

Activity Versus Reactivity in Psychology and Neurophysiology

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The traditional reflex approach in neurophysiology is incompatible with modern psychology's concern with goal-directed activity. We try to show that a neurophysiological approach based on the theory of functional systems may help to solve this problem. According to functional systems theory, all the elements of the organism are organized in systems that are neither sensory nor motor, but functional; the elements of these systems are defined in terms of how they enable the achievement of useful results of behavior. To make our case for this functional systems approach, experimental data are reviewed to illustrate the significance of the behavioral context in determining the activity of both central and peripheral neurons. One key indicator of the functionally specific organization of neural elements is the role of efferent influences in the coordination of the central and peripheral neural processes, and this is discussed at some length here. We offer the present approach as a basis for a new integration of neurophysiology and psychology (systemic psychophysiology), an integration which aims not at correlations of psychological with neural phenomena, but at their methodologically consistent unification through an understanding of the organization of different levels of the organism-environment system.

METHODOLOGICAL INCOMPATIBILITY OF MODERN PSYCHOLOGY AND NEUROPHYSIOLOGY

The significance of neurophysiological knowledge in developing psychological theory is widely acknowledged (Bunge, 1990), but the integration of psycholog-

ical and neurophysiological research entails many difficulties related to the ancient mind–body problem. In this context, these difficulties are usually ascribed to psychology which is seen as methodologically differentiated and controversial, whereas neurophysiology is treated as unproblematic, as if it proceeded in a methodologically monolithic fashion (cf. Bunge, 1990). In contrast, the starting point of this article is the notion that, at present, the difficulties in combining psychological and neurophysiological knowledge are due to a marked degree to the concept, held by many neurophysiologists, of the reactive and mechanistic character of neural processes. This reactive approach contradicts the emerging appreciation of the active and goal-directed character of the behavior of organisms, apparent to many psychologists and some neurophysiologists (see, e.g., Alexandrov, 1989; Anokhin, 1978; Jarvilehto, 1982, 1984; John, 1972; Shvyrkov, 1991).

Traditionally, neural processes are studied in neurophysiology as a set of transformations starting from the effects of environmental stimuli and ending in the execution of responses. This analytic methodology has its origin in the dualistic theory of the mind and brain formulated by René Descartes in the 17th century. Descartes (1637/1970) conceived of the nervous system as a machine which could be studied similarly to any other machine. By means of this machine responding to outer influences by pumping vital spirits, the soul could acquire knowledge from the environment and also activate the muscles realizing the behavior. The basic element in the action of this machine was later called the *reflex*, a causal connection between the stimulus and the response. The materialistic philosophers after Descartes abandoned the concept of soul and regarded the reflex as a sufficient basis for the explanation of behavior. The concept of soul, however, was maintained in different notions of mental activity, although its place in the mechanistic model was unclear. Mental activity was thought to be something completely different from the material world, or it was simply identified with the neural activity. At present, the last view seems to be most common among neurophysiologists and psychophysicologists.

During the 20th century, there have been attempts in biology and psychology to reject the analytically linear and mechanistic explanation of behavior. For example, Jakob von Uexküll argued that the behavior of animals cannot be understood as a linear set of events, starting with the excitation of receptors, but instead should be described as a functional circle (*Funktionskreis*). According to von Uexküll, the behavioral environment does not consist of a set of physical stimuli common to all animals, but each animal species has its own experienced environment (*Umwelt*) which it forms according to its needs (Uexküll & Kriszat, 1932/1957). At least since Dewey's (1896) classic critique of the reflex-arc concept, the central idea of an *active*, not *reactive* character of the interaction between the organism and the environment began to emerge within American functionalism, European Gestalt theory, and Soviet activity theory (Bernstein,

1967; Koffka, 1935; Leontjev, 1975; Rubinstein, 1977; Tolman, 1932). Ideas incorporating several of these trends were developed by the founder of ecological psychology, James J. Gibson. According to Gibson (1979/1986) each organism actively divides its environment into *affordances* which allow different kinds of behavior. Organism and environment are not separate entities, but form a functional unity, for which the stimulus-response (S-R) association is not an appropriate unit of analysis. Thus, at a general methodological level, many psychologists have abandoned the concept of reflex or S-R association as a unit of explanation for behavior.

