



The Task at Hand

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1. INTRODUCTION

Most of our actions are directed at objects in the world about us. Key components include our ability to perceive the qualities of an object and, having decided that it is appropriate to a task, to reach for it (with one or both hands), grasp and lift it, manipulate it or use it to act on some other object, and finally place it back down. While holding the object we can appreciate its attributes, confirming and extending the information available from vision. The incoming sensory information from the hand also serves a role in establishing the success of manipulative action, ranging from confirming the stability of the object in the hand's grasp to the provision of information about the relative motion of parts of the object.

This chapter is intended as an introduction to themes such as these, which are taken up in greater detail in the rest of the book. We start with a slightly tongue-in-cheek characterization of the manipulative functions of the hand. This serves the purpose of identifying many of the major issues that recur throughout the book. We then provide a brief summary of a number of the methods used to study neural control of hand function. Although not exhaustive, this section will help orient the reader to the variety of techniques that will be encountered later in the book. A glossary of important terms is provided at the end of the book in order to assist the reader with the wide range of specialist topics covered by researchers working in a variety of disciplines.

2. NEWTON'S APPLE

The ease with which healthy adults pick up, transport, and manipulate objects belies the complexity of the task from the point of view of neural control. Yet this complexity can become all too apparent when we observe the very young, the elderly, or people with neurological damage (e.g., following a stroke due to a cerebral vascular accident, CVA) attempting to perform a simple, everyday task such as pouring a drink. In order to illustrate the control issues involved in reaching, grasping, and manipulation, suppose we could join Sir Isaac Newton in the kitchen garden at Trinity College, Cambridge, where he is pondering the laws of motion in the comforting shade of an apple tree. Suppose further he is beginning to feel somewhat hungry, yet there are several hours to go before he will be able to assuage his appetite at high table in college that evening. At this point his attention is attracted by a shiny red object in the tree, the image of which strikes his retina.

Now, Sir Isaac's brain must solve the following problem; how can it translate the perceived location and shape of the object into a set of muscle commands that will bring his hand to the vicinity of the apple and shape it appropriately for grasping? Fundamental to this process is a *sensorimotor transformation* from a sensory frame of reference (or coordinate system) appropriate to the retina to a motor frame of reference in which commands to the muscles are specified (Chapter 8). This transformation might involve intermediate representations. For example, the apple could be represented in a coordinate system, which would take as input information about eye direction relative to the head and orientation of the head relative to the body. This representation might then be mapped onto an appropriate posture for the arm, defined by particular shoulder, elbow, and wrist angles and only subsequently transformed to specify corresponding levels of activity required in selected muscles.

Of course, it is unlikely that our eminent don would have been distracted from his meditations on integral calculus without first having identified the shiny red object as an apple. Thus, his visual system is not only required to identify object location. It must also provide information that allows object identification based on access to long-term memory. Presumably color, shape, and location in a tree allow our genius to figure out that the object affords eating. However, recent neuropsychological studies suggest that there are *separate visual systems* subserving cognition and action (Chapter 2). Thus, curiously, it is conceivable that, if Sir Isaac had brain damage resulting from a stroke he might be able to use visual information to recognize the apple, that is, perceive it in terms of being able to describe its attributes, but not be able to plan an accurate reach to grasp it!

Let us return to consider how Sir Isaac's central nervous system (CNS)

would define a posture for the hand and arm so as to allow the apple to be grasped. Here, we encounter what has been termed the *degrees of freedom problem* (Chapter 9), which can be cast in terms of the following question. How is a specific posture to be selected from the large number of possible postures, any one of which would result in the hand encompassing the apple (even if some of them would leave our don looking rather inelegant)? Six numbers (degrees of freedom) are required to specify the location of a rigid object in three-dimensional space; three for position (x,y,z) and three for orientation (yaw, pitch, and roll). However, the joints of the arm allow 7 degrees of freedom; flexion-extension, abduction-adduction, and humeral rotation at the shoulder; flexion at the elbow; flexion-extension, abduction-adduction, and pronation-supination of the wrist. Thus, the arm with the hand fixed around an object has one surplus degree of freedom that allows some freedom of choice of elbow position.

