Beyond the Spinal Reflex Arc : Physiology of Supra-Spinal Reflexes

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INTRODUCTION

In 17th century, it was Descartes who first clearly defined the basic behaviour pattern of the reflex. He gave an example of a foot placed near a fire, which, when painfully stimulated, is quickly withdrawn. Such reflex responses can be described as machine like in character, implying a reproducibility of response. They have also been called purposeful, since reflexes are generally of use to the organism. In the last century, the purposiveness of reflexes was taken to indicate that there was some kind of primitive consciousness in the spinal cord that directs reflex activity. Sherrington[1], however, pointed out that the apparently purposive nature of reflex responses represents a selection, during evolution of responses that have survival value. Certain reflexes damaging to the organism, rather than protective, may be elicited, further indicating the lack of conscious direction in reflex action.

A practical use made of reflexes is illustrated in anaesthesiology. Touching the eyelids causes a reflex closure, the eyelid reflex, which is lost with moderately deep anaesthesia. Touching the cornea of the eye causes a corneal reflex; the lid blinks to cover and protects the cornea. This reflex is diminished or lost when the brainstem has been depressed to a perilous degree. The pupillary light reflex, constriction of the pupils to light shining on the eye, is one of the last reflexes to disappear in deep anaesthesia alongwith respiratory and cardiovascular reflex control mechanisms whose centres are in the medulla. Another reflex of value in judging whether the depth of anaesthesia is satisfactory for operative manipulation is the response produced by pinching the skin (one example of nociceptive, i.e., injury-provoking stimulation). This evokes a flexor withdrawal reflex in which the limb flexes away from the site where the noxious stimulus is applied. When this reflex is absent, anaesthesia is generally considered sufficiently deep to permit operative procedures.

The various reflexes are so interrelated in the animal that the result is one continuous, smooth, well-directed beheviour pattern, each reflex succeeding and merging with the next in rapid sequence. The interrelation of one reflex with another is demonstrated in locomotion. An animal in which the spinal cord has been cut some weeks previously to allow it to recover its reflex excitability is suspended in a harness. When the foot is gently but quickly pressed upward, the slight spreading of the toe pads suddenly results in a powerful downward thrust of the leg, the extensor-thrust reflex. During locomotion the limb is flexed and brought up from the ground. After the body of the animal has carried it forward, the limb is extended and comes into contact with the surface. With that contact the extensor thrust is excited, and the limb is converted into a rigid column to give a polevaulting effect to the body, carrying it forward over the extended limb. The reflex is then quickly inhibited, permitting the leg to flex, and the cycle of flexion and extension is repeated.

In the following review, the spinal reflex arcs have been outlined. Also, it has been discussed that reflexes do not depend mainly on the integrity of spinal-reflexes but involve phylogenitically younger, more powerful and adaptable long loop reflexes running through higher centres.

SPINAL-REFLEXES

There are a number of spinal reflexes. The variety of these reflexes function as integrated ones. Various types of spinal reflexes are: MYOTATIC, INVERSE-MYOTATIC, FLEXION, CROSSED EXTENSION, SCRATCH, STEPPING, LONG SPINAL. The normal animal does not use any of these reflexes to the exclusion of the others. The interdependence of spinal reflexes has two morphologic and physiologic determinants: a). Overlap of neuronal circuits in periphery and in the spinal cord. b). The end

product of any single spinal reflex muscle contraction, itself initiates, other reflexes by virtue of the stimulation numerous muscle and joint receptors during the reflex movement.

Organization of Spinal Reflex paths:-

Spinal reflexes have been studied mostly in Spinal cat (By transecting spinal cord at first cervical segment) or Decerebrate cat (By trasnecting the mid-brain at the intercollicular level). These reflexes are characterized by their central delay and the duration of discharge. The greater the number of synapses in a reflex, the longer is the central delay.

