THE TWO ROUTES FOR EXCITATION OF MUSCLE AND THEIR SUBSERVIENCE TO THE CEREBELLUM

By RAGNAR GRANIT, B. HOLMGREN* AND P. A. MERTON†

*From the Nobel Institute for Neurophysiology,
Karolinska Institutet, Stockholm 60, Sweden*

When the motor centres of the brain bring about a movement, descending impulses may reach the muscles by either of two routes (Fig. 1). The more familiar runs directly, or through relays, to the large α anterior horn cells and so to the muscles. In the second, the indirect route, recently investigated by Eldred, Granit & Merton (1953), the small nerve or γ efferents are excited instead. This causes contraction of the intrafusal muscle bundles, in itself giving negligible tension measured externally, but sufficing to stretch the primary (nuclear bag) sensory endings in the muscle spindles and thus, through the stretch reflex arc, to activate the main muscles. Such a roundabout way of initiating contraction naturally introduces delay, but it has the advantage that during shortening the muscles may still enjoy the self-regulating or servo properties of the stretch reflex.

The behaviour of a muscle will be quite different in the two modes of excitation. A constant rate of discharge over the α route sets up tension which, to a first approximation, will be independent of length. The γ efferent system, however, is believed to operate the stretch reflex servo which (by the mechanism just outlined) makes the main muscle follow length changes in the spindle. For a constant rate of γ discharge the muscle will tend to maintain a fixed length independent of tension.

The circumstances under which use is made of one route or the other, or (as seems more likely) various mixtures of the two, are not known, although, for example, it is probable that posture would mainly employ the γ route, and that rapid movements with minimum reaction time go through the α route. If there is truth in these suppositions it is clear that some mechanism must exist to adjust activity quickly between one route and the other, and to vary the proportions of the two routes in use. The experiments to be described suggest that such adjustments may be a function of the cerebellum.

* Guillermo Puelma Foundation Research Fellow of the University of Chile, Santiago.
† On leave of absence from the Medical Research Council, London.

In all previous work on the γ efferents one of the most striking and uniform observations has been the apparent linkage between α and γ systems in reflex activity. As a rule contraction is preceded and accompanied by γ discharge (Hunt, 1951; Kobayashi, Oshima & Tasaki, 1952; Eldred & Hagbarth, 1954). In decerebrate animals, according to Kobayashi *et al.* and Granit & Kaada (1952), γ activity is particularly prominent. Eldred *et al.* (1953), by disrupting the link, showed that in cats decerebrated by intercollicular section the γ route was indeed predominant. They listened in to single spindle afferents from
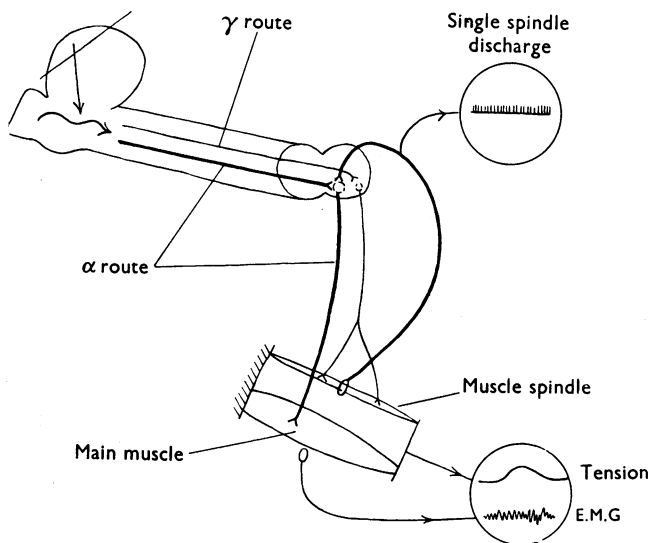

Fig. 1. Diagram of the experiments. Muscle tension and electromyogram are recorded, together with the response of a sample spindle-ending from a fine dorsal root filament (muscle innervation otherwise intact). There are two possible routes, α and γ, from the brainstem to the muscle (indicated very schematically). The experiments deal with the relative degree of usage of the two routes before and after anterior cerebellectomy, etc.

muscles whose innervation was interfered with only to the extent of taking one dorsal rootlet. As passive spindles without γ supply always stop discharging during muscle contraction owing to their 'in parallel' attachment, the observation that in reflex contractions there was an actual acceleration, meant that γ discharge was making the spindles contract ahead of the main muscle. The large spindle afferents are known to excite the stretch reflex, so the experiment also indicated that γ activity was indirectly promoting excitation of the α motoneurones. The importance of this factor was brought out by cutting the dorsal roots; afterwards, although spindle acceleration was observed to occur just as before, there was no muscle contraction. The linkage had been broken.

