

The command neuron concept

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Abstract: The notion of the command cell has been highly influential in invertebrate neurobiology, and related notions have been increasingly used in research on the vertebrate nervous system. The term "command neuron" implies that the neuron has some critical function in the generation of a normally occurring behavior. Nevertheless, most authors either explicitly or implicitly use a strictly operational definition, independent of considerations of normal behavioral function. That is, command neurons are often defined as neurons which, when stimulated by the experimenter, evoke some behavioral response. Even when utilizing such an operational definition, investigators frequently differ on what they consider to be the exact characteristics that a neuron must have (or not have) to be considered a command cell. A few authors appear to treat command neurons in relation to normal function, but a precise behaviorally relevant definition has not been specified. Because of the ambiguity in the definition of command neurons, the term can refer to a wide variety of neurons which may play divergent behavioral roles. In some ways the attempt to label a cell as a command neuron may interfere with the process of discovering the complex causal determinants of behavior. Nevertheless, the notion that individual cells are responsible for certain behaviors is highly appealing, and an attempt to define the command neuron rigorously could be worthwhile. We suggest that a command neuron be defined as a neuron that is both necessary and sufficient for the initiation of a given behavior. These criteria can be tested by: (1) establishing the response pattern of the putative command neuron during presentation of a given stimulus and execution of a well specified behavior; (2) removing the neuron and showing that the response is no longer elicited by the stimulus (necessary condition); and (3) firing the neuron in its normal pattern and showing that the complete behavioral response occurs (sufficient condition). In some cases, groups of neurons, when treated as a whole, may satisfy the necessity and sufficiency criteria for a given behavior, even though individual neurons of the group fail to meet the criteria. We suggest that such a group be termed a "command system" for the behavior in question. Individual neurons in the command system can be termed "command elements" if, when fired in their normally occurring pattern, they elicit a part of the behavior, or "modulatory elements" if they do not in isolation elicit any response, but alter the behavior produced by other elements in the command system.

Keywords: command cell; behavior; motor systems

One of the most influential concepts to derive from studies of the nervous systems of invertebrates is that of the command neuron. The related notion of the command system has been increasingly used in research on the vertebrate nervous system (Grillner, 1975; Mountcastle et al., 1975; Roberts, 1974). Despite the central role that the command concept has played in neurobiology, it has seldom been critically reviewed. A few publications (Bowerman and Larimer, 1976; Davis, 1977; Kennedy and Davis, 1977) discuss the empirical data regarding command cells, but only the reviews of Davis (1976, 1977) and Kennedy and Davis (1977) attempt to deal in depth with a number of problems associated with the concept. Even these authors basically accept the command neuron concept as it is currently used by the majority of investigators, that is, to denote neurons whose experimentally induced activity elicits a recognizable behavioral response. The discussions at several symposia indicate, however, that problems and controversy surround the command cell idea; unfortunately, these discussions are only available in summary form (Bryant, 1973; Davis, 1977). In the present paper we will attempt a critical appraisal of the command neuron concept, incorporating previously published critiques as well as our own ideas. We will attempt to develop the following notions:

1. As originally conceived, the command neuron was not explicitly and rigorously defined.
2. The notion of command has surplus theoretical implications about the neural bases of behavior. Once neurons are la-

beled as command neurons, they are often taken to be relevant behaviorally, even though adequate proof of their behavioral relevance may be absent.

3. Some authors have attempted to define command neurons operationally on the basis of electrical stimulation of neurons, but independently of their possible functional role in normal behavior. Other authors appear to treat the command neuron notion in relation to normal function, but have not provided a precise behaviorally relevant definition.

4. Because of the ambiguity in the precise meaning of command neurons they have come to refer to a variety of neurons, which appear to play widely divergent behavioral roles.

5. Command neurons and command systems are best redefined operationally, in a strictly behaviorally relevant sense.

Historical perspective

The term "command neuron" (or "command cell") was introduced into the literature by Wiersma and Ikeda in 1964. In their paper the term was used to describe neurons in the crayfish which, when fired, elicited rhythmic movements of the swimmerets, small abdominal appendages that normally exhibit rhythmic movements during several types of behavioral responses. In previous publications, Wiersma (1938, 1952) had

described other neurons in crayfish that also could produce complex behaviors when stimulated individually. These pioneering efforts were followed by numerous publications on crustacean command neurons, particularly by Kennedy and associates (see Kennedy and Davis, 1977 for review) as well as by others (Wine and Krasne, 1972; Winlow and Laverack, 1972). Several neurons in molluscs (Gettings, 1977; Gillette and Davis, 1975, 1977; Gillette et al., 1977; Kater, 1974; Koester et al., 1974) and insects (e.g. Burrows, 1975; Pearson and Fournier, 1975) have also been identified as possible command neurons.

The paper in which the command neuron concept was first introduced (Wiersma and Ikeda, 1964) already indicated possible problems with the concept. The term was not formally defined. On first reading it appeared that one could infer a formal definition on the basis of the context in which the term was used and by the examples of other command neurons previously described in the literature. For example, in the introduction to the paper, the expression "command interneuron" was often used and the examples of command neurons cited in the introduction all consisted of interneurons. And yet one could not conclude that what the authors termed command neurons were limited exclusively to neurons that were interneurons as opposed to sensory neurons or motor neurons. No attempt was made to determine unequivocally that the swimmeret command neurons studied were indeed interneurons. (It is possible that some of these neurons might have been primary sensory neurons.) Other problems raised by the lack of a formal definition include the question of whether a command neuron was an operational concept not necessarily linked to normal function, or a genuine functional entity. In other words, was a command neuron simply a neuron that elicited behavior when electrically stimulated under the conditions of a specific experiment, or was it a neuron that was causally related to the initiation of behavioral patterns that occurred normally? Finally, it was unclear whether, in order to qualify as a command neuron, a cell had to elicit a complete behavioral pattern when it acted individually, or whether it could qualify if it acted together with other command neurons to elicit a complete behavior.

Appeal of the command neuron and some theoretical implications

Despite some ambiguity in the command neuron concept as originally developed by Wiersma and Ikeda (1964), it was an attractive notion that stimulated a great amount of research and had a profound effect in invertebrate neurobiology. This idea was attractive, in part, because it provided an elegant neural mechanism to "explain" the release of fixed action patterns by specific stimuli. Various stereotyped and endogenously generated reflex patterns could be triggered by corresponding "neural push buttons," in the words of Wiersma (1952). One could envision the nervous system as composed of sensory analyzers that provide an input to a command neuron when themselves excited by the appropriate sensory input. The command neuron in this model is also affected by other inhibitory and excitatory inputs. When sufficiently excited, the command neuron fires and in turn excites a neural network that is interconnected so as to produce a complex response appropriate to the sensory input. In this schema, the command neuron provides a neat solution to the problem of how the nervous system generates one behavior pattern at a time; and how a "decision" to respond is made. In our opinion, implicit in the command neuron concept, as it is usually employed, is a model of behavioral function of the type schematized in Figure 1 (see, for example, Ikeda, 1976).

It is becoming increasingly clear, however, that even simple ganglia are rarely, if ever, organized into such neat compartments. Nervous systems are characterized by redundancy and extensive feedback loops (see, for example, discussion of Davis,

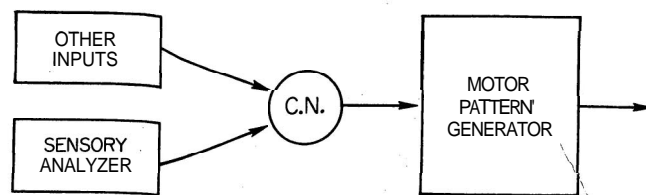


Figure 1. Hypothetical neural circuit utilizing a critical "decision-making" neuron (command neuron, labelled C.N.) in the generation of behavior.

1976). Given the existence of extensive excitatory feedback loops between neural elements in a circuit, it may be difficult to assign a primary command or initiating function to any given element in the circuit, and activity of any of a number of elements within the circuit may be able to initiate activity in other members of the circuit. Consider the following hypothetical example (Harth and Lewis, 1975): A population of neurons randomly interconnected by excitatory connections can exhibit a threshold property, whereby activity of more than a given number of neurons in the population results in sufficient positive feedback within the system to result in sustained activity. In such a system, addition of the activity of one neuron can make the difference between sustained activity and nonsustained activity of the network. Thus, in systems of this type, removal of a single neuron might suppress the initiation of a behavior by a previously effective input. And yet here, behavior is not commanded by any one neuron. Rather, the behavior is the result of the cooperative activity of the population of neurons. This is not to deny the importance of individual neurons and their interconnections. But in the system described above, it simply makes no sense to ascribe a primary initiating function to any given neuron, even though under appropriate conditions the activity of a given neuron can make the difference between success and failure of a stimulus to initiate behavior. Similarly, one can conceive of other circuits in which behavior can be initiated by stimulation of a neuron, and yet that neuron cannot meaningfully be called the exclusive trigger or command of the behavior.

The point is that calling a neuron a command neuron can lead one erroneously to conclude that activity of this neuron is the "cause" of a behavior. In many cases it may be that behavior cannot be attributed to a single cause, despite the fact that the activity of individual neurons or groups of neurons can affect the behavior. There may indeed be instances in which behaviors can be related to single causal events, but this cannot be determined merely by stimulating individual neurons and calling them command cells if they produce some behavior. In some ways, naming a cell a command neuron may interfere with understanding the functioning of the total system and with identifying the causal processes.

Behavioral versus nonbehavioral operational definitions

The early description of the command neuron concept (Wiersma and Ikeda, 1964; see also Wiersma, 1952) clearly implied that these neurons were involved in "commanding" normal behavioral responses in the animal. Unfortunately, however, except in rare instances, neurons were classified as command neurons not on the basis of proof that they normally elicit behavior, but rather on the basis of the observation that electrical stimulation of these neurons led to some observable response of the animal. Thus, in practice, many authors have come to define the term operationally on the basis only of electrical stimulation, and independently of considerations of normal behavioral function (Atwood and Wiersma, 1967; Bowerman and Larimer, 1976; Davis, 1977; Kennedy and Davis, 1977). The attempt to define command neurons independent of their normal function did not arise from any lack of interest in behavioral problems (see, for

example, Davis, 1977). Rather, it appeared to be the result of difficulty in obtaining behaviorally relevant data on the preparations that were being studied.

A narrow definition of command neuron on the basis of electrical stimulation, independent of normal function, avoids the formidable problems of having to provide functional data before a neuron can be classified. Nevertheless, even with a definition independent of normal function, there are numerous problems associated with the "command" notion. Consider the relatively basic operational definition: "Command neurons may be defined as single cells which, at modest discharge frequencies, release coordinated behavior involving a number of motor output channels" (Kennedy, 1969). What is meant by "modest discharge frequencies" and does this have the functional implication that the discharge frequencies are within the range occurring in a behaving animal? How does one define a coordinated behavior and how large must a "number" of motor output channels be? Does the term "release" include instances in which ongoing behavior is modified? Of course, one could arbitrarily define and set limits for all these questions, but it is not likely that, if this were done, any sizable fraction of neurons called command cells would still qualify as such, or that any sizable fraction of neurobiologists would agree that the appropriate limits had been chosen.

An additional and fundamental problem with the current attempts at operational definition independent of normal function is that, stripped of its functional implications, the command neuron concept is deprived of much of its attractiveness. Nevertheless, a behaviorally relevant definition is not easy to formulate because in the vast majority of studies of single neurons in the nervous system it is not yet possible to determine the precise functional role of a given neuron. Thus, on the one hand, divested of most of its surplus meaning, the command neuron concept loses a great deal of its appeal; on the other hand, in the absence of good behavioral data with which to classify the functioning of a cell, a functional definition of the command neuron may be inadequate. Perhaps because of this conflict, one finds the same author using the command neuron notion as either an operational-nonfunctional or as a functional term. In the same paper. Thus, for example, in the thoughtful review of command cells by Davis (1977), he asks, "Are command neurons used as pathways for activating normal movements in freely behaving animals?" This implies a nonfunctional operational definition of command neurons. Later in the same paper, he states, "Information on the organization of central and sensory inputs to a neuron thus becomes critical in determining whether a neuron is properly considered a command neuron" - implying that command neurons should be defined in terms of their function in normally occurring behavior. In some instances, although authors do not rigorously and operationally define command neurons, it is clear that they have in mind a definition that involves considerations of normal behavioral function. Furthermore, the phrase "command neuron" itself linguistically implies normal control over some aspect of behavior and, not surprisingly, in our personal experience we have found that many students and scientists consider command neurons, by definition, to be involved in normal function, despite the fact that, in print, command neurons are rarely defined that way.

Multiple types of command neurons

Perhaps because of the lack of a clear definition, command neurons have come to refer to a wide variety of cell types, which presumably play distinct functional roles in the generation of behavior. The various cell types that could be termed command neurons can be categorized into two dichotomous classifications. The first dichotomy concerns the issue of whether command cells are limited to individual neurons that elicit behavior or can include groups of neurons that elicit behavior when acting in

concert. The second dichotomy is concerned with the issue of whether command neurons *elicit* behavior or whether they can also *gate* or *modulate* behavior. We have used the two dichotomous classifications to form a two-by-two table (Table 1) that includes selected examples of various neurons that might be considered command cells, depending on one's definition and theoretical orientation. The classification scheme given in Table 1 is clearly tentative and likely to change as additional information becomes available. Furthermore many cell types may span more than one classification. Nevertheless the table provides a heuristic framework to illustrate the complexity of the command concept. In the following sections we will briefly discuss the classification scheme outlined in the table.

Individual versus multiple neurons. As originally conceived (Wiersma and Ikeda, 1964), command neurons were thought to act individually to produce recognizable behavioral acts. Kennedy et al. (1967; see also Atwood and Wiersma, 1967), however, introduced the idea that neurons that elicit relatively simple movements could also be called command neurons, and that a complex act might then be due to the activation of a number of command neurons, each contributing an aspect of the complete behavior. This extension was the result of the observation that stimulation of a number of neurons in the crayfish produced distinct movements, but the movements were only a fragment of a recognizable behavior. In some instances, neurons termed command cells produced movements that were not part of the normal behavioral repertoire of the animal (Bowerman and Larimer, 1974). The unintended result of this extension was that it became exceedingly difficult, in principle, to exclude any neuron from the category of command neuron as long as its stimulation produced some movement, regardless of how simple the movement was.

Related to the question of whether command neurons should be restricted to individual neurons or should include multiple sets of neurons is the question of whether groups of neurons whose activity is coupled can be considered a command "unit." Several observations in the literature indicate that activation of a set of homogeneous neurons can initiate behavior (bag cells, Kupfermann, 1970) or modulate behavior (octopamine cells, Evans et al., 1975), although activity of an isolated element may not produce clear effects. The term "homogeneous neurons" refers to groups of neurons with virtually identical inputs and outputs. Since homogeneous groups of cells function as a single unit they have been classified as a subset of individual-action units in Table 1.

In cases where a behavior appears to be associated with the activity of a number of command neurons, each of which can produce a fragment of a complete behavioral act, the neurons

Table 1. Putative command cells

	Individual action		
	Single unit	Homogenous group	Multiple action
Modulatory function	MCC ^a L10 ^b	Lobster octopamine cells ^c	DUM cells ^d
Triggering function	Lateral or medial crayfish giant escape fiber ^e Defense fiber ^f Mauthner fiber ^g	Bag cells ^h	Cyberchroton ⁱ Crayfish posture cells ^j

Note: ^aWeiss et al., 1975, 1977 ^bKoester et al., 1974 ^cEvans, et al., 1975 ^dHoyle, 1974 ^eLarimer et al., 1971; Wine and Krasne, 1972 ^fWiersma, 1952 ^gDiamond, 1971 ^hKupfermann, 1970 ⁱKater, 1974 ^jKennedy et al., 1967

have been classified as a multiple-action system. Included in this classification as modulatory cells with multiple action are the DUM cells of locusts, which appear to affect the spontaneous activity of different leg muscles (Hoyle, 1974). Examples of a possible triggering function for multiple command cells are provided by the cyberchiron neurons, which affect various aspects of feeding behavior in snails (Kater, 1974), and by neurons whose stimulation produces limited movements associated with posture of the abdomen of crayfish (Kennedy et al., 1967).

Elicitation versus modulation. Command neurons are frequently described as neurons that elicit behavior. As originally conceived, the concept was felt to shed light on the question of how neuronal oscillators are triggered into activity (Ikeda, 1976; Wiersma and Ikeda, 1964). Nevertheless, the swimmeret command neurons described by Wiersma and Ikeda could not only elicit swimmeret activity, but could also modulate the frequency of occurrence of swimmeret activity already in progress (Atwood and Wiersma, 1967; Davis and Kennedy, 1972). Similarly, other command fibers in the crayfish were described as having "generalized" effects on behavior (Atwood and Wiersma, 1967) rather than triggering specific responses. It is unclear whether the modulating function of these neurons was considered part of their command function.

Willows and Hoyle (1969, see also Bryant, 1973) have drawn a distinction between the triggering and gating function of a neuron. By "gating," they are referring to the ability of a neuron to permit the behavioral expression of ongoing neuronal activity rather than to trigger the activity itself. Some of the most convincing data on the command function of individual neurons have come from studies of giant fibers that trigger escape responses in vertebrates and invertebrates (Diamond, 1971; Larimer et al., 1971; Wine and Krasne, 1972). Data from several invertebrates suggest that in some cases rhythmic neuronal output is not present until specifically triggered (Kupfermann, 1974; Selverston, 1976), whereas in other cases rhythmic activity may be initiated as a result of the gating in or out of continuous underlying rhythmic neuronal activity (Burrows, 1975).

A notion somewhat broader than that of gating is modulation. This refers to certain neurons' property of modifying the effects of ongoing neural activity. It includes turning on or off the output of ongoing activity (gating), as well as modifying the strength or other aspects of ongoing activity. In molluscs, functional evidence has been presented that the expression of ongoing behavior can be modulated by the metacerebral cell (Berry and Pentreath, 1976; Gelperin, 1976; Gillette and Davis, 1975, 1977; Weiss et al., 1975, 1976, 1977; see following section) and by cell L10 (Koester et al., 1974). Note however that under certain conditions stimulation of these neurons can also elicit behavioral responses.

The metacerebral cell - command neuron or not?

A consideration of whether the metacerebral cells of molluscs are command neurons highlights some of the problems of the concept. The metacerebral cells are a pair of giant neurons in several pulmonate molluscs (snails and land slugs) first described in 1894 by Nabias. Homologous cells are found in a wide variety of pulmonate molluscs (Berry and Pentreath, 1976; Kandel and Tauc, 1966; Senseman and Gelperin, 1974) as well as more distantly related opisthobranch molluscs such as *Aplysia* (Weiss and Kupfermann, 1976) and *Pleurobranchaea* (Gillette and Davis, 1977).

The available data suggest a great similarity in the functional properties of metacerebral cells from quite different molluscan species. Despite the relative uniformity of the functional data, there is a question about whether the metacerebral cells should be termed command neurons. In our studies of the metacerebral cells (MCC) of *Aplysia* (Weiss et al., 1975, 1976, 1977), we found

that their activity produced central as well as peripheral actions on the muscles involved in feeding responses. Both the central and peripheral actions failed to produce functionally significant effects unless other neural elements were active. Thus, activity of the MCC produced depolarization of motor neurons innervating feeding muscles, but the depolarization was generally not very effective in firing the cells unless another source of depolarization brought the cells close to their firing threshold. Similarly, MCC activity by itself produced no obvious electrical or mechanical effects on buccal muscle, which it innervates, but produced a clear enhancement of the contraction produced by motor neurons. In preliminary observations we have noted that stimulation of the MCC of *Aplysia* can increase the frequency of burst activity of the buccal ganglion, but only in preparations in which the burst activity was already occurring. On the basis of the overall data we suggested that the metacerebral cells were not conventional command neurons, in the sense of initiating behavior, but rather were concerned with modulating ongoing behavior (Weiss et al., 1975, 1977).

Gillette and Davis (1975, 1977) in studies of the MCCs of another opisthobranch mollusc (*Pleurobranchaea*) found that activity of the MCC could initiate a feeding movement. Although feeding in *Pleurobranchaea* normally consists of repetitive feeding cycles, when the MCC was fired continuously it usually elicited only a single feeding cycle. If feeding cycles were already in progress, continuous firing of the MCC could increase their frequency of occurrence. On the basis of their data, Davis and Gillette concluded that the MCCs in *Pleurobranchaea* are one of several command neurons that must normally function together to cause feeding.

Gelperin (1976), in studies on the land slug *Limax*, has found that firing of the MCC can similarly increase the frequency of occurrence of ongoing feeding activity, but cannot sustain activity by itself. On this basis, he concluded that the MCC has a modulatory role in the control of feeding behavior in *Limax*. Berry and Pentreath (1976) studied the role of the MCC in the pulmonate snail *Planorbis*. They found that when this cell was stimulated at unphysiologically high frequency it could produce repetitive output of the buccal ganglion, but the movements resulting from this output were not coordinated and did not resemble feeding movements. On this basis they concluded that the MCC was not a command cell for feeding, in *Planorbis*.

Because there are no widely accepted criteria of what exactly a command cell should be, there is no way of unequivocally classifying the metacerebral cell. Davis and Gillette (1977) pay particular attention to the direct behavioral effects elicited by the MCC. On the other hand, we and, presumably, Gelperin, Berry, and Pentreath are impressed by the fact that the MCC does not appear to play any type of critical decision or command role in feeding, but appears to function primarily to modulate the effects produced by the activity of other neurons. It appears that it is still premature to assign a functional role to the MCC. Calling the MCC, as well as many other neurons, a command neuron evokes functional implications that appear to vary markedly from investigator to investigator, and implies a degree of functional understanding that we do not yet have.

Toward a new definition

Our critique of the command neuron concept should not be taken as implying that the concept has not been useful. On the contrary, the past work on command neurons has provided some fundamental insights into the organization of neuronal systems. However, a number of developments in the last decade have greatly improved our ability to relate neural activity to behavior. First, intracellular techniques may now be applied much more readily to the arthropod nervous system. Second, chronic recording techniques in invertebrates have been greatly improved. Finally, individual cells that elicit behavior have now been found

in gastropod molluscs, in which intracellular recording and stimulation in "behavioral" preparations can be achieved readily. Thus, the time may be ripe to sharpen and clarify the notion of the command neuron.

In the present state of the field, the attempt to classify a specific cell as a command neuron is not necessarily useful or desirable. In fact, in some instances this attempt could conceivably interfere with progress toward understanding the precise role of a neuron or system of neurons in generating behavior. Nevertheless, the notion that individual neurons may control behavior is important, and it may prove useful to have a precise definition of command neurons. It is our feeling that if the term is used, because of its obvious functional implications, it should be defined in a way that closely ties it to normal behavioral functions. In this section we will attempt to develop a set of operational criteria that can be applied to determine whether a neuron is functioning as a command cell. We do not view this as a complete solution to the problem, but rather as a contribution to a discussion that will help to clarify some of the highly complex issues concerning the generation and causation of behavior. It should be pointed out that the procedures we suggest for assessing command neuron function have already been applied in an attempt to quantify the contribution of individual motor neurons (Kupfermann et al., 1971) or sensory neurons (Byrne, 1975) to a behavioral response. Furthermore, similar procedures have recently been applied to assessing the behavioral role of complex interneurons (e.g., Getting, 1977; Koester et al., 1974). Thus the present suggestion tries to extend this approach to the development of a specific set of criteria that can determine unequivocally whether a neuron should be termed a command neuron.

In a sense, the command neuron hypothesis implies that responsibility for certain behaviors can be associated with the activity of individual neurons. How can one experimentally define such responsibility? We suggest that responsibility for a given behavior should be attributed to a cell only if its activity is both necessary and sufficient for the initiation of the behavior. The task is not the impossible one of assigning some sort of ultimate responsibility, but rather of identifying the critical decision points in the generation of behavior.

The most direct means to determine whether a neuron is necessary for a given behavior is to remove the neuron from the neural system, preferably in a reversible manner by means of depolarizing or hyperpolarizing currents, and see if the behavioral response to the appropriate stimulus is abolished. Under those stimulus conditions in which the response of the neuron is an inhibition of spike activity, the neural response can be eliminated by depolarizing the neuron sufficiently to maintain its prestimulus activity. A neuron could be said to be sufficient for a behavior when an exact experimental reproduction of its stimulus-evoked firing pattern results in a precise reproduction of the behavior under consideration. This is a rather severe requirement, and a neuron could be said to fail the sufficiency requirement even if stimulation produces an approximate, but inexact, duplication of the behavior in question.

To provide an example of the procedure we are suggesting for establishing the command role for a neuron, let us consider the following hypothetical case. Tactile stimulation of a given receptive field produces a withdrawal response of a certain intensity, with a given latency. In this example, the receptive field, response strength, and response latency define the behavior under consideration. The first step in ascertaining whether a given neuron is a command neuron for this behavior is to determine the response of the neuron during application of the appropriate tactile stimulus and the execution of the response. Now, in the absence of the stimulus, the neuron can be directly stimulated to fire with the precise pattern in which it previously fired to the stimulus. If the response occurs at the appropriate magnitude and phase relationship to the firing, the neuron can be said to meet the sufficiency requirement. Sufficiency, of course, does not mean that no other conditions are necessary for

the generation of the response. Rather, an experimental result of this type indicates that activity of the neuron is capable of eliciting or creating all of the other conditions needed for the occurrence of the response. To evaluate whether the neuron's activity is necessary for the behavior to occur, the stimulus is presented to the animal, and by means of intracellular current, the neuron is kept at its prestimulus firing condition. If the response is completely eliminated, the neuron can be said to meet the necessity requirement. Similar tests could, in principle, be applied to nonspiking neurons by duplicating or eliminating the membrane potential shifts (at the presynaptic region) evoked by the relevant stimulus. In instances in which there is reason to believe a neuron might be a command neuron, but in which not all the tests have been done, we suggest that the neuron be termed a putative command neuron.

It should be noted that we have not attempted to define the nature of the behavior that command neurons control. Any behavior, either complex or simple, prolonged or brief, can be appropriately considered. The requirement that the nature of the eliciting stimulus be specified helps to insure that only meaningful and normal behaviors will be considered. In the case in which a stimulus elicits a series of behavioral responses, we consider it appropriate to define explicitly a part of the behavioral sequence. In practice, of course, it may often prove impossible to find neurons that can elicit an exact duplication of a behavior that is a segment of a more complex behavioral sequence. But where this is possible, it seems reasonable to attempt to establish command-neuron criteria for such a cell. To eliminate the relatively trivial examples of numerous motor neurons that can elicit very narrow segments of a behavioral response, we suggest that motor neurons not be considered as command cells. In some instances, motor cells have interneuronal functions in addition to their motor function, and in these cases it may prove possible to distinguish the command role of the neuron from its purely motor function.

