

DEMAND AND ACCOMPLISHMENT IN
VOLUNTARY MOVEMENT*

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A review is presented of our knowledge of the voluntary motor act, as reflected in electrical records from man and monkey. Thus, the electronic summation technique has revealed complex changes of cortical potentials accompanying the act of volition and preceding execution of the willed movement. Furthermore, by monosynaptic testing with the aid of H-reflexes, preparatory variations in the size of these reflexes have been shown to succeed a warning signal alerting the subject to a demanded movement. Variations in size of the H-reflex occur in a number of muscles, not only in those taking part in the demanded movement, but even in their silent partners on the opposite side of the body. Muscle spindle afferents in man have been recorded from in voluntary movement. Electromyography and myography have been used to analyze the effect of varying the voluntary command and, finally, the timing of motor events in voluntary movement has been successfully carried out at several sites in the brain of the awake monkey. A synthesis is attempted of the available knowledge and the final discussion is centred on the possibilities of advancing in this field of study by considering voluntary acts from the point of view of demand and the checking of its accomplishment.

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In a recent paper, H. C. Longuet-Higgins (1972) gave an excellent account of how I, at the close of my own experimental career, look upon the task ahead, "In so far as the neuro-physiologist is concerned to understand 'how the brain works', he must equip himself with a non-physiological account of the tasks which the brain and its peripheral organs are able to perform: only then can he form mature hypotheses as to how these tasks are carried out by the available 'hardware' -- to borrow a phrase from computing science" (p. 255).

Below follows an attempt at reviewing some relevant aspects of 'hardware' research pertaining to demanded movements and their accomplishment. Demanded movements are by definition purposive and, when after some practice such movements become automatic, this does not destroy their purposiveness. Automatization merely relieves our consciousness of the trouble of keeping the whole movement in permanent focus.

The new knowledge about the widespread occurrence of anticipatory motor activity in central nuclei widely apart in the cortex, thalamus, mesencephalon, cerebellum and the spinal cord (see below) indicates that motor acts are operated by a large number of subsystems of incredible complexity. Considering with Harmon (1970) that if one has n subsystems, the number of parameters may be still larger but even if they were n only, there would be 2^n subsets making "complete assessment... virtually impossible if n is large" (p. 488). Harmon, a physicist and communications engineer, clearly realizes that we need teleological constraints in order to narrow down the number of possibilities in a sensible manner. My view is that demanded movements provide natural constraints with a likewise natural approach to the study of an instrument whose main task is to deal with them.

REACTION TIME

Study of the simple reaction times is the oldest example of attempts at quantifying some aspects of a demanded movement. Electronic summation of changes of potential over the scalp has led to a reactivation of this approach. The technique has mostly involved timing the act of pressing or releasing a telegraph key in response to a stimulus signal preceded by a warning signal. With light signals well-trained subjects (men or monkeys) have

reaction times between 160 and 180 msec (e.g. Donchin and Lindsley, 1966; Evarts, 1966; Miller and Glickstein, 1967) measured up to the electromyographic response. Hufschmidt and Hufschmidt (1954) followed by others have shown that in man inhibition of the antagonist precedes the excitatory response of the agonist by some 15-20 msec. This has also been found by Evarts (1966) in the monkey. In man, values for the efferent time vary from 30-60 msec (Miller and Glickstein, 1967; Vaughan and Costa, 1968). The latency of the evoked potential to light also varies, partly dependent on the retinal latencies which hardly could go below 15-20 msec with strong stimuli. Accepting Miller and Glickstein's value of 30-40 msec to the evoked potential in the striated area, clearly something remains to be accounted for. In his reaction time experiments, Evarts took the time to spiking of the pyramidal cells in the motor cortex of the monkey and found it to be of the order of 100 msec, as against 30 msec in the chloralosed animal. Processing of the demanded behavioural act thus added 70 msec.

