy, with the proviso that the waveforms for different synergies can be staggered in time by amounts that differ from trial to trial. This would be especially useful in tasks where different synergies are used for different components of the task. For example, the transition from motion to exerting a constant force against a surface with the tip of a finger requires two distinct and temporally separate muscle synergies [48•].

Recently, this method was applied to characterize EMG patterns in a task that involving reaching to various objects, grasping them and then transporting them [49•]. The authors found that three synergies could account for 80% of variance. Remarkably, each of the three could be associated with one component of the task: the earliest being related to the reach component, the second to the grasp and the third to the transport phase of the movement. Consistent with this interpretation, the scaling of the second synergy depended strongly on the object shape, while others did so only weakly. A potential drawback of this approach is that the waveforms are not necessarily orthogonal to each other, implying that the primary synergies could change if additional ones were added to the model. However, a recent study showed that the synergies change only slightly when an additional one is added [50].

Tactile sensing in grasp and manipulation

In grasp, the hand is shaped and the contact forces are generated in a largely predictive manner based on prior experience [51,52]. If the grip force is not large enough, peripheral tactile afferents (fast adapting FAI and FAII as well as slowly adapting SAI) signal incipient slip and elicit an increase in grip force at short latencies [53]. A variety of cues are available for adapting the shape of the hand to an object's shape and size. This topic was addressed in a recent study [54•] in which the visual information about an object's size was dissociated from its true size, the actual object being unexpectedly larger or smaller. Subjects adapted their grip aperture to this discrepancy and the investigators showed that neither finger speed nor force at the time of contact provided information about the discrepancy, but that there were reliable timing cues relative to the time of contact.

Behavioral studies have pointed to a role of tactile information from the fingers in a variety of tasks [55]. For example, they have the potential to signal spatial errors in pointing movements of the arm, provided the fingers contact a surface at the end of the movement. How this information is encoded has not been studied, however. Tactile cues are also important in providing information about an object's properties such as shape, size and texture and compliance during haptic exploration [16,56]. Specifically, the orientation of edges contacting the fingerpads is known to be important for shape perception, and this topic has been the focus of a recent study [57–59]. Their studies show a progressive elaboration of this information as one progresses from peripheral afferents to primary (S1) and secondary (S2) somatosensory cortex. Peripheral SAI afferents respond to gratings but they are not tuned to orientation. Orientation tuning is first found in area 3b of S1, with receptive fields restricted to a single finger pad. To the contrary, neurons in S2 are also tuned to orientation, with receptive fields spanning multiple finger pads, providing a potential substrate for encoding object shape.

In haptic exploration, the fingertips are generally swept across the surface of an object, implying that information is acquired serially. Forming the percept of the object's shape thus requires that information be stored in working memory and then integrated. This aspect of tactile sensing has been studied by Romo and Salinas [60], using a task in which monkeys discriminated the frequency of two vibratory stimuli presented in succession. Neurons in S1 responded only to the stimulus as it was presented. However, in S2 and in the prefrontal cortex, the response to

the second stimulus depended on the frequency of the preceding stimulus, thus providing a substrate for the comparisons needed for frequency discrimination.