This emerging psychology of the active and goal-directed character of behavior has been difficult to combine with the "reactive" point of view of neurophysiology. Such difficulties have usually been overcome with the "help" of eclecticism, such as the ad hoc use of the reflex concept when dealing with concrete "mechanisms" of goal-directed action (e.g., Leontjev, 1975). In psychological fields that are traditionally more closely related to neurophysiological research (psychophysics, psychology of perception, several branches of cognitive psychology), Cartesian dualism is still present (see, e.g., Michaels & Carello, 1981; Reed, 1988; Jarvilehto, 1985, in press; Still & Costall, 1991). The other strategy has been to neglect neurophysiological data altogether because of its incompatibility with psychological concepts, as occurs in much of cognitive and social psychology.

It is understandable that neurophysiologists, who study detailed mechanisms of the neural processing of stimuli, relations between neural units, and the molecular-biochemical basis of the processes in the nervous system, belittle psychological descriptions and speculations about the activity or goals of the organisms. For most neurophysiologists, such concepts represent only provisional descriptions which will be replaced by explanations at the cellular or molecular level.

This presumptive reductionism is, in effect, an abandonment of the basic goals of neurophysiology. From its beginnings, neurophysiological research has been aimed at understanding the neural basis of the real behavior of organisms, their adaptive interaction with their immediate environment. However, with the development throughout the 20th century of new methods and with discoveries of new details in the activity and structure of the nervous system (nerve impulse, synapse, inhibitory and excitatory actions, receptive fields, etc.), the original goal was lost by many investigators and research tended to concentrate on subproblems, the clarification of which was thought to be possible without considering the behavior of the organism. The concept of reflex as the unit of behavioral analysis supported this development: It was often thought that when all the details about the reflex arc were known, it would be possible to explain the real behavior of organisms without reference to mental activity or goals of the organism.

ALTERNATIVE TO TRADITIONAL NEUROPHYSIOLOGY

Recently, mechanistic models of neural functioning have been questioned within neurophysiology (e.g., Edelman, 1987; Grobstein, 1989). In fact, over 50 years ago, a neurophysiological approach had already been developed which abandoned the reflex approach and which still may build a methodologically compatible bridge between psychology and neurophysiology. This is the *theory of functional systems*, first formulated by Peter Anokhin in the 1930s (see Anokhin, 1974).

In terms of functional systems theory, all activity of the organism is described as a realization of numerous functional systems such as those for taking food (see next section), avoiding harmful effects, or breathing. Anokhin (1974, 1978) analyzed and described in detail many different kinds of functional systems, their development, and their realization. These systems consist of dynamically organized activity of selectively involved elements (both neural and others) of the organism, the interconnected cooperation of which realizes the achievement of useful results of behavior. Although these systems serve different purposes, have different elements, and operate by different executive mechanisms, they have the same basic "systemic architecture" (Anokhin, 1974)—the same basic organization.

The fundamental concept of the theory of functional systems is the *result of behavior*, a forthcoming event which is in the future in relation to the given behavior. All behavior is goal directed; the goal is conceived as a model of the result which is the factor determining the systemic architecture of the functional systems. The result is a new relation between the organism and environment, an achievement of a concrete adaptive change in the interaction between the organism and environment, that is subserved by the organization of the activity of the organism in behavioral acts. According to functional systems theory there are no sensory or motor mechanisms, special central or peripheral processes. Rather, there are only functional systems in which elements with different anatomical localization are coordinated for the achievement of the result of behavior. Any processes in the organism can be understood if considered in relation to the future, not to the past events.

