

# Constant Errors in the Execution and Appreciation of Movement

BY

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## CONSTANT ERRORS IN THE EXECUTION AND APPRECIATION OF MOVEMENT<sup>1</sup>

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To a large extent our motor acts belong to a subconscious organization of controls. Even those movements which we regard as voluntary are largely automatic. Most of them intrude upon consciousness only at the moment when they are triggered off into action. The final execution of the command follows a beaten track and the event reaches awareness only if something goes wrong. For this reason constant errors of judgement on motor performance, often appearing as illusions, are of considerable interest to the physiologists. Provided that they can be interpreted, they may tell us something about the automatic components in the control of movement and posture, and present knowledge about muscle receptors and motor control (summarized, Granit, 1970, 1972) has advanced far enough to warrant an attempt at reassessing—in terms of neurophysiology—the value of some old and new observations on constant errors in motor performance. Neurophysiological research has been largely devoted to the elucidation of principles of control at the very level at which subconscious and automatic acts take place. The properties of muscle spindles and tendon organs have also been intensely studied.

It is impossible in this brief introduction to review the long history of Bell's (1826) muscular sense which he (1833) defined as a "consciousness of exertion." However, it is equally impossible to bypass the fundamental experiments of Renqvist (1927) in which he used Hill's (1922) inertia ergometer to study flexion-extension around the elbow-joint and proved that his subjects perceived equal force when the physical forces were equal. A weight of 9.59 kg was pulled at two amplitudes related as 4:2. At the lower amplitude the weight had to be accelerated to feel as heavy as at the greater amplitude. Equality of perception was reached when the products of mass and acceleration, by definition equal to force, were adjusted to be equal. When unequal weights were used, the time (duration) was integrated into the percept so that the judgement of equality reflected equal tension-time curves, that is, equal amounts of work. In view of v. Frey's (1914, 1915) precise experiments on what

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he called the *Kraftsinn* (sense of force) those of Renqvist led to results that were to be expected. In both cases active movements far above the threshold were studied. In recent discussions of muscular sensations these fundamental contributions have been neglected.

Another important datum needed for the interpretation of constant errors in motor performance is the notion (Granit, 1955) of alpha-gamma linkage in movement, now definitely shown to be a characteristic feature also of voluntary acts (Hagbarth and Vallbo, 1968, 1969; Vallbo, 1970, 1971). The term means that the muscle spindles are mobilized in willed contractions and by the aid of the stretch reflex of Liddell and Sherrington (1924) automatically influence the motoneurons of the acting muscles. Co-activation of the extra- and intrafusal motor fibres suggests that the spindle component in excitation is included in the expectations related to the accomplishment of motor acts commanded by the will.

### *Hypothesis to be Explored*

It has long been known and often confirmed that the muscle spindles can be activated from the cortex (*see review*, Granit, 1970; Fidone and Preston, 1969; Grigg and Preston, 1971). A fast monosynaptic path to the gamma or fusimotor neurons of the baboon's hand has recently been described by Clough, Phillips and Sheridan (1971). Finally, it has been proved by Oscarsson and his co-workers (Oscarsson, 1965) and by Landgren and his group (Andersson, Landgren and Wolsk, 1966; Landgren and Silfvenius, 1969) that the large primary spindle afferents project to the sensorimotor cortex. Similar projections have recently been discovered in the baboon's sensory field 3a (Phillips, Powell and Wiesendanger, 1971) too. The role of these projections is unknown but the hypothesis to be investigated in this paper is that they form part of a mechanism for checking the execution of movements in relation to commands. This check is assumed to be an automatic process likely to be integrated in the sum total of proprioceptive information and reaching awareness only when something unexpected happens and needs to be attended to, or when for other reasons special attention is directed to sensations from the muscles (as, for instance, in Renqvist's work referred to above). The general attitude taken in this paper is that whatever clue the brain be given, it also is capable of interpreting if need for this arises to serve some sensible purpose. Meaningless pull on muscles is not regarded as serving any such purpose.