Conclusion

Humans are obviously capable of learning a large variety of motor skills required for manipulating objects and using implements. Generally, error information on one trial is used to modify movements on subsequent trials to decrease the error and to improve the probability of success. When the error information is unreliable (because the task is inherently unstable or the dynamics are largely unpredictable), limb impedance can be selectively modified to improve motor performance. However, the precise sensory information and the neural algorithms are largely unknown. Thus, the challenge for the future is not to demonstrate that humans can learn a particular motor skill, but to identify the information and the algorithm that is used to do so.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Flanagan JR, Bowman MC, Johansson RS. Control strategies in object manipulation tasks. *Curr Opin Neurobiol* 2006;16:650–659. [PubMed: 17084619]
2. Brochier T, Umiltà MA. Cortical control of grasp in non-human primates. *Curr Opin Neurobiol* 2007;17:637–643. [PubMed: 18294839]
3. Olivier E, Davare M, Andres M, Fadiga L. Precision grasping in humans: from motor control to cognition. *Curr Opin Neurobiol* 2007;17:644–648. [PubMed: 18337084]
4. Rancourt D, Hogan N. Stability in force-production tasks. *J Mot Behav* 2001;33:193–204. [PubMed: 11404214]
5. Valero-Cuevas FJ, Smaby N, Venkadesan M, Peterson M, Wright T. The strength-dexterity test as a measure of dynamic pinch performance. *J Biomech* 2003;36:265–270. [PubMed: 12547365]
6. Venkadesan M, Guckenheimer J, Valero-Cuevas FJ. Manipulating the edge of instability. *J Biomech* 2007;40:1653–1661. [PubMed: 17400231]. Subjects had to compress a spring with the pad of the thumb in a task that measured subjects' strength and dexterity. If the endcap of the spring is rotated too much, the spring will buckle. Thus, the authors can define a stable domain for this task. They develop a model in which sensory visual and tactile feedback is used to control this parameter and they show how performance is affected in the absence of either or both of these feedback components. This is a simple task that has a rich potential for assessing sensorimotor regulation in the face of potential instabilities.
7. Ernst MO, Banks MS. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 2002;415:429–433. [PubMed: 11807554]
8. Ting LH, McKay JL. Neuromechanics of muscle synergies for posture and movement. *Curr Opin Neurobiol* 2007;17:622–628. [PubMed: 18304801]
9. Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 1994;14:3208–3224. [PubMed: 8182467]
10. Burdet E, Osu R, Franklin DW, Milner TE, Kawato M. The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 2001;414:446–449. [PubMed: 11719805]

11. Franklin DW, Burdet E, Osu R, Kawato M, Milner TE. Functional significance of stiffness in adaptation of multijoint arm movements to stable and unstable dynamics. *Exp Brain Res* 2003;151:145–157. [PubMed: 12783150]
12. Osu R, Burdet E, Franklin DW, Milner TE, Kawato M. Different mechanisms involved in adaptation to stable and unstable dynamics. *J Neurophysiol* 2003;90:3255–3269. [PubMed: 14615431]
13. Burdet E, Tee KP, Mareels I, Milner TE, Chew CM, Franklin DW, Osu R, Kawato M. Stability and motor adaptation in human arm movements. *Biol Cybern* 2006;94:20–32. [PubMed: 16283374]