It is important to note that there are other concepts that seem to be analogous to this approach. One of these concepts is *anticipation* which also describes processes directed toward the future. However, this concept, which was developed in the frame of the reflex approach, is based on the traditional understanding of the sequence of events, from stimulus to response. What supposedly is anticipated is a stimulus and during anticipation the organism is only conceived to be preparing a reaction to the stimulus. Furthermore, this "preparation" is also a reaction to some external or internal stimuli. From the point of view of functional systems theory, which is based on the behavior-to-result sequence, there is no anticipation in this sense, but only organization of the

organism–environment relation as a whole, directed toward results, in which any possible events in the environment (“stimuli”) are integrated.

Similarly, all such concepts as *reafference* (Holst & Mittelstaedt, 1950) or *feedback* are only extensions of the reflex scheme to the explanation of the phenomena of goal-directed behavior. All such approaches, even if defining the reflex not as an arc, but as a circle, retain the linear S–R point of view and describe only possible mechanisms of the arc, or of the circle, but without real change of methodology. Indeed, many reafference models also treat anticipation as the preparation of responses to potential stimuli.

From the position of functional systems theory, the whole methodology of the study of the functioning of the organism changes in principle. S–R relations are no longer the focus, but rather the organization of the activity of the organism directed toward the future. This methodological change is reflected at every level of analysis, even in the study of the activity of single neurons. Because neurons are not seen as having to obey S–R laws, they are not seen as reacting to presynaptic influences by firing; rather they are seen in terms of their activity with other neurons (and elements of the body) in achieving a new relation between the elements of the organism and between the organism and environment as a whole (which is the way neurons influence their own chemical “environment”). Therefore, even the characteristics of single neurons must be studied in this dynamic behavioral context and not in static relation to more or less arbitrarily defined “stimuli.”

To be able to carry out investigations of neuronal unit activity based on such principles it is clear that anesthetized or immobilized animals cannot usually be used. The animal must be able to realize its behavior to achieve its goals. Moreover, in this kind of investigation the behavior of the animal is not used—as is often the case in traditional neurophysiology—as a method of investigation (e.g., as a way to attract the animal’s attention, to fix its gaze, or to get it to perform certain movements), but as the real object of the study.

In the study of the neural basis of motor control, the viewpoint has emerged that the activity of the units in the motor cortex depends on the behavioral situation and is more related to the occurrence of behavior than to which muscle is activated (Fetz & Finocchio, 1975). In contrast, within sensory physiology (which has much more influence on psychology than the study of motor control) such relations to behavior are not usually expressed and the position of traditional Cartesian dualism is especially prominent. Therefore, we deal here with the neurophysiology of “sensory” structures.¹ It is here where the difference between the traditional and systemic approaches can be seen most clearly.

In this article we argue that neural units are not reactive but active in character, their activity being dependent on behavioral results and the context

¹We regard the terms *sensory* or *motor* structures or neurons as referring to anatomical classification of structures of the nervous system (cf. Masterton & Berkeley, 1974; Reed, 1982).

of the experimental situation. We describe, mainly on the basis of our experimental studies, what kind of new explanations of the known "facts" and what kind of new questions emerge from the systemic approach to the study of the neural basis of goal-directed behavior.

GOAL-DIRECTED BEHAVIOR AND THE ACTIVITY OF "SENSORY" NEURONS

Receptive Fields of the Central Sensory Neurons

The study of how the activity of sensory neurons depends on the characteristics of physical stimuli is based on the knowledge of anatomical connections of sense organs with particular brain structures and on the view that these central structures process information about the physical properties of the environment, "coded" by the peripheral receptors. Traditionally, neurophysiological studies of the processing of environmental information are based on testing of the *receptive fields* (RFs) of neurons. It is assumed that the complex environment can only be represented as a set of physical features "coded" by the activity of neurons with RF characteristics corresponding to these features. In these studies, the RF is the unit of analysis of the environmental information, and the activation of a central neuron with a certain RF is interpreted as a response to the activation of a receptor and lower level neurons.

