**Toward a Physiological Understanding of Human Dexterity**

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**Dexterity, defined as the skillful manipulation of the hands, is now amenable to physiological investigation. Two topics are discussed here: grasping (i.e., hand-object coupling) and bimanual coordination. Dexterity depends on powerful, distributed neural networks and is particularly vulnerable to brain lesions. A knowledge of physiological mechanisms is needed to deal with these neurological problems.**

Infants relentlessly grasp and manipulate objects within reaching distance, typically using both hands. During development, this sensorimotor experience is an important learning process subserving goal-directed manipulatory actions. A sensorimotor memory, often also referred to as an internal model or representation, is created that includes the properties of objects, their form, surface texture, weight, color, smell, and taste. Symmetrical reaching to grasp an object emerges within the first year of life, whereas the bimanual coordination used in everyday life by adults develops more slowly in the second and subsequent years. Full achievement of bimanual and skillful manipulations usually takes six or more years and is typically referred to as “dexterity,” a term that implies dominance of the right hand. However, observations clearly demonstrate that the two hands tend to be specialized for different functions. In right-handers, the left hand typically assumes a postural role for holding the grasped object, thereby providing a body-centered reference frame, while the other hand manipulates the object. Grasping a bottle with the left hand and removing the cap with the right hand is a typical example. It emphasizes that grip formation is a particularly important, basic sensorimotor component of the complex act of prehension. This topic has attracted considerable interest and resulted in much methodological and conceptual progress (6). The physiological understanding of goal-directed skillful manipulations, including the coordination of reaching and grasping and interlimb coordination, as well as the role of vision, proprioception, and internal representations, have also been in the forefront of physiological-behavioral research (5, 17). The purpose of this essay is to: 1) provide a short overview of how the grasping hand adequately secures coupling with the object during holding and moving and 2) discuss the problem of bimanual actions as studied in a task representative of everyday manipulations. The basic proposition is that each hand plays its preferred role, often asymmetric between the two, but constrained into a higher unit of performance and ruled toward proper goal achievement.

**Basic principles of force regulation and methodological aspects**

We developed a drawer manipulandum that requires the use of both limbs for successful goal achievement (Fig. 1). It is equally adequate for measuring the forces in unimanual pulling actions. First, we will briefly introduce some methodological principles about the interplay of forces in the drawer-pulling action. Obviously, subjects have to produce a force to overcome imposed constant or transient loads, friction, and inertia during the dynamic phase of pulling. The application of loads is a convenient way to probe the adaptive power of the pulling hand. The total force that the subject needs to generate is commonly referred to as “load force,” which is exerted against the gravitational or inertial loads and tangentially to the pulling direction. The load of the object partly determines the force that has to be generated for grip formation, i.e., the “grip force,” which is exerted normally on the front handle of the drawer. This force also depends on the surface properties between the object and the grasping fingers. However, the important role of friction has been well documented, particularly by Johansson and Smith and their coworkers (see relevant chapters in Ref. 17). When holding or manipulating an object, the grip force has to exceed the load force to ensure a coupling with the object. The grip force-to-load force ratio reflects the extra-grip force one has to produce to avoid slipping. The “safety margin” is measured formally as the difference between the actual ratio and the slip ratio employed by the subject (i.e., with the subject asked to slowly separate the fingers until the object slips). Friction is the determining factor for the slip ratio. In healthy human subjects and under static conditions, the force ratio is usually a constant and the gain in the linear regression depends on the friction. In a dynamic situation, for example when using a hammer, the load and grip forces continuously change, increasing and decreasing in parallel, to compensate for the inertial forces and secure appropriate hand-object coupling. Obviously, the mechanical laws require a precise coordination of the two forces that concern quite different effectors: proximal ones for transportation and distal ones for hand-object coupling. The beauty of this force coordination lies in its complete automatization. The force ratio has another interesting feature. Since it is usually a constant, the two forces may require only one control variable. This is a nice and concrete example of how the organism can reduce the potentially large number of degrees of freedom in motor control, a proposition first made by the eminent Russian movement scientist Nicolai Bernstein (1). As we will show further on, there are, however, situations when the ratio between...
the two forces is not constant. Obviously we have to allow for some flexibility in biological rules when, in a given situation, a fixed ratio would be counterproductive.