Autogenously generated rhythmic behaviors pose a special problem. As pointed out by Ikeda (1976), however, even an autogenously generated behavior can be turned on and off by appropriate environmental events. Where these events can be specified and controlled, so-called spontaneous behavior can be analyzed just like any other behavior. The real problem arises in those cases in which relevant controlling stimuli cannot be identified. Where the adequate internal or external controlling stimuli are not known, the behavior in question is often not understood very well, and a search for command neurons may be premature. However, given a spontaneously firing neuron and spontaneously occurring behavior, one could apply the test for necessity by suppressing the neuron and determining whether the behavior ceases completely. One cannot simply apply the test for sufficiency (firing the neuron in its normal pattern), since a spontaneously active neuron is already firing in its normal pattern. However, rather than merely releasing the neuron and allowing it to fire in its own spontaneous pattern, one can keep the neuron suppressed and, by means of brief depolarizing pulses, specifically drive it in the pattern previously observed when the neuron was firing spontaneously. If the behavior returns, the neuron meets the sufficiency requirement. In the case of neurons that have burst activity phase locked to behavior, the same phase relations should hold when the neuron is driven in its natural pattern.

Command systems

Figure 2 illustrates a circuit in which redundancy exists, with each of two identical neurons able to elicit a full behavioral response. In this type of arrangement, neuron A or B will meet the sufficiency requirement, but will fail the necessity requirement, since when one neuron is removed from the circuit, the other can still fully mediate the behavior. Thus, by our criteria,

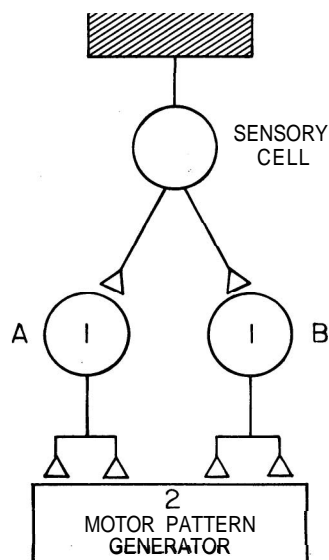


Figure 2. Diagrammatic representation of a circuit in which activation of a sensory cell (top) provides one single unit of input (one triangle) to two interneurons (A & B). Interneurons A and B require one unit of input to reach threshold (indicated by number within neuron). Each of these interneurons provides two units of input (2 triangles) to a motor pattern generator which has a threshold of 2 units of input. Furthermore, we assume for the sake of argument, in these figures, once threshold is reached in the pattern generator further input does not intensify the response, that is, the output is all or none. In this circuit, units A and B are sufficient for the occurrence of the reflex. However, they are not necessary since taking either one of them out of the reflex will not abolish it.

neither neuron is a full-fledged command neuron. Thus, for example, if one of these neurons makes a "decision" not to fire, this "decision" can be overridden by activity of the other, redundant neuron. It is thus unclear which neuron is in command of the response. A situation in which two or more neurons produce *exactly* the same response, including fixed phase relationship to the response, will probably be rare. Nevertheless, it is worthwhile to apply the necessity test since by taking a neuron out of the reflex we may uncover subtle elements of the behavioral response that remain, even when the putative command neuron is not functioning. In this case, stimulation of the putative command neuron may then reveal that it does not produce an exact replication of the behavior in question, but that certain aspects of the original behavior are indeed absent.

In the example provided by Figure 2, the two neurons can be said to form a command system. That is, the two neurons treated as a unit will fulfill the requirements of a command neuron. Fired together in their normal pattern, they produce the behavior; when they are both removed from the circuit, the behavior fails to occur. Each neuron could be termed a command element (in distinction to command cell), since it is part of a command system.

Figure 3 illustrates an alternative circuit. In this case there are two identical elements, A and B, whose simultaneous activity is needed to elicit a behavior. In this example, neuron A or B will pass the necessity requirement for a command cell, but will fail the sufficiency requirement. Here again, however, the two neurons, when treated as a unit, will meet the criteria of a command neuron; thus these neurons also form a command system. Unlike the previous example, these cells, when fired individually do not elicit any behavior, whatsoever. Hence, their activity is expressed only in modulating the effects of other neurons. We therefore may term this type of neuron a modulatory element of a command system. A command system as defined here has certain similarities to the neural centers defined by Doty (1976) in the vertebrate nervous system.

Command systems need not necessarily consist of a group of neurons that form a meaningful unit of similar function. Consider the circuit shown in Figure 4. Here neurons A plus B and C plus D form two command systems that function similarly; neurons A plus D and B plus C also form command systems, but their functional role is different from that of the other command elements. Indeed, although neurons A plus D and B plus C do form command systems as operationally defined, these systems do not constitute a functionally interesting entity. This illustrates that isolating command systems without understanding the interrelationships between the neurons may not contribute significantly to understanding the generation of behavior. One could argue that a neuron should be called a command neuron if its activity is either necessary or sufficient, rather than both. However, we feel that if the activity of a neuron is necessary for a behavior but not sufficient (see Figure 3) then that neuron in itself is not providing a critical decision point for the behavior. If the activity of a neuron is sufficient but not necessary for a behavior (Figure 2) then the nervous system must contain redundant systems for the generation of the behavior, and to our mind it does not make sense to assign responsibility to any *individual* element of the redundant system.

Notice that within the present framework it is meaningless to inquire whether a neuron is a command neuron in the abstract. Rather, the appropriate question is whether a neuron serves a command function for a given, well-specified behavior under well-defined stimulus conditions. It could very well be that for certain behaviors a neuron may serve a command function, while for other behaviors the same neuron may function in a noncommand role.

On the basis of current data, the best candidates for being command neurons, in the sense used in this paper, are the giant escape fibers in crayfish (Larimer et al., 1971; Wine and Krasne, 1972) and the Mauthner "escape" neurons in fish (Diamond, 1971). But even for these very extensively studied neurons, not all of the tests we have outlined have been performed. Nevertheless, the available data, together with some indirect evidence, suggest that these neurons are very likely to satisfy our criteria for command neurons, at least for certain types of escape behaviors. Neurons such as L10 in *Aplysia* (Koester et al., 1974) and

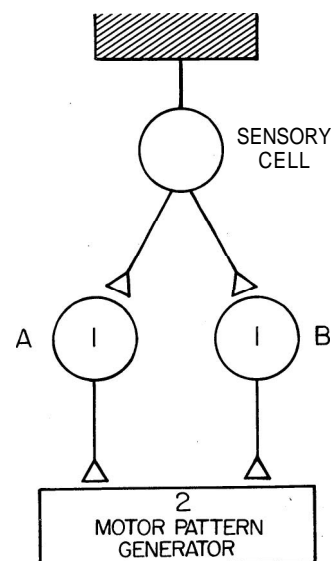


Figure 3. Diagrammatic representation of circuit in which a sensory cell (top) activates identically two interneurons (A & B). Interneurons A and B each provide one unit of input to a motor pattern generator whose all-or-none threshold of firing is 2 units of input. The activity of both interneurons A and B is therefore necessary for the reflex to occur. However, each one of them individually is insufficient to activate the reflex.

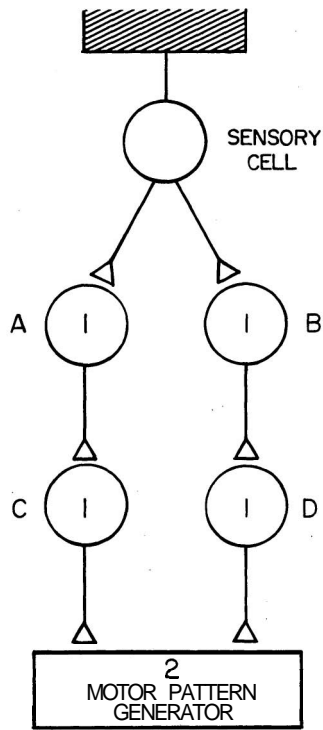


Figure 4. Diagrammatic representation of a circuit in which the proposed tests for isolating a command system could lead to the conclusion that there are 4 command systems. In this case a sensory unit activates in parallel two interneurons A & B each of which in turn activates another interneuron, C and D. Interneuron C and D each provide one unit of input to the pattern generator, which has an all-or-none threshold of 2 units. In this case, the four command systems that could be isolated would consist of cells A plus B, C plus D, A plus D, and B plus C.

C2 in *Tritonia* (Getting, 1977) almost meet the criteria for command neurons, but in one respect or another the data are incomplete. The set of criteria we have suggested is not easy to apply in most neural systems and may define a very small set of neurons. Nevertheless, the establishment of the causal determinants of behavior is a primary end-point of neurobiology and it seems appropriate to demand convincing evidence when claims are made that such causal factors have been determined.

ACKNOWLEDGMENT

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Precommentary by Graham Hoyle

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Where did the notion of "command neurons" come from? During the past 10 years I have on several occasions been an outspoken critic of the term "command" when used adjectivally to classify certain interneurons. During a discussion at a conference on Neural Control of Locomotion (Herman et al., 1976), I claimed that its indiscriminate use was doing more harm than good. The reasons for my objection are several fold, and many of them are clearly exemplified by the approach taken by the authors of this article, especially in the title, wherein lies the crux of the problem. The term "command," used as a noun, adjective, or verb, implies a specific conceptual framework. However, this was neither the act nor the intention of the man who first used the term: Cornelis Wiersma [see also this Commentary]. At that time he sought only to provide an operational definition for some very interesting interneurons which he had discovered. He sought neither to establish a concept nor to beg any questions regarding the functional organization of nervous systems; but he can certainly be accused of making an unfortunate choice.

The term "command" has its roots in a conceptual framework certainly, a very old one, which is the notion of hierarchical control of function that dates

back to Sechenov (1881), and was most explicitly stated in the English language by Niko Tinbergen (1950, 1951), who had adopted the concept from Paul Weiss (1941). A hierarchy invites comparison with a state, an army, or the Catholic church. The ruler, general, or pope issues "commands" which, voluntarily, or under "persuasion," are obeyed by underlings. These are issued to the next lower level in the hierarchy: lords, colonels, or cardinals. They may be intended for them personally, in which case the command stops there. Or they may simply be relayed from them to the next in the chain, until finally translated into actions ranging from individual effort to massive prolonged, coordinated group efforts by vast numbers of subjects or soldiers. If a simple result is called for, the command may be handed on unchanged ("kneel"); but if complex results are called for, it may be progressively altered in detail ("build a 100-room palace"). And so it is implied for the hierarchical nervous system! At each step a "command" is issued, translated and elaborated if necessary, and executed. Every link in the chain, from where the instruction originates to the final executor, transmits the command. In an animal the executors are muscles and glands.

The point is that the command is a unit of information that happens to be backed up by authority. Each is an abstraction. The term may be used as a noun or as a verb, but was clearly never intended to be used as an adjective. The basic mistake was right there in misusing a good word. Once the term is used adjectivally, to describe the conveyer, should it be restricted to the issuer? If the general says "advance," the colonel says "advance," and so do the major, the captain, the lieutenant, and the sergeant. By analogy, command certainly should be applied to motor neurons, yet those who enjoy the term are quick to assert, as do Kupfermann and Weiss, that they want to avoid this usage. The command interneuron, they say, must cause several things to happen at about the same time to be so classified. When pressed, users of the term don't like to include an interneuron that simultaneously excites two follower neurons — or three or even four. They talk vaguely about the need to evoke "behavior." Yet even a single twitch caused by a single motor impulse can constitute an important act of behavior. They might want to restrict the term to the initial issuer in the chain. The king, general, or pope can say, with some justification, that the command is theirs alone. At all lower levels the instruction becomes an "order." The problem with this restriction is that in nervous systems, there is usually no knowledge of where, in the course of behavior, the instruction arises.

Wiersma appears to have waited to use the term until he thought he was close to the pontificating pinnacle (brain), when he found that stimulating an interneuron coming out of the crayfish brain always caused a specific behavior. It was not Wiersma himself but others who chose, later, to apply the term to neurons "lower down" in the nervous system, which he had discovered but chose not to so designate. He discovered the functional attributes of giant fibers of the crayfish nerve cord in the late thirties and, a decade later, a single neuron emerging from the brain that elicits the whole bilateral defensive posture (Wiersma, 1952). When the medial giant axon is excited to produce but a single impulse, it causes movements "throughout the animal, the eyestalks are turned inward, the antennae forward, all legs turn forward, the swimmerets are pulled upwards, and a strong tail flip occurs . . . inhibition of existing leg position must (also) occur." There was a long, published discussion following Wiersma's announcement of these results, to a meeting of the world's most distinguished neurobiologists. Incredibly, this discussion is full of trivia. It is quite clear that none of the famous neurobiologists present grasped the real significance of his findings.

At first Wiersma used the term "trigger" to describe the action of the interneurons he had discovered. The term "command," used adjectivally, appears for the first time much later, in a 1964 paper (Wiersma and Ikeda, 1964). On the second page of this paper, without any prior discussion or statement of reasons for introducing the term, Wiersma and Ikeda wrote: "Interneuronal control of patterned movements is illustrated by experimental reproduction of the typical sound reflex in the cicada (Hagiwara and Watanabe, 1956). A somewhat more complex system is seen in locusts, in which command interneurons (my italics) can maintain co-ordinated wing movements without the mediation of peripheral feedback (Wilson, 1961)." In point of fact, Wilson had not used the term, nor had he stimulated interneurons: concerning interneurons there was only conjecture. Later in his paper with Ikeda, Wiersma applied the term "command" adjectivally to interneurons of the crayfish connective that, when stimulated with a long train, caused coordinated beating of swimmerets.

At a discussion held during the course of a Festschrift for Wiersma (Hoyle,

1977), Wiersma was asked how he came to use the term "command interneuron," and also if he would both explain his original intent and define his current usage. He said that he had borrowed the term from concepts arising at the time in vertebrate literature, but could give no precise origin. The only vertebrate literature cited in his own work around that time is a paper by Lundberg et al. (1962) on the effects of pyramidal tract activity on lumbosacral interneurons activated by somatic afferents. Whilst this paper classified interneurons, it did not use the term and affords no clues to its source.

In both the discussion and his writing Wiersma recognizes the influence of Franz Huber. In a 1959 paper, Huber describes his discovery of centers in the brain of male crickets at which local electric stimulation elicits complex behavior, notably locomotion and singing. Speculating about what is going on as motor patterns emerge during brain stimulation, Huber refers to "vorgeschalteten Interneuronsystemen." There are many possible translations of vorgeschalteten. Technically, its meaning ranges from shifting gears forward, through switching to preceding; *schalten* is in the same class of words as those used by the top people to rule their subjects. There are many synonyms in the German language for command, notably *befehlen*, *gebieten*, *kommandieren*, and *verfügen*, as well as *beanspruchen*, *beheerrschen*, and *fordern*, which are less forceful. All may have been used at some time or other in interpreting neural activities. *Schalten* is weaker than *befehlen* and *gebieten*, but stronger than the others. The hypothetical interneurons in Huber's scheme (for which he had extremely weak experimental evidence) "direct and control the motor activity." Huber's fine wires, placed randomly in the cricket brain, acted "not on the motor centers but rather on a (preceding?) interneuron system."

At a 1962 meeting, at which Wiersma was present (Reiss, 1964), I was faced with a similar need to classify interneurons, also as yet largely hypothetical, which, when active, cause behavior in a locust. I chose the term "driver" interneuron (Hoyle, 1964). I went on to recognize two classes, one that causes widespread general, but not precisely programmed, excitation – general driver – and another that carries neural patterns that elicit discrete movement patterns – specific driver.

Neither of these terms should be confused with the command neuron in the sense that Wiersma used it in the paper with Ikeda. Likewise, a distinction should be made between interneurons, of which several are now known, that require to be activated continually in order to cause behavior, and those in which the behavior greatly outlasts the interneuron burst, the ultimate example of which is the crayfish medial giant axon. The latter may genuinely be "releasing" or "triggering" a response. Both of these terms are loaded with physiological implications. They imply that energy has been stored for the act, but is somehow blocked; when the block is removed, the behavior will automatically occur.

The terms we eventually choose will not be truly satisfactory until a much deeper knowledge exists of interneuron properties, connectivity, and actual roles in intact, behaving animals. That interneurons exist which, when stimulated, cause specific behaviors to appear, should hardly be deemed surprising. There are cells that cause backwards-walking and those that cause forwards-walking in crayfish (Bowerman and Larimer, 1974; see also Larimer, this Commentary). The most compelling question to ask about them, as I pointed out at the 1975 locomotion conference, is: "Are they the neural pathways used by an intact animal when, in nature, it walks in these ways?" With modern recording techniques this should not be a difficult question to answer. If an affirmative answer is obtained, the use of the term "command" to describe them will be well-justified. But if the answer is negative, one would suspect that the appearance of the specific behavior is an irrelevant chance circumstance.

If a study is made by exciting an interneuron *in situ* without cutting its connection to the head, it is extremely important to determine if it is indeed centrifugal. A centripetal interneuron in a feedback loop may also cause a complex behavior, but is hardly going to fit the command concept! The real point here is that in the final analysis only a knowledge of what identified interneurons are doing during natural behavior will lead to a satisfactory classification and understanding. This will come, in time, at least for some invertebrate animals. If terms like "command" are properly defined they may prove to be useful as we grope to understand the principles underlying the cellular bases of behavior. They can be used descriptively at first, and then refined by theoretical considerations. Or, we could set up a theoretical framework first. But who would think this worthwhile when nearly every month a new physiological process is discovered in interneurons?

Because of internal feedback circuits and reflex actions, forced contraction of even one muscle or excitation of one key neuron is likely to lead to whole acts of behavior. When a single postural muscle in a free animal is electrically excited, there is a very high probability that running, jumping, flying, sound production, or whatever, will occur. Here we see the command neuron concept *reductio ad absurdum*.

The unfortunate conversion of a noun/intransitive verb into adjectival form to denote neurons empirically determined to initiate complex movements has resulted in a strange quirk. It has become an important determinant in the conceptualization of neural organization! Well, perhaps the end justifies the means? We may hope that neurobiologists can be prevailed upon to be more logical in the future.

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EDITOR'S NOTE

This pre-commentary by Graham Hoyle was, at his request, circulated to all commentators along with the target article by Kupfermann and Weiss. Hoyle's response appears after that of the other commentators.

by John H. Andreae

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Descriptive and prescriptive names. Is this a little word game that neurobiologists play to while away the time? Why not use words like "command," "control," "decision," and so on, to describe the functions of neurons in a neurochemical circuit? We do the same with electronic circuits in describing how they work. You are quite likely to see a digital circuit diagram with one component labelled "command flip-flop." The word "command" would be a suggestive label introduced to help explain how the circuit worked. In addition to such informal names, electronics engineers use precise terms, like "JK flip-flop," to identify elements of a circuit and other precise terms to identify circuits or subcircuits that perform particular operations. I cannot think of a situation in which we would attempt to *define* a command flip-flop: to define the role of an element in a circuit would be

hazardous for the reasons given by Kupfermann and Weiss. We need to distinguish between descriptive and prescriptive ways of referring to things. "Command" is descriptive because it depends upon the point of view taken, while "JK" is prescriptive because it remains correct regardless of the point of view.

May I suggest that Kupfermann and Weiss's paper becomes more interesting if their criteria for defining a command neuron are seen as an experimental procedure for testing neurochemical circuits? There is some similarity between the problems faced by the neurobiologist trying to understand a functioning nervous system and the problems faced by the electronics engineer trying to understand a malfunctioning electronic circuit: neither knows what is happening! The electronics engineer gets out his multimeter and oscilloscope to try to trace a causal path through the circuit, but he is well aware of the difficulties he faces. Feedback loops play havoc with causality. If he is tempted to short-circuit or open-circuit a component, he knows that the consequences may be far more than the mere removal of that component. He has to consider the effects of d-c and a-c changes in the circuit. All of these difficulties and others face the neurobiologist, but it is not for an electrical engineer to tell neurobiologists how to test their circuits.

Nevertheless, we can put ourselves in a position that combines the neurochemical difficulties of the neurobiologist and the circuit know-how of the electronics engineer by applying Kupfermann and Weiss's criteria to some of the artificial neurons in a well-defined, computer-simulated neurochemical circuit, such as my own (Andreae, 1977, p. 147). No command neurons would be found. As soon as we leave the simplest of nervous systems, a straightforward correspondence between pieces of structure and pieces of behavior is bound to vanish (Gaines, 1976). In Kupfermann & Weiss's words, "... even simple ganglia are rarely, if ever, organized into such neat compartments. ... calling a neuron a command neuron can lead one to conclude erroneously that activity of this neuron is the 'cause' of a behavior. ... the attempt to classify a specific cell as a command neuron could conceivably interfere with progress towards understanding the precise role of a neuron or system of neurons in generating behavior." They convinced me.

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"General" or "general assembly"? On command neuron systems. When a neuron changes from a silent to an impulse-firing state (and some formal criteria for this discharge are met), one can say that a "decision" is made by a cell (or some part of the cell). Similarly, when a distinct behavioral act is performed, some formal criteria are met in terms of a "decision" point of the underlying neuronal net. This concept of a "decision making" point is well defined in an early theoretical work by Bullock (1961, see also this Commentary) that can also be considered as providing a perfectly adequate description of any "command" units.

The definition of the command neuron given in Kupfermann and Weiss's paper is logically consistent, but the ranges of its application have not been adequately described (and this not only due to lack of experimental data). Actually, behavior is not likely to be controlled by a single command neuron (CN), but by a system of command units. In this respect, the reasoning of the authors seems oversimplified.

The command neuron system discovered recently in a snail (Balaban & Litvinov, 1977; Balaban 1978) allows us to confirm some of the postulates of Bullock as well as to show that (1) the present authors' "necessity" criterion cannot always be met, while on the other hand, (2) convergence of all information required for the given type of behavior is really a necessary condition.

We have discovered that an intracellularly induced firing of any of the five giant neurons located on the dorsal side of the parietal ganglia in the snail *Helix lucorum* will elicit escape reactions (a "sufficient" condition for exploring their hypothetical command function). These neurons receive sensory in-

formation from the whole receptive surface of the snail's body and respond to tactile, visual, thermal, and electrical stimulation. (High thresholds prevent spiking to weak stimuli.)

It is impossible to establish the command function of a given neuron unless the hierarchy of behavior in question is determined. In experiments on the intact snail and a half-intact preparation, it has been possible to single out three levels of behavioral response. The first level is represented by a muscular contraction in response to tactile stimulation (intensity: weak, moderate, strong). The short latency of this response (not exceeding the minimal propagating time) led us to the conclusion that it was of peripheral origin. In the putative CNs of avoidance behavior, only subthreshold Excitatory Postsynaptic Potentials are generated during such a response.

Tactile stimulation of moderate intensity evokes, in addition to the just described response, a tentacle withdrawal reflex and pneumostome closure. (This represents the second level: responses of individual effectors). Phasic spike responses are registered in the five putative CNs preceding the effector responses of this second level.

Strong stimulation evokes generalized contractions (representing the third level) of all muscles, including contraction of tentacle retractor and pneumostome muscles. In an intact animal, such stimulation leads to complete withdrawal into the shell. In addition to phasic discharge, pacemaker firing was also evoked in all putative CNs by strong stimuli.

The data allow us to conclude that these five cells act in the snail's normal escape behavior, their input being convergent and polymodal.

Each of the putative CNs differs from the others in terms of either a specific part of its extremely wide receptive field or in terms of the set of behavioral responses released by its discharge. Pneumostome closure (PC) is the escape reaction common to all the five cells firing in their "normal pattern" (0-20 spikes/sec). It is peculiar that two symmetrically located neurons (No. 3) in parietal ganglia only released the PC with short latency at low frequencies of spike activity. The amplitude and duration of this behavioral response increased gradually with increasing discharge frequency.

Low-frequency firing of any of the three remaining neurons does not evoke PC, but their high-frequency discharge elicits generalized contractions (the third level of escape behavior), including PC. The average latency of PC increases fivefold under these conditions, and the response is performed in all-or-none fashion.

It might appear that the snail's CNs for avoidance behavior can be divided into two groups: (1) cells that can gradually evoke specific escape responses and (2) neurons that can release generalized escape behavior in an all-or-none manner. Such a classification would be inconsistent, however, because a high-frequency discharge of a CN from the first group can likewise elicit generalized responses (Balaban 1978). We assume that all five neurons under investigation are equivalent with the respect to their command function and that some of the numerous axonal branches of the first group of neurons go to the peripheral net in the pneumostome region. Absence of any specific interrelations between the five CNs confirms that assumption.

We consider that the CNs of the snail's avoidance behavior meet the "sufficiency" condition of Kupfermann and Weiss's paper, but the "necessity" criterion is fulfilled in only a limited number of cases. Strong adequate stimulation, for instance, can evoke escape responses even if four of the five CNs are removed.

Moderate rhythmic stimulation of one point of the snail's skin with an inter-stimulus interval of less than ten sec. leads to rapid habituation of all CNs except the one whose specific part of the receptive field is being stimulated. This is significant only while hyperpolarization of the given CN yields total suppression of the behavioral response. If response elimination is not total, we cannot confirm that the removed cell is not a command neuron because there is always the chance that a parallel nonhabituated CN is active. On the other hand, only this procedure can make it possible to establish the contribution of any single CN to the functioning of the whole system.

One readily notices that only CNs of escape behavior are confidently described in the literature (such as in Kupfermann and Weiss's paper). This has to do with the CNs all-or-none manner of functioning and the all-or-none nature of the types of behavior in question. However we cannot now exclude that CNs for other types of behavior may have different properties that may be closer to the characteristics of modulatory neurons.

Any "decision making" requires the convergence of all types of sensory information necessary and sufficient for a certain behavioral act. This trivial assumption leads to a nontrivial condition (and one confirmed by recent mor-

phological investigations of the snail's CN with cobalt injection in the laboratory of E. N. Sokolove): any command neuron must have an independent, well-developed "fact-finding input net." This we consider an unnecessary condition for command function.

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Command neurons: know and say what you mean. One can lead a horse to water, but one cannot make it drink. One can propose a definition of a command neuron, but one cannot make everybody use it. However, one can reasonably require that everybody give his own definition when he uses the term in public or publication. A term is useful when it is applicable, if only in saving space in journals and speeding communication. A term becomes more useful as it summarizes more data. A term is dangerous if it implies a hypothesis, that is, suggests that a situation or mechanism exists that has not in fact been demonstrated. Also, unless a term is a complete neologism, its definition should follow from its etymology. A term is virtually useless if it defines an empty set. The term command neuron is probably dangerous, as Kupfermann and Weiss (hereafter K & W) well recognize, and I agree that there is value in clarifying its definition. How useful the term is remains to be seen. Of this K & W are also aware, for they say a "primary command or initiating function" may be "difficult" - really impossible - to assign, by which I think they mean that the term does not apply to the behavior under consideration. Definitions often break down around the edges. Recognizing this, we can go on using them and when in doubt merely state what the experimental observations are without worrying too much whether they fit into a particular terminology.

On the question of "command neuron," I have to agree with a number of commentators. Hoyle's comments [q.v.], although he is perhaps a little more acerbic than is helpful. Nor do I accept his general rejection of the term (for which he will substitute "driver" or "trigger"?). He traces the origin of the concept to a respectably early date in the 1800s. I would add its relation to the Sherringtonian concept of final common path and the terms "command nerve" and "noyau . . . commandant" employed by the Fessards and their colleagues in respect to the electromotor systems of the electric fishes (Albe-Fessard & Martins-Ferreira, 1951; Albe-Fessard et al., 1954). Also there is the converse concept of hierarchy in sensory pathways, which is probably as ancient. I will go no further here than to point out the relationship.