Although coactivation of the α and γ systems seems to be the common pattern of excitation in other types of preparation too (at least in postural reflexes), it is clear that the part played by the γ system is not always quite as decisive as appears in decerebrate cats, for in some circumstances contractions do occur when the γ route is completely blocked by dorsal root section. It was one of Sherrington's fundamental observations that the state of exaggerated posture he called decerebrate rigidity was dissolved by dorsal root section (Sherrington, 1898). This is easily understood if rigidity is due to hyper-activity in the γ system. Pollock & Davis (1930b, 1931) found, however, that in cats functionally decerebrated by tying off the arterial supply to the brain, rigidity remained after deafferentation. Such rigidity must, therefore, be due mainly to excitation over the α route, by-passing the γ mechanism. The essential difference between these two types of decerebrate preparation was elucidated by Stella (1944a, b; see also Moruzzi, 1950). Recalling that in the indian ink injections of Pollock & Davis, in addition to the cerebrum, the anterior part of the cerebellum was also rendered anaemic, he prepared classical decerebrate animals with deafferented (and therefore flaccid) forelimbs. Rigidity appeared at once when the anterior lobe of the cerebellum was cooled or cut off. Cardin (1946) later showed the same effect in the hindlimbs. (See also Terzuolo & Terzian, 1953.) Sherrington (1898) himself had observed that decerebrate rigidity persisted after cerebellectomy, but the above facts indicate that the rigidity before and the rigidity after cerebellectomy really have quite different mechanisms, the former largely γ driven, but the latter by-passing the γ route. Thus we were led to investigate the effect of the cerebellum on activity in the γ system.

We have done experiments on the same principles as Eldred *et al.*, but after various types of interference with the cerebellum. In a successful experiment, when the anterior lobe is out of action, the muscle is switched towards the α mode of excitation; contraction is no longer accompanied by spindle accelera-tion, nor is it abolished by deafferenting. Usually, however, there is evidence that the γ system is not completely paralysed; some γ discharge accompanies α contraction, but the emphasis has shifted. A preliminary communication of the results was given by Eldred, Granit, Holmgren & Merton (1954).

METHODS

The results are based on experiments with twenty-five cats, the technique being that described by Eldred *et al.* (1953), with certain additions. (The essentials are illustrated in Fig. 1.) In ablation and cooling experiments, after decerebration by the trephine method, the cerebellum was exposed by removal of the tentorium, or occasionally by a posterior approach through the occipital bone. Ablations were made with a blunt instrument under brief trichlorethylene anaesthesia. Cooling was by the application of a small piece of frozen Ringer's solution to the cerebellar surface. Action potentials of single spindle afferents were recorded in dorsal root filaments. The customary recording of muscle tension was often supplemented by the electromyogram, taken between a

silver pin in the muscle belly and the fixation drill through the femoral condyles. Soleus was generally the muscle used.