In reaction time experiments a non-demanded electromyographic response may slip through the system at a faster rate than the behavioural reaction. Thus, Luschei et al. (1967, with references to earlier papers), studying the reaction time both to clicks and to visual stimuli, found an early electromyographic response after 30-50 msec. The demanded response to a click would otherwise be of the order of 80 msec. The early electromyogram definitely correlated with the stimulus, visual or acoustic, but not with the behavioural reaction. When the latter was delayed by differential reinforcement, the early response stayed put in its time-dependent relationship to the stimulus while the behavioural reaction slowed down in obedience to the new demand imposed. Training to react 'as fast as possible' does not seem to lead the reaction into pathways responsible for early electromyograms.

As is well known, the evoked potential to light is a long-lasting affair comprising several components. A late wave N_2 , at 250 msec latency with visual signals, was found by Bostock and Jarvis (1970) to relate very strongly, both within and across subjects, to the speed of the reaction. This component was interpreted as an index of the moment-to-moment level of arousal. Karlin et al. (1971) found the length of the reaction time correlated with several of the evoked potential wavelets. While there is a considerable literature to show that the form and magnitude

of the evoked potential varies with the level of alertness, it is worth emphasizing that the latency to the peaks or troughs of the various waves has no relationship to the length of the reaction time (Davis and Yoshie, 1963; Morell and Morell, 1966, using visual stimulation). It is the processing within the instrument that is decisive for the speed of the response. Of this the configuration of the evoked potential seems to be an index.

VOLUNTARY MOVEMENT

The electronic summation technique in the hands of many recent workers (e.g. Kornhuber and Deecke, 1964; Gilden et al., 1966; Vaughan and Costa, 1968, Deecke et al., 1969) has demonstrated the existence of a drawn-out cortical process in man and monkey engaged in performing voluntary movements. There are complex changes of potential preceding such acts (Deecke et al., 1969) which I do not intend to review in their entirety with attention to details. These still belong to the frontline of research. Voluntary movement is preceded by a slow negative bilateral change of potential. It may begin as early as 850 msec before the mechanogram (readiness potentials). Such changes of potential during the time between a warning signal and the signal to react are being eagerly studied today. The experiments need not necessarily be completed with a motor act. Other purposive responses may serve just as well (Donchin et al., 1971). However, about 50-150 msec prior to contraction there appears a more decisive and brisk unilateral change in the same direction, the so-called motor potential, closely related in time to the spike activity described by Evarts (1966, 1967) in the pyramidal neurones of the monkey. The motor potential in man is unilateral and somatotopically located over the specific region in the motor area that is engaged in the motor act. It may precede movement of the hand by 30-40 msec. Deecke et al. (1969) find a latency of 56 msec to the electromyogram of the index finger.

Of particular interest seems to me a paper by Vaughan et al. (1970) in which they describe work on monkeys trained to perform wrist extension at regular intervals. The motor potential and the electromyogram were recorded before and after de-afferentation of the limb. The negative motor potential was followed by a positive deflection that had been regarded as a response to proprioceptive feedback because of its similarity to the recordable effect of joint movements. However, it was seen also in the de-

afferented state and so, if really caused by a feedback mechanism, must have been fed back from elsewhere in the cerebrum, cerebellum or spinal cord. There had been a fresh training period of 4 weeks interpolated between deafferentation and the resumption of the experiments. This would give ample time for the establishment of vicarious feedback in aid of accomplishment of the movement.

I have selected this, rather than any other of the many experiments in this field because it convincingly demonstrates a retardment and prolongation of the cortical process itself after deafferentation. In their work normal values for the delay between the cortical motor potential and its electromyographic counterpart were of the order of 100 msec, never below 80 msec, occasionally as late as 250 msec. After deafferentation the lag regularly was between 200 and 250 msec. The peripheral motor response lasted 200-300 msec in the normal monkey, after deafferentation 500 msec. The experiment shows that the afferent apparatus of a limb is needed for efficient motor performance. Afferent messages must have reached the cortical organization in advance of the motor potential, at the time when the brain was still engaged in processing the voluntary motor act. Thus, in an animal at the monkey's level of encephalization, the cortex must be cognizant of the peripheral requirements conditioning execution of a demanded movement. Except for the retardation, the cortical process itself, in terms of potentials, was not very different before and after deafferentation. The act of processing the demand was merely slowed down and delayed.

