

This is put through an automatic control system of which experimenters have been able to elucidate a number of major facts and some operative principles. I refer to the selection of material presented in this and the preceding chapter: the gamma loop and alpha-gamma linkage, the specification of motor unit properties, the cortical readiness and motor potentials, the colony concept, the ghost movements, and the recording from single cortical and other neurons during intentional wrist movements. The list—by no means complete—represents an impressive number of disclosures won by dint of hard work in the laboratory. And yet the full logic of the automatic control system still eludes us. What, for instance, is the motor role of the cerebellum whose intricate wiring diagrams are quite well known (Eccles, Ito, Szenthágothai)?¹⁶⁷ The answer to this question is that we merely possess a number of hypotheses demonstrating that wiring diagrams have to be infused with a modicum of teleological relevance to be more than an enumeration of inhibitions and excitations at synaptic loci. Five hypotheses are mentioned by Llinás in a recent review.¹⁶⁸

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Motor and Sensory Organizations in Integrated Action

In “sensorimotor processes” in general, localization might tend to a greater degree of minuteness on the receptor than on the effector side. There must be no ambiguity about the localization of an object in the field of vision. But the part used to grasp it may start from many different postures and may reach it by as many trajectories as there are occasions to grasp. (C. G. Phillips, Cortical localization and “sensorimotor processes” at the “middle level” in primates. Hughlings Jackson Lecture, *Proc. Roy. Soc. Med.* 66 (1973):987–1002.)

There are interesting correlations between motor and sensory organizations and also some differences that need to be considered. We have seen that sensory performance reaches its summit in conscious awareness of the external world of which it tries to build up an image, whereas motor perfection in the end implies suppression of the conscious component in favor of automatization of the demanded actions. The pianist and the skilled typist are not conscious of what their fingers are doing as long as they are doing it according to an automatized program. The coactivated alpha and gamma motoneurons follow the instructions, and several feedback mechanisms (eye, ear, muscle spindles, skin, tendon, and joint organs) report on perfection and elicit error correction, conscious or unconscious, as the case may be.

Learning motor acts by secret automatic routes is strikingly illustrated by some patients with severe and persistent anterograde amnesia, which implies inability to store or retrieve new memories (Scoville and Milner; Teuber).¹⁶⁹ When trained to do tracking tasks or to learn minor drawing tests, these patients may acquire increasingly greater skill from day to day without ever remembering that they have seen the apparatus to which they return day after day. Thus a virtually normal capacity for motor learning may coexist with absence of conscious sensory learning. Some aspects of learning and memory will be discussed in Chapter 10.

Visual learning is largely conscious learning, whereas the proprioceptive accompaniments of motor skill do not at all, or to a much lesser degree, reach conscious awareness. Proprioceptive information is not well perceived. We possess length-recording muscle receptors (the spindles) but no

percept of muscle length, only a general awareness of tension. Nevertheless, proprioceptive feedback is important in movement.

Experiments on 20 sec short-term memory have shown that blind kinesthetic learning for moving a lever at a given distance leads to considerable forgetting, although conscious visual locations of position are easily remembered over that time (Posner).¹⁷⁰ However, conscious awareness is the more adaptable mechanism and so, if visual remembering is disturbed by an interpolated purposive act such as a verbalized task, it erases the original engram when inserted in the pause between checkings. By contrast, such interference leaves proprioceptive learning undisturbed.

In creating a body image, the child in fumbling is faced with the necessity of integrating information from many different sources: (1) visual, the most important contribution in normal people; (2) vestibular, from two ears, each with five different sense organs; (3) sensory endings for touch and pressure in the skin; (4) two kinds of spindle endings in most muscles, above all those around the neck, the arms, the legs, and the spine; (5) tendon organs recording tension; and (6) three types of endings in a large number of joints. Schematically speaking, information from at least twenty subsystems is needed, and so there will be adjustment to 2^{20} combinations! The final result will be a body image (postural model) whose existence is demonstrated when destroyed by disease. Patients of this kind are helpless when they are asked to show parts of their body. They may be so to the extent of believing that an eye or an arm is missing when asked to point to it (Schilder).¹⁷¹ The postural model is also disturbed, and they may be incapable of starting a movement. Can we ever go beyond the

anecdotal description of such personal tragedies for a look at the “inside” of the organized high level integrations? I shall come to some kind of answer later.