14. Franklin DW, Liaw G, Milner TE, Osu R, Burdet E, Kawato M. Endpoint stiffness of the arm is directionally tuned to instability in the environment. *J Neurosci* 2007;27:7705–7716.7716 [PubMed: 17634365]. This is an extension of the authors' previous work investigating a task in which subjects had to move their arm in a straight line while it was subjected to potentially destabilizing elastic forces pulling the arm from its intended trajectory. Three different force fields were tested. For each, subjects learned to selectively adapt the arm's stiffness in the direction of the forces. The sensory cues that drive this adaptation and the learning algorithm used in this task remain to be elucidated.
15. Fasse ED, Hogan N, Kay BA, Mussa-Ivaldi FA. Haptic interaction with virtual objects. *Spatial perception and motor control. Biol Cybern* 2000;82:69–83. [PubMed: 10650909]
16. Henriques DY, Soechting JF. Approaches to the study of haptic sensing. *J Neurophysiol* 2005;93:3036–3043. [PubMed: 15911888]
17. Lederman SJ, Klatzky RL. Haptic identification of common objects: effects of constraining the manual exploration process. *Percept Psychophys* 2004;66:618–628. [PubMed: 15311661]
18. Flanders M, Hondzinski JM, Soechting JF, Jackson JC. Using arm configuration to learn the effects of gyroscopes and other devices. *J Neurophysiol* 2003;89:450–459. [PubMed: 12522193]
19. Dingwell JB, Mah CD, Mussa-Ivaldi FA. Manipulating objects with internal degrees of freedom: evidence for model-based control. *J Neurophysiol* 2002;88:222–235. [PubMed: 12091548]
20. Kawato M. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 1999;9:718–727. [PubMed: 10607637]
21. Winges SA, Soechting JF, Flanders M. Multidigit control of contact forces during transport of handheld objects. *J Neurophysiol* 2007;98:851–860.860 [PubMed: 17553950]. The authors investigated a task in which subjects had to move an object in different directions in the horizontal plane while holding it from above in a tripod grasp. Reactive forces in this task could be somewhat unpredictable, when a pendular mass was suspended from the object. Force and finger muscle EMG activity failed to reveal active feedback regulation of the contact force. Instead, the authors concluded grasp stability was maintained by compensating for predictable as well as unpredictable inertial forces by controlling the stiffness of the hand through feedforward regulation of hand muscle activity.
22. Shadmehr R, Moussavi ZM. Spatial generalization from learning dynamics of reaching movements. *J Neurosci* 2000;20:7807–7815. [PubMed: 11027245]
23. Ahmed AA, Wolpert DM, Flanagan JR. Flexible representations of dynamics are used in object manipulation. *Curr Biol* 2008;18:763–768.768 [PubMed: 18485709]. This study attempted to define the frame of reference (extrinsic or intrinsic) within which the dynamics of an object that is manipulated are represented. Subjects pulled on a spring with one arm and actively generated an opposing force with their other arm. Posture of the arms could be changed, as could the complexity of the object's dynamics. The authors concluded that object dynamics could be flexibly represented in different frames of reference.
24. Yoshikawa T, Nagai K. Manipulating and grasping forces in manipulation by multifingered robot hands. *IEEE Trans Robotics and Autom* 1991;7:67–77.
25. Westling G, Johansson RS. Factors influencing the force control during precision grip. *Exp Brain Res* 1984;53:277–284. [PubMed: 6705863]
26. Baud-Bovy G, Soechting JF. Two virtual fingers in the control of the tripod grasp. *J Neurophysiol* 2001;86:604–615. [PubMed: 11495936]
27. Lederman SJ, Wing AM. Perceptual judgement, grasp point selection and object symmetry. *Exp Brain Res* 2003;152:156–165. [PubMed: 12879179]
28. Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and principle of superposition during static prehension in three dimensions. *J Neurophysiol* 2005;93:3649–3658. [PubMed: 15728759]