The advantage of an extra degree of freedom (*kinematic redundancy*) is that it allows flexibility in selecting postures. Thus, even if there were a branch in front of the apple, Newton might still be able to achieve his goal of placing his hand on the apple by keeping his elbow out around the obstacle. The drawback to kinematic redundancy is that the brain must select among the alternative postures. What criteria or rules may be used to narrow down the options to any particular arm configuration? The problem is nontrivial considering just the shoulder, elbow, and wrist. It becomes an order of magnitude greater when we consider the further degrees of freedom contributed by the digits of the hand. These underlie our ability to grasp objects in many different ways employing all variety of grips (Chapter 12), but again this variety contributes to the issue of selection from multiple alternatives.

Thus far, we have considered only the final posture of the hand and arm. However, Newton will have to move his hand from some other position (maybe he had been using it to scratch his head as part of his cogitations). How should the path from initial to final position be chosen? One theoretical approach to movement control suggests that the brain is concerned only with end posture and that the path taken by the hand is merely a by-product of the commands associated with that change in posture. However, our ability to avoid obstacles between start and end points of a movement (and not only avoid collisions with the hand but also with the arm and particularly the elbow), suggests the brain plans a specific spatial path for the hand (and arm) through space. Again, the CNS must deal with a redundancy problem in that it must identify a particular path and associated kinematics (together defining a *goal trajectory*) from many that are possible. Moreover, in reaching to grasp there is the further question: how will *hand shape* develop and be coordinated with arm movement as the hand approaches the apple (Chapter 13)?

Once movement trajectories for the arm and hand have been planned,

Sir Isaac's motor system must determine the forces required to generate the desired motions. In movements involving several joints, this is a difficult problem because of mechanical interactions between limb segments. The motion of a given joint depends not only on the muscle forces acting on that joint but on the motions of other joints as well. Failure to allow for such interactions can lead to large discrepancies between intended and actual movement paths (Chapter 10). These errors could be compensated for by *feedback control* in which corrections are made on the basis of the moment-to-moment discrepancy between the intended and actual paths. However, feedback corrections are necessarily subject to sensorimotor transmission delays in the CNS, which create further problems. Therefore, some researchers have proposed instead that the CNS uses an *internal model* of the dynamics of the limb in order to compute the muscle forces necessary to realize planned trajectories. The advantage of such a control scheme is that if the CNS can specify accurate forces, there will be less need to monitor feedback.

Up to this point, we have considered only the reaching movement to the apple. However, much of the real action begins when Newton's illustrious hand contacts the fruit. The task then becomes one of establishing a *stable grasp*, plucking the apple from the branch, and then transporting it back for inspection and eating. Let us assume that, in order to pluck the apple, Sir Isaac grasps it with a precision grip using just the tips of the thumb and index finger. Because the apple is still attached to the branch, to prevent his fingers slipping over the surface as he pulls, Newton squeezes it. This increases the *grip force* at right angles to the surface of the apple and this, in turn, results in an increase in the friction between his skin and that of the apple, which counters the *load force* created by his pull.

To break the apple from the branch, Newton increases his pull and the rise in load force requires closely coordinated increases in grip force to prevent slipping. It might be assumed that past experience in handling apples, perhaps at the supermarket, would allow Newton to *predict* how hard he has to squeeze an apple for a given load force. However, if the apple is more slippery than he expects (perhaps because the Trinity undergraduates were earlier polishing the college apples as a class exercise in aesthetic appreciation), the grip force will be too low and the apple will start to *slip* from grasp. Fortunately for our natural scientist, this unexpected slip will likely stimulate mechanoreceptors in the skin (Chapter 19). The resultant afferent signal, following a path that probably takes in sensorimotor cortex, leads to a reflex increase in grip force with a delay sufficiently short to reestablish grasp before the fingers slip off the apple.