While papers over a period of a hundred years have shown that deafferentation produces motor deficits, the discovery and analysis of the cortical motor potential adds the demonstration that, in advance of movement, the cortex itself has recorded and made use of available information required for rapid and efficient execution of what is being demanded. How does it inform itself? Along what channels? The solution of this problem seems to be within reach of experimentation and one day we shall have the answer.

While considering the subject of simple reaction times and motor potentials, one should perhaps give a thought to the great variations of estimates of time in this field of work. Any figure can be doubled or even trebled, as we have seen in the papers

dealing with human subjects. Levels of arousal are known to be very important for the outcome of experiments on reaction time (e.g. Garcia-Austt et al., 1964), but variations are likely to depend also on temporal summation of the kind that have been illustrated so well at the spinal level by Phillips and Porter (1964) studying the motoneurons of the baboon excited from the motor area. Porter and Muir (1971) found the motoneurons extremely sensitive to small variations of frequency. In studying this variable in the motoneurons of the m. abductor pollicis they found a range of latencies from 17.6 -66.5 msec. There may be other sites at which similar temporal summations could be equally effective. Both non-specific and specific afferent impulses may be responsible for such variations in levels of depolarization as would be capable of explaining the large span of latencies observed in experiments on reaction times.

'GHOST MOVEMENTS'

There is a considerable literature making use of monosynaptic testing by H-reflexes and tendon jerks in man to investigate the excitability of the motoneurons during the warning period that alerts a subject to the signal in reaction time experiments. During this time the cortical changes of potential indicate processing of the demanded act and the question raised is whether anything measurable also can be recorded at the spinal level. Some recent experiments by Requin (1969), Requin and Paillard (1969) and Coquery and Coulmance (1971) will serve to illustrate what is meant.

Thus, for instance, an experiment was arranged so as to measure the size of the tendon reflex of the two soleus muscles. The warning signal was a click, the signal to react was a light and the response was an extension of the right foot. The monosynaptic testing reflexes were elicited by a bilateral percussion of the two Achilles tendons and recorded by electrodes on the soleus muscles. The right soleus alone was involved in the instruction to react, but both solei exhibited a facilitation after the warning signal. In the muscle engaged in the demanded response the facilitation was gradually replaced by an inhibition of unknown origin. In the motoneurons not involved the 'ghost' movement gradually disappeared.

This experiment has been modified in several ways. In one

case the demand was elaborated as a choice-reaction-time experiment. When the warning signal was followed by a light signal on the left, the subject extended the left foot; when it was given on the right, he was requested not to respond. Random equiprobable signals were used for the two choices. Testing was by H-reflexes elicited from the popliteal fossa. Duration of the preparatory period from warning click to stimulus signal was varied from 100 to 700 msec. During this period there was a facilitation of the monosynaptic indicator reflex that again was seen on both sides and rose more slowly with the extended delay. These experiments provided more examples of the intricate changes of motoneurone excitability caused by a variation of the demand. The expectation raised by the different lengths of the preparatory period may also be regarded as a further variation of what was demanded of the subject: be attentive for a short or a long interval before the signal to react is given. It turned out that processing of the response from the very beginning was adjusted to these instructions.

Timing, localization, the relative significance of alpha and gamma motoneurons (Brunia, 1971), etc., enter into experiments making use of demand as a variable. At the Second International Symposium on Motor Control, in Varna, Bulgaria (1972), Zalkind presented a variety of 'ghost movements' by monosynaptic testing, demonstrating the intimate manner in which the cortex takes part in and prepares for movement down to the spinal level. It would be interesting to have spindle records from subjects responding with 'ghost' movements.