29. Gao F, Latash ML, Zatsiorsky VM. Maintaining rotational equilibrium during object manipulation: linear behavior of a highly non-linear system. *Exp Brain Res* 2006;169:519–531. [PubMed: 16328302]
30. Lukos J, Ansuini C, Santello M. Choice of contact points during multidigit grasping: effect of predictability of object center of mass location. *J Neurosci* 2007;27:3894–3903.3903 [PubMed: 17409254]. Subjects had to grasp an object whose center of mass could be eccentric by grasping it with four fingers opposing the thumb. Subjects were free to choose the location of the contact points of the digits and they reliably altered their locations to counter the effects of the torque generated by the eccentric weight. The contact points of the thumb and the index finger showed the most variation.
31. Friedman J, Flash T. Task-dependent selection of grasp kinematics and stiffness in human object manipulation. *Cortex* 2007;43:444–460.460 [PubMed: 17533767]. The authors illustrate the application of several computational approaches that have been developed by roboticists to human grasp control. They computed matrices that define the extent to which force and movement can be transmitted from the digits to the object, and how these matrices depend on hand configuration. They also computed a matrix defining the effective stiffness of the hand as it grasps the object. The approach is illustrated by several examples (grasping a cup, the lid of a jar, or a teaspoon).
32. Ansuini C, Santello M, Massaccesi S, Castiello U. Effects of end-goal on hand shaping. *J Neurophysiol* 2006;95:2456–2465. [PubMed: 16381806]
33. Zatsiorsky VM, Gao F, Latash ML. Prehension stability: experiments with expanding and contracting handle. *J Neurophysiol* 2006;95:2513–2529. [PubMed: 16319210]
34. Mussa-Ivaldi FA, Hogan N, Bizzi E. Neural, mechanical, and geometric factors subserving arm posture in humans. *J Neurosci* 1985;5:2732–2743. [PubMed: 4045550]
35. Wings SA, Eonta SE, Soechting JF, Flanders M. Multi-digit control of contact forces during rotation of a hand-held object. *J Neurophysiol* 2008;99:1846–1856.1856 [PubMed: 18234979]. Subjects used a tripod grasp to rotate an object in pitch, roll and yaw. Based on a principal components analysis (PCA), two main temporal patterns accounted for the modulation of force and EMG activity of finger and wrist muscles: the largest followed rotational position and the secondary one had a time course that resembled that of rotational velocity.
36. Lacquaniti F, Ferrigno G, Pedotti A, Soechting JF, Terzuolo C. Changes in spatial scale in drawing and handwriting: kinematic contributions by proximal and distal joints. *J Neurosci* 1987;7:819–828. [PubMed: 3559713]
37. Schieber MH, Santello M. Hand function: peripheral and central constraints on performance. *J Appl Physiol* 2004;96:2293–2300. [PubMed: 15133016]
38. Zatsiorsky VM, Li ZM, Latash ML. Enslaving effects in multi-finger force production. *Exp Brain Res* 2000;131:187–195. [PubMed: 10766271]
39. Theverapperuma LS, Hendrix CM, Mason CR, Ebner TJ. Finger movements during reach-to-grasp in the monkey: amplitude scaling of a temporal synergy. *Exp Brain Res* 2006;169:433–448. [PubMed: 16292639]
40. Mason CR, Theverapperuma LS, Hendrix CM, Ebner TJ. Monkey hand postural synergies during reach-to-grasp in the absence of vision of the hand and object. *J Neurophysiol* 2004;91:2826–2837. [PubMed: 14762155]
41. Santello M, Flanders M, Soechting JF. Postural hand synergies for tool use. *J Neurosci* 1998;18:10105–10115. [PubMed: 9822764]
42. Thakur PH, Bastian AJ, Hsiao SS. Multidigit movement synergies of the human hand in an unconstrained haptic exploration task. *J Neurosci* 2008;28:1271–1281.1281 [PubMed: 18256247]. The authors used PCA to characterize finger kinematics during a variety of exploratory finger movements and found that seven principal components could account for >90% of the variance. The analysis assumed that temporal covariation among all of the mechanical degrees of freedom, an assumption that may be overly restrictive.
43. Weiss EJ, Flanders M. Muscular and postural synergies of the human hand. *J Neurophysiol* 2004;92:523–535. [PubMed: 14973321]
44. Flanders M, Pellegrini JJ, Geisler SD. Basic features of phasic activation for reaching in vertical planes. *Exp Brain Res* 1996;110:67–79. [PubMed: 8817258]

