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# COGNITIVE NEUROSCIENCE

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## CHAPTER 5

# Voluntary movement: computational principles and neural mechanisms

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### 5.1 VOLUNTARY MOVEMENT DEFINED

Movements of body parts comprise a large variety of motions (e.g. from small finger movements to locomotion) produced for various behavioural purposes (e.g. reach towards an object, manipulate an object, run away from a predator). Which of these movements are voluntary? Clearly, reaching to an object of interest is a voluntary motor act, but is arm swinging during walking, or running for life from a predator voluntary as well? In a way they are not because, for example, the arms swing while we walk without our intentionally willing them to do so, and we run away from a predator because our life is in imminent danger and, therefore, we have no choice. However, in both these cases, we can do otherwise *if we choose to do so*: we can walk without swinging our arms, and we can stay immobile when the predator approaches. However, we *cannot stop* other movements that are usually the result of brain damage, especially in a group of nuclei within the so-called basal ganglia. For example, people with lesions of a small nucleus in the basal ganglia, the subthalamic nucleus, frequently move their arms unwillingly in wild, throwing motions, a condition called hemiballismus; and the various dyskinesias consist of movements of body parts that happen without the patients willing them to, but also without the patients *being able to stop them* either. Therefore, these movements are called *involuntary*. Strangely, the best definition of *voluntary movement*

seems to be the opposite of involuntary movement, that is a movement that *can be suppressed* (or not initiated at all) *at will*. This comes from the fact that involuntary movements are well defined and possess the cardinal feature that they come and go by themselves, and that they cannot be suppressed or not initiated. This then serves as a good background against which to define voluntary movements.

## 5.2 COMPUTATIONAL ASPECTS OF VOLUNTARY MOVEMENTS

Practically all voluntary movements are quite complex across several dimensions. Consider, for example, reaching towards and manipulating an object of interest: the reaching movement looks graceful and feels effortless, and the hand manipulates the object by continuous, expert movements. This apparently simple, natural act involves the coordinated activation and relaxation of many muscles acting about several joints of the arm and the hand each of which possesses a number of degrees of freedom in motion and which, together, provide an enormously complex system from the computational point of view. Then consider playing the piano, dancing or an acrobatic performance: the complexity now extends to the time as well as the space dimension; not only is a precise coordination of muscles and joints needed to achieve a particular movement, but the movements of different body parts also have to be co-ordinated continuously in time and space for these motor skills to be performed. Lastly, consider standing on a tightrope. In this case you need just the opposite, that is to suppress irrelevant movements and assume a posture that will balance yourself very precisely so that the centre of gravity of your body does not fall outside the safe margin dictated by your stance and you do not fall on the ground. All these cases are quite different and can be performed well after a period of practice. The computations involved, if one were to solve these problems in a straightforward, brute-force manner, are prohibitively large. This is due mainly to the combinatorial aspect of the problem, in the sense that the same goal can be achieved in an almost infinite number of combinations of muscle activations and joint motions; for example, you can reach an object through a very large number of movement trajectories which correspond to a large number of different combinations of muscles and joints. Although these are serious issues for modellers, fortunately, they do not seem to pose problems for the organism because movements are typically performed in a stereotypical manner and with several constraints, so that the degrees of freedom are reduced appreciably. For example, quadruped locomotion involves regular alternation of stance and swing phases associated with cyclical changes in many

joint angles and concomitant activation and relaxation of flexor and extensor muscles acting about those joints; this reduces the practically infinite ways of combining the motion of all the joints in four limbs, and the activation of muscles in these limbs, to specific constrained, co-ordinated motions and muscle activations. Similarly, the reaching movement involves well co-ordinated and tightly linked motions about the shoulder and elbow joints (Soechting & Lacquaniti 1981) that position the hand in desired locations in space. This reduction in the degrees of freedom is a common property in the motor system (Bernstein 1967). It seems that the brain controls movements of the limbs as a constrained, linked system rather than as an aggregate of independent units. In this chapter we discuss the properties of reaching movements and the neural mechanisms involved in their control.

### 5.3 REACHING MOVEMENTS

Reaching movements involve motions at the shoulder and elbow joints. These motions result from the application of torques generated about each joint by the contraction of muscles. The muscles activated and the temporal course of the intensity of their contraction will depend on the movement trajectory in space, the velocity of the movement and the magnitude and direction of fixed or changing external loads. The relations between the temporal pattern of these torques and the trajectory of the hand are complicated even for two-dimensional hand trajectories (Hollerbach & Flash 1982). This is true both for deriving the trajectory given the torques (integral kinematics) and for deriving the torques at each joint given the trajectory (inverse kinematics).

In general, the patterns of activation of muscles during reaching movements are very complicated. This is due to several factors. First, these movements are implemented by the concomitant contraction of several muscles. Therefore, a population of muscles has to be considered rather than an agonist-antagonist pair, as is usually the case for movements around joints possessing a single degree of freedom (e.g. elbow). Secondly, the exact contribution of each muscle to the torques generated at each joint in the course of the movement is often difficult to measure because the direction along which a muscle will exert its mechanical action may change during the movement. Thirdly, a complete analysis of the muscular patterns of activity subserving these movements has to take into account the relative timing differences between the evolving contractions of the muscles involved, because such differences may affect the movement trajectory. This problem is further complicated by methodological considerations. For example,

muscle activation is usually assessed using electromyographic (EMG) methods, yet there is no general agreement concerning the relations between the EMG activity and the force exerted by the muscle. This is an especially difficult problem in the case of pinnate muscles, the fibres of which do not run along the axis between the insertion points of the muscle; in this case, for an approximate assessment of the relation between the EMG activity and the force developed along that axis and within different compartments of these muscles, the geometrical arrangement of the fibres must be considered.

In spite of these complexities, some principles of muscle activation during reaching are evident. For example, in an EMG analysis of movements made by monkeys in eight different directions on a plane, it was found that at least ten muscles acting on the shoulder joint and girdle were involved (Georgopoulos et al. 1984). The magnitude of EMG activation was correlated significantly among several muscles, which suggests that the movements were subserved by muscle synergies. Moreover, these synergies differed in an orderly fashion from the direction of movement. Although similar considerations may apply to unconstrained reaching movements in three-dimensional space, at the present time we lack an adequate description of the simultaneous muscle patterns in this general case.

#### 5.4 PATHS AND TRAJECTORIES

A path is the sequence of positions that the hand follows in space; a trajectory is the time sequence of these successive positions (Hollerbach & Flash 1982). Handpaths of unconstrained reaching movements made on the sagittal (Soechting & Lacquaniti 1981, Atkeson & Hollerbach 1985) or horizontal (Morasso 1981, Gordon et al. 1994) plane are usually straight or slightly curved. Their velocity profile is dome shaped and, if no emphasis is placed on accuracy, it is single peaked. The curve may become slightly asymmetric with practice, with the ascending, accelerating slope steeper than the descending, decelerating slope (Beggs & Howarth 1972). The shape of the velocity profile is essentially unaffected by the location of the movement vector in space, in contrast to joint motion (Morasso 1981).

The shape of the velocity profile is probably determined by the strategy for making the movement (Nelson 1983). First of all, a basic strategy that subjects follow in reaching is to arrive near the target with a single movement that covers most of the distance to be travelled. Moreover, the acceleration of the movement changes continuously, so that there is no portion of the movement in which the velocity is

constant. We do not know why or how this strategy is adopted. It is acquired gradually during infancy, and breaks down in Parkinson's disease. The initial reaching response of infants is composed of a series of smaller movements, and it is only later that the large amplitude, initial component develops (von Hofsten 1979). In Parkinson's disease the first movement component is too small, and a series of smaller movements is employed by the patient to get to the target (Flowers 1975).

### 5.5 ACCURACY OF REACHING

The accuracy of reaching is defined with respect to its target. The trajectory itself is not commonly constrained, although accuracy boundaries could be placed on it as well. P. M. Fitts investigated the accuracy of open-loop reaching at targets in different locations in extrapersonal space (discussed in Georgopoulos 1986). In the first series of experiments pilots memorized the letter-coded locations of 20 targets and reached with a pencil at a requested target while fixating a red light in front of them. The subjects did not see the target areas which were constructed like a bull's eye, so that the accuracy of reaching could be determined directly. Movements directed straight ahead were most accurate, whereas those directed low, on either side and slightly behind were least accurate.

In two-dimensional reaching movements, the errors in pointing comprise errors relating to the direction and amplitude of movement (Gordon et al. 1994). The variability of movement end-points along the axis of movement reflects errors in movement amplitude and increase markedly and non-linearly with distance from the origin of the movement. On the other hand, the variability of movement end-points perpendicular to the axis of the movement reflects errors in the direction of the movement, and is generally smaller than the variability due to amplitude. Moreover, directional errors increase proportionally with distance, which indicates that the directional variability, in *angular* terms, is constant and independent of distance. These findings suggest that the direction and amplitude of movement are planned separately.

### 5.6 MOVEMENT TIME AND THE SPEED-ACCURACY TRADE-OFF

The duration of the reaching movement is a behaviourally important variable because it specifies how quickly the target will be reached.