DEMAND AND ACCOMPLISHMENT

One of the earliest neurophysiological experiments to demonstrate the significance of varying demands was carried out by Hammond (1954, 1956), and interpreted by Hammond et al. (1956). The subject carried a steel tape wristlet connected to a stretching device. The experiments were conducted at an initial tension of 3.06 kg. Tension to pull and the biceps electromyogram were recorded. The demanded acts were: (i) respond to a tendon tap by the strongest possible contraction; (ii) when the wristlet is pulled away without warning, resist the pull; (iii) or do not resist, but let go (this will not be considered below).

Ten superimposed responses were used in each case. To (i)

the tendon tap produced a monosynaptic reflex jerk with a latency of 15-20 msec. This was succeeded by silence in the EMG for some 50 msec. At a latency of about 80 msec followed the subject's response. The whole experiment is thus a study of proprioceptive reaction time.

Knowing now that in such measurements of reaction time the afferent signal reaches the cortex to be somehow processed with respect to the demand for a specific movement (strong biceps contraction in this case), let us consider what could be the minimal, theoretical latency of the behavioural response, if the fastest possible pathways were in operation. There are precise measurements of afferent and efferent times from the work of Phillips and his colleagues on the baboon's hand and arm muscles and their cortical connections. Impulses in the fast primary spindle afferents reach the cortical area 3a after a mean time of 4.2 msec, counted from the dorsal root entry (Phillips et al., 1971). The fast monosynaptic path from the motor cortex to the motoneurons requires a minimum of 2.3 msec (Kernell and Wu, 1967a, b) to 2.5 msec (Landgren et al., 1962).

The additional time required to and from the biceps electrodes can hardly account for more than a few msec. This is on the assumption that the motoneurons are optimally depolarized in advance by (i) the cortical paths to their interneurons and (ii) by the maintained stretch of the arm muscles keeping the spindles active. Adding a generous estimate of 15-20 msec a minimal reaction time would be something of the order of 45-50 msec. Such theoretical times probably presuppose employment of the fast primary spindle afferents and the monosynaptic cortical efferents. The cortical afferent latencies of spindle secondaries are of the order of 20 msec in the baboon (Wiesendanger, 1973). There seems to be no obvious reason why use of the fast pathways should be prohibited, provided that the subject is attentive and well enough trained. Polysynaptic segmental excitation induced from the cortex is present in all animals and is likely always to be engaged.

Brief reaction times are of considerable interest because Evarts (1973) has recently carried out experiments on the monkey suggesting that in a well-trained animal these can be very brief indeed. In this work the monkey grasped the handle of the apparatus to trigger the rapid movement required for reward. It responded by opposing the triggered pull. Records were taken

from pyramidal tract neurones which began to discharge 25 msec after the proprioceptive stimulus. The electromyographic response came at a total reaction time of 35 msec, so that the efferent time would have been 10 msec. The initial monosynaptic jerk at a latency of 15 msec was followed by a pause in the EMG. The reward put a premium on speed of performance, and speed, indeed, was what the monkey delivered. It was noted that the brief reaction times required attention. If the animal let his attention wander, the response time was prolonged.

Here then we have evidence proving that the cortex actually was engaged in very rapid performance. A direct connection of area 3a of the primary spindle projections to the motor area of the baboon has not been found by Phillips and his co-workers (Phillips et al., 1971; Wiesendanger, 1973), but their experiments were carried out in light anaesthesia and we have seen that brief reaction times require full attention on the part of the animal, or of man, for that matter. One would not therefore expect them to have found the key to the lock closing the path. This is tied to a definite demand. However, there are also other meeting places 'en route', for instance, in the thalamus where the actual integrative work may take place. Cerebellar impulses destined for the cortex likewise take this way. Activity in neurones of the thalamic nucleus VL has been shown to precede movement with latencies approximating those of the fastest cortical cells (Evarts, 1970). There is no information available on cortical motor potentials in those experiments. It would be desirable to have some.