From our point of view, the characteristics of the RF of a neuron involved in a system directed to the achievement of the given result should change when the same result is achieved under different conditions, just as the "motor fields" (Fetz, 1981) of neurons change when the behavioral conditions are varied. Thus, RFs should be modifiable.

This is, indeed, what can be seen in many experiments. A sensory neuron may be functionally connected at different times with different receptor elements (Zimmerman, 1983). Furthermore, RFs are affected by stimulation and blockade of descending pathways (Adkins, Morse, & Towe, 1966), heterosensory stimulation (Weingarten & Spinelli, 1966), vestibular influences (Tomko & Barbaro, 1981), anesthesia (Chapin, Waterhouse, & Woodward, 1981), ethanol (Chapin & Woodward, 1982), and by iontophoretic application of biologically active drugs (Dykes, Landry, Metherate, & Hicks, 1984; Zielgansberger & Herz, 1971). In fact, these studies show that practically all RF characteristics are subject to modification: The sensitivity, "on-off" relation, orientation specificity, directional selectivity, size, shape, localization, and even submodality (e.g., shift from tactile to hair or proprioceptive is possible) of the RF of a sensory neuron may be modified. Moreover, the RF of some neurons may disappear under certain conditions and emerge under others. Such changes

are typical of all sensory structures, of the cortical, subcortical, spinal, and retinal neurons.

RF modifications of central neurons are especially observed in behaving animals. They have been demonstrated in experiments with varying behavioral conditions (Dubner, Hoffman, & Hayes, 1981; Hyvarinen, 1982; Mistlin & Perrett, 1990). Differences can be seen in the activity of the central neurons also between the effects of passive stimulation (testing of RF) and active contact with environmental objects (Hyvarinen, 1982; Lemon, 1981).

We (Alexandrov & Grinchenko, 1984) compared unit activity in the somatosensory and visual cortex of the rabbit during RF testing with activity during food-acquisition behavior to determine whether the activity of a neuron in the sensory cortex during food-acquisition behavior could be predicted on the basis of the properties of its RF. RFs were tested when rabbits were maintaining a stable posture prior to and immediately after performance of 20 to 30 cycles of food-acquisition behavior (each behavioral cycle consisted of the following phases: act of approaching the pedal, pedal pressing, turning to the feeder, and taking food from the feeder). The behavior of the rabbit was video-recorded.

In the RF testing, most neurons had low selectivity (i.e., they were activated by receptive surface contact with any object with varying form and area), although the markedness of activation could change with the speed or direction of the movement of the test object. The range of the testing parameters was intentionally wider than the normal range of stimulation occurring naturally during food-acquisition behavior. During the food-acquisition behavior, similar contacts of the receptive surfaces with environmental objects were determined from the video recordings.

The comparison of activity of units in the somatosensory cortex during RF testing with the activity of the same neurons in the food-acquisition behavior revealed three groups of neurons: (a) those whose activity during RF testing enabled prediction of their activity in the food-acquisition behavior (40%), (b) those for which this was only partially true (34%), and (c) those showing no correspondence between the activity characteristics in the two situations (26%). (Neurons in somatosensory cortex with proprioceptive and nonspecific visual RF as well as neurons in visual cortex with a specific visual RF could also be classified into these three groups.)

Generally, differences between the activations were seen for 60% of the units in the sensory cortical areas during RF testing and goal-directed behavior. The results showed that somatosensory and visual cortex units that have a certain RF during RF testing may modify or even lose it during food-acquisition behavior. Therefore, the activity of a unit in the food-acquisition behavior cannot be reliably predicted on the basis of its activity during RF testing. Furthermore, these RF modifications corresponded to the most pronounced RF changes that were described in the analytic experiments (i.e., up to the complete disappearance of the response during the stimulation of the respective receptive

surface). Chapin and Woodward (1982) reported similar data, but with different RF localization, during different behavior and in a different species (rat). Therefore, it seems justified to state that the differences in RFs during "passive" testing and active behavior reflect a basic pattern of variation in the organization of unit activity.