45. Santello M, Flanders M, Soechting JF. Patterns of hand motion during grasping and the influence of sensory guidance. *J Neurosci* 2002;22:1426–1435. [PubMed: 11850469]
46. Klein Breteler MD, Simura KJ, Flanders M. Timing of muscle activation in a hand movement sequence. *Cereb Cortex* 2007;17:803–815.815 [PubMed: 16699078]. The authors describe the temporal pattern EMG activity of finger muscles during 27 letter-to-letter transitions as subjects used a manual alphabet to spell a list of words. The authors describe a main synergy beginning with a burst in the 4-finger extensor and a silent period in the flexors, followed bursts in the thumb abductor, thumb flexor, little finger abductor, and finally the finger flexors. This was demonstrated by a PCA designed to account for temporal asynchrony in muscle activation.
47. d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci* 2003;6:300–308. [PubMed: 12563264]
48. Venkadesan M, Valero-Cuevas FJ. Neural control of motion-to-force transitions with the fingertip. *J Neurosci* 2008;28:1366–1373.1373 [PubMed: 18256256]. The authors investigated a task in which subjects had to make a transition from movement to steady force production (tapping the finger and then pressing on a low-friction plate). They show that the force requirements for motion and static force production are incompatible with each other and that there is an abrupt transition from one to the other that anticipates the time of contact.
49. Overduin SA, d'Avella A, Roh J, Bizzi E. Modulation of muscle synergy recruitment in primate grasping. *J Neurosci* 2008;28:880–892.892 [PubMed: 18216196]. The authors have developed an elegant analytic approach to identifying muscle synergies that can account for temporal asynchronies in muscle activation and the transitions from one synergy to another. In this paper, they have applied the technique to an analysis of muscle activation as nonhuman primates grasped and transported a variety of objects. Three synergies could account for >80% of the variance.
50. Vinjamuri, R.; Mao, ZH.; Sclabassi, R.; Sun, M. Time-varying synergies in velocity profiles of finger joints of the hand during reach and grasp. *Conf Proc IEEE Eng Med Biol Soc.*; 2007. p. 4846-4849.
51. Forssberg H, Kinoshita H, Eliasson AC, Johansson RS, Westling G, Gordon AM. Development of human precision grip. II. Anticipatory control of isometric forces targeted for object's weight. *Exp Brain Res* 1992;90:393–398. [PubMed: 1397153]
52. Salimi I, Frazier W, Reilmann R, Gordon AM. Selective use of visual information signaling objects' center of mass for anticipatory control of manipulative fingertip forces. *Exp Brain Res* 2003;150:9–18. [PubMed: 12698211]
53. Johansson RS, Westling G. Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Exp Brain Res* 1987;66:141–154. [PubMed: 3582528]
54. Säfström D, Edin BB, Roh J, Bizzi E. Prediction of object contact during grasping. *Exp Brain Res* 2008;190:265–277.277 [PubMed: 18592227]. This study investigated the cues available to adapt the maximum grip aperture when the size of an object changed unexpectedly from one trial to another. The authors showed that velocity or force cues at the moment of contact were inadequate to account for adaptation, but that timing cues could do so.
55. Lackner JR, DiZio PA. Aspects of body self-calibration. *Trends Cogn Sci* 2000;4:279–288. [PubMed: 10859572]
56. LaMotte RH. Softness discrimination with a tool. *J Neurophysiol* 2000;83:1777–1786. [PubMed: 10758090]
57. Hsiao SS, Lane J, Fitzgerald P. Representation of orientation in the somatosensory system. *Behav Brain Res* 2002;135:93–103. [PubMed: 12356439]
58. Fitzgerald PJ, Lane JW, Thakur PH, Hsiao SS. Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. *J Neurosci* 2006;26:6473–6484. [PubMed: 16775135]
59. Fitzgerald PJ, Lane JW, Thakur PH, Hsiao SS. Receptive field (RF) properties of the macaque second somatosensory cortex: RF size, shape, and somatotopic organization. *J Neurosci* 2006;26:6485–6495. [PubMed: 16775136]
60. Romo R, Salinas E. Touch and go: decision-making mechanisms in somatosensation. *Annu Rev Neurosci* 2001;24:107–137. [PubMed: 11283307]