Our second goal was to use the drawer manipulandum for assessing the rules of bimanual coordination in an asymmetric task, similar to manipulations of everyday life. The task was to use one hand (the “pull hand”) to fully open the drawer while the “pick hand” reached toward the opening drawer for picking up and reinserting a small peg placed inside the drawer. Most subjects spontaneously used the left hand for pulling. The goal was achieved at the instant that the index finger reached into the opened drawer for picking up the peg (Fig. 1A). A measure of goal achievement was given by the synchroniza-

tion of the two hands as they arrived at the goal and by the correlation coefficient from the pairs of arrival times. Trajectories were recorded with an optoelectronic system (Fig. 1B). Drawer position and timing signals of discrete events were measured by appropriate sensors and digitized for quantitative analyses (Fig. 1C) together with load and grip forces (not shown).

Adaptive mechanisms in grip formation to predictable and unpredictable changes

When one wants to lift an object, the grip has to be established before lift off, i.e., before the weight can be sensed. To produce the adequate grip and load forces, one has to rely on past experience, i.e., on sensorimotor memory of the object’s properties. If the object is not familiar or was not manipulated before, one is left with “an intelligent guess,” usually on the basis of its appearance. Figure 2A illustrates a representative result for a subject pulling the drawer in an initial series of trials. Whereas the first trial is overscaled and the second somewhat less, the third and all subsequent force pulses generated to secure the hand-drawer coupling settle down to a lower level with a relatively small variance. A similar and well-known erroneous force programming occurs when we lift a large suitcase, not knowing that it is empty. This very simple experiment illustrates an important rule: grip as well as load force are programmed on the basis of an estimate and on past experience, with fine tuning occurring within the first trials. Several lines of evidence suggest that fine tuning is achieved on the basis of sensory feedback that updates the central model of grasp properties (sensorimotor memory). The high precision of how the grip force is coordinated with the load force is indicated by their low ratio. In our experimental condition, this ratio was between 1.1 and 1.5 (see Fig. 2C). With smooth surfaces, e.g., when using moist fingers, the ratio may be much higher. The need for sensory feedback is evident from investigations in patients who have lost their large sensory afferents. Since they have no ability to update their internal model, they constantly overscale their grip force, which results in an abnormally high ratio. Interestingly, it has been found that overscaling may also occur in patients with central neurological disorders (e.g., basal ganglia and cerebellar diseases), which might implicate networks concerned with the central representations.

Often our actions are executed in an unstable, disturbing environment. An external perturbation might occur either predictably in cases of regular repetitions or when visually captured before its impact (e.g., catching a ball), or one might occur unpredictably. A typical example from everyday life is going on a walk with a dog on a leash. When the appearance of a cat produces a sudden pull, it is likely that the inattentive master will lose the leash together with the dog. Alternatively, he/she may anticipate the situation and tighten the grip before the dog decides to rush away. By means of the drawer manipulandum, it is easy to mimic the above event, as illustrated in Fig. 2B. The condition when the subject knows that during the whole series no external load perturbation will occur when pulling the drawer to a self-stopped position is illustrated at left. At middle and right, trials from a second series in the same subject in which short perturbing load pulses occur midway...
Our own actions are also prone to self-induced perturbations to which we do not pay much attention. Again, using the drawer manipulandum, one can easily demonstrate that self-induced load impacts also generate the appropriate adjustments. This can be shown when subjects are instructed to pull the drawer until its mechanical stop is reached (11), as is often done with drawers of furniture. Figure 2C displays the temporal profiles of drawer position, grip force, and load force. The vertical dashed line indicates the moment that the drawer hits the mechanical stop. The impact results in an immediate (not reflexive) spike-like peak of load force. The dashed lines, diverging from the grip force and load force profiles, indicate the approximate course of the forces if the subjects had stopped the pulling movement just before the impact. Alternatively, when the drawer is pulled to the end producing the impact, the grip force, after having reached the first programmed peak related to movement onset of the drawer, resumes its increase until the moment of impact. After, a small extra peak follows before a steep decay in grip force. Thus the ramp-like increase in grip force occurs in anticipation of the impending impact. This is a proactive adjustment that prevents hand slippage on the drawer due to the impact. In contrast, the reflexive and small reactive adjustment occurring after the impact is probably of little functional significance, at least in this particular situation. Note that the grip force diverges from the load force that stabilizes or even decreases before impact. This is also expressed in terms of the increased force ratio that prevents slipping at the impact. Here we demonstrate that the rule of a constant ratio can indeed be broken. The primacy lies in goal achievement, i.e., to have the proper coupling force at the time of the impact. If the load force were to augment in parallel with the grip force before impact, the intensity of the impact would increase. This would obviously be a counterproductive situation, with the increased likelihood of losing contact with the drawer at impact. Rather, the amount of anticipation usually correlates significantly with the amount of load force at impact.