Spinal reflex paths are laid out according to a relatively simple plan whose main feature is the segmental organization fo circuitry. It is comparatively easy to study the reflexes under functional isolation of the reflex paths when supra-spinal influences or influences from spinal segments other than the one under investigation are eliminated by an adequate spinal transection. Spinal reflex paths are easily accessible. Reflexes can be evoked by natural or electrical stimulation of identified afferents from various peripheral organs (extensor or flexor muscles, tendon skin receptors) or by electrical stimulation of dorsal roots (see Fig. 1). The reflex response may be recorded from ventral roots or from skeletal muscles as electrical activity or muscle contraction as shown in the same figure. The simplicity in the organization of spinal reflex paths makes it possible to determine the effect of drug on single synapses mediating either excitation or inhibition. The result thus obtained may prove to be relevant not only to the spinal cord but other regions of the CNS as well.

Spinal reflexes have been categorised as a result of particular receptors or afferents to be stimulated in the body.

(a)   *The Monosynaptic reflex:-*

Excitation of low thereshold afferent from extensor muscles (muscle spindle or Ia afferents) activates a reflex path consisting of the afferent (sensory) neurone, the efferent (motor) neurone and the synapse between the two neurones (Fig. 1). Activation of this monsynaptic reflex path with a single electrical pulse evokes a potential in the ventral root which, due to an extremely synchronized evcitatory impulse input into the motoneurones, is short in duration and of relatively high amplitude.

Since the monosynaptic reflex path contains only one synapse and the velocity of impulse conduction in the afferent and efferent nuerone is high, the reflex latency is very short (a few msec.).

(b)   *The Disynaptic reflex:-*

Excitation of afferent from Golgi tendon organs (Ib afferents) activates a reflex path involving two synapses between afferent and efferent neurones. The reflex latency of disynaptic reflex is greater than the monosynaptic one.

(c)   *Polysynaptic reflex :-*

Stimulation of high threshold afferent e.g. afferents from the skin (exteroceptors) or joint receptors (proprioceptors) evokes a polysynaptic reflex. Skin stimulation activates ipsilateral flexor motonuerones (crossed extensor reflex) by way of a polysynaptic reflex path (Fig 1). As the monosynaptic reflex path, it consists of the sensory (primary) afferent and the motor efferent but, inaddition, it contain one or more interneurones in series.

Due to the low conduction velocity of high threshold afferents and to the synaptic delays in the course an impulse has to travel from the primary afferent via consecutive internuerones to the motoneurone, the latency and the duration of the response of the motonuerones to polysynaptic activation with a single electrical impulse are long. Moreover, the long duration of the polysynaptic reflex potential recorded from ventral roots results from pecularity of the interneurones to discharge repeatedly when activated by a single incoming impulse. Thus, the motoneurone in a monosynaptic reflex path is activated only once by stimulation of the afferent neurone with a single, whilst this mode of stimulation evokes repetitive activation of the motoneurone forming part of a polysynaptic reflex path.

SUPRA-SPINAL REFLEXES
(Long loop or Transcortical reflexes)