### *Constant Errors Referable to Reflex Adjustments*

An example of unexpectedness was analysed by Hick (1949) in a study of reaction times. His subjects were instructed to pull as quickly as possible on a solenoid at the moment a click was heard. The reaction time (click to start of pull) was measured and after some practice was reduced to 0.212 second. The solenoid was then unexpectedly magnetized. After a brief abortive starting response, pull against the heavier load was resumed at the longer reaction time of 0.304 second. The difference

is 0.09 second, thus considerably shorter than the pure kinesthetic reaction time which is of the order of 0.130 second. How is this error to be accounted for?

On the principle of alpha-gamma linkage in voluntary movements, the muscle spindle's own contraction was set or biased for a shortening which was suddenly prevented from taking place immediately, because of the increased load. This automatically accelerated the firing of the spindles in so-called load compensation by means of the stretch reflex. This postulate, based upon general spindle properties, was first realized experimentally by Corda, Eklund and Euler (1965) who studied the linked alpha-gamma activity in the intercostal muscles of the cat in response to tracheal occlusion, but the sudden increase of tension would also mobilize Golgi tendon organs. Their likely participation in the response has been shown by Newsom Davis and Sears (1970) and Sears (1971), who introduced sudden changes of respiratory load in subjects maintaining an otherwise even flow of air. Electromyograms from the intercostal muscles then showed an initial inhibitory phase at a latency of 19–22 msec, followed by an excitatory response at a latent period of about 50 msec, both times being too short for voluntary reaction times and therefore held to be dependent on reflexes. The inhibitory response was referred to the tendon organs which, wherever found, always cause ipsilateral autogenetic inhibition (for references, see Granit, 1970). The excitatory reflex of the spindle primaries had to overcome this initial inhibition.

Actually an experiment very similar to that of Hick also shows an initial inhibition by electromyography. This was performed by Hammond (1955, 1956). The subject held his forearm at about 80 degrees against a spring and was instructed to resist a sudden outward pull at the wrist produced by clutching in a velodyne motor connected to it. In Hammond's records there is an initial inhibition followed by a contraction at 71.5 msec (in terms of the electrical response that precedes contraction). Hick only recorded contractions. His constant error of 90 msec can be accounted for by (i) the time needed for the muscle contraction to advance far enough to elicit the reflex from the muscle receptors, (ii) the initial inhibition and (iii) the excitation of the motoneurons leading to a contraction. Ascribing 20 msec to the latent period of inhibition, 40 msec to its duration and 20 msec to the excitatory reflex to overcome it, the total of 80 msec is an acceptable value and reasonably close to the 90 msec suggested by Hick's results. Hammond's time of 71.5 msec to the excitatory phase was wholly kinesthetic, that is, not initiated by a click.

There is now accurate information on the time needed for a cortical response to mature into awareness. Libet and his colleagues (Libet *et al.*, 1964, as reviewed by Libet, 1965) stimulated the exposed cortex of patients, occasionally the subcortical white matter or the VP nucleus of the thalamus also, and they found that "not only is repetition of liminal stimulus pulses required (sc. for a conscious response) but that such repetition must go on for half a second or so to become effective" (Libet, 1965, p. 251). Relative to this time the evoked cortical response was virtually instantaneous and thus preceded the conscious reaction by a margin allowing for the activation of whatever circuits may have been needed for awareness. Interestingly

enough, this figure of half a second recurs in the attempts of psychologists to determine the interval required for two percepts to be separable as such (Craik, 1947-48; Vince, 1948).

In the experiments of Hick and Hammond, the perception of increased resistance must therefore have arisen well after the reflex adjustments it was supposed to engender. How is it then that reaction times are so much shorter than the time required for perception? The reply must be that the reaction times are determined by the subconscious organization on to which they are transferred as soon as the subject has learned to understand what is being wanted. The delayed perception of increased resistance in the experiments reviewed may well in itself be a composite one based on several peripheral components. The high precision of judgments on amount of force perceived, demonstrated in the experiments of v. Frey and Renqvist, makes it extremely improbable that the muscle's most sensitive organ, the spindle, could be negligible in this complex. Its sensitivity, after all, is of the order of 4-5  $\mu$  of extension at the tendon (Brown, Engberg and Matthews, 1967; Stuart, Mosher, Gerlach and Reinking, 1970). The present tendency to ignore the cortical projections of spindles in sensory experiments is based on a traditional "isolationist" standpoint, inherited from psychophysics, implying that if it is impossible to detect a conscious response when a sense organ is stimulated in isolation, its message can never implicate consciousness.