Proactive anticipatory adjustments rely on the ability to recognize potentially dangerous situations. This is a cognitive mechanism that is expressed as “motor set.” It can be assessed both quantitatively and objectively. In the case of self-induced perturbations, we have observed that children up to about eight years of age do not use the same strategy as adults. Initially, they often lose the drawer when they hit its mechanical stop. In subsequent trials, they use slow, probing pulls. Adults almost invariably use the strategy illustrated in Fig. 2C. Again, subjects are not aware of this proactive adjustment. Nor are they aware that they increased their grip during random load perturbations. We have observed that the above proactive adjustments are often lacking and/or replaced by a default strategy of overscaling in patients with cerebrovascular accidents (4), which interfere with cortical functions, and those with cerebellar (12) and basal ganglia (10) lesions.

The bimanual drawer task is performed with a goal invariance

Video sequences of our subjects have already revealed a perfect coordination of the two hands as they reached the goal in near synchrony. For quantification, the most valuable measures were interlimb synchronization and correlation (9). Since an opened drawer is the prerequisite for picking up the peg in
the drawer recess, the pull hand arrived at the goal with a small phase advance. Synchronization at the goal typically occurred with an interval of 50–100 ms and a smaller variance compared with the variance in the timing of the individual limbs. Figure 3 illustrates the results from a representative healthy human subject. In Fig. 3A, the histograms of time intervals between the go signal and the arrival times are shown for the two limbs, respectively. Interlimb measures are shown in Fig. 3B, with synchronization intervals and a regression plot between the movement times of the two limbs. Typically, the timing of the individual limbs is more variable than the synchronization interval (in this particular case, 61 ± 54 ms). The high correlation coefficients further indicate that the two limbs covary, i.e., are under a common control. A goal invariance of the coordinated action with variable movement components of the individual limbs is a characteristic feature of goal-directed actions (1). It has also been termed the “principle of motor equivalence” (8).

Demonstration of motor equivalence by imposing task constraints

One could argue that, in the above drawer task, bimanual coordination was controlled visually. It was clear, however, that when subjects were blindfolded, the goal invariance did not deteriorate. Although the two limbs moved more slowly, synchronization and correlation were preserved and were sometimes even better than that achieved with vision. When an asymmetry was introduced by increasing the load on the drawer that slowed down the action of the pulling arm, the other limb immediately adjusted its speed for maintaining goal synchronization. A cutaneous nerve block of the index finger and the thumb used for pulling the drawer greatly disturbed and prolonged the pulling action, with frequent slips of the grip and high variability of the reach trajectories. As a consequence, the other arm also slowed down in reaching toward the drawer. But again, the goal invariance was essentially preserved due to the covariance of the two limb movements, with high correlation coefficients of ~0.9. These adjustments in the unaffected limb were completely automatic, and none of the subjects was aware of what had happened. Some of the human subjects, and particularly monkeys that were trained over long periods in a similar drawer-pulling task, were equally well or even better limb synchronized at the goal than at movement onset. These cases are particularly interesting because they show that a coordinative control may intervene while the synergy is unfolding between movement onset and reaching the goal.