The monosynaptic reflex between primary muscle spindle afferents and alpha motoneurones has had an important role in the development of our understanding of reflex mechanisms. This is due to the simplicity and the accessibility of this reflex for experimental study. However, in recent years it has become clear that the response to more prolonged stretch of a muscle involves many mechanisms beyond that of the monosynaptic connection bet-
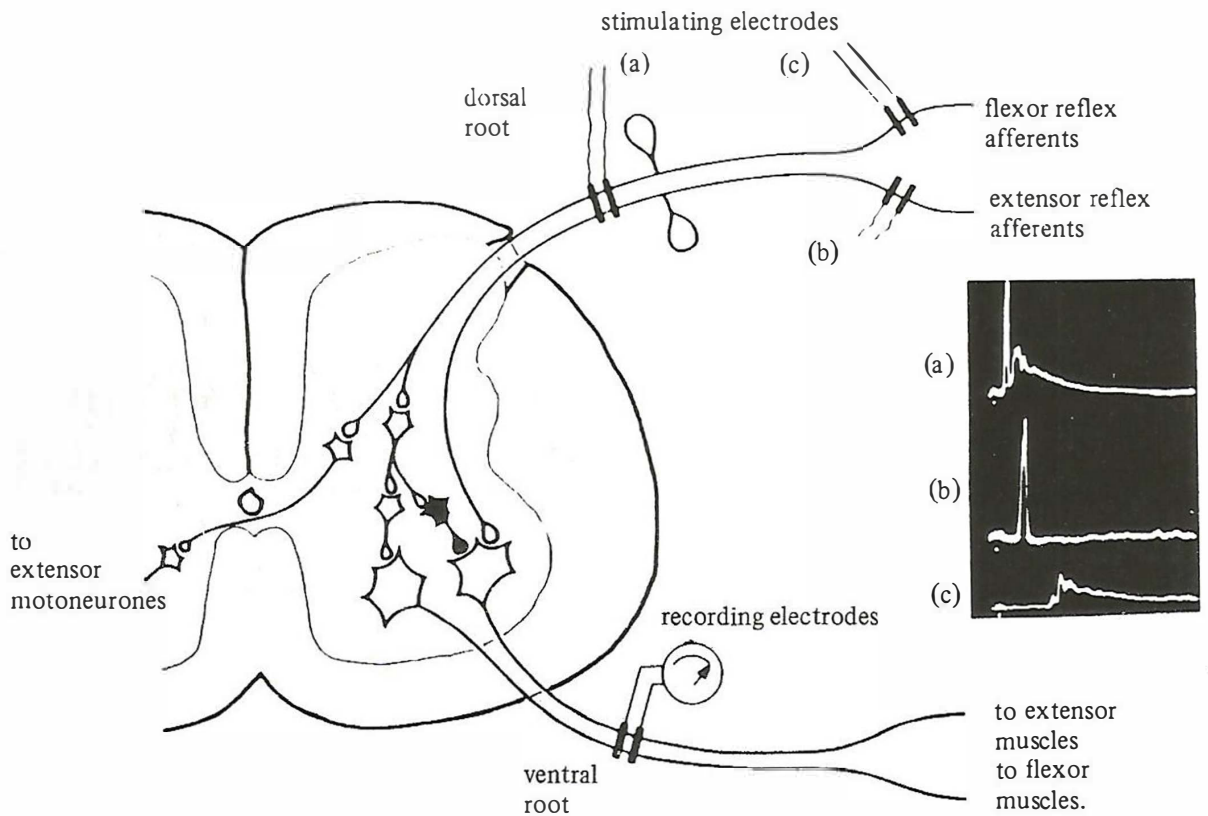
Fig. 1: Schematic presentation of monosynaptic and polysynaptic reflex path in the spinal cord. An inhibitory neurone from the polysynaptic flexor reflex path to the extensor motoneurone is marked in black. The inset shows reflex ptoentials recorded from the ventral root. The potential (a) presents mono and polysynaptic reflex activity evoked by stimulation of the dorsal root. The potential (b) is the monosynaptic reflex response to stimulation of flexor reflex afferents. Time calibration is 5 ms. The difference in the latencies of corresponding mono-or poly-synaptic reflex responses to stimulation of dorsal roots or afferents is due to differences in the distance of the stimulating electrodes from the spinal cord.

ween primary muscle spindle afferents and alpha-motoneurones, At the spinal level evidence has been presented to suggest that secondary muscle spindle afferents have a powerful multisynaptic effect[2] and evensome monosynaptic connections[3] on to motoneurons. The reflex effects of Golgi tendon organs, even at relatively low levels of active contraction, have also been stressed[4] Fig. 2 (A).

The relative roles of these three types of muscle receptors at the spinal level under various conditions remains quite controversial and is an active area of current research. In addition, evidence has been accumulating for the importance of supra-spinal mechanisms in response to stretch during human voluntary contraction. Hammond[5] first noted a large response intermediate in latency between the spinal stretch reflexes and a voluntary reaction time. These responses were dependent on prior instructions to the subject and were more dispersed in time, but other-wise similar to reflex mechanisms. Further data from non-human primates led Phillips[6] to suggest that during the course of evolution more flexible supra-spinal mechanisms had, to some extent, been overlaid on top of the basic spinal reflexes. He saw such transcortical reflexes as providing a focusing action for muscle spindle feed back. Among the data which are consistent with the participation in motor control by a transcortical loop is the finding that motor out-put response to a sharp pulse of torque is fractioned into distinct peaks[7], which have become known as M_1 & M_2 (Fig 2B). While the latency of M_1 is consistent with a segmental conduction delay, the timing of M_2 provides ample time for its mediation by the cortex. Furthermore, it was found that precentral units in the cortex respond reflex action[8,9]. Lee & Tatton[7,8] showed that M_2 is abolished following a lesion of the post central cortex. This suggestion has been corroborated in human studies[10,11,12].