As long as vision and hearing are excluded, most readers may willingly admit that there must exist an important subconscious organization capable of dealing with movements within the body space. But neither eye nor ear can be left outside these integrations. Both sense organs have extensive subcortical projections, and even in the monkey the kind of blindness produced by ablation of the geniculostriate projections to the visual area leaves the animal capable of visual orientation and of reaching for desirable objects (Weiskrantz).¹²³

Need for Stimulus-Bound Approaches

The components of an integration can hardly be analyzed unless a beginning is made with stimulus-bound approaches. And if the problem then is taken to the level of single-cell recording, at least some kind of insight can be reached. For example, a monkey can be trained to follow the movement of a small target with an equally fast eye movement. In the hindpart (flocculus) of the cerebellum Miles and Fuller have discovered neurons that specifically respond to this velocity signal.¹⁷² These cells are independent of head movement. The input signal is the slippage of the image across the retina. The cerebellar neurons translate this signal into a command for the brainstem motoneurons of the eye muscles to pursue the target and keep it in focus. The will enters into this operation by deciding which target should be placed into the fovea of the retina. The execution of the command is left to the automaton, and so slavish pursuit proceeds until some whim of the ani-

mal urges it to use its saccadic system—another independent mechanism—to redirect the gaze elsewhere.

At the level of systems analysis the same problem recurs. There is no escape from the stimulus. Specific systems or organs are engaged in selecting the speed at which any movement is supposed to be performed. These deliver the instructions to the motor apparatus (Bouisset and Lesienne).¹⁷³ We know that there are cells in the so-called basal ganglia (pallidum) which preferentially respond to slow movements (DeLong and Strick).¹⁷⁴ It has furthermore been found that cooling one of the cerebellar nuclei (dentatus) slows down movement (Conrad and Brooks).¹⁷⁴ Such cells are likely to be concerned in issuing the instructions regarding the speed of a muscular act. Such instructions are likely to be reformulated within the cortical motor area after a preliminary elaboration of instructions in the cerebellum and the basal ganglia. We are familiar with the presence of cells in the motor area whose activity precedes motor acts and demands force or velocity of application of force from the motor apparatus in the spinal cord (Evarts).¹⁶⁶ But independently of whether force at this or that velocity of performance is urged upon an organism by external stimuli or is ordered from the store by an act of willing, the same executive mechanisms are likely to be employed.

Purposive Sensorimotor Integrations

Motor action takes place within a sensory envelope whose presence and stability is constantly confirmed by daily renewal of the same experiences. This perpetual confirmation has created the neural organizations engineering the constancies and frameworks of reference discussed in

Chapter 6. These developments are taken into account in motor activity. Within the surrounding space such as a room we move with the greatest ease between objects whose size is constant rather than variable with the retinal image. Because our movements are scaled to this invariant world, it should be possible to detect cells in the cortex that somehow have the properties of coordinating the motor and sensory spheres. In a sense the pyramidal cells of the motor cortex and the motoneurons of the spinal cord represent stimuli and movements combined. But, in looking for cells inserted into our established organizations for movement within spatial coordinates, a more sophisticated response pattern is required than that of pyramidal cells and motoneurons which deliver force and rate of change of force to commands from elsewhere.

The signs of the postulated sophistication are somehow related to varieties of behavior, and by accepting behavioral criteria we have chosen to adopt a number of psychological concepts such as motivation, attention, interest, or demand. Alternatively, we have abandoned the urge to use whatever means are at our disposal for making experimental observations meaningful. Units within the parietal cortex exemplify the required properties. This part of the brain lies behind the sensory area and above the temporal lobe. Clinical experience testifies to the complex and variegated symptomatology of parietal destructive processes (Critchley).¹⁷⁵ Though the threshold for skin sensations may be little altered, there are striking defects in the synthesis, interpretation, differentiation, and comparison of the elementary sensory experiences. "Touch and vision are partners when it comes to affording us information as to the nature, physical properties and identity of objects around us" (Critchley, p. 109). They also contribute to the

building-up of the body image and the coordinates of the postural model. Postural loss and defects in recognition of passive joint movements are seen with parietal lesions. The body image is needed for movement. Single-cell analysis again has shown a way of closing in on these problems (Mountcastle and his colleagues; Hyvärinen and Poranen).¹⁷⁶

One of the cell types in the parietal area could not be activated by any passively delivered stimulus but was fired in movements aimed at securing something the monkey desired like food. For this purpose it had to close a switch or pull a lever. Outwardly similar, active movements of an aggressive or aversive character did not excite these neurons. The cue used for detection of the desired object was unimportant—it might be visual, tactile, or acoustic; nor was the trajectory by which the goal was reached or the length of the time of expectation after the first warning signal of any significance. Thus the real stimulus appeared to be anticipation of what the reward was good for. The cellular discharge actually ended before the movement itself was completed. Because the neuron began firing in anticipation, the movement could not have been the cause of the discharge; it seems more likely that it was a consequence of the internal stimulus taking a routine course and using the required movement from the available repertoire. The significant point appears to be that the neuron was imbedded in an internal organization for signaling something like "Eureka, this is worth going for," a kind of purpose detector related by the affective quality of the stimulus to the movement signaling accomplishment.