Planning, goal achievement, and postlesion motor equivalence

Intuitively, conscious planning of an action is centered on the goal of the action, rather than on the selection of individual effectors or on the single limbs in the case of bimanual actions. Walking, playing games, writing, and so forth, are all learned actions that we perform easily under many different conditions. An often-cited example is writing a letter with

FIGURE 3. Time structure in a control subject performing a series of 25 bimanual actions on the drawer manipulandum. Note the relatively larger dispersion in the time histograms of the individual limbs than in the histogram of goal synchronization. The synchronization value and the correlation coefficient for the arrival times at the goal are the quantitative measures for temporal coordination.

movements confined essentially to the hand and fingers, writing larger characters on the blackboard by use of whole arm movements. These are examples of the motor equivalence mentioned by Lashley (8) and Bernstein (1). In the case of bimanual synergy, it appears that the two limbs are constrained into one “virtual limb,” which also allows, however, for asymmetric task assignments (e.g., the drawer task). This means that the individual limbs are controlled in a subordinate fashion in a “top-down” coordinative bimanual control system.

Bethe (2) in Germany, Lashley (8) in the United States, and Bernstein (1) in Russia were well aware that purposeful goal-oriented actions require the selection of effectors to be flexible and adaptable to the actual environment. Bethe particularly emphasized the enormous flexibility in switching effectors for the appropriate condition. He and Lashley also insisted that these physiological adaptations come equally into play at peripheral or central neurological lesions. For example, stroke patients soon learn to write with whole arm movements while the proximal effectors are regaining their function. Shifting to other effectors (i.e., motor equivalence) can sometimes manifest itself even quite shortly after lesions.

We were able to confirm the occurrence of motor equivalence after cortical lesions in monkeys performing a bimanual drawer synergy (7). The drawer task was essentially the same as described above for human subjects, except that the reaching distances were adapted to the monkeys’ particular limb geometry. The animals were highly motivated and very well trained. They received a reward for each trial, i.e., a small piece of a cookie, which they picked up from the opened drawer recess.
Between the bilateral lesion’s effects on the individual limbs was an evident difference in their coordination. Figure 4 shows the striking difference in synchronization between the limbs before and after a bilateral lesion in the mesial-frontal cortex of a monkey trained to perform the bimanual drawer task. Arrows indicate time of the lesion. Whereas the lesion resulted in a massive prolongation of the individual limb movements (A and B), goal synchronization ($C = B - A$) and the interlimb correlation coefficient (before lesion, $r = 0.927$; after lesion, $r = 0.956$) were not significantly changed. This is a clear-cut and quantitative demonstration of motor equivalence.

Following mesial frontal cortical lesions, including the supplementary motor area, the goal invariance (i.e., the coordination of both hands) was not disrupted. In two cases with relatively small unilateral lesions, we found a postoperative delay in movement initiation of the contralateral limb compared with the control values. In one case with a large and bilateral lesion, initiation was also delayed and, in addition, the reaching movements were conspicuously slowed down. All monkeys adapted to the situation, however.

After development of an asymmetric deficit due to a unilateral lesion, the delay in the leading pull arm was quickly matched by a similar delay in the unaffected limb. In another monkey with a similar unilateral lesion, the contralateral non-leading arm was delayed. After a few training sessions, however, this monkey adapted to the delay by speeding up its reaching to match the delayed onset. As a result, both of these monkeys with unilateral lesions were again well synchronized shortly after the surgical intervention.

In the case of the animals with large bilateral lesions, synchronization was also soon restored due to an exquisite covariation of their two limbs. Figure 4 shows the striking difference between the bilateral lesion’s effects on the individual limbs displaying a high variance; but these limbs’ “bimanual coordination” was at low variance, with almost unchanged interlimb synchronization and correlation.

The characteristic adaptive behavior, which underscores the high flexibility of the organism, also comes into play in the context of postlesion recovery processes. This aspect of “plasticity” (in a broad sense) is much neglected in the currently topical field of neural repair in animal plasticity research. To cite Paul Weiss (15): “Since coordination exists at all levels, disturbance of coordination at any one level need not imply disturbance or disruption of coordination at the others. Disregard of this fact accounts for much of the confusion in past discussions of functional regulation, re-integration, re-education, compensation, etc.”