An experiment by Hollingworth (1909) in which the subject was pulling on a carriage moving along a track on which it could be stopped unexpectedly by an upright is also instructive. The order was to shift the carriage 1, 2 or 3 feet, at a constant speed that also was well held. Errors of judgement of extension (displacement) were small as long as the movement was free. When the movement was momentarily arrested by the upright that then was quickly removed, the subject, who was supposed to indicate one of the standard distances by continuing the movement, made positive errors of the order of 155 per cent of the standard. These gross constant errors are illusions caused by the impact. The error was found to increase with the force of the impact (in terms of velocity of movement) and to decrease if the upright was placed late in the wanted displacement. The illusion could not be abolished by training, and is therefore likely to be based upon a sensory message inevitably causing an excitatory reflex.

The arrest of the planned displacement implied that an isotonic contraction had been made isometric. This would have caused a forceful spindle discharge facilitating the motoneurons which therefore would have responded to the supraspinal command by increasing their output. There may have been other sense organs contributing to the effect of the impact but only the spindles have the properties of responding with a smaller discharge, the later the upright was placed in the planned movement. As to joint receptors, there seems to be no obvious reason why they should have failed to set the angle correctly, block or no block in the path.

The positive error is an illusion because the subject does not recognize that he has failed to notice it. The articular sense was "cheated" by the reflex during the

actual movement and is not very sensitive to maintained positions. Long ago Bloch (1896) stated: "While a movement is in progress, the impression of position is perceived with some accuracy; it deteriorates during immobility and gradually vanishes as the moment of action recedes" (p. 82). Recently Paillard and Brouchon (1968) have confirmed and extended this observation. In Hollingworth's illusion the subject therefore is badly guided by his sense organs after the accomplishment of the act. He is compelled to judge by intent only.

#### *Clinical Implications of Previous Section*

The common denominator of the experiments described in the previous section is that they are explained by the process of load compensation by spindles acting in alpha-gamma linkage. Inasmuch as the neurologist needs simple methods for the study of the exquisitely organized mechanism of spindle co-operation in movement and posture, the experiments reviewed are of the kind that could easily be adapted to that end. The results can be obtained by objective measurements calling for very little from the patient. Their precision should be high.

#### *Illusions of Intent and the Sensation of Innervation*

The realization that we are capable of adjusting our commands to the motoneurons in proportion to the requirements of expected performance is as old as physiology (see, for instance, J. Müller's textbook of 1840, p. 500). This experience led Müller to suggest as a possibility that we might also have a sense of innervation, the *Innervationsempfindung* of several subsequent authors. This notion recurs in recent writings under various terms such as *corollary discharge*, *sensation of effort* and *efferece copy* together with more or less elaborated theoretical appendages which cannot be reviewed in the present context. All these terms and explanations were invented to account for absent peripheral information before it was known that the periphery itself is "corollarized" by alpha-gamma linkage to one of our most highly developed sense organs which also projects to the cortex.

These problems are sharply brought into focus by Charpentier's illusion (1891). He had two equally heavy spheres, one 4, the other 10 cm in diameter, in his palm or on his fingers. On lifting the weights he felt the larger sphere to be the lighter. Flournoy (1894) extended these experiments to a large number of observers and made them compare the weights of objects of different shape and volume. In his paper Flournoy tabulates results from experiments in which 50 subjects lifted ten different equally heavy objects of 112 grammes varying in volume from 10 to 2,100 cc. The subjects were asked to rank them according to perceived weight along an arbitrary scale of ten divisions. The table provides a most convincing demonstration of the validity of Charpentier's observation; the larger objects appeared lighter than the smaller ones. In the end Flournoy asked his subjects to add small balls and shot to the apparently light weight of 2,100 cc in volume until it felt equal to the small weight of 10 cc in volume. The amount required turned out to be 111.5 grammes in the averages.