Generating force with the thumb and index finger to hold the apple in a stable grasp produces a variant on the degrees of freedom problem described

earlier. Several muscles act on each digit (Chapter 4) and there is considerable redundancy in their contribution to increasing grip force. How should their relative contributions be determined? One way in which Sir Isaac's motor system might solve this problem is to reduce the number of individual elements that need to be controlled by exploiting coordinative *synergies* between muscles. That is, if subsets of muscles are constrained to act as a unit with a fixed relation between their levels and timing of activation, then the CNS could control these units rather than individual muscles (Chapter 3).

Having plucked the apple, Sir Isaac's grip must be directed to produce a frictional force to counter the force of gravity acting on the apple. At this stage his prior judgment of the apple's weight might help him select a grip force sufficient to prevent the apple dropping out of his hand. However, once the apple is detached from the tree, sensory information from cutaneous receptors will provide him with indications of grasp stability. Taken in combination with information about the level of effort required to hold the apple, this might lead him to revise his *weight estimate* (Chapter 20). With the apple free of the branch Newton can then begin to transport the apple toward him. This requires he first accelerate and then decelerate his hand. This creates *inertial forces*, which, in combination with the apple's weight, will tend to cause the apple to slip from grasp. So, as an addition to the trajectory planning required in moving the hand, transporting the apple implies preparing commands to the hand muscles to take account of the forces created by the kinematics of the planned path (Chapter 15).

Let us now imagine a different scenario and suppose that at the very moment Sir Isaac spots the object of his desire (or the apple of his eye), it starts to fall from the tree above him. Ever quick, he reaches to catch the apple. This *interception* task is considerably more complex than reaching for a static object, since it requires prediction of the path of the apple in time and space. Moreover, he also has to deal with the impact when the apple strikes his hand; here, he is assisted by reflexes probably involving sensorimotor cortex (i.e., *supraspinal reflexes*) that help stabilize the hand at the time of collision. Unlike fixed spinal reflexes that involve response only in the stretched muscle (Chapter 18), the anticipated collision means the supraspinal reflex triggers responses in both wrist flexors and extensors in a manner that contributes to absorption of the apple's impact (Chapter 11).

Whichever route brings the apple to hand, Sir Isaac now wants to inspect it in case some insect has gotten to it before him. Here he has a number of options. Holding the apple in one hand he may run the tips of the fingers of his other hand over it, seeking any softness or blemish in the otherwise smooth rounded form of the apple. This is termed *active touch*; through his own voluntary movements he picks up sensory information about the apple

(Chapter 21). By using active touch, Newton can extract richer sensory information than that obtained under passive touch conditions created, for example, by a colleague moving the apple for him while he rests his fingers on the surface. During active touch, cutaneous (and proprioceptive) sensory information is likely modulated by the CNS. This modulating, or *gating*, presumably enables Newton's brain to attenuate unwanted sensory information and enhance information that is important to the task at hand (Chapter 16).

Vision provides an alternative to touch for inspecting the apple. However, bringing all parts of the apple into view requires that Newton manipulate it to rotate it in his hand. If carried out without the help of the other hand, this involves *dexterous manipulation* with contrasting movements of several digits. For example, one strategy involves the application of force (or more accurately, torque) around an axis defined by the line between the thumb and index finger grip points. This torque can be supplied by movements of the ring finger. However, the fingers share a number of muscles in common (these are located in the forearm and attached by long tendons running over the wrist). Therefore, when commanding ring finger movement, Sir Isaac's motor system must compensate for the potential concomitant disturbance to the index finger (Chapter 5). Given the complexity of the underlying neural circuitry required to achieve this, it is perhaps not surprising that, as a preschooler, Izzy (as he was known to his friends at that time) could not achieve such dexterity. In fact, the fine finger control improves over a number of years and likely reflects the *development* of specialized neural connections in the spinal cord (Chapter 7). A further issue in such dexterous manipulation is the role of sensory feedback in controlling the induced motion. This includes information from receptors not only in the skin but also in muscles and joints (Chapter 17).