I have taken up Evarts' experiment in such detail because we have a pendant to it in Hammond's second type of experiment. This shows up other aspects of the interpretation of brief reaction times.

To (ii): in this case Hammond introduced an unexpected pull on the wristlet and the instruction was to resist it when it came. Again the first effect of stretch was the monosynaptic reflex jerk at 15-20 msec, followed by a pause shortened to 35 msec. The command to resist took effect after a reaction time of about 50 msec. Evarts' results suggest that in Hammond's very similar experiment the cortex was informed and had time to act upon this information. Evarts and Hammond both used a fully awake aroused preparation, monkey or man.

At the time one could only postulate (Hammond et al., 1956) that the alpha and gamma motoneurons would be co-activated but we have since had the evidence of Hagbarth and Vallbo (1968, 1969) and of Vallbo (1970, 1971) by direct recording from spindle afferents in man that voluntary movement is executed in alpha-gamma linkage, leading to co-activation of the direct and indirect motor systems.

In Hammond's first type of experiment there would have been voluntary activation of the spindles involved in the requirement for a maximal response to a tendon tap. Assuming that in both cases the sensory message from the stimulus itself reached the cortex and was reflected back to the muscle in alpha-gamma linkage, why was the time shortened when the subject was requested to resist the pull? Very likely the effect was caused by the spindles' increased firing in load compensation to the more isometric mode of contraction implied in the instruction to resist stretching. Considering that the cortical monosynaptic path to the motoneurons operates within a span of 18-67 msec at the motoneurone, this may provide a sufficient margin for the variations of delay observed in the cases compared. (It might be remarked that there are monosynaptic corticomotoneuronal paths also to the gamma motoneurons, at least in the baboon (Clough et al., 1971). There may well be more of them in man.)

Finally, what can we say about the period of silence after the monosynaptic jerk of constant brief latency in man and monkey? This clearly precedes and, for a moment, curtails load compensations on the part of the spindles. Is it merely caused by an after-hyperpolarization of motoneurons synchronously engaged in delivering the jerk, supported by recurrent inhibition? I am inclined to be skeptical. It may well be caused by Golgi tendon organs and, in places, by spindle secondaries. However, knowing as we do that antagonist inhibitions have shorter reaction times than agonist excitation, we cannot exclude that it may be one of the properties of motor processing to sweep a path clean by a cortically generated inhibition before action. The corticomotoneuronal inhibitory path in the baboon is as fast as its excitatory counterpart and a single intercalated synapse only adds a negligible time of the order of a millisecond. More work should now be done on the inhibitions in the antagonists and their extremely brief latencies.

CHECKING ACCOMPLISHMENT

Knowing that pyramidal and extrapyramidal motor paths branch off to several nuclei on their way to the motoneurons, we have to reckon with means of internal feedback of information at many sites. Another matter is how to attack such problems in terms of 'hardware' and in their precise relation to specific motor acts. In this situation my standpoint is that one should begin with the muscle spindles and the tendon organs. These structures are situated in the contracting muscles and are accessible indicators of both force and length, of the first derivatives of these quantities and, in the case of spindles, also of the misalignment between them and the main muscle. If we cannot solve such problems, what chance is there of solving the obscure ones of internal feedback? There is little likelihood that an organ like the spindle, which is co-activated from virtually all sites capable of initiating movements (Granit and Kaada, 1953) and which returns information to both the cerebrum and the cerebellum, ever could be neglected in trying to formulate ideas on accomplishment as checked by feedback. Vallbo's (1971) recent work on afferent spindle responses from the human hand shows that even brief isometric twitch-like wrist movements are carried out in alpha-gamma linkage.

It has now become necessary for further progress to entertain some precise ideas about the structural nature of the link between the alphas and gammas that is responsible for their co-activation. I have recently (Granit, 1973) put forth a simple model which could serve as a guide in such endeavours. Its postulates should not be too difficult to test by experimentation.