In the abstracts of the K & W paper the term's referent is a neuron whose activity is both necessary and sufficient for the initiation of a given behavior. At first glance this is clear, an unambiguous and attractively simple, esthetically pleasing definition. I particularly welcome the "necessary for," meaning that the command neuron controls the behavior in the intact organism, a point of ambiguity in the literature well worth resolving.

However, there are several aspects that merit discussion: 1) The question of integrative and relay functions of command neurons under this definition. 2) A command nucleus versus a command neuron. 3) The point of specifying "initiation." 4) The definitions of behavior and activity. 5) The state of the organism when tests for necessity and sufficiency are applied, as well as the meaning of modulatory.

The question of integration. Late in the text of their paper K & W finally give as their definition "responsibility for a given behavior should be attributed to a cell only if its activity is both necessary and sufficient for the initiation of the behavior" (italics theirs). They immediately add that the "task is not the impossible one of assigning some ultimate responsibility, but rather of identifying the critical decision points in the generation of behavior." This qualification brings out a weakness in their definition that I think can be easily remedied. For indeed we are trying to assign ultimate responsibility in terms of neural activity. I think it would be better to define "command neuron" as the

highest level of the final common path of the neural activity necessary and sufficient for the given behavior. The highest level of the final common path could be a motoneuron, although one ordinarily would not call these command neurons. (In agreement with Hoyle [q.v.] I see no natural way to exclude motoneurons, particularly in the K & W definition.) Alternatively, there could be one or more higher neural levels. In the latter case the lower levels can quite naturally be termed "relay" neurons. (The command fibers of Wiersma and Ikeda could well be relay neurons in this sense, although they carry a neural command for swimmeret movement.) My point is that the command neuron should be integrative (that is require multiple inputs for its activation), which a relay cell is not. (And this is implied in K & W's discussion of Wiersma's ideas [see also Wiersma, this Commentary].) We can, in Hoyle's prose, maintain that the command is the king's alone.

Obviously we do not completely understand the control of a behavior when we know only the highest level of the final common path of the activity mediating it (assuming that such exists). We could then define the next higher level of neural command as any member of the set of activity patterns in neurons presynaptic to the command neuron that elicits the activity producing the behavior. And so on to sensory neurons or those that are active without inputs. (Feedback loops must also be taken into account.) Understanding of this degree of complexity is required for an adequate description of the behavior; it is good to keep in mind that this is where we hope to go, even if we do not know how, or whether, it can be done. (Heisenberg's uncertainty principle has not been shown to apply to investigation of neurons at our present levels of resolution.)

One problem in K & W's definition (and in their Figures 2-4) is that sensory cells can be command neurons. If activity of a single sensory cell elicits the behavior (and, as Kennedy has pointed out in this respect, stimulation of single sensory hairs was shown by Dethier to elicit proboscis protraction in the blowfly), then its activity is sufficient for the behavior, and if the stimulus is carefully defined, necessary as well. Here, as with motoneurons, I think the command concept becomes somewhat trivialized, if again there is no natural way to exclude sensory neurons (Dethier, 1963).

One possibly useful variant of the command concept is the self contradictory notion of "bifurcation of the common path." If a single cell is fired by activity in any one of a group of cells presynaptic to it, the higher level cells themselves being integrative, then one might consider the higher level cells as command cells. The highest common element acts as an or-gate. The higher level elements are integrative. To be sure, in the fly, if a single cell were the highest level of the final common path for many sensory inputs, each itself adequate, one would probably still call the highest common cell a command neuron.

Command neurons versus command nuclei. Aside from motoneurons and a few giant axons, I do not know any command neurons. But I do know a number of cell groups that I would call command nuclei, that is, groups of equivalent neurons coupled together (electrotonically as it turns out) and acting as a single unit in normal function. I would call these command neurons as well, while K & W would consider these cells to be a "command system." I find their usage unnatural, for to me a command system implies all the neurons controlling the behavior, from what I have termed the command neurons on down. Moreover, a "command system" ought to apply to a network with feedback loops with no highest level, and it should include other neurons whose activity or inactivity is necessary for the behavior. The K & W definition of command system for any behavior is simply satisfied by the effector neurons that control it. This is fair enough, but I would not be very interested unless higher level neurons were also included.

K & W get into some subsidiary terminology here that I think is not useful: "command elements" and "modulatory elements." As defined, activity in any one of a set of command elements can initiate part of the behavior. In a command nucleus so closely coupled that an impulse in one cell propagates to all the others, excitation of a single cell can produce part or even all of the behavior. K & W would consider such cells command elements. There are also less closely coupled command nuclei in which an impulse in a single cell only propagates to the other cells when they are depolarized. In this case, stimulation of a single cell produces nothing, but blocking activity of enough cells will begin to disrupt the behavior and each remaining cell will then be modulatory. By these definitions, a difference between command and modulatory elements could arise from quantitative aspects of coupling and need not reflect significant organizational features. It might be useful here to define modulatory cells as anatomically distinct from command nuclei. More of modulation below.

Why "initiation of the behavior?" K & W specify that the command neuron should be necessary for the initiation of the behavior. I suppose the point is that the behavior can outlast activity of the command neurons themselves and that command neurons can serve what might be termed a triggering or releasing function. However, if "the initiation of" is omitted, nothing is lost. Not only is the inclusion of "initiation" unnecessary; it is undesirable. As the definition stands, we might reasonably infer that initiation is specified because the activity of some command cells is not necessary or not sufficient for the later parts of the behavior. Yet K & W clearly mean that activity of the command neuron should be necessary for the entire behavior, not just its onset. Substitution of "production" for "initiation" would be another way of clarifying the meaning.

The definition of behavior and activity. Kennedy would restrict the term command neuron to one eliciting complex motor outputs. Although that might be acceptable usage, it is very hard to define how elaborate is complex (as noted by K & W). And certainly if one allows that command nuclei can be validly included, complexity of controlled behavior varies in tiny steps from motor twitches to complex swimming movements. No fewer than six pertinent examples are found in electromotor systems (Bennett, 1968, 1971). (One reason for writing a commentary is to be sure your own work is referred to.)

Several entries in K & W's Table I of putative command neurons present problems for me. Bag cells are neurosecretory and, granted that their activity is followed by the behavior, they do qualify as neurons that command it. Nonetheless, I would have restricted neural commands to synaptically relayed activity. If hormone secretion is the behavior, then the bag cells are the ultimate effectors without even a nerve-effector junction intervening. I would think the cells controlling inking in *Aplysia* were a better candidate. Other homogeneous groups that are omitted are in the electromotor systems mentioned above. These groups include command and relay nuclei in electromotor systems of gymnotids, mormyrids, the electric catfish, and the stargazer and, less well defined, the Torpedo. In the mormyrids there appear to be two command nuclei, one on either side, driving a common relay nucleus acting as an or-gate as described above. The entries in K & W's Table reflect the common invertebrate chauvinism (and occasionally ignorance) about vertebrate work.

Inclusion of the Mauthner cell is straightforward if the behavior meant is the tail flip to the contralateral side. The ipsilateral motoneurons are inhibited however (Diamond, 1971 *op. cit.*) and the reflex also involves bilateral contraction of a number of pectoral and cranial muscles, and mediating circuitry has been described for the pectoral fin muscles of the hatchet fish (Model et al., 1972). The command to depress the pectoral fins can arise in either Mauthner fiber, both of which innervate the same population of giant fibers activating the motoneurons. The giant fibers (which are not coupled and which relay the Mauthner fiber activity) are the highest level of the final common path for pectoral fin depression, but the Mauthner fibers are the integrative elements. Either Mauthner fiber is sufficient for the pectoral fin depression, so for this behavior there is no command neuron in the K & W sense. When both are active simultaneously, the motoneurons for axial musculature are inhibited while the pectoral fin muscles are still activated (Diamond, 1971 *op. cit.*; Auerbach & Bennett, 1971). But depending on whether the behavior is defined as a tail flip to one side plus pectoral fin depression or as pectoral fin depression alone, there is or is not a K & W command neuron. Yet the two components are unequivocally part of the same behavior and are controlled by the same neurons. This definition is losing some of its usefulness.

Although the concise K & W definition states "activity," the text indicates that "the appropriate (pattern of) activity" is meant. K & W recognize that a single neuron might be a command neuron for one behavior yet participate in other behaviors when differently active. An example may be the motoneuron of the crayfish abdominal musculature that appears to activate one muscle at low frequencies and another muscle at high frequencies (Grossman et al., 1973). Further, the electromotor system of the electric eel activates the weakly electric organ at low frequencies and both strongly and weakly electric organs at high frequencies (Bennett, 1971).

Command implies, and may be most useful in dealing with, discrete responses, yet there is gradation from what can be considered a unit of behavior to ongoing regulatory activity. It might be better to speak of control neurons and systems for regulatory behavior, provided one remembers the existence of a spectrum from discrete to continuous.

Some behaviors involve feedback loops, none of whose members can be

at the highest level. Here the K & W definition has an advantage over mine in that stimulation that reproduces the evoked response opens the loop. Thus, command neurons in the K & W sense could exist in such loops for ballistic kinds of movement and behavior but not for behavior in which the feedback signal corrects for variability in the system. For example, a command to jump a particular height might exist in a feedback loop, whereas a command to walk along a tight rope would not.

The state of the organism and modulation. It is implicit in the K & W definition that the behavior should be produced "under given or constant conditions." Thus, where a K & W command neuron exists, there may be other neurons that are contributory. There could be neurons that are not affected by the stimulus, but whose activity provides a tonic background excitation or inhibition. I would consider these cells modulatory if their effects were not very strong. I suspect that there are few systems in which a command cell cannot be prevented from firing by other neurons, or where the command cannot be aborted by inhibition at lower levels. These inhibitory neurons are certainly part of what I would term the command system, although they are not command neurons. Sometimes we deal with a factorial situation; where a number of neurons are required for the exact response, one cannot say that one is more necessary. Suppose 90 percent of the (evoked) command postsynaptic potential in a relay nucleus comes via one group of cells and 10 percent from another morphologically or physiologically distinct group. Then I, but not K & W, would term the first group command neurons and the second group modulatory neurons. I would be even happier if the modulatory group similarly affected a number of behaviors, as the metacerebral cells might do. Modulatory neurons, by my definitions, may or may not be excited by the stimulus that evokes the behavior.

There are lots of ways in which behavior is controlled other than by command neurons *sensu stricto* (anybody's). As K & W note, it appears likely that a command may be diffuse (as in neurons presynaptic to a command neuron *sensu Bennett*) and arise more from a gestalt than a center. Where this is true, the concept of command neuron really is inapplicable. I suspect that we need not be overly precise in our definitions. Even with the relatively small amount of data we have now, we know many different neural circuits involved in controlling behavior, and a strict but inclusive categorization evades me, for one. There are many instances in which neurons appear to have some function to which we would naturally apply the concept of command, considered loosely. But these lie across a spectrum sufficiently wide that an encompassing definition becomes too complex for usefulness. And besides, few other scientists would abide by such a definition. We can go with Supreme Court Justice Potter Stewart who wrote that although he might find it impossible to define hard core pornography, he knew it when he saw it (Jacobellis vs. the State of Ohio 378 US 184, p. 197). In the last analysis, the question of whether a particular cell is or is not a command neuron is unimportant: what matters is how the neuron operates.

To summarize my concerns: 1) A command neuron should be integrative and not a relay. 2) A command nucleus is a simple and useful extension of the concept. 3) Activity of a command neuron leads to generation of the entire behavior. 4) How behavior is defined greatly changes what constitutes a command neuron. 5) Command neurons may be only one part of the overall system controlling the behavior. 6) Too much rigor in the definition may not be useful.

A comment on commentaries: It is my understanding that K & W's paper cannot now be changed, but that they will write a further commentary or rebuttal. Supposedly this will expose the workings of all our minds in arriving at our conclusions. It would seem more direct for the various authors to exchange comments until they know the points where they remain in disagreement. Moreover, I, for one, would be more likely to defend a nonoptimal position taken publicly than one adopted more or less privately, from which a quiet retreat was possible. [And after consultation with K & W, I have indeed significantly revised this commentary, in some respects clarifying and in others retreating.]

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"Command" is heuristic until we know better. I like Kupfermann and Weiss's paper. It is constructive and helpful. At two points I would add a few words to clarify important aspects of the command neuron concept. I regard these additions as fully congruent with their construction. In the abstract, at the end of the third sentence, the somewhat obscure phrase "... independent of considerations of normal behavioral function" presumably means "without any claim that the neuron is necessarily the initiator or the only initiator of the same behavior when the animal performs it in natural conditions." However, I think most authors do at least imply that the behavior elicited by stimulation of the command neuron is so very much like normal behavior as to be equivalent if not indistinguishable from it. Again in the abstract, at the end of the third defining criterion, I think it is important to add "given a set of background conditions that are at least permissive and perhaps also conducive."

Turning to Hoyle's precommentary, the message gradually comes through that the main objection is one of personal taste.

Adjectival use of "command" is well accepted, as in "command post." Note that under the stated conditions, the term command neuron "will be well justified," so it is not the adjectival use that is the basic problem. Just the fact that a sergeant can clearly issue a command to a private does not destroy the usefulness of the term. It is easy to build into the definition of command neuron, as we all use it, the idea that its application is not at the level of a small fragment of a normal act in the ethologist's sense. A single twitch in a single motor unit may be such an act if by itself it causes a major part of, say, a normal startle response, but not if it is one of many motor units or normally partakes in non-twitch-like movement.

I agree that it is highly desirable to show whether or not these cells are used in natural behavior of intact animals, yet they need not be the only way the animal calls up that act. Alternatively, the differences between those acts called up by the command cell and quite similar acts called up otherwise may be subtle and difficult to show. Eaton, Bombardieri, and Meyer (1977) have recently shown that it takes high speed cine photography - 200 frames/sec. - and careful measurement to reveal the very real early component of the startle response of fish that is, presumably, uniquely due to the command cell called Mauthner's neuron. Without it, other neurons can probably mediate superficially quite similar but crucially different behavior.

Before we have the eventual, desirable demonstration, it is quite in order - to my taste - to use the name for a highly interesting cell meeting stated criteria to express a hypothesis about its normal significance.

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"Command" as functional concept rather than cellular label. When I was asked to provide a commentary on Kupfermann and Weiss's paper "The

Command Neuron Concept," my initial reaction was surprise, since I have no direct experience in this field. I accepted because I think the commentary is a stimulating format and because I have found the command neuron idea useful in musings about the vertebrate motor system. Because I write largely on the basis of secondhand information, my remarks will be brief.

The most obvious point to be made by a student of vertebrate nervous systems about the command concept is already noted by Kupfermann and Weiss, that is, the vertebrate central nervous system (CNS) probably does not contain individual neurons capable of a "command" function. With much less premium on space and numbers of neurons, one imagines the vertebrate CNS to contain sets, some probably quite large, of nerve cells with functions more or less analogous to those subserved by some individual neurons in "simpler" systems of invertebrates (Grillner, 1976 and this Commentary). Even in the latter, however, the "command function" appears in some cases to be distributed within sets of neurons (Davis, 1976 and this Commentary; Kennedy & Davis, 1977 *op. cit.*).

The next point that can be made is to distinguish between the use of the term "command neuron" to label or describe particular nerve cells versus its use as a conceptual model for certain proposed neural organizations. With regard to its use as a label, Kupfermann and Weiss make the point that "identifying" a particular nerve cell as a "command neuron" may induce a false sense of accomplishment that can be counterproductive if the matter is left to rest there. They do, however, suggest in detail some criteria that can be used for such cellular identification.

The vertebrate neurophysiologist should be sympathetic to this desire for precise and functionally meaningful neuronal labels. The vertebrate CNS also contains what we like to think of as meaningful categories of motor and sensory neurons, including sensory interneurons of rather high order, all of which seem to have evident functional roles, interneuron labeling is difficult in the vertebrate, but there has been recent progress in the development of methods and conceptual models required to permit identification of functional classes of CNS interneurons in the mammal (Lundberg, 1969; Jankowska, 1975).

What, then, about the command neuron as concept rather than as cellular label? The concept is, for me, encapsulated in the phrase often used by Don Kennedy: "... permissive but not instructive ..." (Kennedy & Davis, 1977 *op. cit.*, p. 1060). This phrase, in context, implies the existence of a neural network that can produce complex sequences of movements, or even whole behaviors, when activated by an input signal that itself contains no information that can specify the output sequences. Further, the phrase suggests that the "permissive" input must be present for some relatively long period, during which output is generated. Thus, the notion of a permissive but not instructive command differs from the allied idea of a "trigger" input, in which the input signal can be very brief and still release a movement sequence of much greater duration (Willows, 1976). In both the command and trigger concepts, the detailed neural control of movement is viewed to reside in the properties of the target neuronal network, or neural center (Doty, 1976 *op. cit.*). The input signal and the neuron or neurons that deliver it are viewed as external to the network. It is here that the command concept seems clear but its application to cellular labelling gets into trouble. How can one demonstrate that a specific neuron, in synaptic contact with many other neurons, is nevertheless functionally autonomous and not a part of the network postsynaptic to it? This point was made repeatedly by Jack Davis at a recent symposium on locomotion in vertebrates and invertebrates (Davis, 1976 *op. cit.*, and see also his remarks in the conclusion to that symposium's proceedings, pp. 804-8).

As useful as I find the phrase "... permissive but not instructive ..." I find that it also leads to some problems. "Permissive" carries the connotation of a simple gating function and some command situations fit this idea well (Ikeda, 1976 *op. cit.*). However, there are other examples, as in the lobster swimmeret system (Davis & Kennedy, 1972), in which "command" input frequency is related to a range of output frequencies, or in other cases may produce a qualitative difference in output effects (Larimer, 1976 and this Commentary). In such cases, the input signal does appear to have some "instructive" features. Thus, the spectral character of natural phenomena once again foils our attempts to use an imprecise language to formulate precise generalizations.

With regard to the command neuron concept, it seems simplest and perhaps best to recognize that our interpretation of such formulations will necessarily change as more is learned about existing nervous systems at all evolutionary levels. Experimental observations can be communicated only

with imprecise words used in the context of imperfect conceptual frameworks. We must be ready to change both when they are no longer useful, that is, when the then-available evidence dictates too many exceptions. My impression is that the command neuron concept has not yet reached that stage, but it is certainly undergoing a rapid evolution.

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Do we need "command" neurons? Kupfermann and Weiss's arguments are convincing, but they lead to a conclusion that the authors are reluctant to draw: the term "command neuron," with its behavioral associations, theoretical underpinnings, and general fuzziness, should be scrapped. Continued use of the term imposes an artificial unity upon a heterogeneous group of premotor interneurons. It implies a serial generation of stereotyped behavior with a single neuron or group of neurons as the critical link in the chain of causation. It suggests a dichotomy between "simple" invertebrate behavior and higher vertebrate motor systems (Denny-Brown, 1966) in which movements are generated by interacting elements from many different areas of the central nervous system. Even in the more rigorously defined context of a "necessary and sufficient" neuron involved in the generation of a specific behavior pattern, the "command neuron" concept is no longer useful in advancing our understanding of the role of interneurons in behavior.

Two kinds of problems seem to me to be associated with even so restricted a definition of command neuron as Kupfermann and Weiss propose. Implicit in the concept is that in a given species there exists a fixed discrete repertoire of behaviors that can be associated with discrete neurons or groups of neurons. To demonstrate this, the boundaries between different behavior patterns must be quite precisely specified—something that is seldom done. Moreover, establishing that a cell is both necessary and sufficient, while conceptually appealing, is likely to prove difficult, if not impossible, in most preparations. If it is not technically possible to remove reversibly a cell from a behavioral pathway by hyperpolarization, the presence of extensive feedback and parallel pathways allows for the existence of some neuron in the neuropil, undiscovered by conventional stimulation techniques, that can produce the "same" movement, thus rendering the term "command neuron" useless. Let us look at these objections in more detail, concentrating on these limitations inherent in the command neuron concept.

First, one of the most troubling features of the command neuron literature has been the qualitative nature of the descriptions of movements produced by stimulating such neurons. In most cases, neither the variability nor the range of behavior produced by stimulating command neurons has been described. Before we can decide whether a putative command neuron is necessary and sufficient for a particular behavior, we must differentiate that behavior from others. I am not simply making a piecemeal quantification; Bentley's work (1977) on cricket song shows how important adequate quantification is. He was able to demonstrate (by using sound spectrographic analysis) that stimulating a single interneuron at three dif-

ferent frequencies resulted in three behaviorally distinct songs. Only if we know how precisely we are describing a movement elicited by a single command neuron, how it varies at different stimulus frequencies, and how much intertrial variation there is, can we judge the discrete role of that neuron in behavior. Questions about the overlap between movements produced by the same or different command neurons and whether "one" behavior can be produced by many neurons must be answered quantitatively.

A second difficulty in characterizing the output of command neurons is that the techniques used to record the behavior produced by stimulating the putative command neuron may not be adequate to identify that behavior reliably. Three popular techniques in particular must be used with some caution: (1) In addition to the technical difficulties of producing a film record of a movement with sufficient photographic quality and appropriate camera angle to permit the analysis of a series of movements, there is the additional problem with film that many important behaviors consist not only of overt movements but also of the controlled exertion of forces, as in postural adjustments. In the latter case, two units that produce the same movement, but under different load conditions, will be indistinguishable by this technique. (2) Extracellular multiunit recordings of motoneuron discharge in nerves innervating the relevant muscles often cannot be used to distinguish, on the basis of extracellular amplitudes, between two units innervating different muscles. Furthermore, the summation of many extracellular potentials during high frequency discharges accompanying evoked movement often produces an incomprehensible record. (3) EMG electrodes, particularly in small animals, can record spurious signals in adjacent muscles, leading to an inaccurate description of command neuron output. As a result of these errors, categories of discrete behaviors (if they exist) produced by command neuron stimulation are arbitrary in many cases and cannot support any particular model of command fiber function.

Thirdly, the existence of parallel routes for evoking a particular behavior is very difficult to disprove. As Kupfermann and Weiss, as well as other workers, have pointed out, it has been difficult in many preparations to ascertain how command neurons are normally activated. It may turn out that the movement appears in the absence of activity in the neuron, once the afferent input is identified and stimulated; this has been shown in an interneuron associated with statocyst-related righting behavior in crabs (Fraser, 1975). In this case, the interneuron no longer satisfies the "necessity" criterion of Kupfermann and Weiss. Moreover, since these cells receive input from several different stages of afferent processing (direct statocyst afferents, leg mechanoreceptors, and "non-specific" inputs), it is difficult to conceive of them as elements in a serially hierarchical process.

In most studies of command neurons, little effort is made to look for evidence contrary to the command neuron hypothesis; and counterevidence in the form of parallel pathways that may replace or alter the form of the final behavior is ignored. For example, the giant fibers of crayfish are often cited as paradigmatic command neurons. Even though the medial and lateral giant fibers are among the best studied examples of interneurons producing a stereotyped response (Zucker, 1972, a, b, c and this Commentary), the variability in the form of the escape response mediated by the lateral giant fiber has not been extensively studied. There are other problems in this example, since extensive parallel pathways are now known to play an important role in the lateral giant fiber response. Inhibition from other parts of the nervous system can apparently modify the threshold and output of this system (Krasne and Wine, 1975; Wine, 1977 and this Commentary). The presence of numerous "corollary discharge interneurons" (Wine, 1971; Wine and Mistick, 1977) indicates the presence of additional parallel pathways that also modify the response. These interneurons are driven by the lateral giant, first root afferent—and possibly more rostral inputs, and they are presynaptic to many of the motoneurons activated by the lateral giant. There is some indication (Zucker, 1972c) that different fast flexor motoneurons are not activated in the same way by the lateral giant each time. Thus, a case can be made that the lateral giant fiber is an important part of a network of interneurons involved in the escape response. A tail flip of a specific form might depend upon the previous activity in inhibitory and excitatory interneurons synapsing on the motoneurons; the lateral giant fiber might simply trigger a class of escape responses. If this is the case, the lateral giant would be necessary, but not sufficient, for a specific escape response.

Furthermore, escape involves not only the two giant fiber systems (Wiersma, 1947; Larimer, et al., 1971 op. cit.) but also the less studied nongiant systems (Schrameck, 1970; Wine and Krasne, 1972). Both the giant and nongiant fiber systems produce different movements that are under control

of different pathways of sensory activation (Wine and Krasne 1972) whether the nongiant fibers produce the same movements as either of the two giant fibers is not clear. As a result, even in this paradigmatic example of a command neuron parallel pathways and extensive feedback suggest that the model of serial hierarchy with its command neuron as the linchpin of behavior, is oversimplified.

It seems to me that in the use of terms like "command neurons" we are placing the cart before the horse. The premature construction of qualitative categories of premotor interneurons before adequate quantitative observations have been made tends to impede our interpretation of how these neurons actually contribute to behavior. We must define our categories on the basis of quantitative descriptions of interneurons influencing specific behaviors: if we emerge with discrete classes of interneurons that are necessary, sufficient, and consistent in their effects on an adequately defined pattern of behavior, then we can begin to talk about commands in nervous systems.

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On the trail of the command neuron. The concept of the command neuron is stimulating much discussion among neuroscientists these days for reasons that are clearly and comprehensively reviewed by Kupfermann and Weiss. Briefly stated, the difficulty is that the term "command neuron" implies something that has seldom been proved: namely, that such neurons are actually employed by an animal to control behavior. Kupfermann and Weiss suggest that the phrase "command neuron" be reserved for any neuron(s) that can be proved both necessary and sufficient to the occurrence of a particular behavior. The "sufficiency" criterion (#3 in their abstract) would be met only if stimulating the neuron(s) caused the behavior in question. The "necessity" criterion (#2 in their abstract) would be met only if silencing the neuron(s) by hyperpolarization blocked the behavior. Behavioral relevance (criterion #1 in their abstract) would presumably be met only if the putative command neuron(s) responds as expected to the sensory stimuli that normally release the behavior, and if the neuron(s) is active in predictable association with the corresponding behavior.

These three criteria are logical and rigorous, and in those few cases in

which they can be applied, they comprise a powerful test for command neurons. But as the authors explicitly recognize, the criteria are "not easy to apply" and they "may define a very small set of neurons." Because command neurons may be ubiquitous in the animal kingdom, I think we need a set of operational criteria that are more broadly applicable, in addition to those proposed by Kupfermann and Weiss. My purpose here is to evaluate briefly their proposed criteria, and then to suggest additional criteria that may have wider application.

The sufficiency criterion. The original criterion for identifying a command neuron is the one employed by Wiersma and Ikeda (1964) in the crustacean swimmeret system, namely, "sufficiency." Kupfermann and Weiss add stringency to the criterion by requiring that, when stimulated, the putative command neuron release an exact replica of the behavior. This stringency is certainly useful in those few cases in which single central neurons are responsible for a complete behavioral act, but such cases are probably rare. As developed in more detail elsewhere (Davis, 1976 *op. cit.*), motor systems are probably seldom controlled by single neurons. Instead, behavior is usually initiated by a variably sized population of central neurons, operating not individually but in concert (the principle of consensus). Individuals among such neurons cannot be expected alone to elicit an exact replica of the behavior.