With respect to dynamics, changing the time of moving between two points involves a substantial recomputation of the joint motion dynamics. Hollerbach & Flash (1982) found that these computations could be simplified by scaling the joint torques according to the speed desired. Indeed, it seems that human subjects adopt a strategy compatible with this scaling procedure (Hollerbach & Flash 1982). These results suggest that the overall movement speed could be specified at a behavioural level and implemented with no increase in computational load. This would be a behavioural advantage for the subject, especially during motor learning. For example, "one might conceive of a practice strategy beginning with slow movements to learn the basic torque profiles, then simply scaling these profiles to increase the speed of movement" (Hollerbach 1982: 192).

In the absence of accuracy constraints, the movement time tends to remain constant as the amplitude of the movement increases, due to an increase of movement speed with movement amplitude. However, in the presence of accuracy constraints, there is a trade-off between the speed and the accuracy of the reaching movement such that more accurate movements are performed more slowly, and, conversely, faster movements are less accurate. This phenomenon has been studied extensively (see Keele 1981, for a review). It seems that the increase in movement time under conditions of increased accuracy requirements results from an increase in the number of corrective movements that bring the hand on the target following the large amplitude, first component of the movement.

### 5.6.1 Information transmission

Fitts (1954) applied an information-theoretical approach to the relations linking movement time, accuracy and distance. He calculated the rate of information transmission during an aimed movement as follows:

$$I_p = -\frac{1}{t} \log_2 \left( \frac{W}{2A} \right)$$

where  $I_p$ , the index of performance, is the information transmitted in bit/s,  $t$  is the movement time,  $W$  is the target width, and  $A$  is the movement amplitude. The term  $-\log_2 (W/2A)$  is the index of task difficulty. It is a composite measure of informational load, relating to both accuracy and distance. The upper limits of information transmitted by human subjects vary with the task (Fitts 1954) and decrease with age (Welford et al. 1969).

### 5.7 DEVELOPMENT OF REACHING IN INFANCY

The capacity to reach to objects of interest develops gradually over a period of several months after birth. However, a rudimentary form of eye-hand co-ordination is present in the newborn (von Hofsten 1982), and it is on this background that visual reaching is established. The characteristics of forward extensions of the arm towards a moving target were investigated in infants from the 15–18th to the 36th week of age (von Hofsten 1979). Remarkable changes in reaching skill were observed, so that at the end of the observation period it closely resembled the adult pattern. At the age of 12–16 weeks, reaching consisted of a series of movements, as judged by the zero crossings in the acceleration record. About 80% of reachings consisted of three or more serial movements. This resulted in long, fragmented movement paths, in which the first movement covered no more than 40% of the total distance. In contrast, at 36 weeks of age, the first movement covered more than 70% of the total distance. In addition, there was a decrease in the fragmentation of reaching. In fact, the essence of the development lay in the gradual build-up of a dominance of the first movement towards the target, so that at the end of the observation period the reaching response consisted predominantly of one forceful movement that brought the hand near the target, a pattern which resembles that observed in adults. It is interesting that reaching was better to a fast-moving target (15 and 30 cm/s), as compared with a stationary or slowly moving (3.4 cm/s) target. In fact, there were clear indications that some of the reaching movements were predictive in nature (von Hofsten 1980).

### 5.8 VISUAL GUIDANCE OF REACHING

The behavioural repertoire of reaching to a target does not consist of the arm movement alone but includes concomitant movements of the eyes and the head towards the target. All these responses are generated in parallel, for the latency of *muscle* (EMG) activation of the head and arm muscles, and of changes in the electro-oculogram are almost identical when subjects are instructed to track a visual target, when it appears, by eye, head and hand as quickly as possible, without specifying a sequence in those movements (Biguer et al. 1982). In contrast, the latency of the onset of the *movement* of the eyes, head and arm differ, that of the saccade being the shortest and that of the arm being the longest (Biguer et al. 1982). This is due to the different inertial loads that have to be overcome before movement begins. These observations concerning the practically simultaneous muscle activation and the rank

ordering of the onset times of the eye, head and arm movements in reaching seem to reflect a central pattern, because they were unaffected when vision of the arm was eliminated (Biguer et al. 1982). The sequencing of movement onsets can be of particular significance, because the eye movement may be completed before the arm movement has even started, due to the high velocity of the saccade (Biguer et al. 1982). In fact, if eye or head movements are not allowed, reaching to eccentric targets is very inaccurate (Prablanc et al. 1979a). The contribution of the eye and head movements to the accuracy of reaching is probably due to both the foveation of the target *and* the visual monitoring of the hand movement, because allowing the saccade to occur in the absence of vision of the hand did not improve reaching accuracy at eccentric targets (Prablanc et al. 1979a).

This brings us to the question of visual guidance of reaching. There are at least three aspects of this problem: first, visual localization of the target in extrapersonal space and suitable coding of that information for use by the arm motor system; secondly, visual monitoring of the hand before and during its movement through space; and, thirdly, visual adjustment of the final position of the hand to touch, grasp or retrieve successfully the object of interest.

The coding of absolute target position in space is a large subject that is usually treated in the context of perception rather than movement. It will suffice to mention that the perceived location of the target need not coincide with the location used by the motor system to direct the arm. This was shown, for example, in experiments in which subjects were asked to hit with a hammer targets illuminated at different positions in space during the onset of a saccade (Skavenski & Hansen 1978). Remarkably, the subjects hit the targets accurately, despite the fact that they were uncertain about the location of the target and their high success rate.

The monitoring of the arm and hand motion throughout reaching is apparently important for accurate performance. Reaching is more accurate in the presence than in the absence of vision of the arm just before (Prablanc et al. 1979b) and during the movement (Conti & Beaubaton 1976, Prablanc et al. 1979a,b). Since this improvement was observed even for movements that were completed within 200 ms, it was proposed (Paillard 1982) that visual cues from arm motion are being processed at higher speeds than the times (190–260 ms) assumed necessary to utilize external visual feedback (Keele & Posner 1968).

Two visual systems that process information related to the movement of the arm and hand during reaching have been identified (Paillard 1982, Jeannerod & Biguer 1982). Their contribution to the visual guidance of movement and the cues they use have been studied

in experiments that allowed separate control of target and hand vision through a coloured filter in normal and split-brain monkeys (Beaubaton et al. 1978). In other experiments, continuous or stroboscopic illumination was used to dissociate position from motion cues during the course of prismatic adaptation in human subjects (Paillard et al. 1981). It was found that one system utilizes central vision ( $8^\circ$ ), is facilitated by the presence of a foveated target, and analyses positional (displacement) cues, because it is unaffected under conditions of stroboscopic illumination (Paillard et al. 1981). Presumably this system subserves the accurate placement of the hand on the target near the end of the reaching movement. The other system employs peripheral vision and analyses motion cues, as evidenced by its impairment under conditions of stroboscopic illumination. More importantly, the motion cues that seem to be meaningful to this system are those arising from the motion of the arm when *actively* moved by the subject but not when passively moved by the experimenter (Paillard et al. 1981). These findings are consistent with earlier results which suggested that the development of visually guided reaching depends on "self-produced movement with its concurrent visual feedback" (Held & Hein 1963). In general, the two visual systems mentioned above resemble the distinction made previously by Trevarthen (1968).

Paillard (1982) has summarized the implications of these findings as follows. There are three aspects of visual information that are utilized in reaching. The first concerns the visual localization of the target in space. Although this information can be restricted to one hemisphere, it can effectively be used to trigger reaching by either arm. The second piece of visual information concerns the relative position of hand and target; and the third comes from the motion of the limb across the visual fields. The last two cues are processed most efficiently by the hemisphere contralateral to the moving arm (Beaubaton et al. 1978).

### 5.9 SPATIAL PLANNING OF REACHING

Reaching as a behavioural act is the result of a complex sensorimotor coordination. Reaching itself is a complicated multijoint movement directed to a defined point in space and performed under behavioural and biomechanical constraints. In self-paced, cyclical tasks in which alternate reaching movements are performed between two targets, the planning, initiation and execution of successive movements will overlap partially in time. In contrast, in reaction time (RT) tasks in which, for example, a fast aiming movement has to be made in response to a stimulus, it can be assumed that a good part of the planning process

happens during the RT. Several aspects of this process have been studied successfully using RT paradigms, such as the specification of the direction and extent of movement (Gordon et al. 1994), as discussed above.

In general, it has been assumed that the duration of the RT reflects the difficulty in generating a response, given a certain stimulus. The least complicated case is that of a *simple* RT task, in which a response (e.g. movement of the hand) is required as soon as a stimulus is presented. In contrast, in *choice* RT tasks the response is contingent on making a decision concerning specific attributes of the stimulus. For example, given a set of two responses (e.g. movement of the left or right hand) and two stimuli (e.g. a blue and a red light), a choice RT task could be as follows: "move the right hand in response to the blue light, and the left hand in response to the red light". Choice RT increases with the number of alternatives  $N$  involved in decision-making; in fact it is a linear function of stimulus uncertainty ( $\log_2 N$ ) (Hick 1952).