Furthermore, if a neuron of a sensory structure can be activated by stimulation of a certain receptive surface in one behavior (during RF testing the organism also behaves—i.e., it performs some form of defense or orienting behavior), but not during another (e.g., food acquisition), it is natural to suppose that the opposite situation may also be possible: Activation of the unit may occur during the stimulation of a certain receptive surface in the "active" behavior, but not during RF testing. This proposition is supported by the data reported by Sakata and Iwamura (1978). They found units in the primary somatosensory cortex of the monkey that had no RF on the palm during RF testing and were not activated with passive hand displacement. They were, however, activated during grasping of certain objects. Also in the postarcuate cortex of the monkey, units were found with RFs that could be determined only when the receptive surface contacted an object during execution of goal-directed movements (Rizzolatti, Scandolara, Gentilucci, & Camarda, 1981).

If the RF of a neuron is not its stable, behaviorally independent characteristic, what then is the meaning of the receptive field? Receptive field may be treated in two ways: (a) as an experimental observation (phenomenon) or (b) as a concept describing basic regularities of "information processing" in the sensory "systems." The RF *phenomenon* refers to the experimental relation of unit activity with specific parameters of stimulation of the receptive surface. The RF *concept*, however, is based both on this observation and on certain assumptions about the specific function of the sensory structures ("sensory information processing"). The RF concept thus includes the assumption of a hierarchical analysis of stimulus objects, proceeding from groups of lower level, specific receptive elements with fixed RFs to feature detectors, and to the higher level integration that finally corresponds to or is identical with the perception of the given object.

Despite widespread assumptions to the contrary, when it comes to the RF concept, the activity of single neural units to stimulation parameters does not reveal the relation of that unit to the stimulation as such, but to the behavior in which such stimulation is involved. Therefore, when relating the activity of units to stimuli there is necessarily variability, which has even been considered a basic characteristic of neural systems (Burns, 1968). However, if the activity of a unit is related to specific behavior(s), it will be constant after varying stimuli with the same behavior (John & Morgades, 1969) as much as it will be variable after identical stimuli with different behaviors (Travis & Sparks, 1967). In experiments in which the behavioral significance of stimuli is not fixed, repeated stimulation may be associated with variable and uncontrolled behaviors. Thus,

variability increases in awake animals and may be reduced by training the animal to perform specific behaviors after given stimuli (Miller et al., 1972).

Thus, in behavioral situations, the receptive fields of the units may be stable, or modifiable up to their disappearance, because the units are related to different kinds of behavior. For a given neural unit, one type of behavior may in general be related to the contact of the organism with a certain object, but for another unit involved in a different behavior, such relation may not be constant. Such different relations may be due to the formation of specialization of units during different stages of individual development (Alexandrov, 1989), especially during early ontogenesis (Grobstein, Chow, Spear, & Mathers, 1973). The difference between stable and modifiable RFs is thus relative and dependent on the method of analysis. Even very stable RFs of peripheral units may be modifiable (see next section).

In conclusion, the activation characteristics of a central sensory neuron in relation to the stimulation of a given receptive surface depend on the context of the behavior during which this stimulation occurs. The differences in the neuronal characteristics can be observed both in the *activity characteristics* (change of RF) of the neuron and in the *set of the neurons* activated (disappearance or appearance of RF) when applying similar stimulation in behavioral acts characterized by different goals.

Properties of the Peripheral Receptors

It is a common view today that activity in the peripheral afferent system rigidly reflects physical characteristics of stimuli. Its formulation, as Reed (1982) noted (and its persistence, we must add), is based on the concept of the reflex, which presupposes peripheral constancy of the sensory input, whose relation with motor output may be modified only by changes in the central neural circuitry.

However, both data and theoretical notions exist indicating that modification of the activity of the peripheral receptors may occur when the behavioral context changes (Alexandrov, 1989; Jarvilehto, 1990). The principle of functional systems theory concerning the dynamic unity of center and periphery (Anokhin, 1974) in systems directed toward useful results presupposes that the dependence of unit activity on behavioral situations applies not only to central, but also to peripheral units. Therefore, in contrast to traditional input-output methods, receptor activity should be studied in relation to the task of the subject as well as to the stimulus parameters as such.