In several cats decerebrated by the anaemic method of Pollock & Davis (1930 *b*) the parts of the brain deprived of blood were delimited by indian ink injections. Like them we found that anaemic decerebration corresponds to a section through the fore part of the cerebellum and pons. Sometimes, however, small islands of ink were seen in the basal ganglia, suggesting that occlusion had not been complete, or that collateral circulation might develop in a long experiment. For this reason, in the later experiments, after tying the vessels the skull was opened and an intercollicular section made.
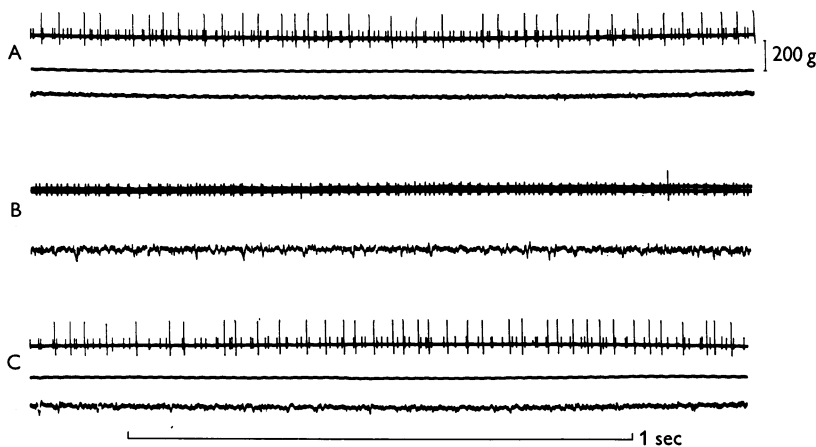

Fig. 2. Effect of cooling the cerebellum on decerebrate rigidity. Precollicular section; left side of tentorium removed; records from left soleus muscle. In this and subsequent figures the top trace is the response of a single spindle afferent ending; middle trace, muscle tension; lowest trace, electromyogram. A, basal activity. B, frozen Ringer applied to left side of culmen; spindle virtually silenced; rigidity increased (tension trace lifted into and just above spindle trace). C, cerebellum rewarmed with Ringer at 38° C. (Spikes retouched.)

RESULTS

In the decerebrate animal, as Eldred *et al.* (1953) described, the spindles are biased by γ activity and keep up a rapid and irregular discharge. Any increase in rigidity is heralded by acceleration to a still higher rate (as previously suggested by Hunt's (1951) results). In the present series of experiments on similar preparations, when the anterior lobe of the cerebellum was cooled, rigidity might even increase, but it was observed that the former association with spindle acceleration had reversed. As tension rose spindle discharge, instead of accelerating, was arrested. An instance of this is shown in Fig. 2 A and B. Rewarming the cerebellum restored the original picture (Fig. 2 C).

These experiments illustrate two important phenomena. First, a relative paralysis of the γ system. Instead of anticipating and supporting α contraction the spindle behaves passively, pausing during contraction as it does in isolated muscle. (The degree of γ bias is also less when the muscle is relaxed, as we have

observed in other experiments.) Secondly, heightening of activity in the α system. Were γ paralysis the only result of cooling the cerebellum, its effect on rigidity should be the same as that of cutting the dorsal roots. The fact that rigidity, on the contrary, may be intensified can only mean that the proprio-ceptive excitation of which the motoneurones are deprived has been replaced, or even exceeded, by activity in the α pathway. (See previous work on α arousal by Bremer (1922) and Stella (1944a, b))
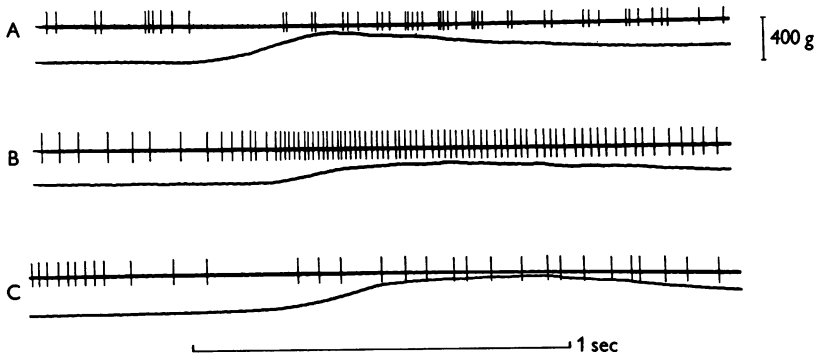

Fig. 3. Effect of cooling or ablating the anterior lobe of the cerebellum on the responses in soleus to head flexion. A, culmen cooled with frozen Ringer. B, rewarmed to 38° C. C, culmen and part of lobulus medius ablated. Spindle response reversed in A and C; tension response similar. Intercollicular section; entire tentorium removed. Tension scale applies to all records. (Spikes retouched.)