Is the RT of a movement aimed at a target a simple or a choice RT? It is not a simple RT because the response is constrained by the location of the stimulus, but if it is a choice RT, what are the choices? Assuming that the movement starts from the same point in space and is of constant amplitude and accuracy, it is reasonable to suppose that the choices will be determined by the number of targets presented in a task, because each target specifies a different movement. Yet, it is remarkable that the RT under these conditions may increase only slightly, or not at all, with stimulus uncertainty (Sanders 1967, Georgopoulos et al. 1981), probably because reactions toward the source of stimulation are fast (Simon 1969) and because aimed movements are usually highly practised and possess a high degree of spatial compatibility with the target. Both of these factors have been shown to reduce the effect of stimulus uncertainty on choice RT (Mowbray & Rhoades 1959, Brainard et al. 1962). Therefore, reaching movements seem to be generated very efficiently, as if there were a short link between the target and the movement directed to it. This link is probably based on the strong similarity between the ways in which the target and the aimed movement are coded spatially, according to theories of stimulus-response compatibility in the spatial domain (Fitts & Seeger 1953, Wallace 1971, Duncan 1977).

Another interesting feature in the planning of reaching movements is that they can be elicited in quick succession as responses to changing targets during the RT, without the delays usually observed in other tasks under similar conditions; that is, without a psychological refractory period (PRP). The PRP is a delay beyond the normal RT that is observed in the response to the second of two stimuli presented in quick succession. The occurrence of a PRP has been well documented (for a

review see Bertelson 1966). The most widely accepted explanation is the single-channel theory, which postulates that there exists a gated channel of limited capacity that cannot handle the stimulus-response requirements of both stimuli simultaneously; therefore, the generation of responses to the two stimuli are treated sequentially and without overlap. When the second stimulus is presented during the RT to the first stimulus, the successive processing of information results in a delayed response to the second stimulus (i.e. in addition to its own RT); this additional delay equals approximately  $RT_1 - ISI$  (where  $RT_1$  is the RT to the first stimulus, and ISI is the interstimulus interval). Indeed, a PRP of the predicted magnitude has been observed in several studies (for a review see Bertelson 1966). It is remarkable, therefore, that a PRP is practically not observed when the required responses are reaching movements. This has been documented in behavioural experiments in monkeys (Georgopoulos et al. 1981) and human subjects (Soechting & Lacquaniti 1983, Massey et al. 1986), and in neurophysiological studies in the motor cortex of monkeys (Georgopoulos et al. 1983b).

These results probably reflect the highly efficient information processing of aimed movements due most probably to the high spatial stimulus-response compatibility and extensive practice, as discussed above. In fact, the information transmitted during the second of two reaching movements made in quick succession was much more than that of a single reaching movement (Massey et al. 1986), as evidenced by its shorter duration in spite of its larger amplitude and constant accuracy.

### 5.10 EFFECTS OF BRAIN LESIONS

Reaching to targets is affected by general motor disorders that affect the initiation, performance or braking of the movement. These disorders include, for example, paralysis or paresis, akinesia, hypotonia and ataxia. In some cases it is difficult to distinguish between such a fundamental disorder and a particular defect in reaching. In contrast, the accuracy of reaching can be affected in the presence of normal motor function. This is mostly observed with lesions of the posterior parietal areas of the cerebral cortex. Defects in reaching have been observed in both human subjects and subhuman primates. For example, lesions of the posterior parietal cortex of monkeys result in defective reaching to visual targets in space (Ettlinger & Kalsbeck 1962, LaMotte & Acuna 1975).

The most interesting cases are furnished by patients suffering from "optic ataxia" (Hécaen & de Ajuriaguerra 1954, Rondot et al. 1977,

Perenin & Vighetto 1993). These patients usually do not have impaired vision or impaired hand or arm movements, but show a severe impairment in visually guided reaching in the absence of perceptual disturbance in estimating distance. In several cases an oculomotor disorder may be present, but in others eye movements are normal. Misreaching cannot be accounted for by motor disability of the limb or a visual defect. Thus, other movements are performed well, and visual functions in the field where misreaching occurs are carried out normally, despite the occasional presence of amblyopia.

The syndrome of optic ataxia is complex, and several variants of it exist. The brain damage in cases of optical ataxia has been localized in the parietal cortex (angular and/or supramarginal gyrus), its underlying white matter and/or the posterior part of the corpus callosum. Although some of the defects in eye-hand co-ordination in that syndrome can be attributed to the destruction of the parietal cortex itself, others are best understood as disconnection syndromes produced by the interruption of pathways linking the posterior parietal and prestriate cortex to the precentral premotor and motor areas on the same (ipsilateral) and the contralateral side (Ferro et al. 1983). For example, suppose that the pathway connecting the right parietal cortex with the right frontal cortex is interrupted, then: (a) the visual control of the left hand (i.e. contralateral to the side of the lesion) will be affected, since the corticospinal pathway from the precentral motor areas is crossed; and (b) the eye-hand co-ordination will be affected in the left hemifield, because the parietal cortex controls spatial operations in the contralateral hemifield; a patient with such defects has been described (Castaigne et al. 1975). Suppose now that, in addition to a lesion of the right parietal cortex, the crossed pathway connecting the right parietal with the left frontal cortex has also been interrupted; then, the visual control of both hands will be impaired when operating in the left homonymous half-fields; such a case has indeed been described (Castaigne et al. 1971). Cases with various combinations of lesions corresponding to a rich variety of defects in eye-hand co-ordination have also been described (Ferro et al. 1983).

### 5.11 NEURAL STUDIES OF REACHING

Several brain areas are involved in the initiation and control of reaching. The study of the role of the various areas in this function was made possible by the advent of a technique that allowed the recording of the activity of single cells in the brain of behaving animals during reaching. This technique (Lemon 1984) is indispensable for the study of neural

mechanisms underlying motor aspects of behaviour. Typically, monkeys are trained to perform various motor tasks and then microelectrodes are inserted through the dura into the brain area of interest to record extracellularly the electrically isolated action potentials of single cells. This combined behavioural-neurophysiological experiment provides a direct and sensitive tool with which the brain mechanisms underlying performance can be studied. An important finding from such studies has been that several brain areas are involved in reaching, including areas of the cerebral cortex and various subcortical structures. The first cortical area investigated was the posterior parietal cortex (Hyvärinen & Poranen 1974, Mountcastle et al. 1975). It was found that cells in Brodmann's areas 5 and 7 changed activity with reaching in the absence of driving from the somatic periphery. Although the changes in cell activity associated with reaching could be observed in the absence of visual guidance (Hyvärinen & Poranen 1974, Mountcastle et al. 1980), cell activity was usually modulated more strongly when the animal reached with the eyes open. Indeed, a particular class of cells could qualify for an "eye-hand co-ordination" function because the changes in their activity was most intense when the monkey tracked a moving visual target with both the eyes and the hand (Mountcastle et al. 1975).

Porter and Lewis (1975) studied the changes in activity of motor cortical cells while monkeys reached out and manipulated a handle in front of them. It was found that single cells changed their activity during the task and that the latency of activation of different cells shifted to later times as more distal parts of the limb became involved in the motor act. This question of the sequential activation of motor cortical populations in reaching and grasping was investigated in more detail by Murphy et al. (1985). The activity of single cells in the forelimb area of the motor cortex was recorded in a task in which monkeys pointed to targets in front of them. The functional relation between the recording locus and the joint of the arm was determined by intracortical microstimulation. Thus a cell could be classified as relating mainly to movements at the shoulder, elbow, hand or fingers. It was found that in the pointing task cells were generally activated sequentially, from proximal to distal, reflecting the sequential engagement of successively more distal parts of the arm.

Murphy et al. (1982) also investigated the possible relations between motor cortical cell activity and joint motion and EMG activity in muscles of the forelimb during reaching. There were three main findings of this study. First, no simple relation was observed between single cell activity and the EMG, even when the muscle from which the EMG was recorded was activated by intracortical microstimulation. Secondly, single cells related to motion about the shoulder or elbow joints

behaved similarly in the task, although the motions produced about these joints could be quite different. Thirdly, the discharge of shoulder-related cells seemed to vary systematically with the movement trajectory. These results indicate that the relations between single-cell activity in the motor cortex and components (joint rotation, EMG activity) of reaching are complex.

#### **5.11.1 Directional tuning of motor cortical cells**

Reaching movements possess two spatial components, namely direction and amplitude. The activity of single cells is directionally tuned, in that cell activity is highest for a given direction ("preferred direction") of movement (for reviews see Georgopoulos 1990, Georgopoulos et al. 1993) or isometric force (Georgopoulos et al. 1992) and decreases gradually with directions farther and farther away from the preferred one (Fig. 5.1). Typically, the frequency of discharge is a linear function of the direction cosines of the movement vector (relative to its origin), or, equivalently, of the cosine of the angle formed between the direction of a particular movement and the cell's preferred direction (Fig. 5.1). These relations have been documented for planar pointing movements (Georgopoulos et al. 1982, Kalaska et al. 1989, Fu et al. 1993), for free pointing movements in three-dimensional space (Schwartz et al. 1988, Caminiti et al. 1990), for continuous planar movements (Schwartz 1993), and for isometric force pulses (Georgopoulos et al. 1992). Changes in cell activity relate the direction, and not to the end-point of the movement (Georgopoulos et al. 1985). Directional tuning is observed for cells with different types of resting firing pattern, including cells with low-rate, regular spike trains, cells with bursting patterns, and cells with high frequency of discharge (Taira & Georgopoulos 1993). Preferred directions differ for different cells and are uniformly distributed in three-dimensional space (Fig. 5.2, reproduced on p. 151) (Schwartz et al. 1988, Caminiti et al. 1990). They are multiply represented on the cortical surface and tend to cluster in columns (Georgopoulos et al. 1984). The preferred direction is very similar for movements of different amplitudes (Fu et al. 1993), although it can change when the origin of the movement changes (Caminiti et al. 1990). Finally, cell activity during the reaction time relates predominantly to the direction of the upcoming movement. In contrast, relations to movement amplitude are more prominent during the movement time (Fu et al. 1995).