To test experimentally whether this hypothesis is accurate, Astrand, Hamalainen, Alexandrov, and Jarvilehto (1986) used microneurography (Jarvilehto, 1977) and compared the responses of human cutaneous mechanoreceptors during two different tasks: (a) magnitude estimation of sensations produced by tactile pulses, and (b) counting of deviant tones in a series of quickly

repeated tones. During both tasks, physically identical pulses were delivered to the RF of the receptors. (see also Soininen & Jarvilehto, 1985).

The main result of the experiments was that for 48% of the recorded mechanoreceptive units, lower receptor thresholds, a larger number of impulses, shorter interspike intervals within response bursts, or shorter response latencies were found in the magnitude estimation situation as compared with the counting of deviant tones. Thus the sensitivity of the units was higher during magnitude estimation than during the counting task.

These findings point to task factors that may modify the activity characteristics of cutaneous mechanoreceptors. Analytic experiments have demonstrated that the activity of the cutaneous mechanoreceptors may be affected by both direct and indirect influences (Janig, Sundlof, & Wallin, 1983; Roberts, Elardo, & King, 1985). Furthermore, investigations of the activity of the human sympathetic nerve fibers (Hallin & Wiesenfeld-Hallin, 1983) indicate that efferent influences may change receptor activity in behavior.

The dependence of the activity characteristics of the peripheral sensory neurons on the behavioral context indicates that this activity is a result not only of external influences, but also of central (efferent) effects. Such interaction clearly undermines concepts of unequivocal peripheral "coding" of stimulus features by the receptors. It may be further hypothesized that the modifications of the receptor activity during different behavioral acts are related to those behavioral changes of central sensory neurons discussed in the previous section.

IS "SPECIFIC STIMULATION" NECESSARY TO ACTIVATE THE SENSORY NEURONS?

Behaviorally Related Activations of Neurons in the Visual Cortex

According to our conception, the dependence of sensory neuron activity on the behavioral context indicates that the activity of all neurons, sensory units included, subserves the achievement of some behavioral result. If this is true, then activation of sensory neurons could occur without contacting the parts of the environment that are "modality-specific" for these neurons and that are traditionally related to activations of these neurons.

We examined this assumption in experiments (Alexandrov & Alexandrov, 1982) with rabbits trained to snatch carrot pieces presented on a moving rod, either with their eyes open or with their eyes closed by nontransparent cups preventing any visual influences from the environment (controlled by visual-evoked-potential technique). Unit activity was recorded from the visual cortex during the different phases of the behavior when the eyes were open or closed.

After the eyes had been closed, in some neurons activations related to certain

phases of the food-taking behavior disappeared or occurred at another phase of the behavior (as compared to the trials with the eyes open), or sometimes the structure of the activation was changed.

The fact that the activity of the units in the visual cortex changed after the "visual" environment was abolished is certainly not unexpected, as there is the widespread view that the neurons in the visual cortex realize specific "visual" functions. We point to another aspect of the results in this connection: Even when there was no "processing of the external visual information from the environment":

1. Activations of the units in the visual cortex were observed during all phases of behavior.
2. In the trials with the eyes closed, some neurons displayed activity at the same behavioral phase as they did with the eyes open.
3. Neurons that displayed no activations with the eyes open became activated with the eyes closed.

Thus, the "specific stimulation" that is considered to be the primary determinant of the activity of the units in the visual cortex was not necessary for the activation of many visual cortex units (about 60% of the units that were activated with the eyes open) to appear in behavior.