In another part of the parietal lobe, Mountcastle's group discovered neurons that fired when the monkey became interested in a visually fixated object within reach. The fir-

ing of these cells diminished when the object was moved farther away from the animal. The three discernible components integrated into the discharge were (1) successful fixation, that is, the object had to be foveally located; (2) it had to be within arm's length; and (3) it had to be interesting. These neurons also discharged when the animal was grooming itself. If the visual cue was blocked, the cell was silenced. Similarly it failed to respond if the target fell within a part of the visual field that was prevented from picking up the object by fixation. Like the neurons previously described, this type also required motivation for a definite purpose, but it differed from the former by being tightly bound to the act of fixation of a visual target at a short distance. Its explorative character was directed and restricted to the immediately surrounding space.

A third type of neuron in the parietal lobe was a sensitive indicator of steady joint position. Many of the neurons related to joint position were more active during active movements than when the limbs were passively displaced.

Other types of neurons have been found in this region but cannot be discussed here. As an assembly of different properties they help us to understand why an authority in the clinical field has been compelled to state: "To seek to establish a formula of normal parietal function is largely a vain and meaningless pursuit, however attractive" (Critchley, p. 410).¹⁷⁵ Partly, of course, a pathological process may not be restricted to the parietal lobes, but it seems more important that localized integrative acts end up in single neurons combining information and action in many different ways. A cortical lobe, or even a cortical field of considerable homogeneity from the histological point of view, contains highly differentiated cell patterns. These are not easily distinguished by conceptual subdivisions based on the re-

sources of our language. Disease may hit them indiscriminately. Nevertheless the clinician somehow adumbrates gross function, as does Critchley: "The peculiar role of the parietal lobe—or lobes—in the building-up of the postural schema of the body leads to an important association with corporeal awareness, imagery and memory. Hence the appearance of unusual disorders of the body-image with parietal disease" (p. 411).

Active vs. Passive Sensorimotor Activity

It has been briefly mentioned that the central nervous system is organized for active selection of the stimuli whose effects it for some reason or other wants to incorporate—that is, use for its integrations—while rejecting the rest. When conscious, we can of course decide what the selection should be, but most of the acts of selecting are carried out by teleologically organized processes over which we do not retain control. We encountered such processes when discussing adaptability in Chapter 3.

The experience of behavioral physiologists from animal work is that selecting and interpreting information to establish visually guided motor activity requires that the actual movements of the limbs are both made and seen to be made. Without self-produced movements the necessary coordinations do not develop in kittens (Held and Hein).¹⁷⁷ And a large number of physiological experiments show that improvement of performance takes place when active movements are substituted for passive ones. In the previous section I mentioned the single cells in the parietal cortex that only responded to active movements at the joints. An interesting case from this point of view was reported by Lashley in 1917.¹⁷⁸ He investigated the motor

behavior of a man with a gunshot injury that had left one leg without sensitivity to movement at the knee joint. The blindfolded patient was unable to detect large passive swings of the nonsentient leg, but when told to swing it himself, he judged about the extent of movement with remarkable accuracy. The finding can be explained in several ways, but it is used here merely to illustrate the significance of active versus passive sensorimotor activity.

Vision, with its 2 million afferent fibers in the optic nerves and its large cortical representation, tends to dominate over proprioceptive and skin senses. If the arm is swung up and down at the elbow joint in the dark, and, suddenly, a flash illuminates the limb, the subject feels his limb to be at rest in the position at which it was caught by the flash (Hagbarth).¹⁷⁹

Principles Applied in Explanations

The preceding references to some properly analyzed sensorimotor integrations in single neurons and to the role of self-activation for the development of motor skills in orientation have been chosen to illustrate essential steps toward understanding sensorimotor integrations. At one time it was commonly held that the fundamental principle behind cortical operations was merely one of association, and from this period stems the name of "association areas" for the fields that did not represent direct projections from sense organs or else were motor in character. Association may also be used in the vague general sense of standing for the fact that motor and sensory events *are* associated in the phenomena described. But the old association theory, in addition, implied an explanation by association caused by

proximity in time and space of objective stimuli or events, which by virtue of this coexistence became semipermanently coupled in memory. This notion balanced emphasis wrongly.