#### **5.11.2 Direction of reaching and neuronal populations: the neuronal population vector**

The broad directional tuning indicates that a given cell participates in movements of various directions, and that a movement in a particular

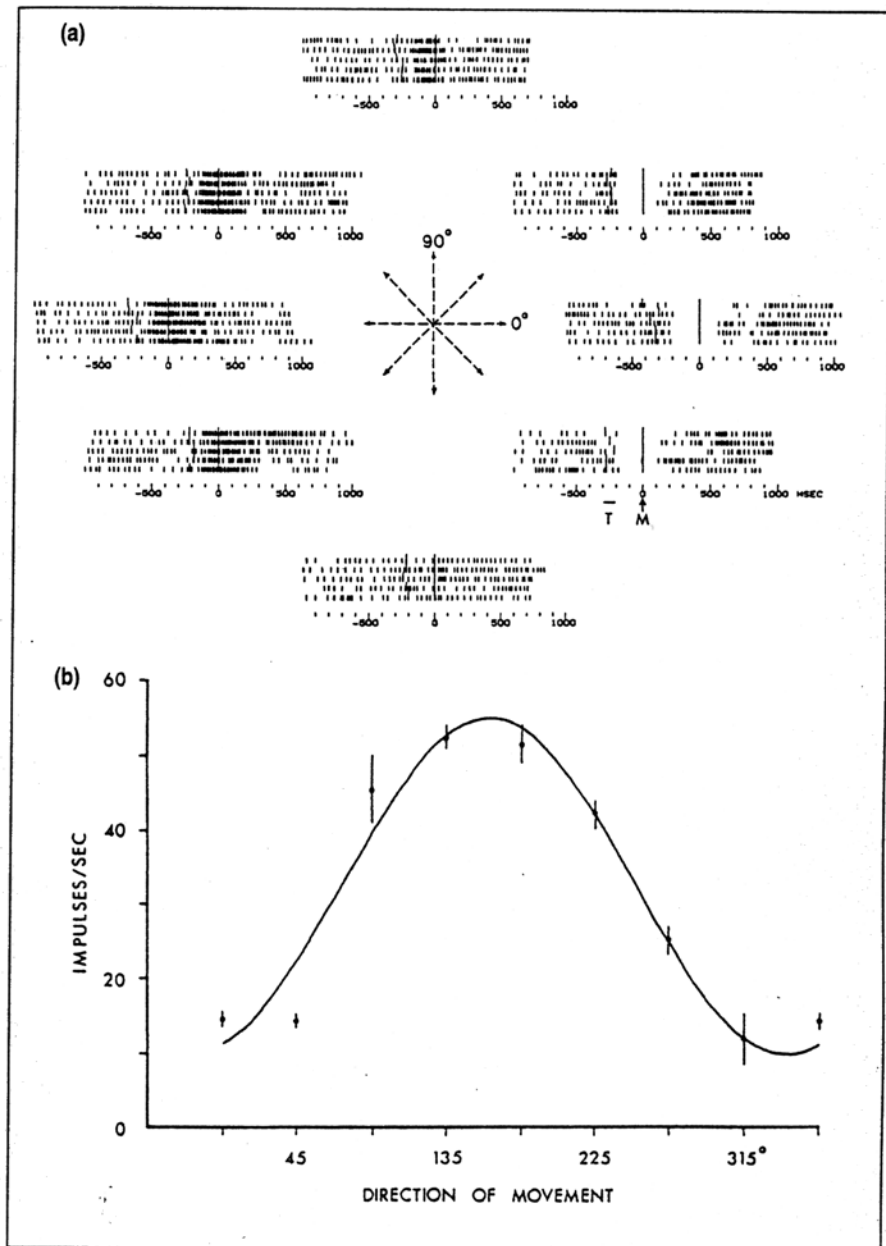


FIG. 5.1. Directional tuning. (a) impulse activity during five trials in which equal-amplitude movements were made in eight directions from the centre of the working surface towards peripheral targets, as indicated by the diagram in the centre. The rasters are aligned to the onset of movement M. Longer vertical bars preceding movement onset denote the time of stimulus onset (target) onset T. (b) Plot of the average frequency of discharge during the time interval from the onset of the target to the end of the movement against the direction of the movement. Points are means of five trials  $\pm$  SEM; the curve is a fitted sinusoidal function. From Georgopoulos et al. (1982). Reproduced with permission of the publisher. Copyright by the Society for Neuroscience.

direction will involve the activation of a whole population of cells. Given that single cells are directionally tuned, we proposed a vectorial neural code for the direction of reaching by the neuronal ensemble (Georgopoulos et al. 1983a, 1986, 1988): (a) a particular vector represents the contribution of a directionally tuned cell and points in the cell's preferred direction; (b) cell vectors are weighted by the change in cell activity during a particular movement; and (c) the sum of these vectors (i.e. the population vector) provides the unique outcome of the ensemble coding operation. The population vector points in the direction of the movement (Fig. 5.3, reproduced on p. 151) (Georgopoulos et al. 1983a, 1986, 1988). The population vector approach has proved useful not only in studies of the motor cortex but also in studies of other motor areas (for a review see Georgopoulos et al. 1993). Moreover, it can be generalized to other, non-motor problems, such as the coding of faces in the inferotemporal cortex (Young & Yamane 1992). The following are some general properties of the neuronal population vector.

#### 5.11.2.1 The neuronal population vector predicts the direction of reaching for movements of different origin

In these experiments monkeys made movements that started from different points, were in the same direction but described parallel trajectories in three-dimensional space. Under these conditions, the population vector in the motor cortex predicted well the direction of the reaching movement (Kettner et al. 1988, Caminiti et al. 1991).

#### 5.11.2.2 The direction of reaching is predicted well by neuronal population vectors in different cortical layers

The average absolute angle between the population vector calculated from cells in the upper layers (II and III) and the direction of movement was  $4.31^\circ \pm 2.98^\circ$  (mean  $\pm$  SD,  $N = 8$  movement directions), compared with  $2.32^\circ \pm 2.06^\circ$  for the lower layers (V and VI) (Georgopoulos 1990). This finding suggests that the ensemble operation of the population vector can be realized separately in the upper and lower layers. This is important because that information can then be distributed to different structures according to the differential projections from the upper and lower layers (Jones & Wise 1977).

#### 5.11.2.3 The neuronal population coding of the direction of reaching is resistant to loss of cells

The population coding described above is a distributed code and, as such, does not depend exclusively on any particular cell. This robustness was evaluated by calculating the population vector from progressively smaller samples of cells randomly selected from the original

population (Georgopoulos et al. 1988); it was found that the direction of the population vector can be reliably estimated from as few as 100–150 cells. In fact, recent work has shown that the population vector can be optimally calculated from a much smaller number of cells (Salinas & Abbott 1994).

5.11.2.4 The neuronal population vector predicts the direction of isometric force  
This finding (Georgopoulos et al. 1992) established the fact that the coding of directional information applies to the motor output in general, even in the absence of joint motion. Moreover, it showed that the direction specified by the motor cortex is not that of the total force exerted by the subject but that of the dynamic component of the force, that is the component of the force remaining after a constant, static force is subtracted.

5.11.2.5 The neuronal population vector transmits directional information comparable with that transmitted by the direction of movement  
In the usual studies in two-dimensional space, monkeys (Georgopoulos et al. 1982) and human subjects (Georgopoulos & Massey 1988) moved a manipulandum from the centre of a planar working surface to a target on a circle. In this case, the direction of the target is the ideal direction: if the subject's movements were straight lines from the centre to the target, the subject's performance would be perfect, and we could say that the movement transmitted the maximum possible information. However, movements rarely end dead on target, and therefore, the information transmitted is rarely maximal: the more the dispersion of the movement endpoint around the target, the less the information transmitted. Now, this dispersion can be split into errors in the amplitude of movement and errors in the direction of movement; accordingly, the information transmitted by the amplitude and the direction of movement can be studied separately. As we were interested in the control of the direction of movement, we asked subjects to "move in the direction of the target" without imposing restrictions on the amplitude or the end-point of the movement: this provided a purely directional task (Georgopoulos & Massey 1988). The calculation of the information transmitted by the direction of movement involves the construction of a "performance matrix" in which the ideal and actual directions are tabulated, and from which the information transmitted can be computed (Georgopoulos & Massey 1988). Essentially the same technique can be used to calculate the information transmitted by the direction of the population vector. Since the population vector is the vectorial sum of weighted contributions of individual cells, and since these weights can vary from trial to trial due to intertrial variability in neuronal

discharge, then the direction of the population vector can vary somewhat from trial to trial. This variation in the direction of the population vector can be treated in exactly the same way as the direction of movement, and the information transmitted calculated. Indeed, we calculated the information transmitted by the direction of movement and the direction of the population vector (Georgopoulos & Massey 1988) and found the following. First, the information transmitted by both these measures increases with input information but more slowly than the maximum possible, and it tends to saturate at high levels of input information. This loss of information is probably due to noise generated during the initial (perceptual) and successive (perceptual-motor) processing stages. Secondly, the information transmitted by the population vector was consistently higher than that transmitted by the movement by approximately 0.5bit. This means that an additional loss of information is incurred between the motor cortex and the movement. However, this loss differs from the previous one, as it does not increase with increasing stimulus information but remains constant at about 0.5bits at all levels of input information. This loss could occur during processing in other motor structures or at the stage of biomechanical implementation of the movement.

