The origin of motoneuron synchronization

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TO THE EDITOR: In recent years, De Luca and colleagues (De Luca et al. 1993; De Luca and Kline 2014) have expressed considerable scepticism for the conventionally accepted view that motoneuron synchronization results from activity in common inputs to the motoneurons concerned. Now Kline and De Luca (doi:10.1152/jn.00452.2015) have gone further. Exploiting the EMG decomposition technique developed in their laboratory, together with their own statistical approach (De Luca and Kline 2014), they measured motoneuron synchronization from a large number of pairs, using different force levels and taking account of firing rates and recruitment thresholds. The relationships between these parameters and the strength of synchronization, they say, are not supported by the common input explanation. This is now more than scepticism; it appears to be outright opposition.

The results themselves constitute a unique set of data and are of considerable interest: because of the decomposition technique, the sample size was large and individual pairs could be followed to different levels of excitation, within naturally produced voluntary efforts. Motoneuron pairs recruited at similar levels of force (high or low) showed stronger synchronization than those recruited at disparate levels, and pairs followed from low to high forces showed a decrease in the synchronization strength. These seem like secure results, but I do have some problems with the interpretation.

One difficulty here is that the authors do not define carefully enough what they mean by common inputs. In the influential early paper in this area, Sears and Stagg (1976) based their argument on the known anatomical fact that many individual presynaptic axons branch to synapse on many motoneurons, and the observed time course of the synchronization they measured for intercostal motoneurons in the anesthetized cat (“short-term synchronization”) appeared to fit the hypothesis that this arose from the raised probability of firing expected in each motoneuron during the rising phases of their near-simultaneous single-fiber EPSPs. This interpretation was later refined by Vaughan and Kirkwood (1997), who showed that synchronization similar to that in Sears and Stagg (1976), with cross-correlation histogram peaks of mean duration at half amplitude of 3.4 ms, was actually most likely to have arisen from common disynaptic, rather than monosynaptic, connections, for which they proposed an upper limit of 2.2 ms. The longer durations were considered to arise from the extra temporal dispersion that is almost inevitable with an extra synapse. Furthermore, in other conditions, in particular in human EMG recordings, the durations of motoneuron synchronization may often be considerably longer. The synchronization may still be assigned to common inputs, but only by assuming pathways with yet more synapses, where perhaps spinal interneurons or corticospinal neurons themselves are synchronized over a relatively long time scale. I think that many authors in recent years implicitly admit this, and they use the term “common inputs” much more loosely than in the original branched axon hypothesis.

Kline and De Luca (doi:10.1152/jn.00452.2015) relate their measurements to others in the human literature where such loose usage is common, but, from the way the DISCUSSION is written, I suspect the hypothesis they wish to reject is specifically the original one relating to branched axons. Unfortunately, as far as I can see, the durations of many of their examples of synchronization are relatively long, so for me it is not even a sensible question to ask, whether these examples fit that restricted hypothesis. What I do see, though, is that in each of their illustrated examples, comparing high and low synchronization, the duration of the synchronization is less for the low example. Thus, in Fig. 3 where the same pair of units was investigated at two different forces, my interpretation would be that at low forces, the excitation was dominated by synchronized inputs; then, these inputs were either “diluted” by the additional drive for a greater force or became desynchronized or inhibited (e.g., feed-forward inhibition, as in Isa et al. 2006). An analogy for this could be Fig. 5, C and D, of Kirkwood et al. (1982), where “broad peak” synchronization was abolished, leaving only short-term synchronization, when the excitatory drive was increased, in this case via the respiratory drive stimulated by CO2.

Kline and De Luca’s (doi:10.1152/jn.00452.2015) main argument against the common input idea is that the reduction in synchronization with increased excitation is simply implausible (their “Plausibility #1” to “Plausibility #3” paragraphs). Clearly, if one allows for motoneuron inputs to be synchronized, as above, then there are many possibilities and implausibility does not arise, but even within the strict confines of the branched axon hypothesis, I would contend that a reduction in synchronization is eminently plausible. The critical factor here is that even if each of the common EPSPs remains constant, the primary correlation operator (PCO; which, mathematically, transforms the EPSP to the raised probability of firing in a motoneuron) is not at all constant, but heavily dependent on a variety of factors, such as the amplitude of the ongoing synaptic noise (Kirkwood and Sears 1991). These factors will undoubtedly change as a synaptic drive increases, but also the EPSPs themselves may well decrease with increased excitation because of nonlinear summation, especially if voltage-sensitive conductances are additionally recruited.

Overall, acceptance of the branched axon hypothesis, together with Kline and De Luca’s results, does not, in my view, demand that “central neural pathways are systematically adjusted... with increasing force.” It could well be that a large reduction in synchronization could occur via a combination of factors, for instance, a small change in the PCO, together with...
a small reduction in synchronization of inputs, plus a small change in the proportion of common inputs that are active. To understand which of such factors are the most important, I would suggest, as did Vaughan and Kirkwood (1997), that much more useful information can be gained from studying the time course of the synchronization than in deriving some overall single figure for its strength. However, this may well demand narrower bin widths and higher bin counts (i.e., much longer runs of data) than were used by Kline and De Luca.

DISCLOSURES

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AUTHOR CONTRIBUTIONS

P.A.K. conception and design of research; P.A.K. interpreted results of experiments; P.A.K. drafted manuscript; P.A.K. edited and revised manuscript; P.A.K. approved final version of manuscript.

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