The problem is well illustrated in the swimmeret system, where the term "command neuron" was first employed (Wiersma and Ikeda, 1964). In this motor system there are at least ten command neurons, five on each side. Stimulation of any single command neuron never produces a precise replica of the swimmeret locomotor behavior, but instead releases a variable fraction of the normal, cyclic motor program (Davis and Kennedy, 1972a). When the swimmeret command neurons are stimulated in pairs, however, their effects are additive and the resulting motor output is more complete (Davis and Kennedy, 1972b). In other words, if we strictly apply the "sufficiency" criterion, the original command neurons do not qualify for the title. In fact the strict sufficiency requirement proposed by Kupfermann and Weiss would exclude all but an unrepresentative few neurons, such as crustacean giant fibers, from the category of command neuron.

The difficulty posed by multiple command neurons is solved by the authors with the concept of the "command system," defined as a collection of "command elements" that normally operate together to cause behavior. The authors propose that before a command system can qualify for the title, it must be shown that when the entire system is activated as a single, functional unit, it is sufficient to the behavior in question. But consider the consequences of this requirement. Unless every neuron in the putative command system is tightly coupled with every other, the only rigorous way to activate the whole population as a single functional unit is to insert a separate stimulating microelectrode into every member of the population. It is an ideal test, when it can be applied; but with the exception of specialized and probably atypical motor systems, the criterion is not technically realistic. Therefore, the criterion lacks broad operational utility.

Perhaps the major problem with the sufficiency criterion is raised by the recent discovery of central feedback within motor systems. My colleagues and I have studied a population of brain interneurons that serve to initiate feeding behavior in the gastropod *Pleurobranchaea*. These same interneurons receive potent synaptic feedback from neurons in the motor network they drive, and they may be integral elements of the central pattern generator that produces the cyclic feeding output (Gillette and Davis, 1977; Gillette, Kovac, and Davis, 1977; Davis, 1976, 1977 *op. cit.*). Owing to the existence of these internal feedback pathways, stimulation of other neurons in the motor system can in principle synaptically activate the brain interneurons that normally initiate feeding. Therefore, the stimulated motor element could meet the sufficiency criterion even though it does not normally serve the command function.

We see that the sufficiency criterion is an ambiguous test for a command neuron. If the test fails, the neuron involved may still be part of a command system; and if the test succeeds, the neuron may not normally play a command role. The criterion is thus helpful only if the outcome of the test is positive, and if central feedback can be ruled out as the cause. Under these restricted conditions, the criterion provides a powerful and persuasive test. But when the criterion is applied in the strictest sense, it excludes neurons that I think are legitimately classified as command neurons.

The necessity criterion. The "necessity" criterion proposed by Kupfermann and Weiss is subject to some of the same difficulties as the "sufficiency" criterion; that is, because the command function is probably normally shared among several neurons, no individual neuron is likely to be necessary to the

occurrence of a given behavior. To demonstrate that the entire population as a unit is necessary is a powerful test, if it can be accomplished. But it again requires independent, simultaneous microelectrode control over every member of the population, a feat that is technically unfeasible in most motor systems. Like the "sufficiency" criterion, the "necessity" criterion is useful mainly in those atypical cases in which single central neurons control complete behaviors.

Behavioral relevance. I fully concur with Kupfermann and Weiss on the desirability of applying this criterion, since there is no other conclusive way to find out whether the neuron is actually used by the animal to initiate behavior, as implied by the term "command." But the criterion is not without its own problems. To begin, if a behavior is truly commanded by several neurons, none of which is either necessary or sufficient, what shall we conclude if a putative command neuron is sometimes silent during the execution of the behavior? Are we to deny the cell its rightful title simply because it takes an occasional rest? In fact, it seems plausible that Nature might deliberately arrange for such relief; perhaps, for example, gradations in the intensity of behavior are caused by recruitment of command neurons from a pool of such cells, as is typical among motor neurons. And what can we really conclude even if the putative command neuron is active during behavior? Perhaps it is not itself a command neuron, but rather one of those central elements of the motor system that is reciprocally connected to command neuron(s).

There are ways around these criticisms, but they are not easily realized, nor for that matter is applying the behavioral criterion in the first place. Recording from single, identified neurons while an animal is free to behave "normally" has been accomplished mainly in gastropod mollusks, and there only because of the unique technical advantages of their nervous systems. Indeed, with the exception of giant fibers, it has not yet proved possible to apply intracellular techniques to putative command neurons outside the gastropod mollusks.

In summary, behavioral relevance is indeed a crucial criterion for identifying a command neuron. But it is not free from ambiguity, and it is of technically limited application.

The epistemology of the command neuron. I think that much of the present dilemma with the concept of the command neuron is directly attributable to our changing concept of how motor systems are organized. Most neuroscientists, including those who first used the phrase "command neuron," appear to have originally conceived of such neurons as single nerve cells capable of eliciting a complex behavior pattern. We detect shades of such thinking in the paper by Kupfermann and Weiss, they imply that unless a single neuron is both necessary and sufficient to a given behavior, it does not provide "a critical decision point for the behavior," and therefore should not be considered a command neuron. But Kupfermann and Weiss also note that "even simple ganglia are rarely, if ever, organized into such neat compartments." We are finding that Nature seldom invests such crucial decision-making power in single cells, preferring instead the safety of numbers, in this case, the fault lies not in the concept of the command neuron, but rather in the narrow way it has been conceived and applied. To some extent we may have allowed our definitions to shape our concepts, and in the process painted ourselves into an intellectual corner.

Where does this leave the concept of the command neuron? I think most neuroscientists would concur that abundant evidence – much of it admittedly circumstantial – supports the existence of a class of neurons, typically descending interneurons, that is specialized to initiate a given behavior. Because of the way the nervous system is organized, individuals among such neurons are probably seldom necessary to the behavior they collectively drive, and they are probably seldom sufficient; but such neurons nevertheless serve the command function, in the sense that together they comprise the central nervous locus of behavioral initiation. We cannot exclude the possibility that such neurons also play a pattern-generating role, indeed, evidence from *Pleurobranchaea*'s feeding system and *Tritonia*'s swimming system (Gettings, 1977 *op. cit.*) strongly supports such a role. The problem, as I see it, is to decide upon a set of practical operational criteria by which individuals among such cells can be identified and labeled with whatever term we choose. (I am not personally enamored of the term "command." It is too militaristic in tone, implying the existence of "authority" that may be but an artifact of our anthropomorphic projections. The term may also evoke a hierarchical image of motor control, which is not in full accord with recent data (see Davis, 1976 *op. cit.*). But the phrase "command neuron" is so firmly entrenched that it will not dislodge easily. In any case, as long as we are clear about definitions it should not matter what term is used. Our terminology

should serve, not master, our concepts. As noted by Einstein, a rose is a rose is an onion.)

Toward a definition of the command neuron. What are the required characteristics of neurons that participate in the command function? First, we would expect that the output connections of such neurons are organized so as to excite the central nervous elements of a motor system, and thereby produce some recognizable component of the corresponding behavior. Sensory neurons are excluded from the category of "command neuron" because they comprise the peripheral input to a motor system rather than a central locus of initiation. Command neurons are probably typically descending interneurons, but I am not sure we can reasonably exclude certain motor neurons. In *Pleurobranchaea* we have analyzed an efferent neuron that makes the esophagus contract and that may be a motor neuron; and yet the same neuron plays a potent command function for the feeding output of the buccal ganglion (the "ventral white cell"; Gillette et al., in preparation; Davis, 1977 *op. cit.*). Neither am I certain we can meaningfully distinguish between cells that "modulate" and those that "command" a motor output program. If several neurons share responsibility for initiating a behavior, the effect of individuals among such neurons may be too weak to detect easily unless the behavior is already in progress. Especially under the trauma of acute experimental conditions, we might expect an individual command neuron to reveal its effect only by modulating an ongoing behavior.

As a second working criterion for defining a command neuron, we might expect such a neuron to enjoy "privileged access" to the sensory and/or central inputs that normally initiate the behavior. Owing to central feedback within motor systems, any neuron in the system may in principle have the capacity to initiate behavior. In this case, output effects are insufficient alone to impart the command role; instead, command neurons may normally play their initiating role largely because their input connections are organized appropriately. The hypothesis that the initiating function is imparted by selective routing of inputs to command neurons has not been tested satisfactorily, but in view of the possibility of feedback connections within a motor network, the hypothesis would seem reasonable if not essential. There is little evidence for the alternative of diffusely routed simultaneous activation of all elements of a central motor network.

If the above "output" and "input" conditions are met, I think a neuron can be considered a likely candidate for a command neuron. But unless the neuron can also be shown to be active during normal behavior, we will not transcend the present discussion. Thus, difficult as it is to apply, the "behavioral relevance" criterion proposed by Kupfermann and Weiss would seem indispensable. If a given neuron truly participates in behavioral initiation, then under behaviorally "normal" conditions it should be among the first members of a motor network to fire, and its activity should at least be very well correlated with the occurrence of the behavior.

If all three of these criteria are met, the neurons involved meet the criteria expected of a "central nervous locus of behavioral initiation," and are legitimately classified as command neurons. If the more stringent criteria proposed by Kupfermann and Weiss are also met, the case is even more conclusive. But we should not deny a neuron the title of "command neuron" if it fails either the "necessary" or the "sufficient" criterion that they propose. For these two criteria are openly tailored to the specialized and almost certainly unrepresentative condition in which single central neurons elicit complete behavioral acts.

Conclusions. The concept of the command neuron is a central one in contemporary neurobiology, and the proposals of Kupfermann and Weiss are a welcome contribution to the dialogue. My counterproposals, like theirs, are not offered as the ultimate solution; we know too little about the neural mechanisms underlying behavior to expect ultimate solutions. Rather, the need at present is for general, if temporary, operational constructs. The immediate goal, it seems to me, is to use these constructs to establish the validity and generality of the command concept, that is, to demonstrate that there really are central nervous loci of behavioral initiation, in as many preparations as possible. As is characteristic of the neurosciences, "complete" proof will most likely be forthcoming only in a limited number of especially favorable preparations.

In parallel with this primary goal, we can begin to address a host of fascinating questions about command neurons, answers to which are certain to illuminate the causal determinants of behavior. What are the operating principles by which a population of command neurons controls a given act of behavior? Do command neurons represent a heterogeneous class of cells that have clearly differentiated functions in controlling behavior? Are command

neurons also pattern generators? Do different command populations interact, directly or indirectly, to establish the "singleness of action" (Sherrington, 1906) that characterizes animal behavior? How do command neurons figure in behavioral concepts such as motivation? And if command neurons comprise a neural locus of behavioral initiation, might they not also comprise a neural locus of behavioral modification by hormones and experience? These impress me as among the most exciting technically plausible questions that can currently be asked of the nervous system.

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Functional descriptions of neurons that influence behavior. It was never expected that observations on the effects of changes in activity of certain invertebrate neurons that initiate and control overt movements relevant to behavior and satisfy many criteria indicative of higher interneuron status would develop into a major concept in neurobiology.

A little over ten years ago, Donald Kennedy and I reported the results of stimulation of nerve fibers in the crayfish CNS that repeatedly produced characteristic postures of the abdomen (Evoy and Kennedy, 1967). We had shown that stimulation of single central fibers produced precisely repeatable, multiganglionic motor outputs to evoke the observed postures and, following isolation from sensory inputs, that the general pattern of these effects did not depend on sensory feedback. These cells demonstrated characteristics of higher order interneurons in that they integrated a wide variety of sensory inputs, and had high thresholds as well as restricted and predictable outputs. We therefore felt justified in adopting the terminology of "command fiber" introduced in Wiersma and Ikeda's 1964 [op. cit.; see also Wiersma, this Commentary] report of similar central control of crayfish swimmerets. However, we also showed that the effects of several fibers could summate. Although not examined in sufficient detail, there is some evidence that command neurons may interact and that they possess a vaguely hierarchical organization in their connections from sensory inputs (Kennedy, 1969, op. cit.). The original observation that stimulation of a single fiber is sufficient to evoke a behaviorally relevant motor output is extended by the observation that in some instances activity in two or more cells is necessary to produce a recognizable output, as in postural extension in the abdomen of the crayfish, *Orconectes virilis* (Page, 1975). Thus the characteristics of these cells are suggestive of the "multiple action systems" described in Table 1 of the Kupfermann and Weiss paper.

If the concept of a complex motor act initiated or modified by a single central neuron served only to stimulate a more sophisticated search for morphologically identifiable interneurons with specific functions in the CNS, use of the term "command neuron" for purposes of discussion would have been justified. Few ideas in science are ever totally correct or incorrect. A more descriptive and grammatically correct term would have perhaps been desirable. However, neither Kupfermann and Weiss nor Hoyle in his precommentary, appear to have come up with a more appropriate substitute.

In its original formulation, the command neuron concept differed from other proposed mechanisms of initiation and modulation of behavior in that it consolidated evidence from direct observations on the stimulation of individual physiologically identified cells having known output connections for a particular well-characterized behavior (Kennedy, 1969). Now that much more precise assessment of the roles of individual neurons is becoming a

reality (Pearson and Fournier, 1975, op. cit.; Selverston, 1976 Zucker, 1972 a,b and this Commentary), we can look forward to consigning the "command neuron" to its proper historical place along with the "engram" and the "center," in the development of concepts of neuronal organization of behavior. The demise of the older terminology in favor of more accurate explanations based on current information does not detract from the former's original heuristic value, nor should any sentimentality defer natural extinction.

The terminology of functional cell types in neuroethology is already complex and sometimes contradictory. Kupfermann and Weiss equate command with trigger. However, it is entirely possible that there are, in fact, at least two separate functional classes of cells that affect motor output, only one performing a trigger function in that, akin to the "release" mechanism of ethology, it initiates activity upon appropriate sensory input. The interneurons heretofore referred to as command neurons would then perhaps be the cells relaying the trigger signal to motor systems. However, Getting (1975) has raised questions regarding satisfaction of the necessity criterion by the cells that have been regarded as the best example of a neuronal trigger for behavior, the TGNs of the *Tritonia* escape response (Willows, 1976).

Another concept the authors relate to commands is "gating," which they argue, is a separate function, but they also tend to lump both concepts under the broader term modulation. The descending contralateral movement detector of the locust (Rowell, 1971) serves one particular type of modulatory function in arousal of motor activity. It is probably pretty safe to predict that many more functionally distinguishable mechanisms of behavioral output exist, and that they will need names of their own.

In several instances, apparently similar motor acts have become distinguishable when the neuronal networks responsible for them have been examined more closely. The rapid abdominal movements that occur in crayfish escape responses are now known to include at least three separate central networks that control the fast flexor muscles. Lateral and medial giant fibers differ in their receptive fields and in the segmental distribution of output connections (Larimer et al., 1971 op. cit.; Wine and Krasne, 1972). The cyclic bursting of flexor motor activity in swimming is for the most part independent of the giant fiber networks, and some evidence for a multineuronal smaller fiber system has been provided (Schrameck, 1970; Bowerman and Larimer, 1974, op. cit.). Additional complexities in the organization of fast flexor control are almost sure to exist.

The command idea developed in parallel with ideas of an endogenous motor score (Hoyle, 1964, op. cit.; Wilson, 1972). The motor score, or built-in pattern generator network, contains all of the necessary components for producing complex and precisely repeating output patterns such as the stomatogastric rhythms of the lobster and flight or ventilatory cycles of insects. However, the motor score is always subject to inhibitory and/or excitatory inputs from other parts of the nervous system by direct chemical or electrical inputs or by hormonal influence (Delong, 1971). Similar organization of segmental networks for output generation, interconnected to produce multisegmental coordination and controlled from descending inputs and feedback pathways, has been proposed for vertebrate motor systems (Miller et al., 1975; Grillner, 1975, op. cit.) on the basis of logical inference from a wide range of experimental evidence. Whether we ultimately choose to designate control inputs as "commands," "triggers," "gates," or something else will depend on analysis of their functional characteristics as well as our need for a taxonomic scheme for purposes of further discussion and improved understanding.

It would seem far more productive to pursue the approach of organizing the principles of neuronal interaction that produce emergent properties of discrete networks than to be overly concerned with definitions and nomenclature, except as necessary to refer to the particular cell. Although the command neuron concept is clearly in need of modification and perhaps substitution of more generally applicable vocabulary, it originally provided the basis of a useful paradigm for exploration of species-specific natural motor behaviors. The sort of rigorous testing against criteria proposed by Kupfermann and Weiss will be more usefully applicable to a systematic exploration of cell types and connections than to an attempt to clarify terminology.

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On the sufficiency of command neurons. The command neuron concept implies identifiable and independent elements in the nervous system that trigger relatively complex patterns of behavior that are themselves intrinsically organized. As such, it is an important departure from earlier, and inadequate, stimulus-response models of behavior. It also suggests links with ethological models of integration and offers some promise that traditionally disparate levels of analysis may be joined together for the common good. As Kupfermann and Weiss recognize, future progress will depend upon evaluation of this concept of command neuron (or command system) with both factual and conceptual rigor in terms of both neurobiology and behavior. It is in this spirit that I outline here my reactions to the authors' thoughtful review.

1. Trigger functions versus modulation. There are many instances in which it is difficult to draw this distinction precisely; stimuli and/or neural activity may not only "release" behavior, but also alter its course of expression in important ways (Hinde, 1970; Davis, 1976 op. cit. and this Commentary). And furthermore, our conclusions with respect to emphasis can depend upon our particular analytical perspective, such as the time scales we employ in our analyses (Fentress, 1976, 1977 Heiligenberg, 1976). Finally, the detailed characteristics of a given input in terms of its quality, strength, and timing can also alter its consequences. For example, behavioral work with vertebrates has shown that a given stimulus can act primarily to modulate (i.e., affect the "intensity" of) one or more classes of behavior at certain stimulus strengths and serve to trigger these or other classes of behavior at other (usually higher) stimulus strengths (Fentress, 1973, 1976a, 1977a). Studies by Rowell (1970) and Krasne (1975) on invertebrate neurobiology suggest similar considerations.

2. Context of control. Individual neural elements operate within a broader context, and changes in this context can alter their functional properties. For example, how do we define "command" in terms of its function in sexual behavior independently of the animal's hormonal state? If under the condition of inadequate hormonal background the firing of a single, previously defined, "command" cell fails to generate a copulatory response, does this imply that we are forced to change our definition of the cell, which at other times meets the "necessity and sufficiency" criteria proposed by the authors? Extended manipulations of the context of command cell activation could be of great value here. To take one further illustration, it might be interesting to see what happens to a command to copulate when the animal is actively engaged in

fighting. Ethologists have spent much effort in describing and analyzing the complex rules of relationship between different (functionally defined) classes of behavior, a trick that could be applied to advantage in future neurobiological studies (Davis, 1976; op. cit. and this Commentary; Fentress, 1976, 1977).

3. Measures of response profiles. It is an error to assume a unitary (i.e., all or none) nature of response production. To take an analogy, commands may in some sense act like a phonograph arm that, when dropped upon a record, "triggers" an intrinsically coded performance, but we should not forget such potentially independent qualities as turntable speed, volume control, and tonal setting (see point 1 above). To continue the analogy to music, are we examining behavior in terms of isolated notes ("acts"), themes, or melodies? At what level does the concept of command start, and stop? And how "fixed" must a behavioral act be, and from what descriptive perspective, to qualify? Kupfermann and Weiss begin to address such issues but the problems of description and interpretation of behavior go much further (Hinde, 1970; Golani, 1976).

4. Redundancy. While the authors raise this issue, it also depends upon the broader context of evaluation. For example, there is much evidence from human performance that a subpopulation of control elements may be adequate for the production of functionally integrated patterns of behavior under favorable conditions, but inadequate in times of stress, fatigue, and so forth. (Broadbent, 1971). Precisely when, therefore, are elements outside the immediate subpopulation investigated "redundant"?

5. Concepts as abstractions. This brings us back to the problem of evaluating command neurons (or systems) as if they occurred in a vacuum. The following pair of sentences by the authors represents the potential dilemma here: "Sufficiency, of course, does not mean that no other conditions are necessary for the generation of the response. Rather, an experimental result of this type indicates that activity of the neuron is capable of eliciting or creating all the other conditions needed for the occurrence of the response." If other conditions are created, do they become part of the command, consequences of the command, or peripheral noise/support? The point is that command as an abstraction will necessarily have its limits due to boundaries of function and causation that remain imperfectly defined. The authors deserve credit for helping us to recognize this; a necessary first step that may not in itself be sufficient.

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by C. A. Fowler and M. T. Turvey

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The concept of "command neurons" in explanations of behavior. We have chosen to focus on two issues that we take to be fundamental to an

evaluation of the concept of command neuron. In general form, the first issue bears on the kinds of concepts that can properly be invoked in an explanation of some phenomenon. The particular concern here is whether, under any circumstances, a neuron's functioning can be said to explain the control of an organism's behavior. The second, and closely cognate, issue concerns the way in which the control of behavior is invested in living systems.

Explanations of behavior. For Kupfermann and Weiss, the primary aim of neurobiology is to establish the causal determinants of behavior; and their theoretical efforts are directed at formulating a set of criteria for deciding whether a given individual neuron, or a small group of them, is indeed a causal determinant of some behavior of an organism.

We believe, however, that it is a conceptual error to ascribe to a neuron's functioning causal responsibility for the functioning of an animal. While it is true that neural activity accompanies and enables psychological functions, it cannot, in itself, have a causal role with respect to them.

By way of clarification, let us contrast two kinds of explanations for some behavior, a "common-sense" explanation and a physiological explanation or in Dennett's (1971, and this issue) terms, an explanation from an intentional stance and an explanation from a physical stance. A common-sense explanation for why an animal executes a given act invokes aspects of the animal's "design" in reference to relevant properties of its current environmental situation. After Gibson (1977), we can describe an animal's environmental situation as a set of "affordances," where an affordance is a unique combination of properties of surfaces and substance taken with reference to a particular activity in that animal's, or species of animal's, repertoire. A common-sense explanation, therefore, can be said to describe the animals species-specific intents and needs and how the animal's behavior addresses those intents and needs by exploiting affordances (Gibson, 1977). In contrast, a physiological accounting of the same behavior ideally describes the neural activity that consistently precedes the behavior.

Clearly, a perceived affordance is a different rationale for behavior than that which Kupfermann and Weiss have in mind when they ascribe causal responsibility to "command neurons." Implicit in their discussion is a distinction between distal environmental provocations or invitations to behavior and proximal neural causes. A schematic representation of that view is approximated in Table 1.

Table 1 depicts a combination and mixture of two levels of analysis of the animal-environment relation, a psychological level and a physiological level. The first two terms and the last term in the figure are psychological terms; they refer to properties, information about properties, and activity, respectively, that are significant to an animal as a coherent system – but are not significant to the animal's individual neurons. (This is not to say that the light as structured by an environment conveys no information that is of significance to neurons. It is only to say that the grain-size of information relevant to individual neurons is not represented in the depicted schematization of the control of behavior.) In contrast, the third and fourth terms are physiological terms; they refer to the activity of a number of fine-grained components, that is, some of the animal's neurons.

From the observational perspective of the detailed level of analysis represented by terms 3 and 4 of Table 1, the concept of the animal as a coherent system is absent (in the sense that, for example, the concept of a leaf as a coherent entity is absent in the view of it given through a microscope), as is the behavioral significance of the environment. In short, the view represented in Table 1 implies that the psychological realm of existence and functioning is lost at an earlier stage and is regained at a later stage in a causal chain of events leading from environmental stimulation to behavioral response.

Table 1. A causal chain of events leading from environmental stimulation to behavior

environmental properties relevant to current needs of animal
information about those properties conveyed by some medium (e.g., light)
neural activity in response to input
neural activity precipitating behavior
behavior

Note: length of time increases from top to bottom of table

Table 2. A set of contemporaneous events at two levels of analysis characterizing the event of an animal acting in reference to what it sees

Psychological realm	Medium
affordances ^a	fundamentally physical particles governed by the laws of motion
affordance-specific invariants	light rays distinguished on the dimensions of wavelength intensity
perceived affordances and embodied dispositions to act	activity in individual neurons
behavior	muscle contractions etc

^aEnvironmental properties relevant to animal's needs

This is the conceptual error to which we referred earlier. To our way of thinking, a now prudent perspective is that neither translation nor causal transaction takes place between levels of analysis. Table 2 illustrates this conception.

We can clarify our view by first considering a tiered description of the light to an animal's eye (the second term of Table 2). The ambient (structured) light that reflects off environmental objects or events can be described in a maximally detailed way by cataloging its component photons. A somewhat less detailed description selects rays of light as its descriptive primitives and specifies their individual wavelengths and intensities. Both of these descriptions are environment- or source-neutral because they fail to capture the patterning across the rays of light introduced when light contacts environmental events. A third description is more abstract than these and catalogs exactly that source-related patterning across rays of light. By hypothesis, this patterning is specific to its source and hence specifies it to a sensitive observer. A description of the light at this level of abstraction is of affordance-specific invariants and is environment-related.

These three alternative descriptions of the light, the first two in the physical realm and the third having psychological significance, are contemporaneous: that is, the light does not first consist of photons, then of light rays, and finally of patterned light rays. Given their contemporaneity, there can be no causal relationships among them. Furthermore, and importantly, the descriptions are not equivalent or redundant: only the most abstract of them specifies the environmental properties that are significant to an animal.

We claim that an analogous story can be told in reference to an animal's physiology when, for example, it is stimulated by structured light. Under these conditions (term 3 of Figure 2), neural functioning can be given a tiered description. The levels of functioning that are captured in each description are contemporaneous, nonredundant, and are noncausally related. Only an abstract description that captures the functioning of populations of neurons, as that functioning has been constrained by the structure in the stimulating light, also captures the message in the light about environmental properties that are significant to an animal. And we believe only that descriptive level can properly be invoked in an explanation of an animal's behavior (see also Fitch & Turvey, in press; Fowler & Turvey, in press).

The investment of control in a living system. Let us consider our second objection to the term command and to the concept of command neuron. In a complex living system, a physical component may be invested with a message function (i.e., with a function outside the ordinary repertoire of components of that type and a function whose significance is biological or psychological) by virtue of its organizational location in the system and not by virtue of its physical properties, which may well be ordinary. That is to say, the extraordinary functional role does not inhere in the component as such but arises from the special organization among the set of components that defines the system as a particular kind of living system. On this understanding, responsibility for the function cannot correctly be ascribed to the component, but only to the component as it participates in a superordinate organization (Weiss, 1969; 1971). In short, the function is not a property *sui generis*.

Pattee (1973) expresses this argument in reference to molecules that appear to execute command functions: "At the lower level of the gene, the authority relation of the hierarchy is often popularly expressed by referring to DNA as the 'master molecule' of life, but here again we must emphasize that

there is no intrinsic chemical property of DNA that allows it to hold this office. It is the integrated collection of "ordinary" molecules we call the cell that endows DNA with this authority."

We pursue this argument through a consideration of different kinds of organization. To claim that a given neuron commands other neurons is to ascribe to an address-specific (individualized) style of control, of which a pure hierarchy is the premier embodiment. A pure hierarchy is characterized as follows: centralization of control (an executive node); immutability of dominance relations between nodes; one function per node; one node type per function; and linear transitivity of dominance relations (i.e., if node A dominates node B, and B dominates C, then A dominates C, cf. Turvey and Shaw, 1977; Turvey, Shaw, & Mace, in press).