### 5.11.3 Time-varying properties of the neuronal population vector

#### 5.11.3.1 The neuronal population vector predicts the movement trajectory in continuous, tracing movements

In this experiment (Schwartz 1993, 1994) monkeys were trained to trace smoothly with their index finger sinusoids displayed on a screen, from one end to the other. The direction of the population vectors, calculated successively in time along the trajectory, changed throughout the sinusoidal movement, closely matching the smoothly changing direction of the finger path. Moreover, a neural "image" of the sinusoidal trajectory of the movement was obtained by connecting successive population vectors tip-to-tail. This finding suggests that the length of the population vector carries information concerning the instantaneous velocity of the movement.

#### 5.11.3.2 The neuronal population vector predicts the direction of reaching during the reaction time

This is the simplest case of predicting the direction of an upcoming movement. Given that the changes in cell activity in the motor cortex precede the onset of movement by approximately 160–180ms, on average (Georgopoulos et al. 1982), it is an important finding that the population vector predicts the direction of the upcoming movement during

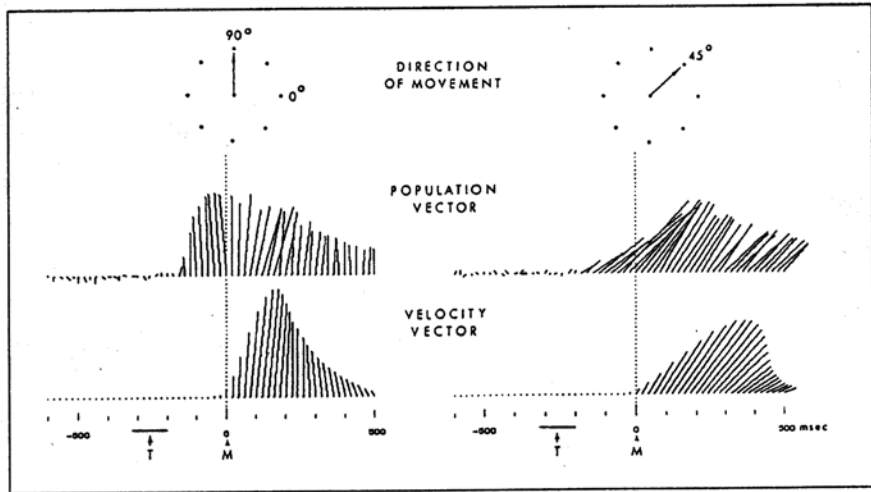


FIG. 5.4. Time-varying population vector. The population vector points in the direction of movement well before the movement begins. The results for two movement directions in two-dimensional space are illustrated (top); the population vector was calculated every 20ms (middle); the average instantaneous (20ms bin) velocity of the movement is also shown (bottom). Before the target onset  $T$ , the population vector is very small in length and its direction varies from moment to moment. Well before the onset of movement  $M$ , it increases in length and its direction points in the direction of the upcoming movement. This finding suggests that even the earliest inputs to the motor cortex are relevant in the direction of the upcoming movement. From Georgopoulos et al. (1984). Reproduced with permission of the publisher.

that period during which the movement is being planned (Georgopoulos et al. 1984, 1988) (Fig. 5.4).

#### 5.11.3.3 The neuronal population vector predicts the direction of reaching during an instructed delay period

In these experiments the monkeys were trained to withhold the movement for a period of time after the onset of a visual cue signal and to move later in response to a *go* signal. During this instructed delay period the population vector in the motor cortex computed every 20ms gave a reliable signal concerning the direction of the movement that was triggered later for execution (Georgopoulos et al. 1989a).

### 5.12 NEURAL MECHANISMS OF COGNITIVE PROCESSING: NEURONAL POPULATIONS AS KEYS FOR UNDERSTANDING

The results summarized above underscore the operational usefulness of the neuronal population vector for monitoring in time the directional

tendency of the neuronal ensemble. We took advantage of this property and used the population vector as a probe to decipher the neural processing of directional information during two cognitive operations, one involving memory holding and the other mental rotation.

### 5.12.1 Memory holding

In these experiments (Smyrnis et al. 1992), two rhesus monkeys were trained to move a handle on a two-dimensional work surface in directions specified by a light on the plane. They first captured with the handle a light on the centre of the plane and then moved the handle in the direction indicated by a peripheral light (*cue* signal). The signal to move (*go* signal) was given by turning off the centre light. The following tasks were used. In the *non-delay task* the peripheral light was turned on at the same time as the centre light went off. In the *memorized delay task* the peripheral light stayed on for 300 ms (*cue period*) and the centre light was turned off 450–750ms later (*delay period*). Finally, in the *non-memorized delay task* the peripheral light stayed on continuously, whereas the centre light went off 750–1050ms after the peripheral light came on. Recordings in the arm area of the motor cortex showed changes in single-cell activity in all tasks. The population vector was calculated every 20ms, following the onset of the peripheral light. There are two aspects of the information carried by the population vector. One concerns its direction, which can be interpreted as the directional information carried by the directional signal; the other aspect concerns the length of the population vector, which can be regarded as the strength of the directional signal carried. The direction of the population vector during the memorized delay period was close to the direction of the target (Fig. 5.5). The length of the population vector reflects the strength of the directional signal. It is interesting that the population vector length was similar in the cue period but was longer during the memorized versus the non-memorized part of the delay. This is shown in Figure 5.6, which illustrates the time-course of the length of the population vector in the two delay tasks. Three phases can be distinguished in this time-course. First, there is an initial increase of the vector length during the 300ms of the delay period; this increase is similar for both tasks. Secondly, this increase subsides during the rest of the non-memorized delay period but continues at a somewhat higher level during the memorized delay period; the latter difference is indicated in Figure 5.6 by stippling. Finally, there is a steep increase in the population vector length following the *go* signal, at the end of the delay period. Thus the memorized task is distinguished from the non-memorized one by the higher population signal during that part of the delay period during which the instructed direction had to be kept in memory.

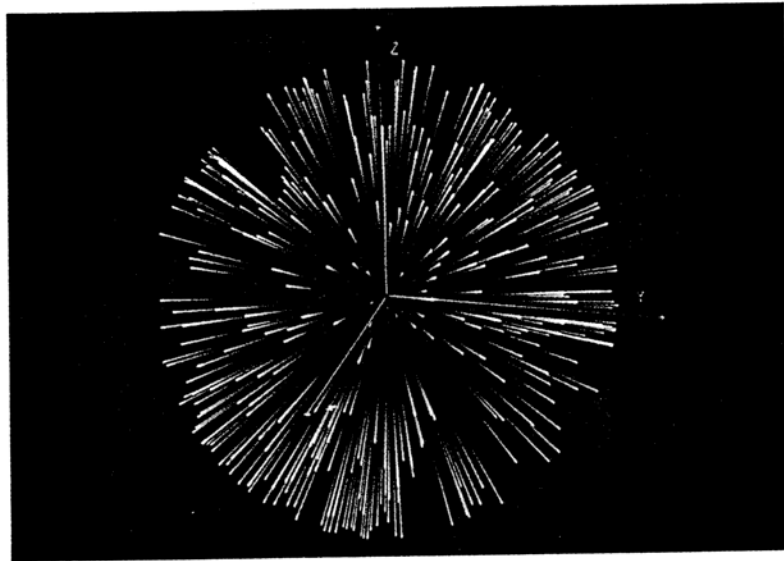


FIG. 5.2. Preferred directions (unit vectors) of 475 motor cortical cells in three-dimensional space. From Schwartz et al. (1988). Reproduced with permission of the publisher. Copyright by the Society for Neuroscience.

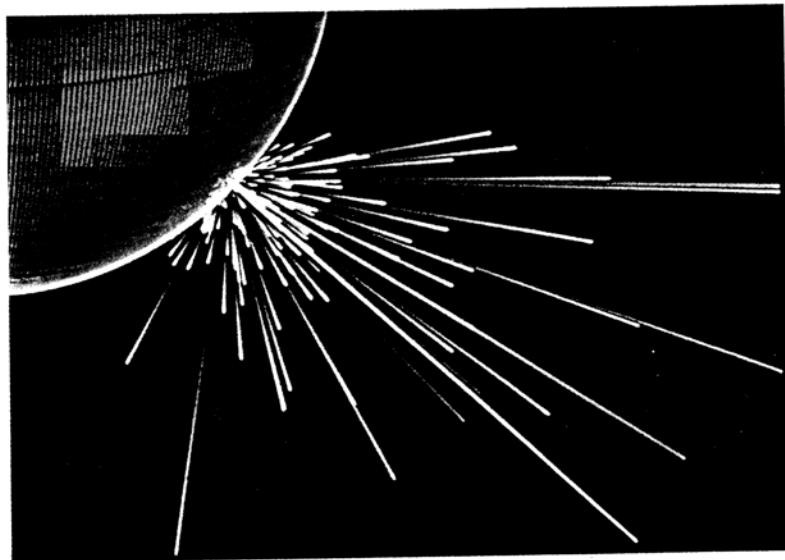


FIG. 5.3. Population coding of movement direction. The *blue lines* represent the vectorial contributions of individual cells in the population ( $N = 475$ ). The movement direction is in *yellow* and the direction of the population vector in *red*. From Georgopoulos et al. (1988). Reproduced with permission of the publisher. Copyright by the Society for Neuroscience.