Flournoy rightly emphasizes that "this illusion is direct argument against the sensations of innervation" because the voluntary anticipation to be "corollarized" would have implied a stronger command for lifting the larger volume. In the language of today the stronger command would have caused a greater spindle discharge acting to facilitate the motoneurons. As a consequence the biceps would have produced a stronger and faster contraction while the tendon organs, if playing a role for the sensory experience, would have recorded tension objectively. During the actual contraction the spindle activity would have diminished at an unexpectedly fast rate owing to the rapidity of the shortening of the muscle. (The postural after-contractions, to be discussed below, are also giving a perception of lightness, and essentially there is the same imbalance in that these contractions likewise encounter motoneurons facilitated beyond expectation by so-called post-tetanic potentiation.)

At the turn of the century Sherrington (1900) declared the sensations of innervation unproven, "provided that memory revivals be not included under that term" (p. 1005). Goldscheider (1898) who faradized the joints and virtually obliterated the perception of movement stated that he had no sensations of innervation. In his well-known textbook, Starling pointed out that weights can be arranged in order of heaviness by purely electrical contractions. Campbell and his co-workers (1963, 1967, 1969), in experiments on curarization of the respiratory muscles did not report any sensations of innervation. During recovery from a spinal anaesthetic I myself ordered one of my legs, stretched out in bed, to be lifted. It felt dead and heavy and I was utterly unaware of the fact that it actually did move, until my toes bumped against the blanket and I had a blunt feeling of something like a thud.

Thus it seems legitimate to reiterate Sherrington's conclusion that there is no evidence for a sensation of innervation. Besides, to postulate such sensations in a normal subject with normal limbs means to abstain from chances of progress and prefer a "dead end" of research to a "live wire."

#### *Postural After-contractions and Vibratory Reflexes*

Among the best-known illusions are the postural after-contractions which even in the twenties gave rise to scientific publications but then seem to have been neglected except as parlour games. Well known is a striking illusion of this kind: the subject stands in an open door and presses his extended arms forcefully against the posts. Moving out after some twenty seconds he experiences a curious sensation of lightness while at the same time seeing his arms rising like wings in flight. The recent reopened studies of vibration reflexes in man (Hagbarth and Eklund, 1966; Lance, de Gail and Neilson, 1966) seem to provide an avenue of approach to the understanding of postural after-contractions. The common denominator of the two types of movement is that both are non-volitional extrafusar contractions lacking the specific intrafusar component of co-activation that is integrated into normal movements based on alpha-gamma linkage. In this respect they fall outside the framework of normal experience.

Hagbarth and Eklund describe a "feeling of relief or lessening of tension" when the biceps contracts in response to vibratory stimulation at the tendon. The frequencies are of the order of 100 to 150 Hz. The reflex movement is correctly assessed as to direction, and it seems reasonable to ascribe this judgment to a functioning articular sense responding as in passive movements. The mismatch in this case lies in the "cheated" muscular sense which is forced to experience something as unique as an active contraction which is essentially "passive" in nature (if this expression be permitted to describe), the spindles acting by themselves disconnected from any sensible programme of action. This unbalanced information the central interpreter refuses to connect with a feeling of "exertion" and quite sensibly it reacts as if an outer force had made the limb lighter.

However, it is possible to introduce a sensation of movement into this experiment on vibration of the biceps muscle if it is performed isometrically. If the muscle is prevented from shortening, there arises an illusion that a "gradual change of position occurs, corresponding to the movement which should have occurred if the contraction had not been 'isometric'. Such illusions (they continue) seem to arise and subside in parallel with the motor effects of the stimulus" (Hagbarth and Eklund, 1966, pp. 179-80).

An interesting development along these lines is an experiment by Goodwin, McCloskey and Matthews (1971) on the arm flexor of a blindfolded subject. If the movement of the vibrated arm was tracked with the other arm, the tracking arm lagged behind it, showing that part at least of the reflex response was inadequately perceived. When, however, the vibrated arm was prevented from flexing by an external constraint, as in the isometric experiment of Hagbarth and Eklund, the subject experienced a feeling of extension though no actual extension could occur. When these events were followed by the tracking arm, it first reproduced the flexion, but at the moment when the subject's vibrated arm felt the non-existent extension against the constraint, the tracking arm responded with an extension. The Oxford workers interpret the sensation of the non-existent extension, as demonstrated so vividly by the tracking arm, to be a consequence of the mismatch between information received and expectation.