Mersden et al[13] described a Servo-action in human voluntary movement: Whenever in the course of a voluntary movement we meet with an unexpected obstruction we soon exert our muscls harder to overcome, to explain a possible mechanism for the gain control in the servo loop postulates an input to the servo which, as the demanded force alters, has the function of altering the number of a motoneurones that are sensitive to spindle excitation, in proportion. A demand for increased force would be met (in whole or in part) by increasing the number of motoneurones responding to spindle input in proportion (or at a slower rate if the larger motor units are recruited later). Loop gain would automatically increase in proportion, as the number of active motoneurones increased. It is known that the number of a motoneurones active does increase with force and that all motoneurones receive a spindle input. They defined in this regard few experimental points (1) that there is Servo-action, sensitive, brisk and so early as clearly to be automatic, involuntary movements. (2) that the gain of the servo loop is proportional to the force exterted (3) that the gain of the servo loop is automatically compensated against contractile fatigue in the muscle (4) that the latency of Servo-action is the same as the latency of transcortical stretch reflexes. Finally it has become clear that in man[11,12] as well as in other species[14,15] al there may be more than one supra spinal pathway involved.
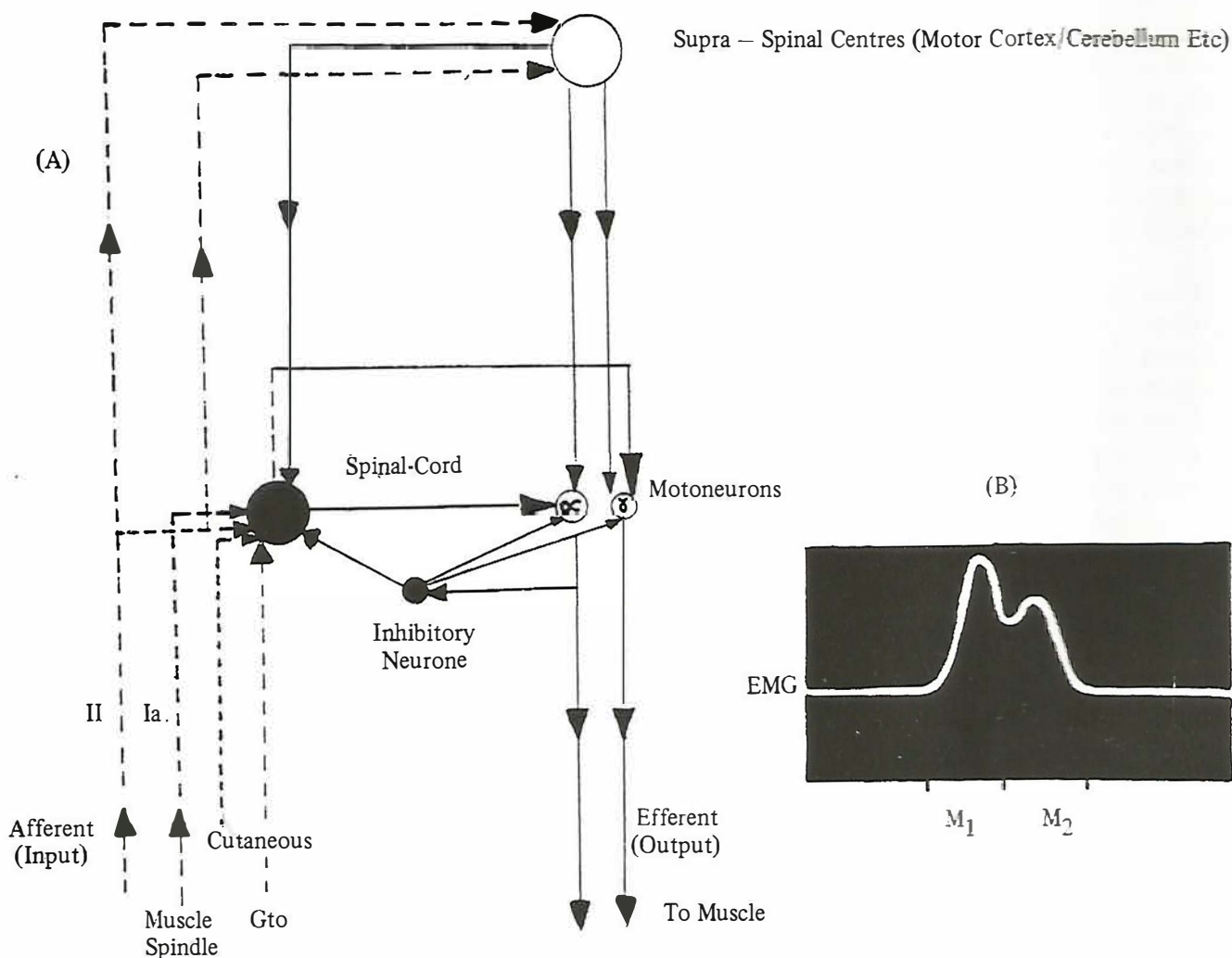