The present series is too small to allow a valid comparison of the tensions exerted in similar reflexes with the muscle in the α and γ modes of excitation. That there is not necessarily any change is shown in Fig. 3. The reflex con-traction of soleus when the animal's head was bent down differs little in the three records, the first during cooling of the anterior lobe, then after warming it up to 38° C again, and finally after ablation of the area previously cooled. The relative passivity of the spindle when the anterior lobe is out of action is clearly demonstrated (records A and C), both by the slowing of discharge during contraction and its acceleration as the muscle relaxes. Thus a muscle certainly *can* be switched towards the α mode without change of the tension it develops in a reflex. By contrast Fig. 4, from the same experiment, compares the effect of twisting the pinna on the discharge of a spindle in soleus. Although a reversal in spindle behaviour is again evident, the tension developed is much larger with a warm cerebellum.

A total of five cooling experiments was done; in three of them results of the type just described were obtained, but in two cats no reversal of spindle behaviour was produced, the only effect being a general depression of reflex excitability. In ablation experiments the proportion of failures was even

greater. Removal of the culmen in a further two cats gave results similar to those already described (Fig. 3), but in several cats lesions involving the culmen, lobulus medius and lobulus centralis did not reverse the spindle response. One cat behaved quite exceptionally. Initially it gave the responses
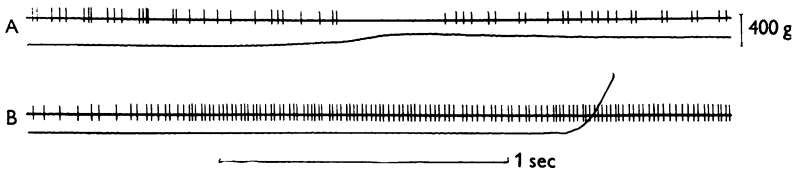

Fig. 4. Responses in soleus to twisting the pinna. A, during cooling of the cerebellum; B, after rewarming to 38° C. Same experiment as Fig. 3. Tension scale applies to both records. (Spikes retouched.)
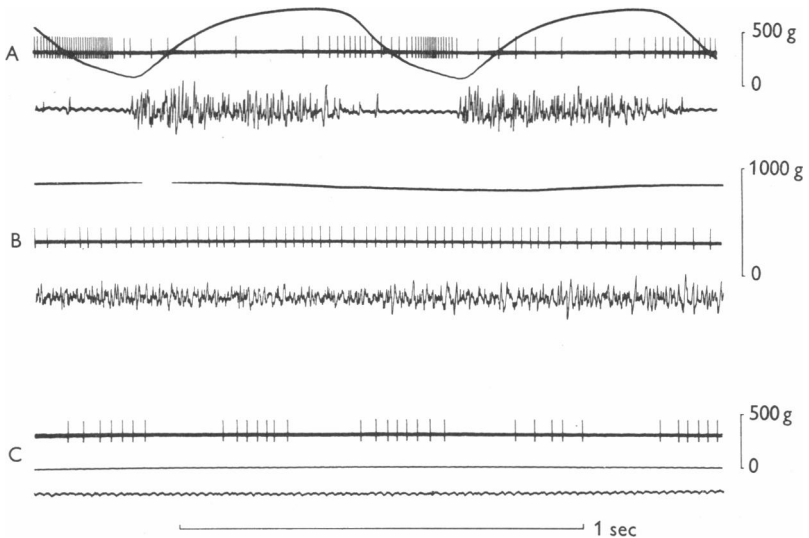

Fig. 5. Precollicular decerebration and ablation of culmen and lobulus medius. Records from soleus muscle and spindle. A, spontaneous clonus with passive spindle response; B, tonic contraction with rapid spindle discharge indicating γ bias, but with passive pattern of response to slow changes in tension; C, muscle flaccid, spindle clonus. (Retouched.)