The notion of command, however, is much less appropriate to a pure heterarchy, characterized as follows: devolution of control—nodes participate in decision making; mutability of dominance relations: several functions per node; several node types per function; and circular transitivity of dominance relations (A dominates B, B dominates C, C dominates A, see Turvey, Shaw, & Mace, in press). There is reason to argue that the style of control manifest in a heterarchy may be described as address-approximate (equivalence class) control. Greene (1971, 1972) has suggested that control functions relating nodes in a heterarchy can rarely be specified more precisely than to place them within fairly broad classes of possible realizations. Consequently, it is assumed that various kinds of equivalence classes comprise the systematically behaving units of information in which components of the system communicate. We can imagine, therefore, a node specifying an equivalence class of functions computable by an equivalence class of nodes. Since the particular function computed and the particular node computing it are not specified, the control is address-approximate.

There is a third style of control that, following a suggestion of Tsetlin's (1973), might be designated addressless (dual complementation) control; its embodiment is an organization that can be termed a coalition (Turvey, Shaw, & Mace, in press). Simply defined, the subsystems of a coalition are so structured that for any one subsystem the remainder provide the requisite context of constraint. In a minimal coalition of two subsystems, the degrees of freedom of one are dissipated by the degrees of constraint of the other; one subsystem may be considered the dual of the other and the relation between them a duality. The concept of coalition expresses a principle of mutual compatibility that recognizes the synergy among systems that have coevolved and have been codesigned: Those (natural) systems coexist that are mutually compatible to do so (Shaw & McIntyre, 1974; Turvey & Shaw, in press). Crudely, the idea is that controlled behavior arises from the mutual fitting together of simultaneously changing subsystems (Fitch & Turvey, in press). This characterization seems to us to capture the styles of control in a living system that Pattee describes in the quoted passage (and attributes to a hierarchy), and for which Weiss has also argued (1969, 1971).

The point we wish to make, and with which we conclude, is this: The term "command" is a substitute for the analysis of complex collective behavior; neurons, as fine grained components of a complex organization, relate in some fashion, but they do not command.

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Vector coding and command fibres. The notion of a single command fibre controlling a behaviour is dimensionally unsound for many behaviours. Consider the hypothetical example given in the article by Kupfermann and Weiss: "Tactile stimulation of a given receptive field produces a withdrawal response of a certain intensity with a given latency. In this example, the receptive field, response strength and response latency define the behavior under consideration." This statement is not complete, because withdrawal implies a movement, and movement parameters are vectors having direction as well as magnitude. The behaviour must be directionally defined, for example, tactile stimulation in direction x of a given receptive field produces a withdrawal response of a certain intensity with a given latency in direction y (x and y being directions in three dimensions). Now an infinite number of command fibres is required to produce withdrawal in any direction because a single nerve cell must be considered one dimensional, coding only magnitude. When a behavioural output is a vector, we require some means of fractionating the command into "one-dimensional" pathways, equivalent to splitting a vector into components (at minimum, three components requiring a command set of three nonspiking or spontaneously spiking command elements coding orthogonal components of force or torque are necessary to code a behaviour in three dimensions). If the cells produce spikes and are normally silent, then the minimum number of command cells required is six, defining positive and negative directions for three orthogonal planes. Directional information is coded by the relative activity in three (or six) parallel pathways. Complete behaviours controlled by single command cells must be recognised as special cases occurring within defined coordinates where movement (behaviour) is limited to one dimension, for example, withdrawal into a shell. How are real command fibres organized to code vector components? This is known for crab equilibrium interneurons that satisfy command fibre criteria (Fraser, 1974, 1975a, b; Fraser and Sandeman, 1975).

These equilibrium interneurons receive input from thread hairs in the statocyst that are the receptors in a well-defined orthogonal semicircular canal system (Sandeman and Okajima, 1972). The interneurons can be separated on the basis of their directional sensitivity to angular acceleration (see Fraser, 1974, 1975a; Fraser and Sandeman, 1975) because each interneurone is optimally excited by one direction of fluid displacement in the plane of one semicircular canal. In addition to statocyst input, the cells receive input from leg proprioceptors (reinforcing statocyst input for a rotation of the body of the crab relative to the legs) and a central input that can be abolished by cutting the optic tract (Fraser, 1975b). The central input is manifest as a maintained high frequency train of action potentials that precedes and outlasts overt leg movements. The input pathways and output leg movements are best seen in giant fibre 5, which is a command fibre for the righting reflex— involving cyclical beating of both fifth legs (more strongly ipsilateral to fibre 5 axon) and rhythmic movements of the other legs (Fraser, 1975b). This is best considered as a directional antagonist to the swimming reflex, which is also stimulated via equilibrium interneurons. Although it is hard to demonstrate directly, all observations are consistent with

the view that the particular motor pattern evoked by each equilibrium interneurone generates torque (in a uniform medium and over a period of time) sufficient to counteract the torque producing the angular acceleration that fired the cell in the first place. The equilibrium interneurons hence fit into negative feedback loops, each responding to and counteracting one direction of torque in one of three orthogonal planes. There is evidence that these equilibrium interneurons drive swimming and the righting reflex and participate in walking and the rearing reflex (Fraser, in preparation). The cells are the command points for compensatory reflexes, yet, during central driving of the behaviour, serve only to pass on a higher command from the optic lobes (which in crustacea contain the hemieilipsoid bodies equivalent to the corpora pedunculata of insects), and so the central decision to fire a given equilibrium cell must come from the optic lobes. Logically the decision channels (which have not been shown to be single cells) for the separate equilibrium cells must be separate to code direction, and this separation must represent a fundamental division of the nervous system (into six in the case of the crab).

Consideration of this system raises a query regarding other arthropod command fibres. Could all described arthropod command fibres fit into directionally orthogonal systems similar to crab equilibrium interneurons, but coding different combinations of sensory modality? This question cannot be answered, because directionality of interneurons has seldom been measured, and, indeed, directionality is often hard to measure where the input is distributed (thus directionality of crab equilibrium cells could not have been easily measured in terms of leg proprioceptor input), and directionality functions may be altered by experimental conditions (Fraser, 1977b). However, statolith and visual systems that are known to drive behavior in the crab must at least form orthogonal command sets. There are eight large equilibrium interneurons in the crab. If there are six statolith and six visual cells in similar negative feedback loops, then we can account for twenty command cells and it is not difficult to see that all command cells could be included. Escape tail flips in crayfish are oriented behaviours, demanding that we include crayfish giant fibres. Furthermore, the recent finding that cockroach cerci (which form an orthogonal system with regard to the directional sensitivity of filiform hairs) function as equilibrium organs during flight, allows us to consider cockroach cercal interneurons as being organized into an orthogonal command system (Fraser, 1977a).

In conclusion, the crab equilibrium system shows how a command fibre group can be organized to code the direction as well as the magnitude of behavioural output. The cells are central in negative feedback loops, but act simply as relays for commands (not necessarily via single cells) from higher centres. It is suggested that this form of organization is widespread in arthropods.

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Command neurons or central program controlling system? During the last several decades it has been demonstrated that both primitive and more elaborate nervous systems can elicit certain action patterns or behaviors us-

ing very simple signals, analogous to "push button" control (Wiersma, 1952 *op. cit.* and this Commentary; Larimer, 1976, and this Commentary). In the tailflip-escape response (in crustaceans), one or a few neurons may be directly connected to the appropriate motoneurons, so that whenever the former are activated, a tailflip in the desired direction will result (different cells being activated when responses in different directions are required). In such cases, it is appropriate to trigger the behavior by simultaneously activating all muscles taking part in the behavior: in other cases, it may be necessary to trigger a central program controlling a whole sequence of events, as in the vertebrate "swallowing reflex." Furthermore, in still other cases, the fibers may drive the network to generate a repetitive behavior such as locomotion or mastication.

The object of this commentary is to provide a critique of the term "command neuron," specifically in relation to the accompanying article by Kupfermann and Weiss. I should first like to state, however, that it would be useful to have one term for neurons (or groups of neurons), whose function is to elicit an inherited behavior governed by a "central program" (fixed action pattern) or at least a significant part of this behavior, such as the walking movements of one limb. Such a "functional term" should be applicable regardless of how the neurons activate the network. In seeking such a "functional" term, designating the control of a variety of inherited behaviors in the entire animal kingdom, one would expect the following: (a) Mechanisms of operation may vary. (b) In some cases the division between command element and pattern generator will be clear-cut, in other cases it will be ambiguous; it is presumably wiser to accept this ambiguity rather than to spend time trying to force a neuron into one category or another. (c) In some animals, one or a few fibers may be sufficient to control the behavior while in others a whole group of fibers may be required; several alternative systems with the same function may even exist. (d) In many instances the control system may be a series of neurons that relay a "brain" command to a segmental central program. In different relays there occurs an interaction with other inputs (e.g., cutaneous) that could block or facilitate the descending "command." (e) Each control system within each animal will presumably be unique and contain features unshared with other systems.

This entire "functional class of neurons" has been called "command neurons" by some authors, including myself (1976). Wiersma, working with some particular examples, developed the concept that one group of neurons could be used to elicit activity in a "central program." Other workers have preferred to use Wiersma's term in a more limited way. The most extreme case is represented by Kupfermann and Weiss, for whom a neuron must not only be necessary for the behavior to be elicited but also sufficient. With such a narrow definition, the term "command neuron" can be used only very occasionally in a few rare systems. No doubt this term is very controversial and several invertebrate workers prefer to use different terms in connection with different central signals, such as "trigger neurons," "command driver neurons," and so forth. In the vertebrate literature, the term "command" has been used in a variety of different ways depending on the field of interest, and only a limited number of vertebrate workers would connect "command system" with a system controlling central pattern generators.

In view of the controversy surrounding the term "command neuron system," and what it can be taken to mean, I think it may be useful, while keeping the general concept of Wiersma, to introduce a new, purely descriptive term, such as central program controlling systems ("CPC-systems"). This would include any type of neuron whose main function is to elicit simple or complex behaviors by activating a central program (central pattern generator). Such a system can initiate activity and, in some instances, act to maintain the activity (as, presumably, in locomotion). Furthermore, the degree of activation of the control system can, for example, decide the degree of activation of different muscle groups in locomotion and the related frequency of step cycles.

Probably many borderline cases will emerge in which neurons will perhaps control only one muscle taking part in a complex behavior. In my opinion, such neurons should rather be regarded as part of the pattern generator. On the other hand, neurons that control a more substantial part of a behavior, such as walking movements in one particular limb (but not the ninety-nine others), should be accepted as "CPC-systems." Besides such neurons, there are other inputs that will influence the activity of certain pattern generators. One consists of peripheral feedback signals that may, for example, influence the step cycle of both vertebrates and invertebrates (e.g., Pearson and Duysens, 1976). In the crustacean swimmeret system there has been described another class of neurons (coordinating neurons) that coor-

dinate simultaneously active central pattern generators in the different segments (Stein, 1976 and this Commentary). These neurons do of course profoundly influence the activity of the pattern generators. In certain simple systems, motoneurons may be part of the pattern generator itself; in other systems, such as the tailflip response, the pattern generator and Wiersma's "push button" are contained within the same neuron.

It should be recognized that to date only in a few cases do we know the exact mechanism of control of central programs and the precise activity of the CPC neurons when the behavior is naturally elicited. The term "CPC-system" can thus be used regardless of how such a system exerts its control on the central program. Along the line of thinking of Kupfermann and Weiss, it seems advisable to call a neuronal system that has been shown by only electrical stimulation to elicit a certain behavior a "putative" CPC-system. Only when it has, in addition, been shown that the particular system is normally used when eliciting the behavior may the system be called a CPC-system without other qualifiers. In vertebrates, and presumably invertebrates, it may well be possible that two different anatomical systems can be used to elicit the behavior under different conditions, that is, either system is sufficient but not necessary (see also above).

When considering "descending" motor control, it should be recognized that this is by no means exclusively exerted by CPC-systems. It may be useful to define in a conceptual rather than an anatomical way four types of "descending" systems (see Figure 1). Needless to say, such a gross division will be somewhat arbitrary.

(1) CPC-systems

(2) Corrective systems. Consider walking, in which the actual behavior may be driven by a CPC-system. In each step, movements must be adapted to the environment, and the foot positioned in the appropriate place. Such rapid adaptations are achieved by small correction signals superimposed on ordinary movements. In almost any type of movement, whether learned or inherited, there is a need for rapid correction in connection with basic or associated movements or postural adjustments.

(3) Output systems. Learned behaviors, such as writing, with very "complex central programs" located in higher nervous structures may utilize descending neurons for activating the appropriate motoneurons. Some pyramidal, rubro-, or reticulospinal neurons would in this case be on the output side from the generator just mediating the signals. In tracking and exploratory movements, and ballistic movements to certain targets, it can be assumed that descending neurons are used in the same way. (The borderline with (2) is here very arbitrary.)

(4) Reflex gain controlling systems. A number of different descending systems control the effectiveness of certain reflexes, such as the "flexor reflex" by controlling the interneuronal transmission (Lundberg, 1966).

CPC-systems have been discussed above primarily in relation to inherited movement patterns. However, it would perhaps be useful to consider the possibility that the same type of control may be used to recruit learned movements, say the program for writing a small "a," located somewhere in the

central nervous system; later in the course of the process, the size of the "a" will be specified as well as exactly which muscles should be used, and so forth. It may be assumed that the fast descending fibers contribute to activation of the specified muscles at the appropriate time, thereby acting as a mediating system in this case.

In conclusion: I suggest that a new general term be introduced: "central program controlling system." Within this class of neurons a variety of subgroups can then be accurately defined, depending on the exact way in which they exert their control over the pattern generators. Current difficulties with the term "command neurons" may stem from conflicting needs for both a general term that can be used to express part of Wiersma's "push button control" concept and for very well-defined terms related to how the actual control is exerted.

ACKNOWLEDGMENTS

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Command fibers: *only* strategic points in neuronal communication systems. Commands are initiated, transmitted, processed, and carried out. Available evidence indicates that nervous systems are organized hierarchically and that commands are processed in this way. Orders are formulated by higher nervous centers (i.e., brain). The term "command neuron" would be most usefully applied here, although we have no understanding of decision-making processes and hence no idea as to how a command is evolved. The transmission of an order is accomplished by a single neurite or bundle of nerve fibers that usually links the higher nervous center to lower order nervous systems. The order processing circuit can be one or more interneuronal system(s), motoneurons, or various motoneurons that are interconnected with pattern generation capabilities. The motor act is accomplished by the muscles in cooperation with their scleroelements, which also contribute to the performance of a command by their specific arrangements and properties.

The "command neuron concept" now seeks to connect the activity in a single fiber or in a neuronal tract directly to a specific behavioral act. This is helpful in analyzing behavior and its neuronal background since defined behavioral acts can be repeatedly elicited by stimulation of certain fibers. Exclusion of complicating sensory inputs as well as of the central nervous system or parts of it allows a more simple approach to an understanding of aspects of neural processing in the remainder of the system. When considering whole animal preparations, the "command neuron concept" can lead to pitfalls due to uncontrolled variables (see Hoyle's precommentary). Recently, however, preparations have been introduced (i.e., simple nervous systems) in which analysis of entities necessary for setting up a behavioral act appears to be feasible. If we know the basic output pattern from a neuronal subsystem for a certain behavior and are able to find input fibers

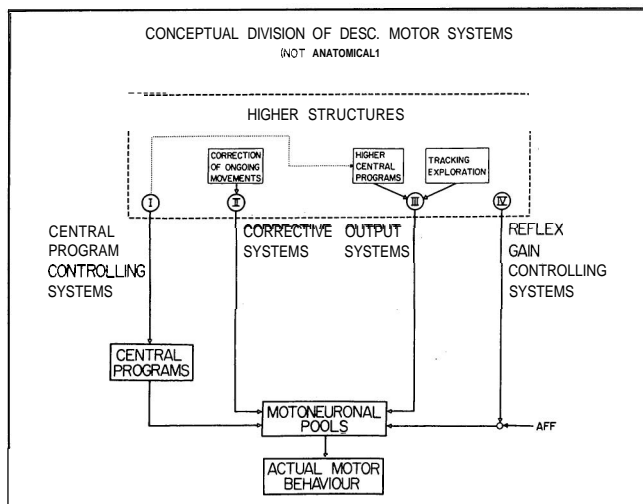


Figure 1 (Grillner). Schematic representation of the different types of descending motor control.

that can initiate or modulate this pattern, it is possible to analyze the pattern of connections of this "command input" as well as properties of the subordinate neuronal subsystem in great detail (i.e., in terms of neuronal wiring, electrical, biochemical, and anatomical aspects).

A danger of the conceptualization of the term "command neuron" is that it can result in an overestimation of the function of these neurons. Command fibers occupy strategically important positions in the neuronal communication system by virtue of their central and peripheral connections, but are otherwise ordinary nerve fibers.

The originators of the term "command fibers" are accused of not having defined it strictly. It appears, however, that they did not intend to do so, and this is presumably one of the reasons for its success. This does not mean that it should never be reconsidered. In any event, it would be more useful to consider "command fibers" as a tool rather than an explanation.

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Nouns, neurons, and parallel pathways. The commentary by Hoyle is a useful record of how the term "command neuron" came into use, but now the usage is so thoroughly embedded that history will soon become History. Such items should be read from time to time by the novices so that they understand the development of their subject, and by old hands who are reminded of the perspectives of others. No harm in that, and something may come of it in the mind of a revolutionary. My own comments on Kupfermann and Weiss are concerned with quite different aspects that relate to the way analysis is carried out.

To start with, a terminology is not forged in theoretical papers or discussions of models, but is generated by the acts of discovery that force the discoverer to use language in ways never used before. Many of the basic terms of experimental psychology were introduced by Pavlov in his papers describing new experiments. Later, of course, there is much purification, distillation, and labeling when the ideas have fermented a little in other minds. Even then, there is no reason to suppose that single nouns (or adjectives) can ever describe adequately the common identifying features of an open-ended class of neurons. Any term would be unsatisfactory. Moreover, new kinds of neuronal interaction repeatedly enter the discussion.

The use of terms, however, gives the clue as to how we analyze the nervous system. In the first place, the way the observations are gathered governs the kind of result. In the case in question, command neurons are discovered and described by recording and stimulating with a single channel of equipment. This leads to the discovery here and there of clear effects attributable to a single neuron. But that is not necessarily the way the rest of the neurons and the muscle cells look at the neuronal activity. They respond to all simultaneous ongoing activity, most of which is not seen by our single electrode. Therefore it is easy to get a partial picture, impute all the response to a single neuron, and systematize the simplification with a simple terminology. Let me illustrate an alternative situation from my own experience with the insect compound eye.

In the insect eye and optic lobe there are thousands of neurons in parallel circuits. They never can be identical because every member of each successive rank looks in a different direction. Yet there are situations in which a very small number of receptors, backed by one or two second-order neurons in parallel, are able to elicit a response. An example is the initiation of an orienting response to a small movement of a point source in the visual field. We have here a situation in which the driving neurons at one particular time could fit the behavioral and also the operational definition of a command neuron, but plainly all the neurons of the array would then have this status. The same condition must hold in many conditions among central neurons in the vertebrate, and in forms like medusae, with great numbers of neurons in parallel, which is perhaps why the term "command neuron" is restricted to the arthropod and mollusk literature. Only the economy of neurons of nervous systems in some phyla makes the term worth preserving at all for some clear-cut cases.

In the second place, in all our analyses we seek the interactions and particularly the functions of components. The interactions are discovered by our recording instruments and it is most important to stress that this is not the same observation point as that occupied by the neurons lower down the line. We have a hard task to determine the function when our point of observation,

the electrode, does not necessarily abstract the important part of the neuron's activity that acts on other cells. We assume that neurons have functions that can be assigned to them as a result of analysis. The basis for this can be traced to the idea that the whole performance and connections of a neuron, both input and output, are a product of natural selection, and we might define the function by a circular argument as that on which selection acts, because it is only the normal neuronal activity that eventually appears in behavior that is acted on by selection. So we have to know the normal behavior before we can give the neuron a name related to function, or even progressively work out its action in more and more detail. Command neurons are simple cases that generate behavior rather obviously.

Expecting a neuron to have a definite function implies that the neuron can be identified and returned to again and again in different animals. The identification is essential for the analysis to this level, which has proved to be possible in only those systems limited to a few neurons. Otherwise, the result is only statistical, thus precluding much analysis at the level of individual cell interactions. There is not an a priori reason why all neurons, even of an insect, should be individually identifiable, and the ultimate detail can be described only statistically at some level near that of the single cell.

The test criteria given by Kupfermann and Weiss are all very well as an elementary outline on paper, but they break down in practice for the simple reason that there are many neurons in parallel. In such a system, what may actually happen is that we first establish the response pattern of a neuron during a well-executed behavior pattern. On extensive exploration, however, we find that numerous neurons go through a family of well-defined response patterns. We remove neurons temporarily, one by one, by hyperpolarization, or permanently, by killing them (assuming no side-effects of these treatments), and find that the behavior pattern always persists, though it may be modified. We then fire single neurons in the normal pattern and find that many neurons, or groups of them, evoke the response. With one electrode, the evidence for command fibers is inconclusive. This is the actual situation in many parts of the arthropod nervous system, and is almost universal in vertebrates.

Kupfermann and Weiss outline a similar example where neurons in a network with many lateral interactions can never be individually identified as command neurons, but they suggest that at any one time one of them is presumably controlling the others in a way that fits the definition. The point is that they present the model in their mind. Then, in their summary, they introduce the above tests, which in fact cannot provide the positive conclusion by ruling out other models. I speak from experience of insect nervous systems: the clear-cut command fibers of arthropods are from crustacean preparations analyzed with a single electrode, and it is possible, on the evidence, that Wiersma and others oversimplified the situation in Crustacea with an erroneous interpretation that the command neurons were unique and that they were able to evoke reasonably normal behavior when active alone.

In insects, we have situations where obvious large neurons such as the giant fibers of cockroaches make connections indirectly with motoneurons, but the part they play in normal behavior has proved peculiarly difficult to determine. Because these look like command fibers, a great many students have jumped to the conclusion that each giant fiber is a command neuron in the cockroach escape response. The situation is still not clear; maybe a thin fiber in parallel with them really controls the metathoracic legs; maybe many long spiking interneurons acting together generate the appropriate configuration of depolarization in a network of nonspiking interneurons, which then are able to drive the motoneurons of the legs and elsewhere. In such a situation, the idea of a command fiber really does lay a false trail for the experimenter, who would be better off if he started with a multielectrode array. At the other extreme, where natural selection has conveniently concentrated the function into one neuron, the faith that command fibers exist may lead the experimenter to a correct conclusion more quickly than would have happened if he had not had the preconceived idea. Excuse me if I talk, not in terms of models or of definitions, but from the outlook of the man engaged in the analysis, trying to make sense of the partial picture that the techniques provide.

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The command neurone concept in mammalian neurophysiology. The command neurone concept originated and developed in studies of

Invertebrates. In higher animals, command functions for behaviour are more likely to exist in systems rather than be invested in single cells. This in itself leads to difficulties in devising criteria to establish a command function, and I wish to consider the usefulness of the concept in mammalian neurophysiology.

The best documented examples of command neurones are giant fibres of crustacea, which coordinate escape responses. Adaptive withdrawal of a limb can be elicited in spinal mammals but is usually classified as reflex. An arbitrary definition of the types of behaviour characteristically associated with command neurones is thus necessary. However, difficulties may still arise since in the spinal cord reflexes and voluntary acts share much of their neuronal circuitry.

Grillner (1976 and this Commentary) has discussed the similarities between command neurones that excite segmental networks responsible for swimmeret beating in crayfish and a system implicated in activating spinal machinery for locomotion in mammals. Noradrenalin released by neurones projecting to the spinal cord from the brainstem can initiate locomotion in the cat. There is simultaneous activation of rhythm generators and γ motoneurones, and also changes in reflex transmission. The activity during normal locomotion is not documented and therefore it is not known whether activation of this system alone to a comparable degree would be sufficient to induce locomotion. Nor have pharmacological blocking experiments yet succeeded in demonstrating that the system is necessary. Anatomically distinct but parallel command systems probably exist. Nevertheless, although neither of the Kupfermann and Weiss criteria of sufficiency and necessity are fulfilled, the command system concept can be provisionally applied.

In crayfish, there are command neurones that, when stimulated, activate groups of motoneurones and lead to characteristic postures of the abdomen. In mammals, single axons descending from higher centres could branch to activate groups of motoneurones. That coactivation of finger flexor, wrist extensor, and elbow fixator muscles during grasping in the primate might be 'hard wired' in just this way was considered explicitly by Beevor (1904). There is little experimental evidence, but single pyramidal cells in monkey motor cortex may directly excite motoneurones of several related forelimb muscles (Fetz et al., 1976). Such cells could constitute command neurones for elemental movements, but their actions are likely to be contingent upon activity in other systems since pyramidal tract neurones may fire at high frequency during sleep without producing movements (Evarts, 1964). A second example of contingency concerns the vestibulospinal tract in the cat, which disynaptically excites extensor motoneurones through the same interneurone as is employed by the crossed extensor reflex (this is in addition to a direct monosynaptic pathway). In cats, pathways projecting from higher motor centres such as cortex and red nucleus do not terminate on motoneurones. Instead, there is widespread convergence from several systems and sensory input on to propriospinal neurones that in turn synapse with motoneurones (Illert et al., 1977). Here command functions may not be localised in single neurones or even in anatomically distinct pathways, but, rather, shared between parallel systems. Should then finer localisation of command functions be sought at higher levels in a putatively hierarchical motor system?

As may be anticipated from the above references to contingency and to sharing of command functions in systems, there are considerable difficulties in establishing a causal relation between activity of a neurone in the higher central nervous system and motor behaviour. The usual experimental approach is to record from unanaesthetised animals and seek neurones whose firing is correlated with movement. Indirect evidence is then adduced to support a causal relation. It may be noted that this is the reverse of the usual direction of progress in invertebrate studies where command neurones are operationally defined by the effects of stimulation and evidence is then sought for a role in normal behaviour. An example of this approach is a study of parietal cortex in the monkey (Mountcastle et al., 1975 *op. cit.*; Lynch et al., 1977; see also Lynch, this Commentary). Some neurones were recorded that fired only when the monkey made a goal-directed arm movement, others fired during visual fixation or tracking of desirable objects. The hypothesis was advanced that these cells constitute high level command neurones for arm projection or visual attention. The temporal correlation of activity before and during the behaviour is clear, but can a causal relation be established? One alternative hypothesis would be that these are sensory neurones of high order with no direct motor role but whose response is conditional upon a particular motivational state that also predisposes to the behaviour (cf. lateral hypothalamic neurones: Rolls et al., 1976). Another possibility is that the neurones are activated by efference copy from a motor area. Direct sur-

face stimulation of parietal lobes occasionally induces reaching movements or deviation of the eyes, but this is hardly a satisfactory way of activating one set of neurones intermingled with others and does not constitute a test of sufficiency. After lesions of parietal lobes, monkeys show a diminished capacity for purposive limb movements in contralateral extrapersonal space (Denny-Brown et al., 1975). In its simplest form a similar syndrome occurs in man. These observations are consistent with the command hypothesis, but loss of a movement following a local lesion does not necessarily indicate direct involvement of that part of brain (small lesions may induce a generalised akinetic mutism). There is clearly no simple and unambiguous way to demonstrate the causal relationship implied by the application of the command concept to these neurones, but the hypothesis could be greatly strengthened by following projections from parietal lobes to other areas with more direct motor outputs [See Roland et al., this issue].