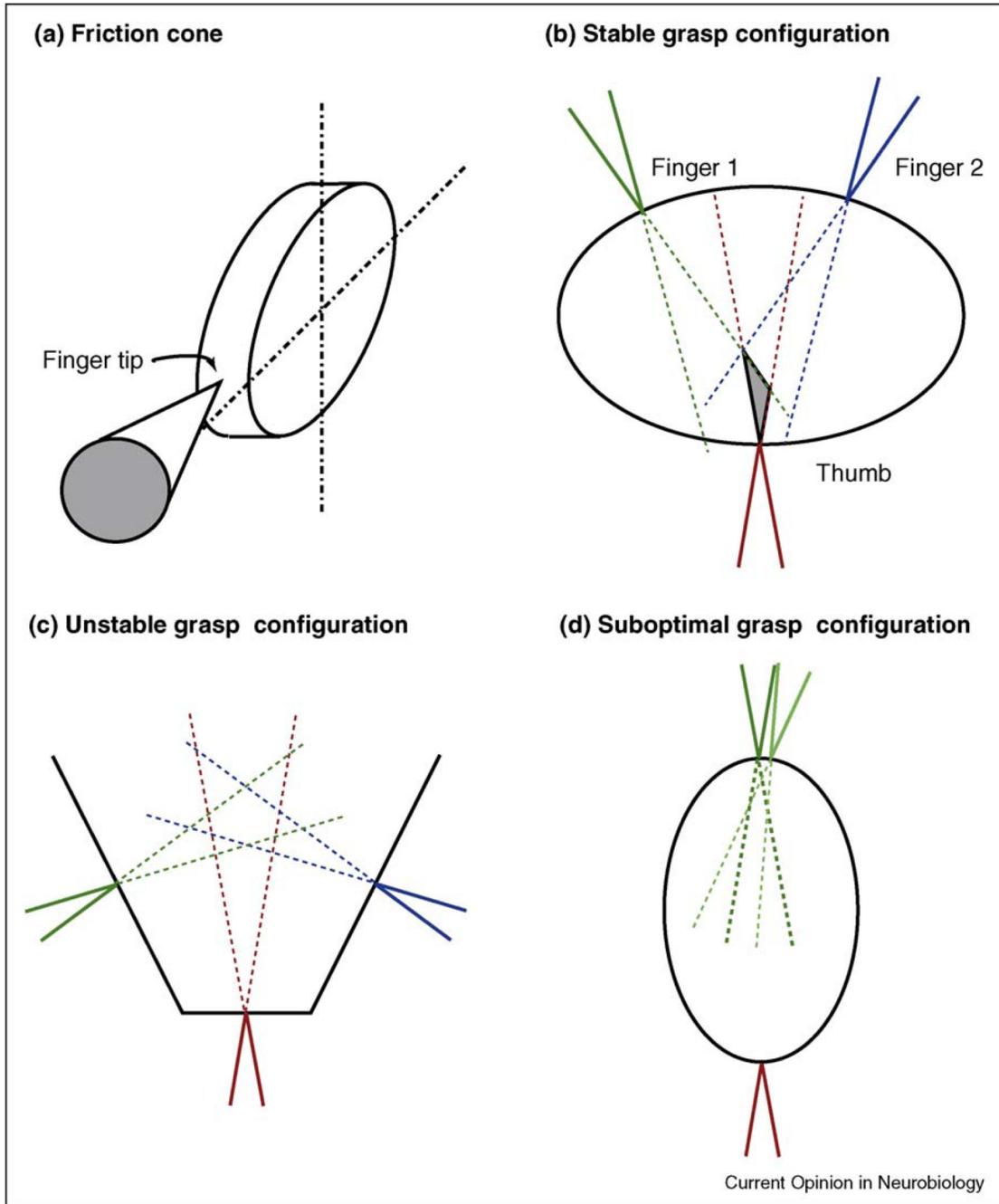


Figure 1.

Criteria for a stable grasp. Friction restricts the force exerted by the finger tip to lie within a friction cone (a), else the finger will slip. The angle of the friction cone is defined by the ratio of the tangential and normal components of the applied force, which must be less than the coefficient of friction of the surface. In a tripod grasp (e.g. the thumb opposing two fingers), the horizontal components of the force exerted by the three digits must intersect at a common point (the force focus, b). The permissible location of the force focus is determined by the intersection of the three friction cones (dark shaded area). Part (c) illustrates an unstable grasp configuration, because the permissible forces exerted by the two fingers cannot oppose the force exerted by the thumb. Part (d) shows contact points in a two-digit grasp that are

suboptimal, because a small change in the location of the contact point (dark green and light green friction cones) alters the direction of the friction cone by a large amount, requiring a compensatory change in the direction of force produced by the opposing digit.

