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The common input notion, conceived and sustained by conjecture

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REPLY: Dr. Kirkwood is correct in indicating that our work on the synchronization of motor unit firing instances since 1993 has progressively questioned the relevance of the common input notion as a cause. However, we suggest that his designation of "opposition" to our opinion on the common input notion may be too assertive for the arguments we present in our recent paper (Kline and De Luca doi:10.1152/jn.00452.2015). We examined the notion of the common input by measuring synchronization, with robust statistical tests (De Luca and Kline 2014), between fixed pairs of motor units. We found that the degree of synchronization changed as the motor unit firing instances progressed within a contraction from a relatively low force level to a higher one. We considered several scenarios involving the notion of the common input to account for the changes in synchronization. But, we could find no empirical support for these scenarios in our data or in the literature spanning the past 40 years.

In our paper, we present an empirical association between two simultaneously occurring physiological variables that relate the behavior of synchronization to the behavior of the motor unit firing rates. We make it clear in the Abstract and the DISCUSSION that our results do not prove a causal explanation for synchronization. We are fully aware that a correlation does not provide a proof. But our interpretation that synchronization is an epiphenomenon of the onion skin property provides a testable hypothesis that can be subjected to further investigation.

Dr. Kirkwood proposes to explain our data by a concatenation of previous conjectures. His explanation may be plausible, but it is not a proof in support of the involvement of the common input. It is as most other preceding explanations, a presently untestable conjecture, which per se cannot provide a factual explanation that leads to the truth. Therein lies our concern with his argument. If it were posed as a hypothesis that could be tested with direct evidence from the voluntary activation of human motoneurons, then it could lead towards a path that reveals the truth. But, conjectures such as those posed by Dr. Kirkwood involving the common input cannot be tested until we understand the structure and the workings of the central nervous system in greater detail than we do now. Therefore, they are best left in abeyance until such time.

To understand the conjectural nature of the common input notion, consider the premise upon which it was originally proposed. Sears and Stagg (1976) were among the first to claim that common synaptic inputs shared by motoneurons have the potential to cause synchronous motoneuron firing instances.

The support for this premise was based primarily on the results of mathematical models used by Moore et al. (1970) that demonstrated various configurations of inputs to neurons could elicit different patterns of correlated firing behavior, such as synchronization. Although the use of models driven by synthesized data has some value for generating or testing hypotheses of physiological behavior, their results are insufficient proof of a specific physiological construct because the choice of the synthesized configuration of input data influences the output of the model. Proof requires empirical evidence from direct experimentation under realistic physiological conditions. Consequently, the results from Moore et al. (1970) are incapable of proving that any one configuration of inputs to the neurons is more closely related to the actual physiological configuration of inputs in human motoneuron pools activated during voluntary contractions. Similar limitations apply to other models invoked to substantiate the common input notion, including those referenced by Nordstrom et al. (1992) and Vaughan and Kirkwood (1997), among others. Even more recent studies (Farina et al. 2014) that incorporate models to justify that common synaptic inputs can be determined based on measurements of coherence between trains of motor unit firing instances should be reevaluated based on the lack of empirical substantiation.

Even if the premise of the common input notion were true, it still would not prove that synchronous motor unit firing instances are caused by common inputs. To illustrate this point, consider the following progression of propositional logic. The premise underlying the common input notion has been used to substantiate the conditional statement:

> *If common synaptic inputs exist between two motoneurons, then the motoneurons may produce synchronous firing instances.*

All reported studies on motoneuron synchronization do not measure common inputs directly, but infer common inputs based on observed measurements of synchronization. Thus, these studies have assumed the converse of the conditional statement:

> *If two motoneurons produce synchronous firing instances, then common synaptic inputs exist between the motoneurons.*

However, according to the rules of propositional logic, validity of the first conditional statement does not prove its converse. In other words, the fact that common inputs may have the potential to evoke synchronization does not mean that observations of synchronization during voluntary contractions in human subjects are in fact caused by common inputs. The original study by Moore et al. (1970), upon which the common input notion was based, was among the first to acknowledge this fact. They cautioned that proof of any configuration of inputs to neurons, such as common inputs, required additional evidence beyond the occasional correlation (synchronization) of the firing instances. This fundamental point has been uni-

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versally disregarded by virtually all reports on the common input published during the past four decades, as well as by the modified interpretation offered by Dr. Kirkwood.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

C.J.D.L. and J.C.K. conception and design of research; C.J.D.L. and J.C.K. drafted manuscript; C.J.D.L. and J.C.K. edited and revised manuscript; C.J.D.L. and J.C.K. approved final version of manuscript.

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