From Chapter 6, Studying brain function with neuroimaging  
(Frith & Friston), pp. 169–96

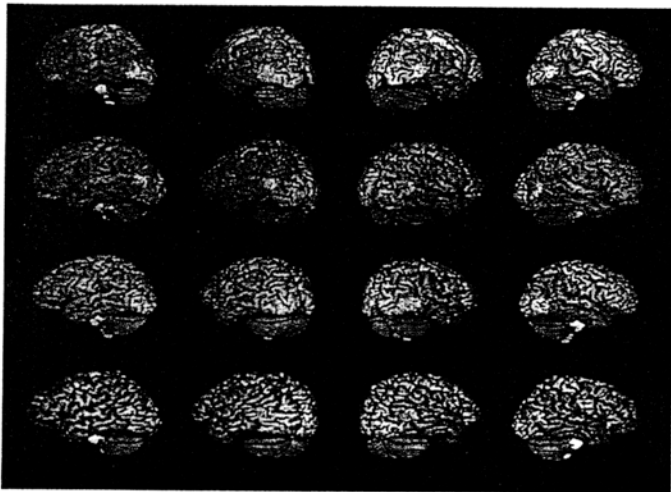


FIG. 6.2. The location of the brain activity associated with the passive viewing of visual motion: human V5. Reproduced from Watson et al. (1993).

From Chapter 8, The architecture of working memory  
(Jonides & Smith), pp. 243–76

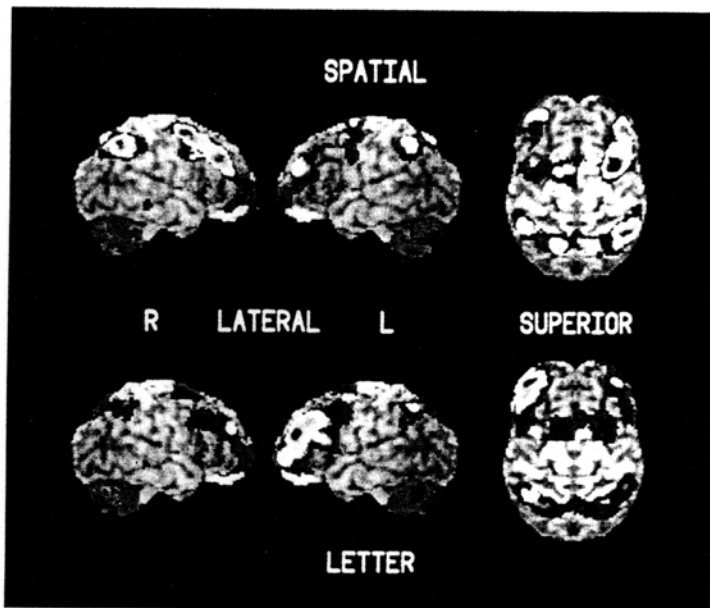


FIG. 8.4. Six PET images from the three-back experiment described in the text. Each row contains right and left lateral views as well as a superior view of a reconstructed brain (from a structural magnetic resonance image) on which have been superimposed PET activations that are shown in colour code. Red and bright yellow areas indicate the highest levels of brain activation. The top row presents images that resulted from subtracting the spatial control from the spatial memory condition; the bottom row presents the images for the verbal memory minus the verbal control conditions.

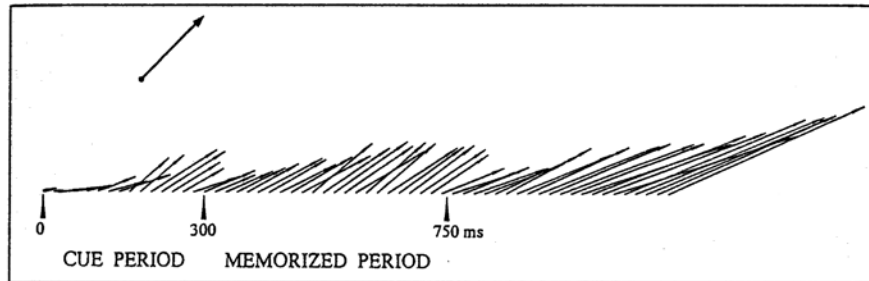


FIG. 5.5. Memorized population vector: direction. Population vectors in the memorized delay task for the direction indicated are plotted every 20 ms. The arrow on top indicates the direction of the cue signal present during the first 300 ms of the delay period. From Smyrnis et al. (1992).

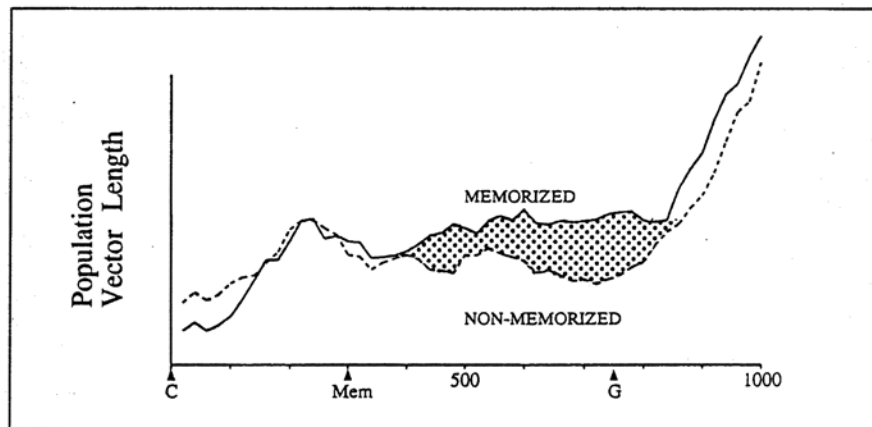


FIG. 5.6. Memorized population vector: length. The length of the mean resultant of the population vector is plotted against time for the two delay tasks. G, Minimum time of onset of the go signal. From Smyrnis et al. (1992).

The directional information carried by the population vector in the memorized task identifies the memorized information in a direct fashion. Moreover, this analysis provided an insight concerning the time-course of encoding and holding directional information. For that purpose we used the length of the population vector, which can be regarded as reflecting the strength of the directional signal in the neuronal ensemble. The population vector length showed an initial increase which started approximately 100 ms following the cue onset and peaked at 250 ms. This increase was very similar in both the memorized and the non-memorized delay tasks (Fig. 5.6). This initial peak can be interpreted as reflecting an encoding process. A second phase

followed which differed in the memorized and the non-memorized tasks in that a higher, sustained signal was present during the memorized delay period but not during the non-memorized delay (stippled area in Fig. 5.6). This could reflect a holding-in-memory process. Following the onset of the *go* signal, the population vector length increased similarly in all tasks used. These findings are interesting because the increase in the signal during the memorized delay period was observed in the absence of the target; however, one would have expected that the signal would be stronger in the presence rather than in the absence of the visual stimulus. This finding strengthens our interpretation of this increase as a memory signal, in contrast to a sensory one and raises the more general possibility that the motor cortex may be particularly involved when only part of the visual information about an upcoming movement is provided.

### 5.12.2 Memorized trajectories of complex movements

The studies summarized above dealt with motor cortical activity during tasks requiring memorization of simple pointing movements. A different question concerns the neural mechanisms subserving memorized, complex movement trajectories. This problem was investigated in a recent study (Ashe et al. 1993) in which two monkeys were trained to perform from memory an arm movement with an orthogonal bend, first up and then to the left, following a waiting period. They held a two-dimensional manipulandum over a spot of light at the centre of a planar work surface. When the light went off, the animals were required to hold the manipulandum there for 600–700ms and then move the handle up and to the left to receive a liquid reward. There were no external signals concerning the *go* time or the trajectory of the movement. Following 20 trials of the memorized movement trajectory, 40 trials of visually triggered movements in radially arranged directions were performed. The activity of 137 single cells in the motor cortex was recorded extracellularly during performance of the task. A good percentage (62.8%) of cells changed activity during the waiting period. Other cells did not change activity until after the 600ms minimum waiting time was over, and, occasionally, cell activity changed almost exactly at 600ms after the centre light was turned off. However, the most interesting observation was that a few cells changed activity exclusively during the execution of the memorized movement (see Ashe et al. 1993: Fig. 5); these cells were completely inactive during performance of similar movements in the visually guided control task. These findings suggest that performance of a movement trajectory from memory may involve a specific set of cells, in addition to the cells activated during both visually guided and memorized movements. This

idea is in accord with the results of modelling studies summarized below.

### 5.12.3 Mental rotation

The second cognitive process we chose for study involved a transformation of an intended movement direction. In these studies we first carried out psychological experiments in human subjects. Then we trained monkeys to perform the same task and recorded the activity of single cells in the brain of these animals during performance of the task. Finally, we tried to connect the neural results with those of the human studies and interpret the latter on the basis of the former: the objective is to get as close as possible in relating neurophysiology and cognitive psychology. I describe below these steps as they were applied to a particular problem of a mental transformation of movement direction.