Of course, such activations of the units in the visual cortex in behavior with the eyes closed could be explained by nonspecific influences (through, e.g., vestibular or proprioceptive afferents). Such an explanation, however, does not help us to understand the functional role of these activations. It is important to emphasize the possible role of the activations in the organization of the behavior: The behavior-related activations indicate that the visual cortex neurons have a behavioral role even in the absence of the effective visual environment. That such activity may really subserve behavior is indicated by Lashley's (1950) results: Rats that had no contact with the "visual component" of the environment during the learning process demonstrated behavioral disorders following lesions of the visual cortex.

Behaviorally Related Activations of Peripheral Neurons

Because peripheral receptive elements are traditionally considered as transducers of specific stimulus energy, it is very difficult (if possible at all) from the traditional point of view to suppose that these elements could display behavior-related activations, in the absence of "modality-specific" stimulation. However, the fact that many peripheral neurons are "spontaneously" active may have functional significance. For example, the retinal "darkness light," is considered as a necessary factor in proper functioning of the central neurons; its absence would mean "natural deafferentation" of the central areas (Granit, 1955).

Because we observed behavior-related activations in the neurons of the visual cortex even when the animal's eyes were closed, it might be supposed that the absence of specific stimulation does not necessarily lead to deafferentation, but peripheral visual neurons could serve central units by producing behavior-related activations even without external influences. To examine this possibility, Alexandrov, Grinchenko, Shvyrkov, Jarvilehto, and Soininen (1986) recorded activity of the fibers in the central part of the optic tract² in rabbits performing the food-acquisition task with open eyes and with eyes closed by nontransparent cups.

The most important finding in these experiments was the existence of activations in the majority of fibers of the optic tract, which were organized in relation to the phases of the behavior also when the animals' eyes were closed (i.e., when there were no external influences on the retinal receptors). From the traditional point of view, this would be understandable if the fibers were not afferent, but efferent ones. However, all the observed effects of the closure of the eyes were typical of afferent fibers of the optic tract (i.e., for the retinal ganglion cells; for detailed classification criteria, see Alexandrov et al., 1986).

Why are there Efferent Influences in the Periphery?

Activity of the retinal ganglion cells in darkness is quite a common phenomenon (Witkovsky, 1971). It is obvious that the changes of this activity in relation to the phases of the behavior can be accomplished only by efferent influences on the retina. At present, much data has accumulated demonstrating the existence of efferent fibers in the optic tract and of efferent influences on the retina in different species ranging from frogs to man (e.g., Hasselt, 1972; Livingston, 1978; Eason, Oakley, & Flowers, 1983) and including rabbits (Cragg, 1962). However, the significance of these influences was usually either considered unclear or explained as modulation of peripheral sensory elements' responses to the stimuli of the specific modality, related, for example, to intermodal interaction (Granit, 1955; Santini, 1976; Witkovsky, 1971). As noted by Collet (1973), the behavioral role of these influences was hardly considered, because most experiments were carried out in paralyzed or decerebrated preparations under conditions having nothing to do with actual behavior.

Our experimental results concerning the task effects on cutaneous mechanoreceptors (Astrand et al., 1986) could be interpreted as showing that efferent influences only modulate the sensitivity of peripheral elements to specific stimuli, depending on the attention of the subject. However, existing evidence indirectly supports the view that the retinal ganglion cells may have efferently

²The retina is generally treated as a part of the brain moved to the periphery. However, when the retina is compared with other morphological levels of the visual system it is referred to as a "peripheral system" (Burns, 1968; Granit, 1955; Witkovsky, 1971).

mediated activations in behavior during the change of the relation between the organism and environment, independent of any changes in the "visual part" of the environment: Intermodal influences may reorganize the activity of the retinal ganglion cells in absence of visual stimulation (Sandeman & Rosenthal, 1974; Spinelli & Weingarten, 1966). Our results on behavior-related activations of peripheral visual neurons show directly that efferent influences may determine the activity changes in the peripheral sensory neurons, which are related to the phases of the behavior in absence of any specific stimulation. In the absence of visual stimulation, there can be no way of "coding" the external "optic information" and so there would be no need for modulating retinal activity.