to be expected of an ordinary intercollicular decerebration. The entire lobulus medius and culmen were then removed by the posterior approach. On recovery from the anaesthetic intense clonic activity developed. We cannot account for this clonus, but, whatever its cause, it was clearly driven predominantly through the α route. Records from a spindle in soleus (Fig. 5A) show a typical passive type of response, pausing during contraction and, indeed, reaching its highest frequency at a time, during relaxation, when the electromyogram was quite silent. Later the muscle went into a sustained tonic

contraction. The frequency of the spindle at this time indicated that a moderate γ bias still persisted, but the reaction to the slight spontaneous swings in tension that occurred was of the passive type (Fig. 5B). After a further clonic outburst the muscle became completely flaccid, but now the spindle itself gave feeble 'clonic' bursts, another indication that γ paralysis was not complete (Fig. 5C).
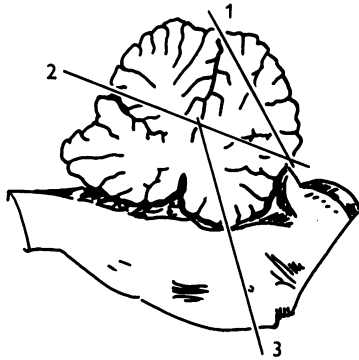

Fig. 6. Diagram of the brainstem in an experiment with a precollicular decerebration and with wide exposure of cerebellum. In this cat sections numbered 1 and 2 did not reverse the spindle response, but section 3 did, as shown in Fig. 7.
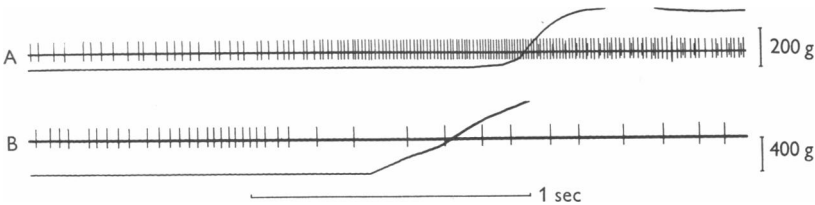

Fig. 7. Responses in soleus to twisting the pinna. A, with cerebellum and brainstem intact; B, after the sections 1, 2 and 3 depicted in Fig. 6. (Spikes retouched.)

In three of the cats with cerebellar lesions a section was subsequently made extending into the pons. In two of these animals sections, involving the middle and posterior parts of the pons, merely depressed reflex activity and soon proved fatal. In the third, a section passing obliquely through the anterior pons (section 3 in Fig. 6), reversed the spindle response during a pinna reflex (Fig. 7) and increased rigidity in the muscle, the resting tension rising some 300 g.

With anaemic decerebration (Pollock & Davis, 1930b), the anterior cerebellum is excluded from the start, so it is not possible to compare γ behaviour with and without an active cerebellum in the one animal. There is no doubt, however, that in general the muscle spindles were less biased in anaemic preparations than in those decerebrated by inter- or pre-collicular section.

(Moderate γ bias in a Pollock–Davis cat is illustrated in Eldred *et al.* (1953), figs. 1 and 6.) A typical response to twisting the pinna is shown in Fig. 8, contrasted with that obtained in an animal with an intercollicular decerebration. The α route to soleus also predominated during neck reflexes; the spindle
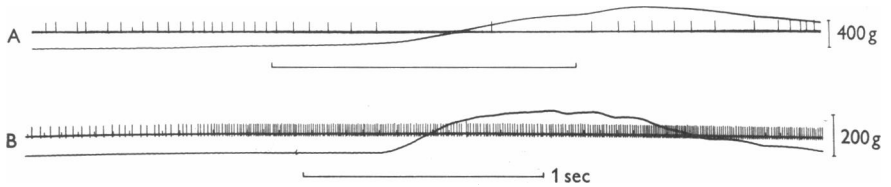

