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**Institutions:** Radboud University Nijmegen

**Published on:** 01 Dec 1995 - Behavioral and Brain Sciences (Cambridge University Press)

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## Reciprocal and coactivation commands are not sufficient to describe muscle activation patterns

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**Abstract:** Recent results have shown that the relative activation of muscles is different for isometric contractions and for movements. These results exclude an explanation of muscle activation patterns by a combination of reciprocal and coactivation commands. These results also indicate that joint stiffness is not uniquely determined and that it may be different for isometric contractions and movements.

It was one of the attractive features of the  $\lambda$  model that the threshold muscle length  $\lambda$  was the only control variable (CV) necessary and sufficient to characterise the activation of muscle (by the difference between muscle length and  $\lambda$ ) and its contribution to stiffness. When several muscles are involved, just as many control parameters are necessary, one for each muscle. With these CVs it was possible, according to the model, to control the position of a limb (by the position at which forces by external loads and those exerted by the limb are in equilibrium), limb velocity during movements (by controlling the rate of change of  $\lambda$ ), and EMG patterns.

Recent experiments have provided evidence that nature is more complicated than the simple view described by the  $\lambda$  model. These new studies have shown that the relative amount of EMG activity in human arm muscles is different under conditions in which subjects are instructed to exert an isometric force at the wrist or to move the hand very slowly against the same external force (see Miller et al. 1992; Theeuwes et al. 1994a; 1994b). In terms of the  $\lambda$  model, this implies that the rest-length of these muscles is changing in a different way for each of these instructions. The important point is that the amount of EMG changes in a different way for different muscles: for some muscles the recruitment threshold of motor units decreases (and as a result the corresponding EMG activity increases); for other muscles, the recruitment threshold increases corresponding to a decrease of EMG activity. Further experiments by Theeuwes et al. (1994b) revealed that for movements assisting an external load the relative activation was different from that in isometric contractions and from that observed for movements against an external load. These results demonstrated that the relative activation of muscles is different for various motor tasks.

Tax et al. (1990a; 1990b) did an experiment in which the instruction to the subject was either to control force at the wrist or to control position of the wrist. In this way the physical state of the wrist (position, velocity, and force) was the same; only the instruction to the subject was different. The results revealed a different relative activation of human arm muscles, indicating that the differences were the result of a different central command, not simply of changes in reflex-induced activity. Any explanations to describe the different relative activation based on the force-velocity relation or the muscle-length relation could be excluded (see Theeuwes et al. 1994b). Because both position and force are the same under all conditions, the only explanation provided by the target article could be based on a change in activity resulting from a coactivation command. However, this, too, could be excluded for two reasons: (1) no change of activity was found in the three heads of *m. triceps* (in fact, no activity was found at all in *m. triceps*) and (2) this explanation cannot explain why EMG activity increases in some muscles (like *m. biceps*) but decreases in other muscles (like *m. brachialis*). Therefore, neither changes in the R nor those in C commands can explain these results and the present state of the  $\lambda$  model cannot explain the results described above.

This review of the differential relative activation of human arm muscles in isometric and movement tasks indicates that the threshold for muscle activation is modulated differently for various muscles. More than one setting of muscle-length thresholds generates the same physical state of the arm. This indicates that the  $\lambda$  model cannot explain the redundancy problem (i.e., that the number of muscles is greater than the number of degrees of freedom of the arm.) There is no unique relation between muscle rest lengths on the one hand and position and/or force of the limb on the other.

Several hypotheses have been proposed to explain the different relative activation of muscle by considering biomechanical constraints (Gielen & van Ingen Schenau 1992; van Ingen Schenau 1989). The activation patterns predicted by these hypotheses can be translated directly into rest lengths of muscles and changes in their rest lengths. Whether these hypotheses can really provide a satisfactory explanation remains to be seen.

Although there can be some criticism of it, I really think that the  $\lambda$  model has been a good one. Like any good model, it has stimulated a lot of experiments trying to falsify it and we have learned a lot from the results. In my opinion, the model is outdated now, being too simple; what we need is a new model, just as good as the  $\lambda$  model, which incorporates all of its good ideas.