In conclusion, at the lowest level in mammalian motor systems, where an operational definition of command systems might be possible, the presence of parallel pathways suggests that the systems used in behaviour are unlikely to be anatomically discrete. The neurophysiologist is then driven to seek localised command functions at higher levels where evidence for a causal relationship with behaviour is technically difficult to provide. The command concept implies localisation of function and a hierarchical organisation of the nervous system for which there is as yet little evidence. It may therefore be premature or misleading to apply this concept to mammalian neurones, and one is tempted to adapt a quotation from Trotter (see Walshe, 1957): 'desired classifications are apt to be mistaken for physiological principles'.

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Is "command" at the top of the hierarchy? We would like to avoid a restrictive definition of the term "command neuron" until more examples provide information about the types of inputs that impinge upon interneurons governing motor programs and the types of synaptic interactions such neurons have with the motor programs that they influence. The details of input-output relationships could prove to be all-important for classifying command interneurons.

At the present time we need to provide constructive guidelines that will promote the development of a classificatory scheme for neurons in the context of behavior. There have been numerous informal attempts to pigeon-hole the command neuron concept. In addition to the discussions at the symposia referred to by Kupfermann and Weiss, there have been other entire

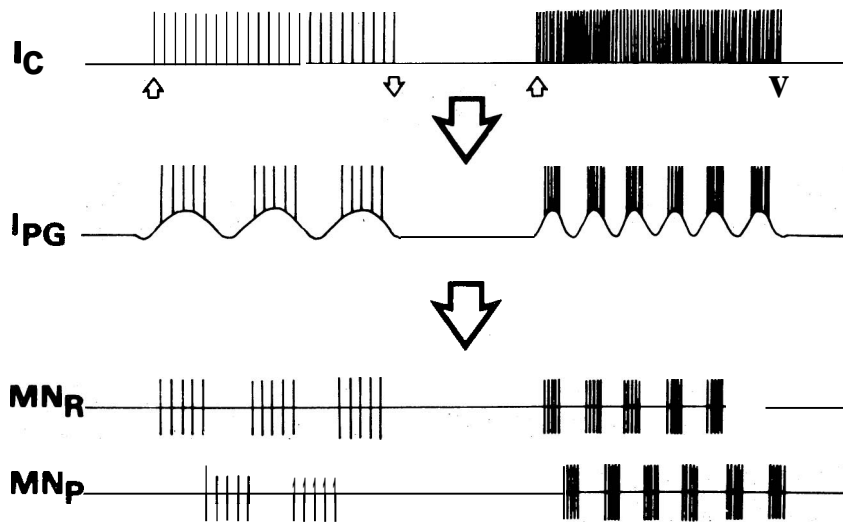


Figure 1 (Kater and Granzow). A hypothetical hierarchical organization of neurons that is apparently common for various cyclically recurring behaviors. Each trace represents the type of activity occurring in the neuron(s) of that particular tier in the hierarchy, with the large arrows in-

dicating the direction of information flow in the system. The small arrows on the top trace indicate the injection of intracellular depolarizing current into I_c , I_{PG} = Interneuron(s), command, I_{PG} = Interneuron(s), pattern generating; MN_p = Motoneuron(s), protractor.

symposium sessions devoted to this topic. One of the more constructive of these was held in 1973 at the Winter Conference for Brain Research at Vail Colorado. This session was chaired by Donald Maynard and addressed two questions: (1) Should there be an attempt at restrictively defining the notion of command interneuron? and (2) If so, what would such a definition entail? The proceedings of this symposium were heated. Though published only in abstract form, those who attended came away with concrete ideas for the use of the command concept in directing research. A most influential idea, for us, was the definition, which we attribute to Don Kennedy, stipulating that a command interneuron functions in a "permissive but not instructive" fashion. That is, activity of the command interneuron governs the read-out of a motor program but does not itself determine the quality (i.e., patterning) of the motor program's content.

The accompanying figure illustrates a set of relationships among neuronal elements that is characteristic of a large variety of actual behaviors. At the lowest level there is the alternating cyclical bursting of antagonistic motoneurons. Few of us would care to call these command elements and we shall not belabor this point. At the next level, for many cyclically recurring behaviors, there exists a stratum of pattern-generating neurons. These directly drive the motoneurons and determine their activity patterns, that is, their information content is instructive. Above the pattern generators is a level of neurons that we have come to regard as command interneurons. The rate of command interneuron firing may ultimately influence the rate of the overall cyclical motor output but not the temporal interrelationships of the motoneurons' activity. Consideration of these neuronal relationships allows us to examine the implications of the guidelines we here propose for distinguishing between instructive and permissive classes of interneurons. It is the latter class to which we would like to assign command interneurons. This guideline, while significantly looser than the definition proposed by Kupfermann and Weiss, has the advantage of not restricting us to a set of proofs that may be impossible for the majority of experimental preparations available.

The reasons for refraining from a definition of command interneuron until more data are available can be emphasized more directly by a consideration of the concrete example of the cyberchρον neurons – the pattern generating core for the feeding behavior in the snail *Helisoma*. The cyberchrons are a network of electrically coupled interneurons contained in the buccal ganglia whose bursting activity drives and times the patterned bursting of the motoneurons innervating the buccal musculature mediating the feeding behavior of this animal (Kater 1974 *op cit.*). Bursting activity in the cyberchrons is both necessary and sufficient for patterned feeding motor output to occur in the buccal ganglia. For instance, "spontaneous" motor output can be abruptly terminated by hyperpolarizing current injected into members of the active cyberchρον network (Kater et al. 1977). Despite the fact that these neurons fulfill the necessity and sufficiency criteria prescribed

by Kupfermann and Weiss, we should never have referred to the cyberchrons as command interneurons. In fact, we now have evidence that the cyberchρον network receives input from "higher order" interneurons (The term "higher order" refers to those neurons apparent relationship to the cyberchρον system in an inferred hierarchical organization of neurons). We have found a pair of bilaterally symmetrical cerebral ganglion cells that have an excitatory influence on the feeding motor output (Granzow & Kater 1977). Activity in either of these cells, experimentally evoked with intracellular current injection, can initiate and maintain motor output from previously quiescent buccal ganglia. The patterning of the motor output is not a function of patterned activity in the cerebral ganglion interneuron, since tonic activity can elicit patterned buccal motor output; that is, these neurons are permissive, but not instructive. However, the rate of motor output can be altered by changing the rate of firing in these cerebral ganglion interneurons. Thus, the cerebral ganglion interneurons are apparently involved in governing the activity of the cyberchρον network. In fact, these cerebral interneurons in *Helisoma* have the characteristics of those crayfish ventral cord fibers associated with swimmeret beating to which Wiersma and Ikeda (1964 *op cit.*, and Wiersma, this *Commentary*) first applied the term "command interneuron." However, Kupfermann and Weiss have referred to the middle tier in this hierarchical organization – the cyberchρον neurons – as a command system. We much prefer the concept that commands are issued by neurons nearer the apex.

The notion that individual neurons may, as a result of their specific activity, unleash a coordinated and often complex behavior from among the various alternatives within an animal's behavioral repertoire has excited the imagination of investigators in the neural and behavioral sciences for nearly a quarter of a century. It will undoubtedly continue to stimulate research whether or not the term "command interneuron" is specifically defined. Most of us now feel the inevitability of the creation of a neuronal taxonomy that can be applied across phyla. However, before a taxonomy useful in classifying the diversity of the animal and plant kingdoms could be constructed, a knowledge of the individual plants and animals comprising these kingdoms had to be acquired. Many a naive observer might have been contented to have classified a large portion of the invertebrate population as either "squishies" or "crunchies." However, the insight of sharper minds and more critical examinations produced far more useful classifications. The term "command interneuron" is unique in that it has meaning for both behavior and physiology. We are reluctant to jeopardize its usefulness by restricting its scope before a critical array of examples is available.

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The crayfish giant fibers as *decision* and command neurons. Kupfermann and Weiss's very useful discussion of the command neuron concept prompts me to make two remarks.

First, the crayfish lateral and medial giant interneurons (LGs and MGs) have been described as among the most convincing examples of command neurons with a triggering function. Given this, it should be clearly understood that whereas direct electrical stimulation of these interneurons does produce tail flips that are quite similar to the naturally evoked flips in which the LGs and MGs normally participate, these command neuron evoked flips are often not identical to natural ones. This means that stimuli which excite the giants also affect tail-flip motor pattern generating circuitry via routes that bypass the giants; thus, in this regard, as in some others, the circuitry of the LG reaction is not perfectly hierarchical. Nevertheless, it remains useful to call the crayfish giants "command neurons."

Second, I must say that I agree with some of the sentiments expressed in Hoyle's pre-commentary. The operational criteria of Kupfermann and Weiss do not seem to provide a good way to distinguish the *issuer* of an order from essential conveyers of the order. Of course, any neuron in the chain of command might properly be called a "command neuron," however, the entity we seek is the ultimate source of the order, the decision neuron. A possible problem arises even for the well-behaved crayfish LG reaction. The LGs fire when and only when caudal type tail flips of short latency occur, and direct stimulation of the LGs does a good (if not perfect) job of evoking the normal behavioral response. Moreover, I feel confident that when we do the experiment of removing the LGs from the circuit by hyperpolarizing them, the behavioral reaction will, as expected, fail. However, it could still be that the LGs are fed in each ganglion by a special neuron whose input (either alone or taken together with the excitation that the LGs receive directly from primary afferents and first order tactile interneurons) is decisive in firing the LGs. If there were such neurons, they would be the true issuers of the escape command and the LGs would be mere distributors of excitation, despite the LGs having met all three of Kupfermann and Weiss's criteria.

To make matters worse, one can imagine that direct stimulation of these hypothetical pre-LG decision neurons might not fire the LGs (and produce a behavioral reaction) unless the LGs were already primed by excitation from primary afferents and first-order tactile interneurons. Therefore, these hypothetical neurons would, in a sense, be the issuers of the order to escape and yet not meet Kupfermann and Weiss's sufficiency criterion. Obviously, this problem would not arise in a perfectly hierarchical system. But the pervasiveness of feed forward and feedback effects makes it unlikely that many real systems will be strictly hierarchical [cf. Roitman et al., this issue].

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Difficulties in applying a functional definition of command neurons. The article "The Command Neuron Concept" by Kupfermann and Weiss clearly documents the need for a more precise definition of command neuron. The authors propose a reasonable set of criteria for establishing a cell as a bona fide command neuron, namely that it must be active during the behavioral act in question and that its activity must be both necessary and sufficient to produce the same behavioral act. They suggest experiments for demonstrating necessity and sufficiency that should give insight into the function of neurons that produce motor effects. However, there are problems when the authors attempt to apply this scheme. For instance, the only two cells that Kupfermann and Weiss accept as command neurons—the giant fibers in crayfish and the Mauthner cells in fish—have never been tested for necessity in the escape behavior they produce and, because of their geometry, probably never will be so tested. Also, cyberchron neurons in the snail are considered to be pattern generating rather than command neurons (Kater,

1974 op. cit. and this Commentary). Other examples could be cited, but we would like instead to discuss the author's proposed classification scheme in terms of our own research.

We have studied a neuron in the medicinal leech that exhibits command properties for swimming. In our attempts to determine the role of this neuron in the animal's normal swimming behavior, we have encountered many pitfalls when trying to apply the command concept to an actual neuronal system. We have found the concept useful to categorize the properties of neurons at the phenomenological stage of experimentation, when little is known about their connections to other cells. However, as we now begin to consider how neurons are connected and how they contribute to swimming behavior, we find that "command" involves cooperation among many different kinds of neural elements rather than being a simple on/off switch composed of a single neuron; therefore, at this more advanced stage, the command neuron concept is not applicable.

We have been investigating an interneuron in the medicinal leech, designated cell 204, which occurs in each of the essentially identical twenty-one midbody segmental ganglia. When stimulated at low, physiological frequencies, cell 204 initiates and maintains swimming episodes in the whole animal or in the isolated, brainless nerve cord (Weeks and Kristan, 1977). During swimming episodes initiated by sensory stimulation, the normally silent cell 204 produces impulses at 10–30 Hz. While stimulation of any one cell 204 is insufficient to initiate swimming in the whole nervous system, swimming can be initiated by sensory stimulation even when two cells 204 are hyperpolarized; therefore, up to any two of them are not necessary. It is interesting that the swimming activity initiated by any cell 204 seems identical to that initiated by any other, a situation Kupfermann and Weiss thought would be rare.

Since we cannot record from all twenty-one cells 204 simultaneously, we have not been able to test adequately the necessity of all twenty-one for the production of swimming. However, from indirect experiments it seems that some minimal amount of activity must be present within the cell 204 population for production of swimming. Therefore it is likely that these cells constitute a "command system" and each cell 204 a "command element." In addition, since stimulation of a cell 204 during an ongoing swimming episode increases the motor output frequency, cell 204 would also qualify as a "modulatory element."

The potential power of a classification scheme such as that of Kupfermann and Weiss is that once a cell is assigned to a particular category (e.g., command neuron), certain predictions can be made regarding expected connections to other neurons (e.g., sensory afferents or pattern generator cells). One would hope that the categories and predictions would provide insight into the organization of nervous systems in various species. However, as consideration of the following very simple connection pattern based on properties of cell 204 will show, even those neurons that meet all the requirements for inclusion in a particular category (i.e., command neuron) may turn out to have functional roles that are much more usefully described by some other term.

Initial experiments to determine the connections of cell 204 to other neurons involved in swimming have provided the following data:

1. Tactile sensory stimulation activates the swimming pattern generator located within the central nervous system.
2. Tactile sensory input excites cell 204, but by an indirect pathway.
3. Cell 204 activates the swimming pattern generator.
4. Cell 204 is strongly excited during swimming.

Figure 1 is a simple hypothetical network that will explain these four observations. It includes a single tactile sensory neuron, S, and a single interneuron, I, that connects to either the swimming pattern generator (pathway A) or to cell 204 (pathway B), or to both. All connections are excitatory.

This scheme is undoubtedly oversimplified, for several reasons. For instance, there may be one or more interneurons interposed in the pathway between any two connected neurons. Additionally, it is known that this network is repeated in each of the twenty-one segments, and it is likely that this iteration is crucial to the function of the system, since a chain of several interconnected ganglia is necessary for any of them to produce the swimming activity. For the sake of the present discussion, however, let us assume that the network shown constitutes a complete system for the production of the swimming activity pattern. A further assumption is that the synaptic potentials produced are so strong that the reciprocal excitatory connections between cell 204 and the pattern generator maintain the swimming activity for many cycles once either of them is activated.

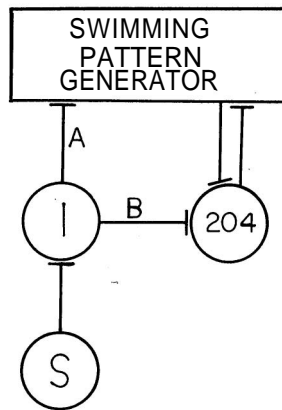


Figure 1 (Kristan and Weeks). Hypothetical neuronal network to explain some of the known properties of cell 204 in the leech. S is a tactile sensory neuron and I is an interneuron. The swimming pattern generator consists of an unspecified number of neurons, all with the same connections to cells I and 204. The pattern generator has further connections directly to motor neurons, which are not shown. All connections are excitatory.

In accordance with the suggestion of Kupfermann and Weiss, we will consider the swimming behavior in response to a specific meaningful stimulus, namely a strong but short-lasting tactile stimulation delivered in such a way as to excite a single sensory neuron, cell S. (Such stimulation can be delivered to a leech and will cause swimming.) First, consider the activity if pathways A and B exist. There are quite distinct differences in the properties, connections, and activity of neurons S, I, and 204 during the swim activity, yet by the tests suggested by Kupfermann and Weiss, they all qualify as command neurons. It seems more reasonable to call cell S a sensory neuron, cell I a relay interneuron, and cell 204 a swim-maintaining interneuron rather than lumping them into a single category. In fact, just as motor neurons were excluded from consideration as command neurons, it might be useful to eliminate sensory neurons from such consideration. This example also shows that neurons connected in series as a relay path are all necessary and sufficient when tested individually.

If the same network is considered, but without pathway B, matters become even more confused. In this condition, cells S and I are necessary and sufficient to initiate swimming, but cell 204 is needed to maintain swimming. Cells S and I would, tested individually, meet the three criteria for considering them command neurons. Cell 204 is sufficient to produce swimming, but only partially necessary, in that a single cycle of swimming could occur without it, and swimming could be prolonged by maintained sensory stimulation. Whether such a neuron should be called a command neuron or a command element is not clear. This seems to be a case in which, as Kupfermann and Weiss put it, worrying about terminology "could conceivably interfere with progress toward understanding the precise role of a neuron... in generating behavior."

We conclude, in direct contrast to the view expressed in the Kupfermann and Weiss paper, that the command neuron terminology provides a convenient means of communicating phenomenology efficiently, but that this way of classifying the properties of neurons is not of great use in defining the functional role of these neurons in behavior. Hence, we are quite willing to call cell 204 a command element in a command system right now; but as we learn more about its connections to other neurons in the system causing swimming, we will almost certainly drop this usage.

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Command neuron, an evolving concept. "We are faced with a historic term and an evolving concept (Bullock, 1977)." Available methodology and the unique features of crustacean preparations dictated the early course of research on neurons of this type and, in a sense, preserved the use of "com-

mand neuron" as the identifying label. For example, Wiersma and his colleagues showed that access to CNS neurons in crustaceans could be gained by isolating their axons from the interganglionic connectives. They had also demonstrated the utility of this approach and had used it extensively to study sensory neurons and various interneurons, including command "fibers." In early experiments, essentially designed to survey and describe the behavioral outputs of command neurons, it was not practical to use intracellular methods; and for the most part, morphological staining methods were not yet available. In addition, the study of synaptic interactions in crustaceans in general requires the penetration of small processes in the neuropil due to the fact that the somata are often electrically isolated from the smaller synaptic events.

Almost from the beginning, neurobiologists were impressed with the richness of the behaviors produced by axonal stimulation and were thus encouraged to pursue the work to the limits of the techniques. For more than a decade, this limited approach continued to reveal important and interesting information on neurons of this type (Kennedy and Davis, 1977 *op. cit.*) and the term "command neuron" remained useful for purposes of labelling these cells as similar to those first described by Wiersma.

Meanwhile, the "command neuron" concept was evolving. In addition to the operational definition applied by Wiersma and Ikeda (1964 *op. cit.* and Wiersma, this Commentary), "command" now has the implied meaning of a cell that not only is used by the animal to produce a normal behavior, but one that is situated in an important position, both in an anatomical and informational processing sense, in the neural circuit underlying that behavior. Experiments oriented primarily around axonal stimulation, while useful for examining and evoking a behavioral output, do not provide data on the activity of these cells during ongoing or naturally occurring behavior, and are not particularly designed to elucidate the organization of the circuitry itself. As a result, the data simply no longer satisfy the concept.

Only when synaptic measurements and neuronal staining were combined with behavioral and neurophysiological studies identifying the input and output of a command cell did we reach some understanding of how these neurons function in the control of a particular behavior. Such an analysis has been performed thus far in crustaceans only on the lateral giant fiber system of crayfish, a system that underlies one form of escape behavior in these animals (Zucker et al., 1971; Zucker, 1972a,b,c, *op. cit.* and this Commentary). Although this analysis was a tour de force, it was only partially complete (Krasne and Wine, 1977 and this Commentary). This was probably the easiest behavior to analyze at the neuronal level in crustaceans because the interneurons are giant, the "command" is immediately premotor, the afferent are themselves large and accessible, and the behavior is unmistakable. This is exactly the kind of analysis that must be made on many other interneuron-driven systems in order to decide whether the driving neuron is or is not a "command" unit. Since there are few known systems as tractable as this in crustaceans, one could predict that the necessary data will be obtained slowly.

The article by Kupfermann and Weiss is a serious attempt to resolve the proper use of the term "command cell," and, at the same time, offers an ideal means of studying the neural basis of behavior. Any neuron or group of neurons that can be shown to be both necessary and sufficient to produce a behavior is certain to be elevated to a level of importance above the average command neuron as we currently understand it. The definition proposed by the authors is therefore extremely useful, but has some aspects that may never satisfy everyone.

At one extreme, this definition retains the term "command neuron" and that fact alone will be unacceptable to some. To others, it will be too much of a departure from the intended meaning of Wiersma, that is, simply an operational term for a neuron without the related implications. More seriously, however, the definition really does not completely distinguish between the related labels such as "command," "trigger cell," "gating neuron," or "driver neuron." And, as Hoyle points out, some of these terms, like "command," are equally loaded with implications about underlying neural organization or function.

The proposed approach for establishing criteria of necessity and sufficiency, although clearly useful, is much more applicable to some preparations than to others. It will, for example, be extremely difficult to apply properly the necessity criterion to a crustacean system that requires the cooperative activity of a group of similar neurons in order for it to be expressed. At this time there is considerable evidence that numerous systems of this type exist (Larimer, 1976 and this Commentary). Although in

crustacean preparations the criterion of sufficiency should be more easily met than that of necessity, the question will remain whether the electrically driven behavior is identical to a normally occurring one or whether or not it is a segment of normal behavior. The latter determination is particularly difficult.

These considerations could have two effects on the overall use of the term "command." First, for technical reasons alone, examples of command neurons that meet the authors' criteria would be found in molluscan preparations more readily than in the arthropods. Yet, examples of neurons similar to those described by Wiersma, Kennedy [op. cit.], Evoy [this Commentary], Davis [this Commentary] as well as others in crustaceans, and recently by Bentley (1977) in insects, are common, but difficult to study in this way. Second, the use of the restricted definition would certainly limit the overall use of the term "command neuron." In this regard, the proposed definition could serve positively in phasing out the term "command" as well as directing our attention to the goals that should be set for studying the neural basis of behavior. It is hoped that restricting the use of "command" does not encourage the proliferation of alternative terms.

As the authors point out, the fact remains that even if we knew the circuit underlying a particular behavior, we might be hard pressed to assign "command" to certain elements and not to others. It is entirely possible that more than one neuron in such an established circuit will be found to be capable of initiating the output or to be necessary for its expression. If this occurs which is the command? Or at the absurd level how many 'commands' are permissible? It seems virtually impossible to define narrowly a command cell on a purely theoretical basis.

The term 'command neuron' is with us, and we should understand its limitations. Most important, we should not overinterpret the data on those cells that have been called command fibers in the past, but should attempt to clarify their role in behavior.

The quote at the beginning of this commentary seems quite appropriate to this discussion. In its original context, however, the quote refers to problems encountered with some other commonly used but much older terms in neurobiology: problems in distinguishing axons from dendrites and input segments from output segments of various neurons! Let us all take a deep breath of dephlogisticated air and proceed.

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Causally oriented devices. Regarding the operation of invertebrate neural networks, "understanding" is often equated with "causal decomposition." A satisfying hypothesis would spell out network operation as a complete causal sequence (event A leads to event B, which leads to event C, and so forth), with a role in the sequence explicitly assigned to each network element. As an electrical engineer, I am sympathetic to this point of view. Analysis and/or design of electrical circuits is much easier when conducted in terms of causal sequences and explicitly assigned roles.

Unfortunately, the passive devices (resistors, capacitors, diodes, transformers, and the like) employed by electrical engineers do not separate cause from effect and therefore do not allow simple causal decomposition. To deal with such devices, electrical engineers have been forced to resort to a concept of network operation that transcends causal decomposition and explicit role assignment. This transcendent concept treats the network as a whole, with whole-network input-output relationships that result from the interactions of all elements. Each element contributes to all aspects of those relationships; no aspect is assignable to any individual element or cluster of elements.

Although electrical engineers can cope with this concept, we often go out of our way to avoid it. We often insert an active device that is causally oriented, in the sense that it exhibits clear separation of cause and effect (achieved by virtual elimination of feedback from output to input), to break the pathways of interaction between one part of an otherwise passive network and another, allowing us to ascribe separate roles to each part. Allowing us to design or analyze the two parts independently, the causally oriented device provides a rest stop midway in the procedure. Furthermore, since the number of design or analysis steps increases approximately as the square of the number of interacting elements, a strategically placed, oriented device simplifies the procedure considerably. (A device that splits the network into two equal parts halves the number of steps for complete analysis.)

For neural networks hypothesis generation requires both analysis and design. When the numbers of steps in these procedures can be reduced hypotheses should be simpler thus easier to comprehend thus more illuminating and satisfying. Therefore a network rich in oriented devices should lead to simple satisfying hypotheses. Unfortunately, the advantages provided by an oriented device are lost if that device is circumvented by feedback loops. Therefore even if a network consists entirely of oriented devices (and a neuron that conveys its output via chemical synapses often is modeled as an oriented device) if it also happens to be rich in feedback loops then causal decomposition is generally so complicated and difficult that analysis and design methods that transcend it are much more illuminating. Faced with such networks the prudent analyst searches for rest stops in the form of oriented devices that do not happen to be circumvented by feedback. Each device of this type immediately provides a partial causal decomposition and its concomitant simplification.

Modelers of vertebrate CNS networks commonly yield to the apparent richness of feedback in those networks and invoke network concepts that entirely transcend causal decomposition. The early network wave-propagation models, the later Fourier-transform models, and the recent statistical-mechanical type models all are based on such schemes. Among invertebrate neural-network models, one finds transcendent schemes applied to coelenterate nerve nets and to lateral inhibition. In spite of the lack of causal decomposition, many neurobiologists consider the models of lateral inhibition to be among the most satisfying.

On the other hand the hope for at least some simple and illuminating causal decomposition survives in both invertebrate and vertebrate neurobiology. In vertebrate CNS studies one sees the hope reflected in the searches for feature detectors and complex pattern detectors. In the invertebrates, I believe, it is reflected in the search for "driver neurons," "modulator neurons," "command neurons," and the like. Any of these neurons might be the rest stop we seek. However, considering the primitive state of our knowledge of nervous systems, I believe that we should seek rest stops in general rather than focus our search on a narrowly defined species of rest stop. Any neuron or group of neurons that serves as a strategically located oriented device uncircumvented by feedback is likely to be of great value to us, whether or not it meets the criteria for command neurons. It seems to me that the neurobiologist's time would be better spent in the search for such devices than in neuronal taxonomy. If and when a large number of such devices has been found, then perhaps one might profitably consider their shared and unshared traits.

If, by misfortune, a long and diligent search uncovers no rest stops, then the weary traveller should reflect upon the example of lateral inhibition and nurture the hope that perhaps, after all, none will be required.