Fig. 2:   (A)   Modle of Input output Relationships in a Long-Ltency Reflex.
               (B)   EMG Response to Illustrate Spinal Reflex (M_1) and Supra-Spinal Reflex (M_2).

In studies on the lower limbs of normal human subjects Melv Jones & Watt[16] noted that the longer latency pathways were much more powerful than the spinal ones and referred to the longer latency pathways as the "functional stretch reflex". These studies were carried out on subjects who were either dropped from some height or were hopping on one foot. The latency of the reflex is such that there must be a number of synaptic relays of unknown properties. The latency could be twice or more that of the corresponding monosynaptic reflex. In monkeys it has been possible to record motor cortical activity correlated with these reflex responses and the latency of the cortex[8] is such that is involves a fast ascending pathway. Thus the most plausible explanation of these reflexes is that it arises from primary muscle spindle afferents and has a pathway involving supra-spinal centres and probably the motor cortex. Recently, Ghori & Luckwill[17] demonstrated a pattern of long latency response to a mechanical stimulus applied to a leg during walking in normal human subjects. They accounted for these responses to be compensatory ones produced from the higher centres to maintain correct upright posture when disturbed momentarily in response to a transitory unilateral resistance.

In human subjects, also it has been hypothesized that long latency compensatory adjustments to mechanical disturbances are triggered reaction processes[18] which are preprogrammed and are thus capable of automatic operation. If this were true, long latency responses would not be dependent on muscle stretch, as any stimulus could be used to trigger a postural adjustment. However, recent experiments by Nashner and Cardo[19] indicated that long latency postural responses to support surface movements always occur before voluntary reaction time movements when both are triggered by or at the onset of platform movement. They observed that these movements could be separated into two distinct entities when examined according to function: (a) stabilizing activites, designed to bring the body centre of mass into a state of equilibrium (Long latency postural responses), and (b) voluntary shifts in orientation (triggered voluntary responses). It should be emphasized that these distinctions were made purely according to function, with no speculation concerning differences in neural circuitry.

Recent work indicates that stability of upright posture on firm ground does not depend mainly on the integrity of spinal stretch reflexes[20,21] but involves phylogenetically younger, more powerful and adaptable long-loop reflexes running through the higher centres such as the motor cortex and presumeably the cerebellum [22] Fig. 2(A).

CONCLUDING REMARKS

A number of groups of investigators have shown that stretch of contracting human muscle evokes not only a monosynaptic spinal stretch reflex at a tendon jerk latency, but also later automatic events, which have been called SUPRA-SPINAL OR LONG LATENCY REFLEXES. It has been proved that long latency reflexes were only apparent when the subject was actively contracting the muscle,either to execute a movement or to hold a position. With the muscle completely relaxed, these longlatency events usually disappeared. The observations, revealed that long latency reflex responses were useful and powerful than spinal ones on the basis of past experience and/or the basis of knowledge stored in CNS.

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