A very similar illusion was reported by Sternberg (1885): the subject flexes the muscles at all joints of his index finger maximally, and, keeping the thumb freely hanging down, extends the remaining three fingers and presses them against a table to produce a maintained state of maximum extension. If he then closes his eyes and starts "willing" to extend the top of the index finger—in the situation firmly locked—he feels after some time that he has been successful. On opening his eyes, it comes as a surprise to him that nothing has happened to the locked finger top. In all these experiments the illusion does not come immediately. Vibration or the voluntary effort must go on for a while.

In these experiments two illusions have been experienced, the feeling of lightness common to postural after-effects and vibratory reflexes and the illusion of having extended a muscle in isometric contraction; a vibratory reflex or a voluntary effort.

It seems that "lightness" of the limb is the natural interpretation of "unsolicited contractions" of limb flexors caused by hyperexcitability somewhere in the path leading to these muscles. In postural after-contractions there is clearly post-tetanic potentiation of the motoneurons and possibly of some supraspinal stations (*see below*). Starting spindle afferents by stretching extensors in the cat, hyperexcitability of the motoneurons lasts for several minutes afterwards (Granit, 1956). In postural after-contractions the spindles are activated during the largely isometric voluntary effort preceding the after-effect. The vibratory reflex in man is largely, if not wholly, caused by the large spindle afferents.

Of very great interest is the illusion of extension in the cases described. It can hardly arise from tendon organs or joint receptors. Spindle activity is generally greater in isometric than in isotonic contractions and what happens when an isotonic contraction is suddenly arrested has already been illustrated by many examples (*above*). In Sternberg's illusion the spindle excitation is a consequence of the voluntary effort in the isometric state of the muscle.

These results serve to illuminate a postulate by Gelfan and Carter (1967) to the effect that we have no muscular sensations whatever, a disturbing conclusion in view of the experiments of v. Frey and Renqvist mentioned earlier, but it was backed by what the authors held to be conclusive evidence: Gelfan and Carter had at their disposal 9 patients with tendons at the wrist freed for about 1 cm so that they could pull on a tendon with a fine-toothed forceps. Pulling in the distal direction, so as to extend the muscles of the arm up to 5 cm, gave no sensation of any definite kind connected with tension or extension, whereas pulling in the opposite direction, causing flexion of the fingers or of the whole hand, led to accurately localized movements of the joints. Visual clues were excluded.

Superficially this experiment seems highly convincing, but it neglects to take into account that sensing or perceiving is an active, exploratory process of some duration and that this act is less concerned with information than with the meaning of information. The cortical projections of the muscle spindles cannot be compared in elaboration and extent with those of the eye or the ear. They may not record position (Merton, 1964; Brindley and Merton, 1960) nor are they likely to tell the cortex much about events in individual muscles considering that organized movement is a multi-muscular event. We have no specific sensations of muscle length but the spindles contribute their share to the inflow of information from the sense organs of muscles, tendons and joints and their messages are included in the expectations of accomplishment created by the higher centres in their operations of control and supervision. There is no need for experiencing movements if all turns out according to expectation. Only the unexpected is perceived. Hence, in agreement with Goodwin *et al.* (1971), it is concluded that the interesting sensations of extension in the experiments described are derived from the activity of muscle spindles which is perceived because of the mismatch entailed. It is likely that normally only properly willed movements are perceived, as in the experiments of v. Frey and Renqvist discussed above. These suggest that co-activated spindles, which are the only end

organs reflecting both demand and execution, play a most essential role in our judgements about muscular exertion, difficult though it be to formulate the proprioceptive experience in the way we can describe things seen or heard.