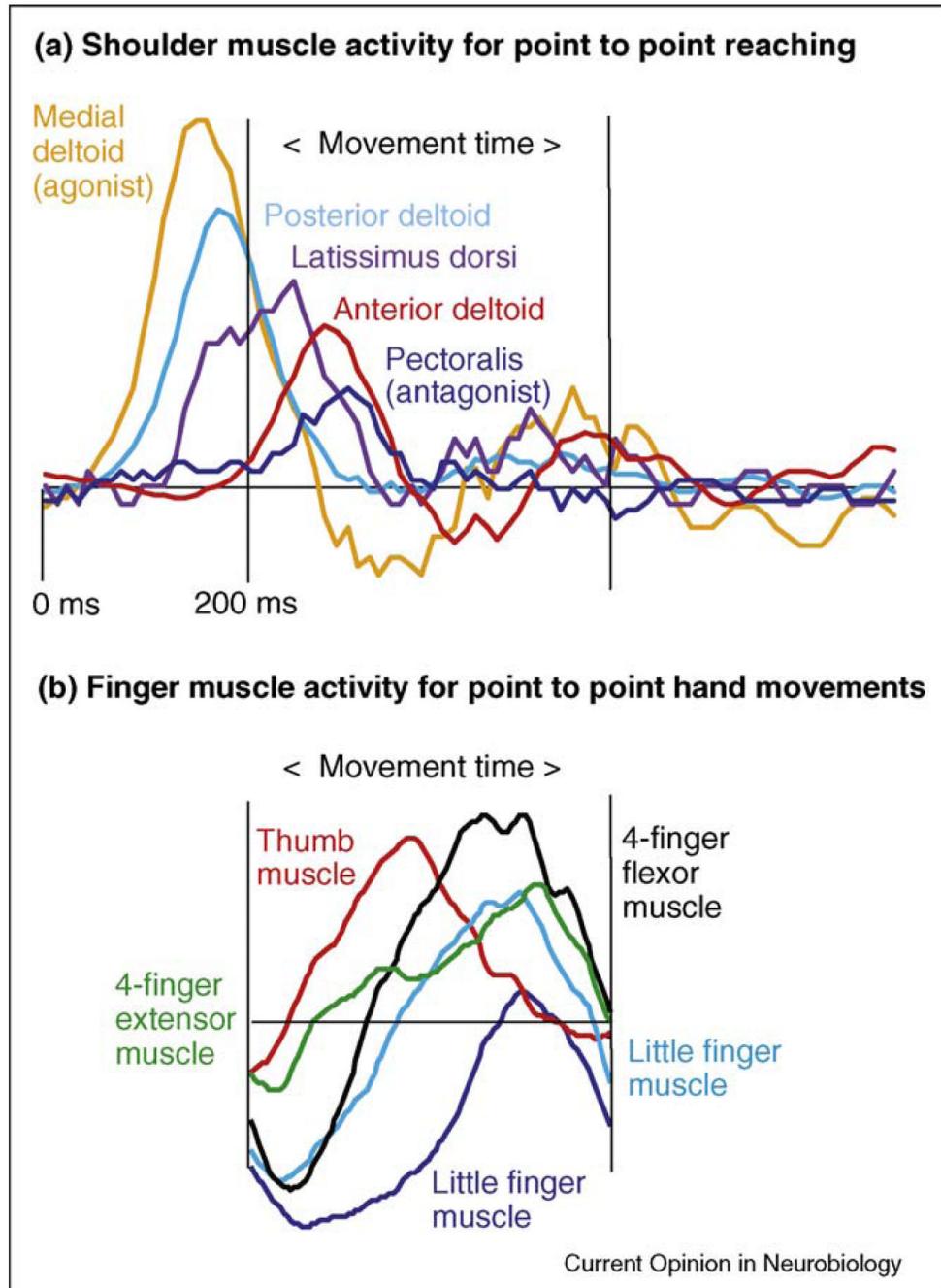


Figure 2. Patterns of muscle activity for arm (a) and hand (b) movements. In (a), EMG activity is rectified, smoothed and averaged across repeated reaching movements. The subject reached with the right arm from a waist-level central target to a target on the right. The EMG related to antigravity forces was subtracted away [44]. In (b), EMG activity was rectified, smoothed, averaged across repeated movement, and normalized in amplitude and time. In contrast to (a), only the first principal component is shown. It was computed across trials for each muscle. The subject made 27 transitions from one hand shape to another as he spelled words using American Sign Language [46]. In both the arm (a) and the hand (b), phasic bursts of muscle activity are staggered across muscles.