Fig. 8. Responses in soleus to twisting the pinna. A, anaemic decerebration by the method of Pollock & Davis (the spindle response is passive); B, active spindle response in a classical intercollicular decerebration. (Spikes retouched.)
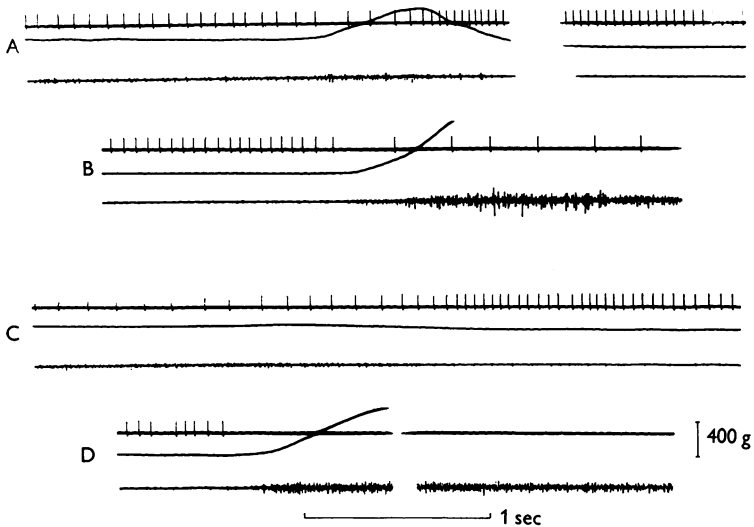

Fig. 9. Responses in soleus to flexion and extension of the neck, showing their indifference to deafferentation in an anaemically decerebrate cat. A and B before deafferentation. A, head level initially, and then bent upwards. After an initial slight contraction (to be disregarded) the muscle relaxes, as expected. Spindle behaves passively and accelerates. (Interruption of traces not successfully synchronized with head movement.) B, head level initially, and then bent downwards. Muscle contracts; spindle again passive and slows. Deafferentation then performed, but without altering the pattern of response. C, head up, as in A; as before muscle relaxes and spindle accelerates. D, head down; responses in muscle and spindle similar to those in B, again despite the deafferentation. (Retouched.)

was passive and reflex contraction or relaxation was not prevented by dorsal root section. Fig. 9, in which this is depicted, is strictly comparable with fig. 10 of Eldred *et al.* (1953), which shows the same experiment in an animal with an active γ system. (In the latter deafferentation completely abolished

muscular contractions.) The important observation that reflex movements in soleus elicited from the neck and pinna are not significantly altered by deafferentation of the muscle in anaemically decerebrate cats was confirmed in three experiments.

Like Pollock & Davis, we have sometimes noted an erratic reflex behaviour in their type of preparation. The Magnus neck reflexes may be completely inverted or, as in Fig. 9, when the head is bent upwards contraction may precede the normal relaxation.

DISCUSSION

The present experiments taken in conjunction with those of Eldred *et al.* (1953) demonstrate quite clearly that overtly similar reflex contractions and rigidities may be produced by either of two essentially different patterns of excitation, to be distinguished most directly by their opposite reactions to dorsal root section. Contractions dependent on intact dorsal roots are associated with a high level of γ activity and are thought to be predominantly γ-driven; contractions that persist after root section show a paralysis of the γ system and are due to primary activity in the α system.

Although it is necessary to emphasize the distinctions between the two modes of excitation they are not mutually exclusive, but may frequently be observed in combination. In relaxed or tonically contracting muscle even spindles that behave passively during phasic changes are seldom without some γ bias (Fig. 5B, C). Similarly, in classical decerebrate preparations with an active pattern of spindle response, there is sometimes evidence of concomitant α excitation. For example, in Fig. 4B spindle acceleration long precedes muscle contraction, and when contraction does occur there is no extra spindle acceleration to account for it. Fig. 8B is similar, and in addition shows a slight spindle acceleration during relaxation. In these instances, therefore, the contraction is mixed α and γ.

The simplest interpretation of our results would be that the cerebellum controlled a neural switch (sketched in Fig. 1) which directed excitation, originating elsewhere, into either the α or the γ route. But this hypothesis would cease to be even a useful representation of our results if it proved that in reflex movements the type of movement or its force were greatly different after the switch were supposed to be thrown. The implication is that the same movement is to be brought about by a different route of excitation, not an entirely different movement produced. It is circumstantial evidence in support of the hypothesis that when Sherrington (1898) cerebellectomized his animals, and Pollock & Davis (1930b) infarcted the anterior cerebellum of theirs, neither commented that their preparations behaved reflexly in any essentially different way from ordinary decerebrate cats. (The fact that their animals remained rigid after deafferentation was apparently attributed by Pollock & Davis (1930b, 1931) to superior general condition, absence of trauma,

etc., although this is not directly stated.) In our experience, too, it would be difficult to tell purely from the general reflex behaviour whether an animal had the use of its cerebellum or not. Neither the pattern of reflexes nor the reflex excitability are consistently different, although it remains true that Pollock–Davis cats are often more rigid, more excitable and more erratic in their responses than the classical decerebrate animal.