The trend of my discourse points in a different direction. Little importance has been attached to the basic coexistence in time and space for the formation of associations. Instead I have emphasized that (1) from simultaneously available information the purposive brain selects what it finds biologically useful; (2) in this way it employs its billions of neurons to create unique cellular organs of high specificity combining information from various sources with action; (3) such organs are mobilized by injecting into them components that we describe in such psychological terms as motivation, interest, anger, demand, or accomplishment—in short, relevance for some biological purpose. From the evolutionary standpoint "teleonomic purposiveness" is involved in addition to the true teleological purposiveness discussed in Chapter 3. These factors are more important than sheer simultaneity in time or space. Most simultaneous events—luckily—go unnoticed.

By far the most revealing information on the tasks of interpretation and action in our purposive brain has come from the study of single neurons, many examples of which have been given in this and previous chapters. Nevertheless it is evident that the individual neuron only represents an elaborate cellular organization within the cortex. Such structures could be columnar organizations (mentioned in Chapter 6) whose existence repeatedly has been confirmed for the visual and tactile spheres.¹⁰⁸ Mountcastle and his colleagues saw something of these also in the parietal cortex, but they were also compelled to introduce the notion

of block formation to account for the orderly presence of specific types of neurons.

At the level of the visual primary projections it is possible to speak of detector or trigger features, but this does not help us much to understand the sophisticated neurons that connect vision to doing. Consider integrated conditions for such activity as "reachability" of an object together with its capability of evoking the anticipation of pleasure leading to the combination of movement with interest; for these neurons the object also had to be fixated within the fovea. This means that whatever detector mechanisms were available for an optimal definition of the object are also likely to have been actively employed. But having delivered their special contribution to the integrated act—to help distinguish and identify the target with maximal perfection—their role was over. Once and for all the object *was* detected. This elementary function was incorporated in the integration as one of the prerequisites for action. The rest of the neuronal properties of the cellular organization to which these neurons belong are held together by realizing some purposive demand and by notifying its accomplishment.

Central sites for recording pleasure are known (Olds and Milner)¹⁸⁰ as well as centers for arousal. For this reason it seems likely that the response of the parietal neurons would require intact connections with these sites. Even if we cannot trace the precise pathways involved in the creation of complex, highly individualized responses of cellular units located beyond the specific sensory projection areas, we can rely on anatomy to supply whatever combinations physiological and behavioral facts might require. No analysis is ever likely to end up with anatomy as the great stumbling block in the way of progress. More often than

not we shall find it difficult to understand the purpose that provides biological relevance to a response found in these hierarchic tiers.

Attention, Demand, and Behavior

In considering motor activity in the highly encephalized primates including ourselves, terms and concepts that belong to the topmost hierarchic stratum are usually introduced into the text.¹⁸¹ Up to a point we can neglect such aspects of movement control and consider the recording of properties of muscles and nerve cells in joint action and the elucidation of wiring diagrams, disregarding the question of why the recorded events take place in the particular manner observed. Such work will often furnish the neurophysiologist with significant knowledge. But then for over a hundred years experimental physiology has been interested in voluntary movement and today, when by an act of willing a subject demands force and a prescribed velocity of performance, it is possible to translate demand into firing rates of motoneurons and muscles and to some extent even into discharge rates of groups of single neurons in the cortex.¹⁸² From these data as a starting point one can proceed "vertically" upward or downward in the hierarchic cascade of strata.

However, by such experiments one has neither explained will as such nor its immense range of demand, its relation to attention, nor its dependence on motivation. Some idea of will power can be obtained by pitting a demanded set of instructions against automatic segmental mechanisms and determining to what extent the latter can be overridden. Both for theoretical and for clinical purposes such studies of the act of willing or demanding are of

considerable importance. Nevertheless will and demand remain what they always were— psychological concepts required in the study of behavior. More will be said about such questions at the end of the next chapter.

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Aims and Limits of Explaining and Understanding

The scientific terms of “explanation” are “not necessarily immediately in evidence. They have to be discovered, and their discovery involves our taking the phenomena to be explained at the right level of analysis and with the right conceptual framework . . . the correlations on one level are explained by those on a deeper level in a way which shows their relation to other possible outcomes.” (Charles Taylor, *The Explanation of Purposive Behaviour*, Cambridge University Press, 1970, pp. 52–53.)¹⁸³