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This paper reviewed the various ways in which the term "command neuron" had been used in the literature, and we suggested that, although the term had clear functional connotations, it was generally used in a manner divorced from function. We offered a definition of command neurons as cells whose activity is necessary and sufficient for a specific behavior. [The *SCI*<sup>®</sup> and *SSC*<sup>®</sup> indicate that this paper has been cited in over 145 publications.]

### The Concept of the Concept of Command Neurons

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At the time of the publication of this paper in the late 1970s, one of the relatively few general principles that was emerging in integrative neurobiology was that complex information may be encoded at the level of individual neurons. On the sensory side, neurons had been discovered that responded to highly complex stimulus features. On the motor side, particularly in invertebrates, there appeared to exist so-called command neurons, which, when stimulated, could evoke complete and often complex behavioral acts.

We had been working with the giant serotonergic neuron (the MCC) of *Aplysia*, a cell that appeared to be an ideal candidate for qualifying as a command neuron. The neuron had been reported to have a very extensive synaptic output, exerting different types

of synaptic actions in its various follower cells. In addition, it had the curious feature of sending peripheral axons to various muscles. We found, however, that stimulation of the cell never evoked a behavioral response. Instead, our studies indicated that the cell is an unusual neuron, a modulatory cell, which can affect ongoing activity but has little or no effect unless it interacts with the actions of other neurons.<sup>1</sup> In the course of these experiments, other investigators began to report that homologous cells in other molluscan species could evoke behavior, and some authors<sup>2</sup> referred to the MCC cells as command neurons. We felt that the term was being used in a loose fashion and, more important, was being used in a manner divorced from serious functional considerations.

In order to clarify in our own minds what was really meant by the term "command neuron," we reviewed the literature on this topic, then engaged in endless discussions with one another and with other members of the lab (e.g., Josh Cohen and Steven Rosen), and finally presented our analysis in a departmental seminar. Some in the audience felt that it was a waste of time trying to define this concept better, but when the new peer-commentary journal *Brain and Behavioral Sciences (BBS)* was scheduled to begin publication, we felt that this was an ideal topic for discussion. The article prompted a lively discussion, largely revolving around the issue of whether our narrow definition of the term was useful or not.

The criteria we proposed (necessity and sufficiency) had been long used in other contexts, but they provided a relatively clear methodology for relating a neuron to behavioral function. Thus, our paper was both a review as well as a methodological description, and it is probably most cited for its methodological content. Despite some limitations in its solution, the paper may have provided a clear statement of a way to examine the role of individual neurons in behavior, and it emphasized the importance of attempting this. Recently the topic was reassessed in *BBS*,<sup>3-11</sup> and the comments indicate that indeed our conceptualization is not without problems but that a number of investigators have found it useful.

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