The above description and contrasting of the α and γ routes are quite independent of the particular manipulations to the brain of the animal used to demonstrate them, and the exact site and extent of the lesions necessary are less well established. In Pollock–Davis cats γ paralysis and indifference to deafferentation are regularly observed. Following Stella (1944b), Cardin (1946) and Terzuolo & Terzian (1953), we have attempted to show that the cause of this lies in the cerebellum. While it seems clear that elimination of parts of the cerebellum may exchange the leading role in muscular excitation from the γ to the α route, the failure to reverse the type of spindle response in many ablation, and in some cooling, experiments cannot yet be explained. Neither the level of the original decerebration nor the site and depth of cerebellar ablation were standardized, although the importance of the depth is now realized from the recent discovery by Sprague & Chambers (1953) that destruction of the cerebellar cortex or of the underlying nuclei has opposite effects on rigidity. It is also true that, even when the spindle response did not become passive, in many instances it seemed less active after an unsuccessful ablation and certainly never more active. Thus failure of a spindle to reverse the pattern of its responses may well be a matter of degree or of technique. We, therefore, feel justified in emphasizing the positive experiments demonstrating that the normal link synchronizing α and γ reflexes is broken by anterior cerebellectomy or local cooling.

The fact that when the α mode of excitation predominates the γ efferents are passive may explain the interesting observation of Sprague & Chambers (1953) that such preparations are not plastic, for Eldred *et al.* (1953) showed that an important component in the lengthening reaction was the inhibition of γ bias described by Hunt (1951), which cannot occur if there is no bias to begin with. Plasticity may thus be an exclusive property of the γ mode of excitation. (In agreement with Sprague & Chambers, Pollock & Davis (1929) had shown that their preparations had no reflex lengthening reaction; their interpretation, however, was discordant.)

There are two obvious applications of these ideas to clinical neurology. First, of the two commonest types of hypertonia, the spasticity of hemiplegia and the rigidity of paralysis agitans, the former is plastic (in the Sherringtonian rather than the clinical sense) and the latter is not. It would be dangerous, however, to conclude that they employ respectively the γ and the α routes, for Pollock & Davis (1930a) and Gordon Holmes (1946) state that both are

abolished by dorsal root section. Secondly, the spindle paralysis produced by cerebellar ablations puts out of action the muscle's length servo, or, in other words, it deprives the muscle of the services of its private length measuring instruments. The symptom of dysmetria in human cerebellar disease may be a manifestation of a similar spindle paralysis, a suggestion we base on the evidence, reviewed in the introduction, that in many reflexes the α and γ systems normally work in close co-operation. Central evaluation of the spindle messages comes to presuppose γ-α linkage.

SUMMARY

1. Previous work showed that reflex contractions of the hindlimb extensors in classical decerebrate cats are largely dependent on an intense inflow of excitatory impulses from muscle spindles, in its turn set up by activity of the γ efferents to the intrafusal muscle bundles.

2. This paper shows that when the anterior part of the cerebellum is eliminated, paralysis of this γ mechanism results. Under static conditions γ bias is diminished and in phasic contractions spindle responses are passive in character (i.e. in reverse phase to the α efferent discharge). Rigidity and reflex contractions are no longer abolished by dorsal root section.

3. If cerebellectomy only caused γ paralysis it should be equivalent to deafferentation. As, however, the muscles are not paralysed but remain perfectly accessible reflexly, it follows that more excitation must be directed on to the α motoneurones.

4. Hence arises the idea of two routes of excitation, α and γ, equally able to undertake reflex movements, the proportions of the two in use at any time being in some way dependent on the cerebellum.

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