On inspecting the apple, Sir Isaac discovers a blemish in the form of a small hole in the apple and suspects that there may be an unwelcome visitor in it. He therefore takes out his handy Swiss pocketknife (presented by a visiting scholar) to investigate. The functional use of a tool requires *bimanual coordination* whereby the apple is supported in one hand and operated on by the other. Bringing the hands together and working on the apple requires that movements in one hand be precisely matched by complementary moves of the other to preserve their relative positions (Chapter 14). The cost of an error in such skill is a cut (which makes laboratory study of such tasks difficult to get past today's ethical committees!). Such coordination of the two hands calls on additional neural resources including the supplementary motor area (Chapter 6). With deft use of the blade, Newton uncovers a worm. He puts down the knife and pulls the worm out, which requires a particularly sensitive precision grip so as not to squash it, then proceeds to enjoy the fruits of his labor.

3. METHODS USED IN THE ANALYSIS OF THE MOTOR FUNCTION OF THE HAND

Our extended example in the previous section illustrates certain key problems in hand movement control, and these recur throughout this book. In particular, the issues of coordination of multiple degrees of freedom and of sensory guidance are to be found in both behavioral and neurophysiological studies. While tasks (and the subjects performing them) vary widely, the common underlying theme is how does the brain control complex movement for effective goal-oriented action.

The research described in this book includes a wide range of methods, from several different scientific disciplines, which have contributed to our understanding of the relations between brain activity and hand function. Some of these methods may be unfamiliar to some readers, and we now briefly review a few of the principal methods that have been used to study manual dexterity. These are: kinematic recording, recording patterns of muscle activity using electromyography, the tracing of neural connections using specialized chemicals, electrophysiological recording from single neurons in the brain, magnetic stimulation of the brain, and functional brain imaging.

In recent years, optical tracking systems have been developed that allow simultaneous quantitative measurement of the trajectory in three-dimensional space of several points on the moving limb. These systems have allowed researchers to study the coordination between different parts of the body during a single movement, as, for example, between the preshaping of the hand and the movement of the arm when grasping an object. However, there is no a priori guarantee that the kinematic information recorded directly reflects the neural program that the brain uses to control movement. Therefore, researchers have often suggested that measures that appear consistently under a wide variety of conditions reflect the underlying neural control (the so-called argument from invariance). Alternatively, kinematic recording can be used in conjunction with measurement of forces and a biomechanical model of the limb to infer torques acting around joints, which some researchers take to be more directly relevant to understanding muscle action.

When a muscle contracts, it produces a low-voltage electrical signal that can be recorded with electrodes placed on the surface of the skin over the muscle and suitable high-gain amplification. The recording is known as the *electromyogram* (EMG). The relation between the magnitude of the EMG and muscle tension is somewhat controversial, but it does allow comparisons between the amount of activity in an individual muscle under different circumstances. Problems can arise if comparisons are made of EMG amplitude across different muscles, because differences in signal level can arise from

factors such as the distance of the electrodes from the muscle. However, the temporal pattern of muscle contraction, for example, the times at which each of a pair of muscles increases its level of activity, may be compared. This timing information can provide useful clues to the various neural pathways contributing to a muscle contraction. Different pathways having different lengths and numbers of synapses from a known stimulus site will produce muscle responses at correspondingly different latencies.