The task required subjects to move a handle at an angle from a reference direction defined by a visual stimulus on a plane. Since the reference direction changed from trial to trial, the task required that in a given trial the direction of movement be specified according to this reference direction. In the psychological studies (Georgopoulos & Massey 1987) human subjects performed blocks of 20 trials in which the angle by which the subjects had to move away from the stimulus direction and its departure (counterclockwise or clockwise) were fixed, although the reference direction varied. Seven angles (5–140°) were used. The basic finding was that the time to initiate a movement (reaction time) increased in a linear fashion with the angle. The most parsimonious hypothesis to explain these results is that subjects arrive at the correct direction of movement by shifting their motor intention from the reference direction to the movement direction, travelling through the intermediate angular space. This idea is very similar to the mental rotation hypothesis of Shepard & Cooper (1982) to explain the monotonic increase of the reaction time with orientation angle when a judgement has to be made whether a visual image is a normal or mirror image: in both cases a mental rotation is postulated. In fact, the mean rates of rotation and their range among subjects were very similar in the perceptual (Shepard & Cooper 1982) and motor (Georgopoulos & Massey 1987) studies. Moreover, when the same subjects performed both perceptual and motor rotation tasks, their processing rates were positively correlated (Pellizzer & Georgopoulos 1993), which indicates similar processing constraints for both tasks.

In the *neurophysiological studies* (Georgopoulos et al. 1989b, Lurito et al. 1991), two rhesus monkeys were trained to move the handle 90° and counterclockwise from the reference direction; these trials were intermixed with others in which the animals moved in the direction of

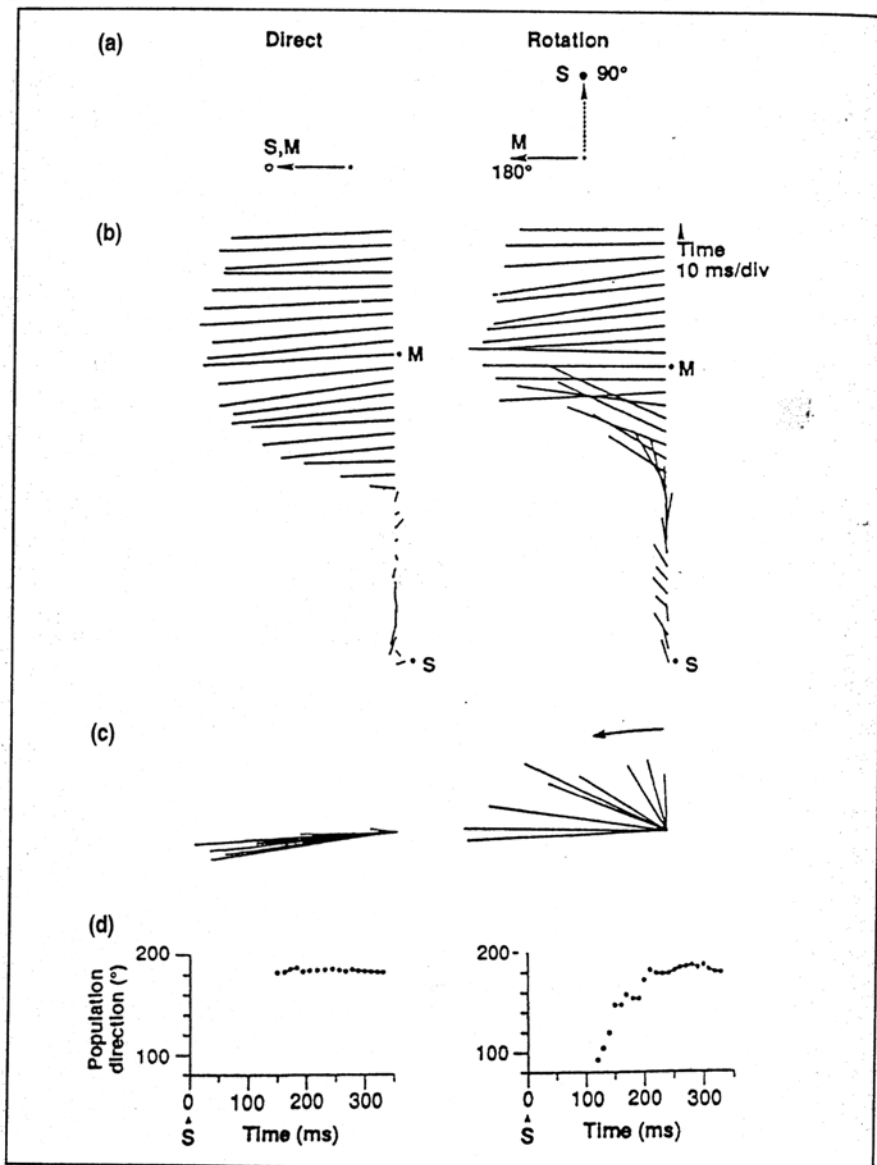


FIG. 5.7. Mental rotation of the population vector. Time evolution of the neuronal population vector when the movement was in the direction of a stimulus or 90° counterclockwise from it. (a) Task: (o) dim and (●) bright light; (....) stimulus S and (—) movement M direction. (b) Neuronal population vectors calculated every 10ms from the onset of the stimulus S at positions shown in (a) until after the onset of the movement M. When the population vector lengthens, for the direct case (left) it points in the direction of the movement, whereas for the rotation case it points initially in the direction of the stimulus and then rotates counterclockwise (from 12 o'clock to 9 o'clock) and points in the direction of the movement. (c) Ten successive population vectors from (b) are shown in a spatial plot, starting from the first population vector that increased significantly in length. Note the counterclockwise rotation of the population vector (right). (d) Scatter plots of the direction of the population vector as a function of time, starting from the first population vector that increased significantly in length after stimulus onset S. For the direct case (left), the direction of the population vector is in the direction of the movement ( $\approx 180^\circ$ ); for the rotation case (right) the direction of the population vector rotates counterclockwise from the direction of the stimulus ( $\approx 90^\circ$ ) to the direction of the movement ( $\approx 180^\circ$ ). From Georgopoulos et al. (1989b). Reproduced with permission by the publisher. Copyright AAAS.

the target. When the time-varying neuronal population vector was calculated during the reaction time, it was found that it rotated from the stimulus (reference) to the movement direction through the counterclockwise angle, when the animal had to move away from the stimulus, or in the direction of the stimulus, when the animal had to move towards it. This is illustrated in Figure 5.7. It is remarkable that the population vector rotated at all, and also that it rotated through the smaller, 90° counterclockwise angle. These results showed clearly that the cognitive process in this task truly involves a rotation of an analogue signal. The occurrence of a true rotation was further documented by showing that there was a transient increase during the middle of the reaction time in the recruitment of cells with preferred directions in between the stimulus and movement directions: this indicated that the rotation of the population vector was not the result of varying activation of just two cell groups, one with preferred directions centred on the stimulus and another in the movement direction. Therefore, this rotation process, "sweeping" through the directionally tuned ensemble, provided for the first time a direct visualization of a dynamic cognitive process. In this respect, it is noteworthy that the population vector is, in essence, a measure that can take continuous values in direction.

In summary, the results of these studies provide the neural correlates of a dynamic cognitive representation (Freyd 1987). The essential contribution of this work is in the neural identification and visualization of the time-varying, dynamic representation of direction in the motor cortex when a transformation of this direction is required and achieved. Interestingly, the mean rotation rate and the range of rates observed for different reference directions were very similar to those obtained in the human studies.

#### 5.12.4 Context-recall memory scanning

The neural correlates of visuomotor memory scanning were investigated recently (Pellizzer et al. 1995). A monkey was trained to exert a force pulse on a two-dimensional semi-isometric manipulandum in eight different directions. The force exerted was displayed as a feedback cursor. The memory task can be divided into three parts: (a) a sequential presentation of three or four yellow stimuli, which stayed on the screen; (b) one of the stimuli, except the last one, changed from yellow to blue which identified it as the test stimulus, and gave the go signal; (c) the correct response was to the stimulus that succeeded the test stimulus during the initial presentation. This task required the memorization of the order of presentation of the stimuli, but not of their position in space which was still available. In a control task, one stimulus was presented and the response was made after the go signal. The

activity of 544 cells in the motor cortex was recorded during performance of the two tasks. The salient finding of the study was that cell activity usually reflected first the direction of the test stimulus, then switched to reflect the direction of the response, when the test stimulus was the second in the sequence. This was true both for the case of single cells, which showed abrupt changes in activity reflecting the two different directions, as well as for the population vector, which also showed an abrupt shift from the direction of the test stimulus to that of the motor response. Another finding was that the time for which neural activity reflected the direction of the test stimulus, and, correspondingly, for which the population vector stayed in that direction, was approximately 100–150ms. These results indicate that the neural process that underlies memory scanning is quite different from that which underlies mental rotation: whereas the latter involves an apparently continuous change of direction of the population vector, the memory scanning seems to involve abrupt shifts of the population vector from one direction to another. Accordingly, the neural events in the mental rotation task reflect a *transformation* of movement direction, whereas those in the context-recall task reflect a *selection* of a direction from a list.