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Restricted applicability of the concept of command in neuroscience

dangers of metaphor. The paper by Kupfermann and Weiss proposes a new operational definition of the concept of command neuron. While this concept has been gaining currency in recent years, it is doubtful that the concept of command makes sense at the cellular level, and that there are operational definitions. Our comments will be concerned with those two issues.

The concept of *command neuron*. Any dictionary will tell us that a *command* or order is an instruction, couched in some symbolic language, to behave in a certain way – and, moreover, one that can be disobeyed only at a risk. A *command(ing)* X is in turn an X that issues or conveys commands or orders to his or her subordinates. Because of their complex nature, commands can be issued or obeyed only by animals endowed with a nervous system capable of making and understanding decisions and of behaving accordingly. Moreover, only animals belonging to a stratified (or hierarchical) society, and occupying a high rank in it, are capable of issuing or transmitting commands and having them observed. Social primates satisfy both the neurophysiological and the social conditions. Whether other species engage in commanding and obeying – rather than in merely threatening and yielding – is a matter of controversy among ethologists. Therefore, most ethologists, animal psychologists, and sociobiologists will be careful not to primatomorphize, let alone anthropomorphize, by using the concept of command out of the primatological context (i.e., metaphorically rather than literally).

While metaphors occasionally have a heuristic power, their essentially figurative nature must be recognized as such lest it become dangerous. This applies, in particular, to the "command" metaphor and its attendant "hierarchy" metaphor. First, this suggests that the "command" unit (e.g., a neuron) has the ability to *make* or *understand* decisions – which ability should be reserved for multineuron systems. Second, it creates the illusion that we understand a behavior pattern initiated by a "command neuron" just because we have brought it home by likening it to a complex decision-making-and-acting process.

Such dangers should not be underrated in neuroscience, in view of the fact that much psychological "theorizing" is little more than analogizing. Recall the role played by animistic metaphors (id, ego, superego), mechanical metaphors (gate, drive, releaser), communication metaphors (information, coding, retrieval), and even military metaphors (ego defense, repression, aggression). Such heavy metaphorizing is not only a manifestation of theoretical indigence but also a stumbling block to theoretical progress. We must try to prevent neuroscience from falling into the trap into which some aspects of psychology have fallen: we must favor the construction of theories over that of metaphors [Bindra, this issue].

The concept of command neuron belongs to a vast family of metaphors related to vitalism. Other members of this family are "hierarchical structure," "goal-seeking behavior," and "genetic information." While the concepts of command, hierarchy, goal, and information are perfectly *legitimate* with *reference* to the highest levels of behavior, they are not legitimate at the cellular level, let alone at the subcellular levels. (The fact that biologists often err in this respect is no excuse for the neuroscientist to follow suit.) When firing, a neuron does not issue or even transmit a command; it just generates or conveys a nonverbal signal that will in turn activate or inhibit some other biosystem (neuron, muscle, gland, etc.). The action of a "command" neuron is thus similar to the template action of DNA and RNA in protein synthesis, to the "seed" or condensation nucleus in vapor-liquid and liquid-solid transitions, or fertilization in the developmental process. In these cases, one can speak of a thing or event as causing, initiating, triggering, or *codetermining* a process, but not as commanding it, because at those levels there are neither commanding agents nor commands nor subordinates. (Recall that if the signals emitted by a "command neuron" fail to activate or block the target, the latter is neither dismissed nor imprisoned nor court-martialed!)

For the above reasons we would prefer to restrict the term "command" to fairly large systems and, even here, to those cases where a genuine commanding process can be unequivocally demonstrated. We suggest using the expression "trigger neuron" – which was the one used originally in invertebrate neurophysiology – wherever "command neuron" is currently being employed. And even in this case, we have reservations concerning the definition of the concept, as will be seen.

The definition of the concept of trigger *neuron*. Kupfermann and Weiss define the command neuron (or, rather, its concept) as the unit necessary and sufficient to produce, when activated, a well specified, stereotyped response. Our objection to this definition is that it conceives of the command

neuron as a prime mover – that is, a thing that modifies other things without being affected by any of them. The universe does not seem to contain prime movers, let alone any at the cellular level. Let us explain.

No element of a circuit – hydraulic, electrical, or neuronal – can be said to act without being acted upon by other elements of the circuit. Moreover, every neuron is immersed in a medium that cannot fail to interact with it. In fact, a neuron is subject to subtle ionic modulations of the extracellular medium or of membrane permeability by transmitters, neurohormones, and so forth, not to speak of the metabolic activity or the possible modifications of the protein matrix in the cell membrane.

In short, since every neuron is influenced by its environment, and particularly by the other neurons in its circuit, there can be no strictly commanding neurons, even waiving the general objections to the concept of command raised in the previous section. For these reasons, we suggest the following redefinition: A neuron is a trigger *neuron* if and only if it starts Markovian processes of neural *conduction*.

Besides, all concern with "operational concepts," or concepts introduced by "operational definitions," should be given up. Operationalism, born in the 1920s, died in the 1960s of logical surgery (Bunge, 1967). Indeed, every definition is a strictly conceptual operation consisting of equating two constructs.

Moreover, not every concept needs to or, indeed, can be defined. The most important concepts are not defined explicitly: they are the basic (undefined, primitive) concepts of a theory. Thus, the concepts of set and set membership are not defined in set theory, and the concepts of mass and force are not defined in Newtonian particle mechanics. Whether the concept of a trigger neuron is definable depends on the (future) theories in which it occurs. In some it may be defined; in others, not. If undefined, it will be characterized by a set of postulates (the way the mass and force concepts are defined in Newtonian particle mechanics). If defined, it will be introduced by an identity, not by reference to laboratory operations.

What laboratory operations can do is to identify things, measure some of their properties, and so forth. For instance, one can identify neurons using electrophysiological techniques. One can, therefore, adopt the following *operational criterion* (not definition): "Any cell in the brain capable of generating action potentials is a neuron." Unlike a definition proper, or a set of postulates, such a criterion tells us not what a neuron is but how to recognize it. Therefore, it cannot belong to a theory, although it does fulfill a role in producing empirical evidence for or against theories.

Conclusion. We have criticized both the concept of command neuron and the proposed new definition of it because the first reinforces vitalism and the second is a victim of operationalism. Our concern may seem Byzantine but it is not, for philosophical ideas can be either noxious or beneficial to science. Some of the very problems about higher nervous system functions in primates, such as *Homo sapiens*, may have been suggested by the philosophy ensconced beneath terms such as "command" and "hierarchy." It is not hard to see that some of the great questions concerning brain function will revolve around the traditional problem of free will, where once again the concepts of will and command may play a central role. Once such terms are embedded in our language, they become either important tools of research or our intellectual orison wardens.

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The command function concept in studies of the primate nervous system. The concept of command neurons has played an important role in the development of the neurophysiology of invertebrates in recent years. Evidence that there are single elements in simple nervous systems, which, when active, cause complex behavior patterns to be executed, has fulfilled widely held intuitive ideas of how the nervous system must surely operate, and has also stimulated a great deal of new and profitable research. The suggestion of Kupfermann and Weiss that the time has come to look again at the concepts behind the term "command neuron" is quite correct. There is no question but that the term has come to be used in many divergent ways, and that the necessary technical methods are now available to the invertebrate neurophysiologist for rigorously defining the usage of the term.

A related concept, that of a "command system" or "command function," has been used in studies of the behavioral neurophysiology of vertebrates, but with more limited implications than those of the "command cell" concept in invertebrate physiology. For example, in describing certain neurons observed in the parietal association cortex of monkeys, Mountcastle and his associates have referred to "command functions" and "command signals" (Mountcastle et al., 1975 *op cit.*; Mountcastle, 1976; Lynch et al., 1977). Here, there is no intention to suggest that activity in a single parietal neuron leads inexorably to the performance of a complex behavior. Rather, the intention is only to suggest that there are cells in this cortical region that are at a later stage of neural processing than the traditionally defined sensory systems, but are not yet a part of the traditionally defined motor systems, and that these cells participate in some way in the conditional initiation of certain behavioral acts. Specifically, the neural activity of posterior parietal reach, hand manipulation, saccade, tracking, and fixation cells is associated with certain specific behavioral acts, but these cells have no demonstrable sensory receptive fields, nor is their activity associated with a particular movement in all circumstances. Saccade cells, for example, discharge before a saccade to follow a fixation target, but are silent before spontaneous search saccades. Fixation cells discharge continuously while the monkey looks at a piece of food that he wants, but are not active if he looks at the food when he is no longer hungry. Some fixation cells are active only when the monkey looks at a target in one specific region of the visual field, and are not active when the monkey fixates the target in another region of the visual field, even though the image on the retina is the same in both instances. These cells cease firing when the target disappears, even if the monkey's eye position does not change for several hundred milliseconds. Reach cells discharge when the monkey extends his arm to take a piece of food, but are not active when the same movement is made to ward off a threatening stimulus.

In describing these properties, the term "command" has been used to indicate that these neurons are believed to be at a stage of neural processing where the details of sensory analysis are complete and information in summary form is brought together to determine the animal's next action. At this level, information from visual input, somesthetic input, auditory input, biological drive level, and affective state all influence the neural activity of individual cells. Furthermore, the activity of some of these cells begins well before certain clearly defined actions, such as visually evoked saccades or visual pursuit, yet the parameters of the burst of neural activity do not seem to be related in any way to the details of the ensuing movement.

The existence of this intermediate, decision-making stage of neural processing is extremely likely. That the neurons described by Mountcastle and by Lynch actually participate in this level of processing appears probable, but is not yet certain. As Kupfermann and Weiss point out, even invertebrate ganglia are so complex that it may be difficult to establish the distinction between a cell that initiates behavior and a cell that participates in the feedback control of that behavior, via either afferent feedback signals or corollary motor signals. This difficulty is greatly increased in the vertebrate nervous system, where it will be particularly hard to distinguish a potential command system element from an element of a mismatch comparator in a servo control system. The saccade cells of posterior parietal cortex, for example, may register only the existence of a mismatch between a new fixation target location on the peripheral retina and the intended target location on the fovea. This information might then be transmitted to some other place in the nervous system for the actual initiation of a following saccade. The criteria suggested by Kupfermann and Weiss for resolving this question will not be adequate for such a complex nervous system, since artificial stimulation in a comparator might produce an artificial mismatch signal and consequent eye movement, while experimental removal of the comparator system might well lead to delayed initiation of saccades to the new target location. This problem has been discussed elsewhere in more detail (Mountcastle et al., 1975 *op. cit.*; Mountcastle, 1976; and Lynch et al., 1977; see also Roland et al., this issue).

The weight of present evidence supports the proposition that the parietal association cortex of primates contains a neural mechanism that participates in the initiation of certain behavioral acts under certain specific sensory, motivational, and affective conditions. It could be argued that "command" is an unfortunate adjective to associate with these cells, and that perhaps some other descriptive term would be preferable. However, the various connotations of alternative descriptors turn out to be even more undesirable than those of "command." Furthermore, much of the meaning of the term "command" is appropriate to a neural mechanism that is linked indirectly to the

several sensory, motivational, and affective systems, and in which neural activity precedes, on a conditional basis, certain well-defined behavioral events. Kupfermann and Weiss wisely remind us that it is our goal as neurophysiologists to discover the complex causal determinants of behavior. In pursuing this goal, we must strive to use the most precise language possible. At the same time, we must not waste excessive amounts of energy arguing about the many possible connotations of a word while possibly neglecting the neurophysiological concepts to which the word refers.

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Command neurons and unitary behavior. A comparison of animals and machines or computer programs may suggest changing the emphasis from the command neuron to the behavior commanded. A *unisource* behavior might be defined as one caused by an event in a small part of a machine or animal whenever the rest of the system satisfies certain general conditions that prevail an interesting fraction of the time. In designing a machine or computer program, one often faces decisions about whether a certain behavior should be produced in a *unisource* way, for example, by a specific subroutine, or whether it must arise from the interaction of many parts of the machine. Thus FORTRAN compilers give error messages on meeting ungrammatical statements, for example, a compiler may print "PARENTHESIS ERROR IN STATEMENT 45." In some compilers, the printing of "PARENTHESIS ERROR IN STATEMENT" is a *unisource* event produced by a routine that detects parenthesis errors. In other compilers, it will be a *multisource* event, namely "ERROR IN STATEMENT" is *unisource*, being produced by a general part of the error routine, while the adjectival "PARENTHESIS" is generated by the part that detected the parenthesis error. In no reasonable compiler will the whole event, including printing "45," be *unisource*, because no one would make a subroutine specialized to detecting parenthesis errors in statement 45. If one found the word "PARENTHESIS" sometimes misspelled in an error message, one would infer that there were at least two different routines that handled parenthesis errors, although the inference would not be completely conclusive.

A second example comes from cryptography. If one successfully concludes that a certain failure of cryptograms in a given cipher is the invariable consequence of the presence of a certain stock phrase in the message, one is well on the way to solving the cryptogram.

It would seem that the discovery that a given behavior in a mollusc has a single source, for example, it is triggered by the firing of a particular neuron, is important. It raises the question of whether *unisource* behaviors in molluscs are usually triggered by single neurons.

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Command neurons and effects of movement contexts. As a psychologist concerned with the programming of body movements, I find the concept of the command neuron potentially useful for describing how movements are selected. If different movements are triggered by different command neurons, it may be possible to select among those movements by selecting among the command neurons associated with them; the number of decisions required if selections were made in this way might be less than if command neurons did not exist. If command neurons are hypothesized to play a role in movement selection, some questions that arise are: (1) How complex are the movements controlled by command neurons? (2) Are command neurons sometimes activated simultaneously, with the effect of producing movements that could not be produced by any individual command neuron or, indeed, by any sets of noncommand neurons? The second question raises the possibility that command neurons may provide an effective means of producing

diverse, and even novel, movements (Rosenbaum, 1977; Rosenbaum & Radford, 1977).

Towards answering these questions, consider Kupfermann and Weiss's criteria for identifying a cell as a command neuron. Suppose some neuron is found to be necessary and sufficient for the production of a given movement. Contrary to what Kupfermann and Weiss assert, it would not be known whether the movement could not also be produced by other means (i.e., whether the circuit containing the command neuron lacked redundancy), or whether the experiments that were done simply failed to provide adequate stimuli for utilizing the redundancy that may have been present. This argument suggests that while the demonstration of a command neuron would be useful for showing that command neurons may in fact exist, it would actually reveal less about the organization of neural mechanisms underlying motor control than the demonstration that a putative command neuron *failed* to meet Kupfermann and Weiss's requirements; in the latter case at least clear-cut evidence for redundant control would have been obtained.

Perhaps instead of trying to certify that a neuron is or is not a command neuron, it would be more illuminating (and also more practical) to establish the behavioral conditions under which a neuron exhibits command properties (i.e., has the ability to trigger a movement or is necessary for the initiation of a movement). To see what kinds of information could be obtained from such an approach, consider a hypothetical example in which a neuron Cm is found to trigger a movement M when stimulated. Cm would qualify for what Kupfermann and Weiss call a "putative command neuron." Suppose it was discovered that whenever some other movement was performed at roughly the same time as M the relationship between the activation of Cm and the performance of M broke down. This could occur in either of two ways. Cm could be found not to fire before M was executed, or M could be found not to occur when Cm fired. Different interpretations of these results could be made, depending on the relationship between M and the other movement.

Suppose that M is a proper subset of a movement N, that is, that all the muscles used to perform M are also used in the same way to perform N, but with the reverse not true. If Cm fails to fire before the execution of M when N is performed, this could be taken to mean that M is subject to redundant control imposed from a higher level. A question of interest would then become: Is the command function of Cm restored as N becomes more complex? If the answer were No, this would imply a type of organization in which control at all levels is usurped by the highest level of control in operation. If the answer were Yes, this would imply a type of organization in which control is relinquished to lower levels as higher levels of control are used.

Now consider the case where, when some movement O is performed, Cm continues to fire but M is no longer produced. Saying that M is no longer produced could mean either that no movement resembling M is produced, or that the movement that is produced, M', only resembles M. If, when O is performed, Cm fires without producing M or M' this would indicate that the control of M (or M') by Cm is aborted somewhere between Cm and the motoneurons. One interesting question in this situation would be: For what relations between O and M does this "collateral gating" obtain and for what relations does it not obtain? As the complexity of O changes, when is the absence of M or M' no longer accompanied by activity in Cm? The determination of this level of complexity would give an indication of the levels of control that are called upon when movements of different complexity are performed.

In this brief commentary I cannot elaborate on all of the kinds of contextual effects that might be used to study neural command systems. Presumably, it should be possible to learn a great deal about command linkages simply by recording from (or stimulating) putative command neurons and observing their effectiveness when other responses are performed by the experimental animal. In view of the fact that there is now abundant evidence for neurons with command properties, it may be more useful to find out how these neurons participate in movement control in a wide variety of behavioral contexts than to find out which of them, if any, should simply be given the tag of "command neuron."

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Defense of the Wiersma-Kennedy concept of the command neuron. One goal of neuroethology is the elucidation of the mechanisms utilized by neurons in the generation of motor behavior. The experimental neuroethologist can attempt to realize this goal by characterizing the relationships linking a particular CNS cell, termed neuron A, to a biologically significant motor behavior, termed movement X. There are many tests that can be performed to determine the role of neuron A in the generation of movement X. Examples of such tests are:

1. Stimulate neuron A. Measure the movement elicited. Compare the movement elicited to movement X. Note: According to Wiersma and Ikeda (1964 *op. cit.* and Wiersma, this Commentary) and Kennedy (1969 *op. cit.*), neuron A is a command neuron for movement X if the movement elicited by stimulation is an excellent replica of movement X.

2. Record the activity of neuron A in a freely moving animal. Record the occurrences of movement X. Correlate the activity of A with a measurement of movement X. Note: Those movements of the animal that occur when neuron A is active comprise the "motor field" of neuron A (see Schiller and Stryker, 1972, and Sparks et al., 1976, for examples of motor fields).

- a) Measure the pattern of neuron A activity during test 2 to determine whether there is a temporal relationship between an aspect of the movement and a component of the neuron A discharge pattern.

- b) Stimulate neuron A directly with electrical current so that the activity elicited in neuron A replicates the activity seen in neuron A when movement X occurred during test 2. Measure the movement elicited and compare to movement X.

3. Determine what sensory inputs can activate neuron A. Measure the receptive fields for these inputs and term them R(A). Determine what sensory inputs can reflexively activate movement X. Measure the receptive fields of these inputs and term them R(X). Compare R(A) to R(X).

- a) Examine the response of neuron A to a sensory input that is a member of both R(A) and R(X). Stimulate neuron A directly with electric current so that the activity elicited in neuron A replicates that seen during such sensory input. Measure the movement elicited and compare to movement X.

4. Prevent the activity of neuron A. Determine whether or not movement X can be produced by a freely moving animal.

- a) Prevent the activity of neuron A. Stimulate the animal with a sensory input that is a member of both R(A) and R(X). Determine whether or not movement X is produced.

The experimenter can now evaluate the results of these tests and then construct a hypothesis concerning the role of neuron A in the generation of movement X. Next, the role of a second cell, neuron B, can be examined by the above tests and a hypothesis constructed concerning the role of neuron B in the generation of movement X. In addition, many other neurons can be studied until the investigator feels that he now has a reasonable working hypothesis concerning the network of cells responsible for the production of movement X. At this stage many further tests can be performed. Examples of these are:

5. Record the activities of neurons A, B, C, and so forth, during behavior X. Indicate which neurons have synaptic activity correlated with electric activity of which other neurons.

- a) Stimulate neuron A directly with electrical current. Describe the set of cells that receive synaptic input from neuron A. Repeat for all neurons being studied.

- b) Determine the chemical and physical properties of each neuron under study and of each of their synaptic interconnections.

After all the above tests have been performed on all the neurons that have movement X as part of their motor field, then it is likely that the experimenter can construct an excellent model to describe the neural mechanisms utilized by the animal to generate movement X.

In this commentary, it may be convenient to state that there was a relationship between neuron A and movement X as determined by test 1. This type of statement can be awkward, however, in the scientific literature. An investigator who wishes to eliminate this verbal difficulty has the option of designating a word to signify that a given operation is satisfied. Such a word may be selected because of the image it evokes, for example, an action potential. Alternately, the word may be selected from existing words in other languages, for example, a cyberchron neuron (Kater, 1974 *op. cit.* and this Commentary). In other cases, the word may be selected for its humor, for example, the barn.

It is a matter of scientific convention that once a word is designated to have an operational definition in a scientific context, then the common language connotations of the word no longer apply in the scientific usage. For example, once the physicist has defined one barn as equal to 10^{-24} square centimeters, then within the scientific context that area need not contain farm animals. In a similar fashion, once the term command neuron is accepted within the scientific literature as a verbal shorthand for test 1, then it is inappropriate within a scientific context to discuss the meaning of the word as applied to a military organization (Hoyle, this issue). Similarly, Kupfermann and Weiss utilize the connotations of the common language meaning of command in their discussion of command neuron as an operational definition. To them, the word "command" implies that the neuron should act as a "critical decision point in the generation of behavior." From their point of view, the term "command neuron" should be redefined to apply to a neuron that has met the criteria outlined in tests 3, 3a, and 4a. I feel that such a redefinition would be confusing to future readers of the literature since they would be faced with two different operational definitions of the same word. In addition, such a redefinition would deprive future experimentalists of a convenient verbal shorthand to utilize in their description of a neuron that satisfied the criterion of test 1. Kupfermann and Weiss view a neuron that satisfies the criteria of tests 3, 3a, and 4a as performing a "critical decision" in the generation of behavior. I suggest that such a neuron be termed a "critical decision" neuron. Such a designation would be a convenient verbal shorthand in the description of future experimental work and would be least confusing for future readers of the literature.

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by Yuko Tsukada

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Ambiguity of the proposed definition. The authors of this article have proposed a redefinition of the command neuron as a cell whose activity is both necessary and sufficient for the initiation of a given behavior. This definition is quite empirical and still intrinsically ambiguous however, a fact of which the authors appear to be quite aware.

There may exist very few neurons that fully satisfy both the necessity and sufficiency requirements, for example, the lateral giant fiber of the crayfish. Such cases appear rather exceptional, and we know many other "command" neurons that may not meet the criteria.

The authors' proposal of calling those neurons that do not fulfill the necessity requirement constituents of a "command system" will leave the possibility of quite a large set of neurons constituting just one command system; and this may lead to the extreme case of nearly the whole population of the CNS, including sensory and motor neurons, being designated the command system for one behavioral output.

If the authors' is to be a conceptual definition, it should provide a distinct boundary between command neurons and other elements of the nervous system. In the present formulation, however, the boundary seems inherently ambiguous, thereby compromising the definition.

We may be fortunate enough to find a number of single neurons that satisfy all the conditions, each eliciting a *single* behavior; however, the logical extrapolation of this would be that there must be a one-to-one correspondence between the command neuron (or system) and the behavior, and thus that the behaviors are as countable as the neurons. Would it really be possible to separate all animal behavior into countable repertoires corresponding one-to-one with command neurons or systems? The chronic recording method in freely moving animals is useful for investigating such a relation. In fact, it has been shown that the activity of the giant fiber is so related to escape behavior (Wine & Krasne, 1972 *op. cit.* and this Commentary) and the activity of the C-99 fiber to defense behavior (Tsukada, 1974). However, other neurons have also been shown to elicit escape behavior similar to that elicited by the giant fiber; there are likewise other neurons, smaller than C-99, that elicit defense behavior (Bowerman & Larimer, 1974 *op. cit.* and this Commentary). These facts throw serious doubt

on the appropriateness of rules of requiring one command neuron (or system) always to have one corresponding behavior.

Though the relation, or at least the correlation, between giant fiber activity and escape behavior is a matter of certainty, any Invariant causal relation between them has yet to be established. This applies to all other command fibers so far known—even the crayfish lateral giant.

Although the generation of behavior may be closely or causally related to command neurons as decision-makers, the actual decision to generate a behavior may not be entirely limited to these cells. One such counterinstance would be represented by a model in which the activity of the command neuron was controlled by an inhibitory neuron connected to it; only when the activity of the inhibitory neuron was absent would the command neuron be able to generate the behavior. In such a system, the experimenter would readily be led to the command neuron, which would satisfy both the proposed requirements, but may not realize that the real decision-maker was the inhibitory neuron.

In spite of all these limitations, "the command neuron concept" has indeed played a certain role in motivating rather extensive studies of invertebrate neuron networks by many investigators. Present arguments clearly demonstrate, however, that the word "command neuron" should be used carefully in a limited operational framework. More rigorous tests should certainly be made to determine whether identified command neurons really satisfy the proposed definition and, above all, whether the causal relation between command neurons and behavior can be established. Further searching for new command neurons may be futile unless we know more of the realities of existing "command neurons."

ACKNOWLEDGMENT

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The original definition of command neuron. As the originator of the term and concept of a "command interneuron," I feel obliged to comment on the discussion of its definition. In contrast to statements that the term was first used in the 1964 paper with Ikeda (Wiersma and Ikeda, 1964 *op. cit.*), I first used it in a 1961 article translated into Russian in honor of my friend Koshtoyants, of which the English version appeared in 1965 (*op. cit.*). A much more detailed presentation, in which similarities between anatomical distributions of this type of premotor unit and sensory interneurons were stressed, appeared in 1962 in a volume of *American Zoologist* (*op. cit.*). On pages 73 and 76, we find "Such 'command' fibers can thus release the whole coordinated pattern without assistance from the sensory feedback." "It is quite feasible . . . that the function of the higher centers consists essentially of activating excitatory and inhibitory command fibers controlling the reflex pathways." ". . . these command fibers are not able to vary their commands to suit the changing conditions in the periphery—they merely have the ability to fire or not to fire. Once the command has been given to the lower ganglionic centers, sensory information coming into the local reflex system will determine to what extent the command will be obeyed."

Note that only units similar to those of the swimmeret fibers, thus those releasing coordinated rhythmic outputs under deafferented conditions, were so named in the aforementioned writings. Later, the central giant axons and the "defense" reflex fibers were also included. But in the latter case it still has not been shown that a main requirement, namely that the deafferented output be similar to that occurring during the reflex, has in fact been fulfilled. However, another requirement with which I agree, namely that during behavior the unit must show appropriate impulse frequencies and durations, was found to hold in this interneuron (Tsukada, 1974 and this Commentary). At present it would seem that a subdivision of command interneurons is indicated. As in all trials to categorize naturally occurring elements into types, this also partially fails, as there are already known intermediates. The three types might be called phasic (giant axons), tonic (defense reflex fiber), and rhythmic (swimmeret) activity releasing units. In the first two, the command

units might make direct connections to a definite set of motor neurons in contrast with the third, where the connections would be to central oscillators driving the output neurons.

Though I thus agree to a large extent with the proposed requirements, there are some important differences. Specifically, I consider that the ability of the command fiber to produce a basic output pattern in the absence of sensory feedback is of fundamental importance. Feedback should cause only variations in the output, as by local inhibition or reinforcement. Secondly, because the command interneurons occur in bilateral pairs in most cases studied so far, it will obviously be necessary to block both to show that their exclusion prevents the behavior. Furthermore, since some behavioral responses may normally be caused by activating several of these units if they are allied in the way of Sherrington's "allied reflexes," blocking one single pair may also not be enough to indicate that they are not command units. In my own prejudiced opinion, this simultaneous activation may usually not occur, but the whole question of the mutual interactions of command units cries for investigation.