**What do we know about neural mechanisms involved in bimanual coordination?**

A number of propositions have been made. Generally speaking, it is reasonable to assume that there are interlimb communication lines and/or a common control system for both limbs. Apraxic patients with lesions in the posterior parietal cortex of the dominant hemisphere may have difficulties in bimanual coordination. There are a number of reports (reviewed in Ref. 16) that mesial frontal lesions may produce coordinative defects of the two limbs. Rather dramatic (albeit rare) cases have been observed following extensive cortical lesions within the frontal-prefrontal midline structures, including the supplementary motor area, and sometimes also including the corpus callosum. Without reviewing details, we can cite Paul Weiss (16) that mesial frontal lesions may produce coordination defects of the two hands. Apraxic patients with lesions in the posterior parietal cortex of the dominant hemisphere may well contribute to coordinated control networks in bimanual actions. At present, however, there is no compelling evidence that one specific structure or commissure is crucially responsible for bimanual coordination. In view of the critical functional importance of a precise and consistent neural control of the coordination of the two hands, it seems most likely that such control is achieved by widely distributed systems, which function in cooperation and include the participation of the cerebellum and basal ganglia. As yet, non-functional imaging techniques have enabled the identification of the brain areas crucially responsible for bimanual coordination. Again, frontal midline structures, including anterior cingulate areas, have been implicated. Few motor tests are amenable to the rather constraining “tunnel” that is required for imaging measurements (PET, fMRI). In most such studies, a rhythmic task was used with the fingers moving in either a mirror-like (in-phase) or parallel (antiphase) mode. It has been shown that the more difficult antiphase rhythmic movements produce more activation than the easier in-phase bimanual movements (14). Whether this is due to the extra load of bimanual coordination vs. a higher demand in attention is still unclear, however.

The existence of covariation of the upper limbs during bimanual actions is indicative of interlimb communication and is also compatible with the notion of common central representations (the “internal model”) for feedforward controls distributed to the two limbs. Alternatively, each limb may be co-
controlled by representations in its contralateral hemisphere. Adjustments might then be generated as the bimanual synergy unfolds. Most synergies last 1 s or more, leaving enough time for propioceptive signaling from one limb to the other, especially from the leading hand to the following hand. This option remains to be further explored. Interestingly, it has been shown that kinesthetic signals may be transmitted from one limb to the other limb within 150 ms (3). Therefore, “online” adjustments may perhaps function as a fine-tuning device for terminal synchronization, leaving the major job to the “internal model” with its feedforward control. It has been suggested, however, that feedback to the internal model has an important role in updating the model according to changing constraints. A potential link might be realized in the cerebellum. We have explored this possibility in patients with chronic bilateral and relatively large cerebellar lesions. As a population, these patients had a clear-cut deficit in synchronization, which is present at both the start and at the goal (13).

Conclusions

Grip force and load force largely vary together, with the ratio being the controlled variable, thus reducing the many degrees of freedom in motor control. The principle of a fixed force ratio can be overruled in dynamic situations, however, when an increased ratio is needed. This was the case with self-induced impact and when load forces tend to go to very low values (not shown). Proper goal achievement (i.e., not losing the drawer) has the primacy.

Adaptive flexibility to external changes in the physical environment is a fundamental property of the organism. Whenever possible, the organism uses a feedforward (i.e., proactive) mode of adaptation, particularly in the case of self-induced perturbations. If external disturbances are expected, even if unpredictable in their exact time, subjects adapt by scaling up their grip force in anticipation of the upcoming perturbations. This important mechanism of motor set requires a research approach at the behavioral level, i.e., with both intact (nonreduced) experimental animal preparations and human subjects. Quantitative probing of the grasp function will undoubtedly disclose deficits in cognitive aspects of motor control in neurological patients.

For bimanual goal-related tasks, the individual neural controls for the two limbs are subordinate to a higher-order cooperative coordinative control system. Changing constraints for one of the limbs is typically compensated for by the other limb, thereby ensuring goal achievement. Similar physiological mechanisms of adaptive behavior, including bimanual actions, can be observed in brain-lesioned animals and in neurological patients.

Although the underlying neural mechanisms subserving bimanual coordination are still poorly understood, there is nevertheless an increasing body of observations that suggests that information from one limb can be retrieved rapidly by the partner limb. The most likely major control is effected from a high-level internal model of the task that can be updated by feedback information, in accordance with changing external and/or internal constraints. In addition, “online” temporal adjustments may operate at lower levels, including the cerebellum, for fine-tuning of an evolving bimanual synergy.

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References