### 5.13 NEURAL NETWORK MODELLING OF MOTOR CORTICAL DIRECTIONAL OPERATIONS

The time-varying directional operations summarized above have been modelled using a massively interconnected artificial neural network that consists of directionally tuned neurons and produces as an outcome the neuronal population vector (Georgopoulos et al. 1993, Lukashin & Georgopoulos 1993, 1994a,b). This network has reproduced well many of the experimental findings and has led recently to a novel hypothesis on how memorized movement trajectories could be stored in the synaptic connections of overlapping neural networks (Lukashin et al. 1994). The idea is that there is a general-purpose network that is involved in all kinds of movements, memorized or not, but which carries no information about memorized trajectories of specific shapes (e.g. circles, ellipses, scribbles) and which, if activated alone, would produce straight-line trajectories. It is now hypothesized that there are also networks highly specific for a particular trajectory (e.g. clockwise circle) which are interconnected with the general-purpose network: when a specific trajectory needs to be performed, the appropriate specific network fuses with the general-purpose network and, as one network now, produces the desired trajectory. It is remarkable that the size of the specific network need only be less than 5% of the size of

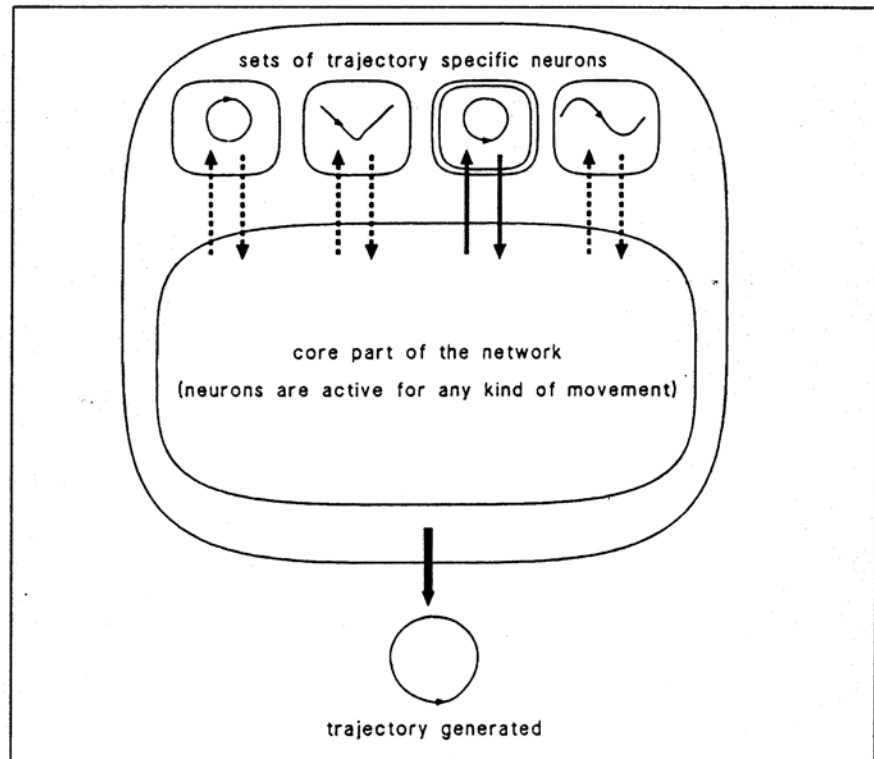


FIG. 5.8. Overlapping neural networks. The neural network for generating four different types of neural-vector trajectories. All units in the core part are interconnected with each other and with all units in the trajectory-specific sets. All units in each trajectory-specific set are interconnected with one another and with all units in the core part. There are no connections between different trajectory-specific sets. Heavy arrows (solid and dashed) indicate that this is a feedback network, and that the connections between the core part and the trajectory-specific parts are adjusted during the training of the network to generate different types of trajectory. The double ovoid indicates that this particular set is currently activated, and connections between the core part and this set (solid arrows) determine the shape of generated neural-vector trajectory. Single ovoids indicate that the other three trajectory-specific parts of the network are inhibited, and that the connections between the core part and these sets (dashed lines) do not interfere with the dynamics. From Lukashin et al. (1994).

the general-purpose network for the desired trajectory to be effectively stored and reproduced (Lukashin et al. 1994). This idea is illustrated in Figure 5.8. It is noteworthy that such very specific cells have been observed at low proportions in neurophysiological recordings during performance of memorized trajectories (Ashe et al. 1993).

The idea of the existence of very specialized networks raises the question of the degree of specialization and of how such networks are created in the first place. We can only speculate on these issues. With

respect to the general-purpose network, it is reasonable to assume that it is present at birth, since it is assumed to subserve all movements. There are several possibilities concerning the specialized networks. One possibility is that a number of small networks, specific for basic shapes (e.g. straight lines, curves, and some combinations thereof—"motor shape primitives"), are present at birth. Then, motor learning for other, complex motor acts would consist of adjusting the strength of the connections between the general-purpose and specific networks. This idea implies that all the specialized primitives are used routinely, although not as frequently as the general-purpose network. Another idea is that innate specific networks code for more complicated shapes and are large in number. The mechanism of motor learning would then be similar to that described above, but in this case only a small number of the specialized networks would be used. This means that a number of the complex, specialized networks may never be used. This situation would be similar to that encountered in the immune system in which there is a large potential for making a large number of antibodies, of which, however, only some may actually be made, depending on the exposure of the organism to specific antigens. In both cases there is a selection (selection of a specialized trajectory or selection of an antibody) from the large ensemble available. Finally, an intermediate hypothesis would be that we start with motor shape primitives but that the more complex trajectories resulting from the combination of these primitives to the general network become themselves very specialized and behave as such in the formation of other trajectories in novel associations.

#### 5.14 SPINAL CORD AND REACHING

Reaching involves motion at the shoulder and elbow joints. Behaviourally, there is little doubt that these two joints are controlled as one functional unit (Soechting & Lacquaniti 1981). Descending motor commands from the motor cortex and other brain areas influence the proximal arm motoneurons, i.e. those innervating muscles acting on the elbow and/or shoulder, through a set of interneurons located at the C3-C4 spinal segments, that is above the segments of the proximal motor nuclei. These interneurons ("C3-C4 propriospinal neurons", Lundberg 1979) have been studied extensively in the cat. They receive monosynaptic inputs from several supraspinal sources, including the pyramidal (i.e. corticospinal), rubrospinal, reticulospinal and tectospinal tracts, and they distribute their axons to several proximal motoneuronal pools. Selective section of the output from these propriospinal neurons to their

target motoneurons results in abnormal reaching with normal grasping, and similar effects are observed when the corticospinal input to the propriospinal neurons is removed (Alstermark et al. 1981). These results indicate that the C3–C4 propriospinal system is concerned with the neural integration of the reaching movement at the spinal level and that the motor cortex and other areas control reaching, most probably through that system. This motor cortical control is also exerted at other levels within the propriospinal system; for example, there is direct corticospinal input on a key inhibitory interneuron which mediates inhibition from afferent fibres to propriospinal neurons (Alstermark et al. 1984). This peripherally initiated inhibition of the propriospinal neurons is important in limiting the reaching movement, because lack of peripheral input results in consistent hypermetria in reaching (Alstermark et al. 1986).

The results summarized above indicate that a large part of neural integration of the reaching movement is accomplished in the spinal cord. In a way, this is qualitatively similar to the sophisticated integration observed in spinal circuits underlying locomotion (Grillner 1981): both cases involve the production of complicated motor outputs, complicated in the sense of involving the time-varying control of several muscles and of more than one joint. It is possible, and even probable, that the detailed organization and the neural integration of the reaching movement need not be the concern, or the burden, of the motor cortex or other motor areas. These various areas could be concerned, instead, with the initiation and ongoing control of reaching according to internally generated goals, as, for example, in drawing, or according to information from exteroceptors, as, for example, in reaching towards a visual or an auditory object. These functions would then be accomplished by the activation of neuronal populations in different brain areas, including the motor cortex, which, in turn, would engage the spinal "reaching" circuits (Georgopoulos 1988).

### 5.15 CONCLUDING COMMENTS

Voluntary movement is still an evolving "hot" topic in behavioural, neural and modelling research. The problems involved are very challenging and not easily amenable to simple solutions. Although simplistic solutions are abundant, true advancements are hard to come by. A major question is, how do such diverse brain structures as the cerebral cortex, basal ganglia and cerebellum co-operate to produce graceful, accurate and seemingly effortless reaching movements? The neuronal population vector analysis is a first step in "breaking" the code by which

individual brain areas process directional information. The fact that this code applies to several areas involved in motor control suggests that the interactions among areas could be expressed within a common, population-vectorial framework. In addition, the fact that the time-varying population vector can provide crucial information on how directional information is being processed in different tasks, opens up the possibility that the dynamic interplay of the areas involved could also be expressed and elucidated within this population-vectorial framework. For this purpose, simultaneous recordings from various areas will be needed, a technically difficult but not insurmountable task. Modern functional brain-imaging techniques (e.g. functional magnetic resonance imaging) could provide useful guidance as to which areas are involved in a task, and, therefore, which areas to record from simultaneously. This combination of approaches should lead to an efficient and effective approach to understanding the real-time, dynamic co-operation of diverse brain areas in planning, initiating and controlling voluntary movements.

#### ACKNOWLEDGEMENTS

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