An understanding of the relations between hand and brain is obviously helped by an understanding of the neural pathways carrying afferent information from hand to brain, and efferent information from brain to hand. Several chapters in this book report anatomical studies that have traced these pathways in monkeys, in order to model their structure and function in humans. The *anatomical tracing* techniques are simple to describe, but technically demanding to carry out. They involve injecting small quantities of a chemical (called the tracer or label) at a known location in the nervous system of an animal, which is often identified by electrophysiological recording (see below). The tracer is then transported away from the injection site throughout the neuron, as part of the cell's normal metabolic transport processes. Depending on the tracer used, this transport may be orthodromic (same direction as the nervous impulse) or antidromic (opposite direction). After a suitable interval, the animal is sacrificed and slices of neural tissue are reacted with further chemicals. Microscopic examination can then reveal sites to which the original tracer has been transported. Tracing studies not only tell us where neurons project, but also what sort of connections they make. Many corticospinal cells, for example, branch in the spinal cord to synapse on motoneurons of different muscles. The physiological contribution of each branch may be unclear, but the consistency of the anatomical finding in tracing studies suggests that this distributed feature of neural control of the hand may be involved in precisely tuning the coordination of the fingers.

While anatomical studies tell us that a neural pathway exists, *electrophysiological recording* from single neurons in the brain tells us more about what the pathway does, since it reveals what aspects of the sensory or motor task the particular neuron is specialized for. The method involves inserting a fine electrode into the brain of an animal with the aim of penetrating a single neuron, and recording the individual neural impulses in that neuron during the task being studied. Single unit studies of the sensory system typically examine the tuning of a neuron by systematically varying the parameters of a stimulus delivered to the animal, and plotting the amount of firing as a function of the appropriate stimulus parameters.

Most single unit studies of the motor system have correlated the discharge pattern with physical parameters such as force or direction of move-

ments made by trained animals or even with motor unit discharge patterns (obtained from EMG recorded with fine wire electrodes in the muscle rather than using the surface electrodes referred to earlier). A complication of working with the motor system is that behavior must be controlled so as to obtain an appropriate range of movement parameters. Moreover, control conditions must be run to check that environmental stimuli are not the source of the observed neural firing patterns. However, a benefit of studying the motor system is that, in principle, the role of the single unit may be studied by direct stimulation while recording effects on motor unit discharge of relevant muscles. (There is now a noninvasive procedure for stimulating cortical tissue; transcranial magnetic stimulation of the brain. TMS involves creating a strong localized transient magnetic field near the scalp, which induces current flow in underlying neural tissue.)

For obvious ethical reasons, invasive physiological recording of brain activity is only rarely possible in humans, for example, when neurosurgical procedures require electrodes be placed on or in brain tissue for functional assessment purposes. In the last century considerable progress in understanding the function of various areas of the human brain came from correlating behavioral deficits associated with information about the underlying neural lesions (e.g., due to a CVA) derived from postmortem examination. Such studies were often made difficult because patients survived for quite long periods following their initial illness and possibly incurred further brain damage. In the second half of this century, this methodological difficulty was alleviated by the development of X-ray techniques (computed tomography, CT) that provided high-resolution images allowing living brain tissue to be differentiated from areas of lower-density tissue associated with brain lesions.

Recently, the endeavor of mapping function onto brain regions has received a considerable boost from new brain scanning procedures capable of providing images of normal brain function. These procedures differentiate areas according to their metabolic activity, which in turn is determined by neural signal transmission levels. One of these (positron emission tomography, PET) relies on the detection of decay of radioactive particles (using a radioactive marker previously introduced through the blood). This procedure requires relatively long periods (several minutes) of sustained activity (e.g., repetitive finger movements) to build up a picture in which elevated activity of the relevant area (finger region of primary motor cortex) emerges from background levels of activity in other areas. In contrast, the technique of functional magnetic resonance imaging (fMRI), which has the advantage of not requiring the use of radioactive markers, can build up a picture over relatively short periods of 10 s. Both procedures obviously have important medical applications, but they are also significant for allowing behavior to be mapped onto concurrently active regions of the brain.