Hoyle's precommentary, in which he appears to play the role of a devil's advocate, is in several respects not defensible. His aversion to the term "command fiber," because it consists of two nouns, is strange. This construction has always been quite common, represented in behavioral neurophysiology by such terms as sleep center and pleasure center. He rightly remarks that I could not quote where I found the term "command center" as such, though central command was in general use. As I recall, it was used for the stereotyped movements made by a monkey's limb on stimulation of a small area of the brain after deafferentation of the limb. The hierarchy questions he raises are also not well taken, since the neural system is definitely not an anarchy, and it is obvious that certain reflexes are suppressed when other more "important" ones are elicited. I see no danger whatsoever, other than that involved in any description of natural phenomena, in the use of "command interneuron."

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Triggering and organizing functions of command neurons in crayfish escape behavior. Progress in neurobiology requires us to forge ever tighter links between neural activity and behavior. As it becomes increasingly possible to establish causal links experimentally, the acceptable criteria for inferring causality become more stringent. Thus a neuron that fires to a dot in the animal's visual field is a candidate "bug detector." and a neuron whose electrically evoked activity elicits an abrupt leg extension is a candidate "jump command neuron," but we are now less certain than we once were that continued analysis will substantiate these convenient labels.

Kupfermann and Weiss perform a valuable service by carefully defining the neurobehavioral evidence required to label a cell as a command neuron for a specific act. They point out that the giant fibers of the crayfish are now among the best candidates for command neurons. Two of the three rigorous criteria they require are met: Activity in the giant axons can always be recorded just prior to short latency tailflips (Wine & Krasne, 1972 *op. cit.*), and direct excitations of the giants elicits escape responses (Wiersma, 1938 *op. cit.*; 1947). "Removal" of the giants by hyperpolarization has not been tried, but it would almost certainly abolish the response, since intracellular recording from the giant axons shows that the tailflip (as monitored by efferent nerve activity) and the impulse in the giant axons are perfectly corre-

lated: the "behavior" and the impulse come and go together as the sensory-evoked EPSP fluctuates around the giant axon's threshold (Krasne, 1969 and this Commentary; Wine, unpublished observations). Since the giant neurons come close to fulfilling the authors' criteria for command neuron status, it should be useful to summarize how they work, since the ultimate evaluation of the command neuron concept will come when a commanded behavior is completely explained in cellular-connectionistic terms. This goal has perhaps been most closely approximated in the case of the crayfish tailflip.

The giant axons trigger escape, and help organize, in both space and time, the pattern of muscular contractions producing rapid flexion and reextension of the abdomen. Triggering is accomplished by having the giants at the apex of a highly convergent sensory network (Krasne, 1969; Zucker, 1972 and this Commentary). Spatial organization, at least of the abdominal flexion, is achieved by an extremely divergent pattern of monosynaptic connections made between the giant axons and flexor motoneurons (Larimer et al., 1971 *op. cit.* and this Commentary; Mittenenthal & Wine, 1973).

Temporal organization is more complex and less direct. It depends, in part, on connections between the giant axons, flexor motoneurons, and a population of "corollary discharge interneurons." An impulse in the giant axons fires both motoneurons and the corollary discharge neurons; the latter transform excitation to inhibition, delay action by virtue of polysynaptic pathways, and prolong action by having delay lines of various lengths converge on a single postsynaptic cell. Timing in the circuit is also influenced by inherent differences in the durations of unitary IPSPs in different parts of the circuit. These central effects are complemented by sensory feedback, which may provide further timing cues. In this way, a 1 msec impulse in the command axons is converted into a 100-msec behavior (Krasne & Bryan, 1973; Wine, 1977a, b, c; Wine & Mistick, 1977; Wine & Hagiwara, in press).

These recent findings partially validate the general concept of a command system as shown in Kupfermann and Weiss's Figure 1. However, they also open the black boxes termed "sensory analyzer" and "motor pattern generator" in Figures 1-4, and show that the command neuron's functions partially overlap each of the compartments

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Command neurons: a more precise definition reveals gaps in our evidence and limits to our models. The imprecision and vagueness of the use of the term "command neuron," and its definition in operational rather than behavioral terms, caused me to call the crayfish lateral giant neuron a "deci-

sion fiber" (Zucker, 1972a). This term was coined to denote the neuron that was responsible for generating a coordinated behavior, in the sense that it was the only neuron whose activity always led to that behavior. The new proposed definition of a command neuron is sufficiently narrow and rigorous to be meaningful. It is also very close to what the evidence (Wiersma, 1938; Zucker, Kennedy, and Selverston, 1971; Larimer, Eggleston, Masukawa, and Kennedy, 1971; Wine and Krasne, 1972, *oper. cit.* and this *Commentary*) indicates is the biological role of the lateral giant fiber. Had this definition been current in 1972, it would not have been necessary to coin a new term to describe the lateral giant function.

The proposed criteria for demonstrating that a certain cell is a command neuron may seem unreasonably severe and frequently unattainable. It is tempting to dilute the criteria, to make them more experimentally achievable. This temptation should be resisted. I am reminded of the criteria for the establishment of a candidate agent as the "proven" transmitter substance at a synapse. These criteria, too, are stringent and rarely fulfilled. However, their rigor, and the unwillingness of neurobiologists to dilute them, have contributed to the high standards in this area of synaptic physiology. Similarly, the insistence on rigorous criteria for the establishment of a neuron as a command neuron might be expected to raise the standards of description and explanation in the field of integrative and behavioral neurobiology. By demanding that "command neuron" denote what it has always connoted, perhaps we shall come to insist that we demonstrate the functions of neurons that have up to now often been assumed.

Kupfermann and Weiss point out that the crustacean giant fibers and fish Mauthner cells are closest to fulfilling their criteria for a command neuron. Yet even the crustacean giant fibers have not been tested against all the criteria. For example, an impulse in the crayfish lateral giant has been shown always to precede a certain escape reaction to a particular class of stimuli (the correlative criterion), to be the only known cell whose activity does so (a weak form of the necessity criterion), and to elicit this behavior when it is stimulated (the sufficiency criterion). Yet, it has not been shown that removal of this neuron prevents the stimulus from eliciting the response (the full necessity criterion). This failure is due to the technical difficulty of inactivating this neuron without generally depressing the physiology of the crayfish. I think the proposed definition of a command neuron serves us well by bringing into sharp focus the limits of our evidence that the lateral giant generates certain escape responses, and by suggesting experiments that would complete the proof.

The new definition of a command neuron is not without its problems. The idea of a command neuron for a behavior carries with it the idea that there is only one cell in the circuit generating that behavior that commands its execution. But consider the input to the command neuron. There must exist, in the neurons afferent to the command neuron, some pattern of activity that triggers the command neuron to fire in such a way that it elicits the behavior. Thus one might think that every command neuron must be preceded by a network of afferents that, by the present definition, would qualify as a command system. Now the properties of uniqueness and localized function that are crucial to the command fiber concept seem to be lost, and the value of the concept becomes questionable.

In some circuits the above situation is present, but fortunately this is not always the case. Consider the crayfish lateral giant escape reflex. The afferent to the lateral giant consist primarily of a population of tactile sensory neurons and interneurons. An appropriate barrage of activity in these cells does precede each lateral giant escape response (correlative criterion) and every such response is preceded by such a barrage (necessity criterion). However, not every such barrage elicits the response (sufficiency criterion). This is because the synapses from the interneurons onto the lateral giant are subject to prolonged depression, during which activity in the tactile interneurons will not be sufficient to drive the lateral giant synaptically to threshold for an action potential (Zucker, 1972b). Extrinsic neurons may also prevent the lateral giant from being activated during tactile stimulation (Krasne and Wine, 1975). Here, a careful application of the proposed criteria for a command neuron or system shows that the lateral giant command neuron is not preceded by an afferent command system. The decision to escape from a phasic caudal tactile stimulus in crayfish is uniquely localized, and the new definition of a command neuron helps us to appreciate this fact.

This example suggests that to understand the function of a command neuron, the details of the circuit generating a behavior and the connections of a putative command neuron must be known. Without this information, no definition of a command neuron is likely to provide enough criteria to unambiguously

define a cell's function. Our ignorance of the molluscan feeding circuit is undoubtedly one of the reasons why we cannot decide whether or not to classify the metacerebral cell as a command neuron.

Kupferman and Weiss propose that only a neuron that elicits a behavior be called a command neuron. This should be a separate class from that of modulatory neurons, consisting of elements that can alter or influence behavior. Likewise, neurons that gate the behavioral expression of neural activity generated elsewhere should be distinguished from the command neuron or system that initiates the activity. It is hoped that clarity and precision of definition can add to the rigor and depth of our comprehension of the neural basis of a behavior. By distinguishing command from modulatory and gating elements, we may come to recognize that in some neural circuits there are no simple command neurons, but rather a complex command network of neurons that individually have only "modulatory" or "gating" functions. The feeding system in molluscs may be an example.

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Postcommentary by G. Hoyle

Who believes in "command neurons?" Interest in the concept of command neurons has clearly been both deep and emotional, judging by the commentaries received on the Kupfermann and Weiss article and my precommentary. I have taken the liberty of assessing subjectively the author's attitudes in the thirty-one commentaries received, and assessing them on a five-point scale ranging from enthusiastic acceptance of the term to strong rejection. Even with so small a sample, drawn from persons with widely different backgrounds and specific research interests, the distribution was gaussian, the median being persons who neither object to current usages nor find the term especially attractive. Only Davis and Stein among invertebrate specialists and Grillner from the vertebrate scene truly favor its use at this time. Seven others like the term, but not strongly. Eleven rejected its use with various degrees of dissent, while the remaining eleven vacillated on the fence. In recent literature there is also clearly seen a dichotomy between users of the term and nonusers referring to the same or comparable interneurons.

The definition and associated contingencies as proposed by Kupfermann and Weiss settled it for some. Clearly no known neuron is able to satisfy all their criteria: strictly speaking there are not yet any "command neurons" to discuss and the concept is just that. If any are eventually found, or if the full set of criteria for neurons that have already been so labeled become satisfied, there is not likely to be any disagreement with the use of this label.

For some commentators the attitude "what's in a name?" prevails. They see no difference between the term "command" and the term "driver," for example, which is preferred by some investigators, including Bentley and myself. Bentley (1977) recently discovered interneurons in the cricket cervical connective that elicit normal song patterns when electrically excited. These interneurons come as close as any that have so far been bestowed with the "command" label to satisfying the original criteria. In discussing the historical origin of the term in my precommentary, I suggested that conceptually it may have arisen out of Huber's work (1959) on cricket song. I was following leads from conversations with Wiersma himself and from discussion at the Ojai conference held in his honor in 1976 (Hoyle, 1977), at which the "command" neuron concept was discussed. Huber found that by stimulating localized areas in the cricket brain he could elicit normal song patterns. He did not consider that he had directly excited the centers, but rather antecedent neural elements (i.e., of command type). In a personal letter regarding my precommentary, he wrote that what he had in mind was "that there exists a premotor (interneuronal) system to trigger or even to switch on and off a certain unit of behavior." In a later letter he emphasized that he intended *vorgeschaltet* to mean "precede." Several persons have told me that common usage in vertebrate neuroanatomical literature

translates the word as "connected before." What I was searching for in the relevant literature was a German word with several shades of meaning that could conceivably have been flipped subconsciously by Wiersma into "command." I still think that I may have hit on the right one. Huber goes on in his letter to say "I have not used the command concept [in 1959], but out of my work one certainly could deduce such a principle."

Huber's former student Wolfgang Kutsch, with Otto Dietmar, eventually showed that the neural pattern generator(s) for cricket songs are not located in the head, as was first thought, but in thoracic ganglia. When Kutsch and Dietmar (1972) summarized this research on song production by headless crickets they wrote: "the cricket can produce songs even in the absence of neural commands from the head ganglia." Here the command concept is correctly used.

So I shall continue to refer to interneurons that others have labelled "command" cells as drivers. To say that an interneuron is a "driver" means only that the net effect of a train of impulses in this neuron generally consists of a specific set of movements. The important distinction is that this term does not imply, as labelling it a "command" neuron does, that it is the natural specific pathway for the elicitation of this same movement in the intact animal behaving naturally, which is the only critical assessment for the command concept.

Whether or not we wish to use language precisely, to cover various restricted conceptualizations accurately, may not seem important to some. But it has been found that careful use of descriptive terms is essential to communication in the hard sciences. Perhaps the differences between us in acceptance or rejection of the "command neuron" concept reflects the depth of our backgrounds in physics, chemistry, and mathematics.

We shall continue to research the neural mechanisms that underlie behavior and hope that some day we shall enjoy the excitement of finding a "command" neuron and studying it in detail.

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Authors' Response

by I. Kupfermann and K. Weiss

Quis imperat? A panorama of perspectives

Our article elicited a very large number of commentaries. This is desirable because the large number helps to insure a reliable sample of current world opinion on this topic. On the other hand, it makes it difficult to respond to the comments in detail. To facilitate our response, we have classified the commentators in terms of seven broad categories that we feel encompass the main thrust of each commentary (see Table 1). The categorization is obviously subjective and we offer apologies to those commentators who may feel misclassified.

The first category is made up of commentaries that contain significant historical remarks, frequently involving the personal role of the commentator. The second category includes those that make broad philosophical and linguistic points. The remaining five categories provide combinations of positive and negative opinion on the two main points of our article. To summarize our original points: a) we argued that there are problems with the notion of command cell as the concept has developed over the years; b) we offered an operational definition that may overcome some of these problems. The third category of commentary disagrees with our first point, that is, it denies that there is a substantial problem with the command notion. A corollary of this position is that our attempt at redefinition is unnecessary. Categories four to seven include commentaries that generally agree

Table 1. Classification of commentaries on the command neuron concept

1. Historical	Evoy, Hoyle, Larimer, Kater and Granzow, Wiersma
2. Philosophical and linguistic	Fowler and Turvey, Hoyle, Llinas and Bunge
3. Command concept is all right as is	Stein
4. Examples from biology or electronics	Balaban, Bullock, Fraser, Fentress, Herman, Horridge, Krasne, Andreae, Lewis, McCarthy
5. Our redefinition is premature	Andreae, Bennett, Burke, Chapple, Evoy, Hoyle, Iles, Lynch, Rosenbaum, Tsukada
6. Alternative definitions	Davis, Grillner, Kater and Granzow
7. Some sympathy for our redefinition, with discussion of problems	Kristan and Weeks, Larimer, Wine, Zucker

with our thesis that there are problems with the notion of command, but differ in their reaction to our attempt at a redefinition. Category four makes little or no reference to our redefinition and instead offers to illuminate the issue by offering examples, either from biology or from electronic devices. Commentaries in category five argue that it is premature to attempt a rigorous definition. Category six includes those that suggest alternatives to our redefinition. Finally, category seven includes commentaries that are sympathetic (in varying degrees) to our attempt at redefinition, but point out new problems associated with this attempt.

We will now very briefly respond to these seven classes of commentaries. For the sake of brevity we have chosen not to respond to numerous points that we feel are either valid, trivial, or are already answered by our original article.

1. Historical commentaries. On the whole, these commentaries were illuminating. That of Wiersma was especially useful in view of his central role in the development of the command cell concept. He confirms our feeling that what he had in mind was a highly specific type of cell that triggered a motor pattern generated without peripheral feedback. That is, the command cell activated a fixed action pattern of the type generally thought to exist at that time. Few, if any, subsequent workers in the field explicitly included this stricture in the use of the term.

2. Philosophical and linguistic commentaries. By and large we did not find these commentaries as useful as we would have liked, perhaps because we could not fully follow the arguments in their compressed form.

Hoyle feels that the field went astray because of some grammatical error. This appears to be a gross oversimplification of a complex problem.

Fowler and Turvey are concerned with the attempt of neurobiologists to find neural causal correlates of behavior. This attempt does not imply a search for a total causal analysis. Neuroscientists study neuronal events causally related to behavior; other scientists study a variety of other variables. Perhaps it is best left to the philosophers to provide a complete causal analysis.

Llinas and Bunge express different concerns. They appear to feel that the attempt to define a scientific term operationally is old-fashioned and outmoded. While, as they say, operationalism has died, it is obvious that it did not take operational definitions with it to the grave. Llinas and Bunge suggest that a concept may be truly defined only within a theory and that definitions of concepts in empirical terms provide only operational criteria rather than definitions. In terms of the real-life behavior of scientists, we fail to see how this alternative nomenclature will make any difference. One can argue that what we have done is to provide a shortcut for a long description of the procedure required to es-

establish a necessary and sufficient role of a cell in a behavior. Since the term as we used it does not involve any surplus meaning, the arguments used against operational definitions of theoretical constructs do not seem to apply in this case. Furthermore, since our "operational criteria" exhaust the suggested meaning of the concept of a command neuron, the concept indeed becomes a definitional criterion. This definitional criterion is expressed in terms of operations necessary to establish the existence of its referent and therefore it is an operational definition.

3. Command notion is all right. Stein stands alone in his unqualified defense of the notion of command cell. He is correct in his belief that one can use any arbitrary term to signify a well-defined concept. However, unlike the term "barn" used in his example, there is no widely accepted definition of command cell. The vast range of opinions evoked by the present article adequately attests to that fact.

4. There are problems with command - with examples from biology or electronics. We personally found the examples of analysis of electronic circuits particularly illuminating, perhaps because they bring to bear the insights of a nonbiological field that is faced with problems similar to those faced by neurobiologists.

Lewis points out that causally oriented devices without feedback may serve as rest stops that are useful in simplifying the analysis of complex devices. It is interesting that a command neuron, as we define it, appears to serve as such a rest stop; but these neurons may receive feedback and yet retain their necessary and sufficient character. Thus, although this type of command cell assists in the causal analysis of behavior, it need not be causally oriented in the sense that it exhibits clear separation of cause and effect.

5. New definition premature. A relatively large number of commentators expressed the notion that neurobiologists do not know a sufficient amount about the organization of nervous systems to come up with a meaningful definition. Chapple feels that the term "command" should be scrapped altogether. Llinas and Bunge point out that the term "command" is used metaphorically in neurobiology. This metaphor is generally a poor one and could be misleading. We agree with this important point, even though we are guilty of suggesting the continued use of the term, albeit in a rigidly defined manner. Our feeling was that indeed the term is not a good one; nevertheless, many neurobiologists will continue to use it, and a relatively precise redefinition might prove useful. Virtually any term selected, other than an unpleasant neologism, will have undesired connotations. For example, the choice of "trigger neuron" by Llinas and Bunge has the problem of using a term that has some unwanted metaphorical content, as well as being a term that is already in use in neurobiology and has accumulated various meanings. However, little would be changed if our necessary and sufficient cell were to be called a "decision unit" (see Zucker's commentary) or "critical decision unit" (Stein). A new term with somewhat less metaphorical content might be "critical control unit."

Some commentators argue that it is premature to define the concept, but leave unanswered the problems associated with the present use of the term. Consequently they suggest by implication that we continue with the notion as it exists. Unfortunately the notion exists in many different forms and thus has become a source of confusion.

Bennett expresses the feeling that too much rigor in a definition may not be useful. We agree that for many concepts the lack of a precise definition is not harmful, and indeed can be helpful. For example, the distinction between mediating and modulating events in the nervous system often depends on a somewhat arbitrary point of view. This distinction is descriptive and largely de-

void of theoretical consequences. Little is lost if two experimenters do not exactly agree on what should be termed mediating and what modulating. On the other hand, for certain terms, such as command, there is a potential for far-reaching theoretical ramifications. Confusion and failure of communication often result if these terms are not carefully defined.

Bennett also raises a large number of other points. He is concerned that our definition is trivialized since it does not naturally exclude sensory or motor neurons. He would probably agree that definitions are designed to assist our conceptualization and that we should not become their slaves. It, therefore, seems perfectly valid to exclude systematically examples (such as motor neurons) that limit the usefulness of a definition.

A second concern of Bennett's is that the difference between command and modulatory elements could arise purely from quantitative differences in coupling between neurons, and hence these differences need not reflect organizational features of the nervous system. One point of our classification is that it is meant to reflect differences in the way elements function in the generation of behavior. Quantitative differences can result in qualitative differences in functional activity. Similarities in organizational features are not important if small differences in the specific properties of the neurons result in major differences in how the system functions.

A third concern of Bennett's is that there are defects in our table of putative command neurons. Perhaps we were not clear, but the table was not meant to be all-inclusive or to review all cases of command cells. The entries are meant only to illustrate the multiple ways in which neurons could be considered to be command cells (or groups), depending on one's predilection for one or the other current conception of what a command neuron should be. We can assure Bennett that the failure to include more examples of vertebrate command cells did not result from "common invertebrate chauvinism" or ignorance about vertebrate work. Rather, the selection reflects the fact that the bulk of the conceptual and experimental work on command neurons comes from studies on invertebrates.

Another concern of Bennett's stems from what we feel is an inadequate appreciation of our conception of behavior. He suggests that depending on how a given behavior is defined, a cell may or may not be a command neuron. The example given of the Mauthner cell is not convincing. Bennett feels that since either the left or right Mauthner cell will elicit pectoral fin depression, both meet the sufficiency requirement, and hence there exists no single command neuron for this behavior (but rather two command elements). On the other hand, if the total behavior (tail flip to one side, plus pectoral fin contraction) were to be considered, then only one Mauthner cell will elicit the behavior, and hence there will be a single command neuron. This argument is faulty. The sufficiency requirement, as we define it, involves firing a neuron in the way it normally fires during the behavior. According to our analysis, the definition of the behavior must include the eliciting stimulus. Since with an asymmetrical stimulus presumably only one cell fires, it makes no sense to test the other cell, since it is irrelevant to the behavior (pectoral fin movement elicited by an asymmetrical, left or right stimulus). We would like to re-emphasize that a critical element of our analysis of command cells involves the use of a definition of behavior that includes the eliciting stimulus. We feel that attention to this feature will answer a number of the other objections raised to our definition.

Definitions serve multiple roles. In some cases they make possible a systematic theory. In this role, a redefinition of command is premature. Another feature of a definition is to help point the direction toward possible experimental approaches. It is in this second function that our definition may prove useful at this time.

6. New definition or guidelines. Kater and Granzow attempt to avoid the problem of definition by offering loose guidelines for

the use of the term. They take as their starting point a notion expressed by D. Kennedy (*op. cit.*) that a command neuron should be permissive, not instructive. They utilize a model of neural function in which one attempts to abstract a "pattern generating system" from a "command" system that triggers the pattern generator into activity. They do not specify how one goes about determining whether or not a neuron meets the criteria set by their guidelines and they make no mention of the problem of behavioral relevance. Furthermore, this approach tends to limit the notion of command to behaviors that are generated by pattern generators (similar to the original conceptions of Wiersma). Our feeling, however, is that command has come to mean something more general to many workers – referring to systems or neurons that "command" behavior, be it complex patterned behavior, simple patterned behavior, or even reflexive responses. On the basis of an approach similar to that of Kater and Granzow, it has been argued that the giant fibers in crustacea should not be classified as command fibers since they elicit a relatively simple reflexive response that does not substantially outlast the stimulus. This is ironic in view of the fact that the giant fibers constitute the best studied example of neurons that are functionally involved in the decision process or command of behavior.

Grillner starts with a notion of neural organization similar to that of Kater and Granzow. He chooses to avoid some of the problems that could arise in association with using the word "command," a term that has come to mean many different things. He suggests that neurons or systems of neurons that activate pattern generating systems be termed central program controlling systems (CPC-systems). He wisely cautions that this term should be reserved for situations where functional significance has been demonstrated and he adopts our suggestion of prefacing the term with "putative" in cases where the behavioral significance has not been adequately demonstrated. We feel that this approach may help clear the air and provide a nomenclature acceptable to a number of different scientists. Grillner does not provide guidelines for determining whether or not putative CPC-systems are involved in specific behaviors. Unquestionably, in contrast to invertebrate nervous systems, this task is highly formidable for vertebrates, and it is unlikely that any generally applicable procedures can be specified at the present time.

Davis is concerned that, due to feedback, a neuron may meet the sufficiency criterion but nevertheless not be involved in command function. In this case, however, the cell will not meet the necessity criterion and, hence, will not qualify as a command neuron. That is one of the points of our argument. The sufficiency criterion that has been traditionally used to define command neurons is inadequate by itself. Davis, as well as several other commentators, suggest that our definition is too restrictive and is overly difficult to apply in actual experimental practice. We fully agree that the definition will probably define a very small set of neurons, although the notion of "command element" should have much broader applicability. Furthermore, we agree that the criteria are difficult to test; indeed, in many instances they cannot presently be tested. Our feeling, however, is that precise behaviorally relevant definitions will always be

difficult to test. Nevertheless, the discovery and elucidation of the mechanisms underlying the initiation of behavior is one of the major aims of neurobiology. Why require that this task be simple? In part, the choice of a definition is a matter of taste. Does one prefer a relatively restricted definition, difficult to apply and test, but relatively unambiguous; or does one prefer a more general definition that is more ambiguous. We feel that the definition Davis offers is quite ambiguous. When dealing with a conceptually rich term such as command, what is accomplished by defining the term in a way that will lead to debates about whether or not a specific instance qualifies?

Davis provides several criteria for considering a cell a command neuron, by which he means one that is part of the central nervous locus of behavioral initiation. These criteria are described as "required," hence they are presumably necessary but not sufficient. The problem with them is that they are so vague that it will be difficult to determine whether a neuron meets any given one. For example, Davis suggests that the output connections must be organized so as to excite elements of a motor system. Does any type of connection, no matter how small, qualify? What constitutes a motor system?

A second proposed command neuron criterion is that it should enjoy "privileged access" to the sensory and/or central inputs that initiate behavior. How does one tell whether a neuron has privileged access? Suppose, for example, a neuron receives input, but the input is very weak relative to other neurons.

In addition to the problem of the ambiguity of the proposed criteria, Davis's definition creates a more fundamental difficulty. Suppose one could specify the proposed criteria more clearly, and a neuron met them. Davis suggests that in this case the neuron can legitimately be classified as a command cell. But these criteria do not in any way demonstrate that a neuron is part of the central locus of the initiation of behavior. That is, the criteria may be necessary, but they are not sufficient to determine that a cell belongs to the class Davis chooses to call command neurons. Indeed, a fatal flaw of this definition is that it will probably prove impossible to specify what exactly is meant by the seemingly innocuous term "behavioral initiation."

7. Sympathy for our redefinition, with critique. To varying degrees, a number of commentators expressed support for our attempt to define operationally command neuron and command systems. In each case they also discussed problems with our definition. By and large we agree with these criticisms. What we came up with was the best we could do. It is likely that the criteria will be of limited usefulness in many invertebrates and will be virtually useless, except in a theoretical context, for vertebrate neurophysiologists. Nevertheless, our hope is that the suggested criteria will contribute toward a sharpening of current ideas on the role of individual neurons or sets of neurons in the control and generation of behavior. Furthermore, our criteria may define a null set or a set with very few members. In that case our definition may contribute to a fading out of the usage of command cell, to be replaced in time, it is hoped, by somewhat more precise terms.