### *Clinical Significance of Vibratory Reflexes and Postural After-contractions*

The clinical significance of postural after-contractions and vibratory reflexes hinges upon the tonic nature of these effects and what they can be made to yield as means of analysing disturbances of posture. Very little can be done without a working hypothesis and the author (Granit, 1956, 1970 and 1972) has for some time experimented on the assumption that tone is organized by a special "postural computer," an organization of its own to which various afferents engaged in postural activities have access, and output of which is mediated by special tonic motoneurons. It has been questioned whether tonic motoneurons (Granit, 1956) and correspondingly slow muscle fibres (Denny-Brown, 1929; Eccles, Eccles and Lundberg, 1958) also occur in man. Recent work (Grimby and Hannerz, 1970; Sica and McComas, 1971) has settled this question in the affirmative.

An important aspect of control of these motoneurons is the fusimotor gamma regulation of the static reflexes by which proprioceptive tone is maintained and adjusted to variations of load on the muscles. These afferents of the stretch reflex have a potent monosynaptic component but their polysynaptic basic organization is equally important. It may be widely distributed in the spinal cord but, even in the cat, the supraspinal component is in control, as shown by spinalization which suppresses both tonic alpha motoneurons and the static gamma motoneurons of Matthews (1964) and his colleagues. The vibratory reflex in this animal is reduced to 20 per cent of its previous size by discrete lesions in the ipsilateral ventral column or by ablation of the lateral vestibular nucleus (Gillies, Burke and Lance, 1971); it can be restored by stimulating the lateral vestibular tract.

The existence of a special tonic organization in man also explains why tonic vibratory reflexes rise so slowly, the latent period of the monosynaptic component being a negligible fraction of vibratory reflex latency. In the decerebrate cat in which the tonic organization is fully activated, the tonic vibratory reflex rises rapidly (Brown, Engberg and Matthews, 1967). Eklund and Hagbarth (1966) have pointed out that during vibration the classical postural reflexes of Magnus and De Kleijn can be elicited. Normally these are subthreshold in man.

The effect of vibration on the nigro-striatal complex and on the cerebellum recommends itself for clinical studies. These will no doubt become properly analysed in neurophysiological laboratories but it seems as if man would be the most interesting and important subject available for decisive conclusions about the role of these structures in postural control.

Study of the postural after-contractions was carried to the point when their use in the clinic merely required an additional effort in order to yield results of considerable interest.

Historically this work goes back to Fechner's (1860) observations, followed up by Müller and Schumann (1889), that lifting a weight a few times leaves an after-effect making a subsequently lifted lighter weight feel lighter than before. Much of the old literature on this subject will be found in the monograph by Woodworth (1903).

Renewed interest in the subject arose from the description by Salmon (1916) and Kohnstamm (1915) of the type of sensation obtained when the arms for some time had been pressed against a resistance and then were released. Pinkhof (1921) demonstrated action currents during the after-contractions and Matthaei (1924) studied them extensively and also confirmed the observation by Müller and Schumann to the effect that pre-contraction of one arm could produce or facilitate the after-contraction of the other. This shows that post-tetanic potentiation at the level of the motoneuron cannot fully explain after-contractions, even if as such it is an unavoidable accompaniment of monosynaptic stimulation of the motoneurons by large spindle afferents. That the effect reaches higher levels is also demonstrated by Hoff and Schilder's (1925) observation that it failed to occur in 6 cases of parkinsonism. A convenient technique for studying after-contractions would be that of Hick (1953). Much new knowledge about motor control and the nature of postural defects and their relief suggests that this old approach deserves to be reconsidered as a diagnostic tool.

#### SUMMARY

Sherrington (1900) expressed surprise that the fine muscular sense could be subject to such gross constant errors (illusions) as were known at the time and since have multiplied in number.

It is being shown that the recent experiments on co-activation of the muscle spindles in voluntary movements and the demonstration of their cortical projections supply a simple explanation of this discrepancy, not needing any special central awareness of innervation (*Innervationsempfindung*).

The basic organization of postural control is discussed and specific suggestions are put forward as to how and why clinical studies of constant errors would be valuable.

Recent experiments questioning the existence of Bell's muscular sense which he described as a "consciousness of exertion" are criticized for taking inadequate notice of the active, exploratory element in perception.

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