Though I now have emphasised the role of the spindles in feeding back information on accomplishment, I do not think of this problem in as simple terms (Granit, 1972). There are receptors from the joints and the skin to be considered in addition to the muscular receptors. Recently Marsden et al. (1972) have studied the responses to loading and unloading of the flexor of the top joint of the thumb. By producing anaesthesia of the hand with the aid of a wrist cuff, the muscle belly (containing the spindles) has been left above the affected region and so the thumb has remained flexible. In this situation Marsden et al. found the compensatory responses to loading disappear showing that, acutely at least, spindles and tendon organs by themselves cannot operate the system. The nature of the contribution from other end

organs is unknown, but it may well be in aid of maintaining the necessary level of depolarization at one or several sites along the passage to the cortex. Marsden et al. (1973) have also been led to the view that a cortical 'reflex' may be caused by stretching a muscle.

In thinking of sensory information and what it may achieve it is necessary to rid our argumentation of the unjustified assumption that isolation of a sensory input necessarily is the most informative way of studying it (Granit, 1972). This assumption is true only for the basic elementary question of conduction, convergence, divergence, etc., relating to sensory projections. Many sense organs, and particularly those concerned with movement, reveal their true significance only when allowed to cooperate in active motor acts with other input channels.

OPERATIVE USE OF 'DEMAND'

Returning finally to the original question of making demands, analyzable in terms of 'hardware' and of the need for teleological constraints, I have chosen my examples to indicate possible means of advancing. Electrodes implanted into different sites can tell us a great deal, provided that we can impose a constraint of variable purpose upon the experiments, as in those mentioned here. Explanations may not always be as plausible and testable as in those discussed above, but, on the other hand, if one merely persists in demonstrating that site a inhibits or excites site b, c or d, neglecting the teleological questions of what purpose all of it serves and how it responds to variations of 'demand', then, in the end one will be in possession of a body of knowledge, to be sure, but knowledge likely to become merely an amorphous conglomerate of well-documented facts.

Let us not underrate the difficulties. We have seen in this exposé that there is widespread cortical activity in voluntary movement, that it moulds both alpha and gamma activity according to demand, as was well illustrated by the increased spindle activity in response to a demand for greater force. We have also seen that measurable acts of preparation for a movement take place as far down as at the level of the spinal motoneurons. Evarts (1966, 1967) and those that have employed his micro-electrode technique of studying wrist flexion and extension in the awake monkey, have demonstrated how widely a movement is

reflected in the brain; thalamic neurones have been mentioned above, the pallidum is informed (DeLong, 1971) and so is the cerebellum (Thach, 1970a, b). It seems likely that the pontine nuclei and the dorsal column nuclei could be added to the list. In the motor area Evarts found both pyramidal tract neurones and non-pyramidal ones participating and also post-central neurones in the sensorimotor cortex, the latter some 60-80 msec delayed. Humphrey et al. (1970) repeated the experiment on the motor cortex with five tungsten microelectrodes inserted into an area 2x3 cm centred on the forearm region. They studied the temporal distribution of the discharges. Clearly, in the motor area alone thousands of cells must be activated in these simple wrist movements. The cortical neurones according to Evarts are concerned with force and velocity of contraction. Such discharges precede muscular contraction also in the thalamus and the dentate nucleus of the cerebellum, but there the cells in addition fire during and after contractions. This suggests that, like the post-central neurones, they respond to feedback messages. For further reference to these results, see Evarts (1973).

In view of all these findings, is it at all sensible to expect us to understand coding in this immense 'computer' without considering that it has been moulded in the course of phylogenesis to deliver purposive reactions in response to demands. These were originally set by the environment, and, after development of a cortex and cortico-subcortical interaction, also by invoking conscious mentation of movements, remembered or created ad libitum for some purpose.

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