Granit (1955) noted that the discharges of the efferent fibers may significantly influence the spontaneous activity of the elements of the "sensitive structures" and alter the frequency of their constant firing to any required level. "Darkness" activity changes in ganglion cells, related to the phases of behavior, confirm this viewpoint, but with one addition: Efferent influences must be organized in relation to the behavioral phases in the darkness also. This is shown by the results concerning the behavior-related activity of the visual cortex neurons in the eyes-closed situation. Similar data have also been obtained for other central neurons in the hypothalamus (Rolls, Burton, & Mora, 1976), in the hippocampus (O'Keefe, 1979), and in the pulvinar and lateral geniculate body (Wei & Marczynski, 1979).

Thus, efferent influences organized in relation to the phases of behavior with the eyes closed form a persuasive argument against the interpretation of these influences in the sense of filtering, modulation, or feedback (cf. Santini, 1976). We suggest that the role of these influences is rather the coordination of the activity of the retinal ganglion cells with other neural elements, this coordination being necessary for the achievement of the results of the behavioral acts both with open and closed eyes. In fact, Livingston (1959), in a review concerning central control of receptors, hypothesized that the mechanism of central efferent control acts as a factor introducing into "perceptual processes the active organizing principle, including the aspect of a *goal*, the principle that determines the selection of messages from the most early stages of their generation" (p. 757, italics added).

In addition to efferent influences there are also other factors involved in retinal, or peripheral-central, coordination. Especially in behavior without artificial limitations, the organization of the activity of the neurons in the nervous system influences the activity of the retinal ganglion cells through the environment (i.e., through the activity of the receptors), because ultimately it is the behavioral goal that determines the direction of head and eye movements toward certain objects. Thus, when behavior is realized without artificial limitations, the efferent influences interacting with the effects of the goal-related changes in the external influences on the receptors form the basis of that organization of the activity of the central and peripheral neuronal elements, which is necessary for the achievement of useful results of behavior.

CONCLUSIONS

The experimental results and theoretical considerations reviewed here show that the activity of both central and peripheral sensory neurons depends on the context of the behavior and that there are efferent means for adjusting the activity of the central and peripheral neurons to correspond to the demands of the behavioral situation. Thus, all neural activity has an active character; that is, it is integrated and coordinated in relation to the results of behavior, not to external "stimuli" as such. A neuronal unit is not a responding element, but is actively subserving the accomplishment of behavioral results. Thus, our view is in agreement with that of Edelman (1987), who argues for the abandonment of information processing as the primary mode of brain function. From this viewpoint, there is no basic difficulty in combining neurophysiological data with theories about the goal-directed character of human or animal behavior. The combination of neurophysiology and psychology becomes possible, although psychologists rejecting traditional neurophysiology have been right: The idea of linear "information processing" by the neurons or sets of neurons and the concept of reflex are both incompatible with the concept of the active character of behavior, not only at the psychological, but also at the neural level.

Our approach may help to develop more general solutions for basic psychophysiological problems. From the systemic point of view, behavior is realized by sets of functional systems which may be analyzed in neurophysiological terms (e.g., by the methods of unit recording or by examining the slow electrical activity of the brain by electroencephalograph during behavior). This does not mean, however, that mental activity could be reduced to the neural one, because mental activity is a systemic characteristic of the organism-environment relation as a whole.

These considerations strongly support psychological experimentation dealing with real behavior of participants and avoiding simple S-R conditions. The results of such experiments should not be eclectically combined with traditional neurophysiological data based on S-R relations, but rather with neurophysiology, in which unit activity or other parameters of the brain's activity are studied to understand the systemic organization of the nervous system in behavioral contexts. Neurophysiology based on such methodology is faced with psychological problems and may be considered as systemic psychophysiology.

Our approach leads to reinterpretation of many old problems about the detailed relation between behavior and neural activity, for example:

1. If there are no separate afferent and efferent components, does it mean that a behavioral act has a homogeneous structure, or can it be divided into "subunits?"
2. What kind of differences exist between the different parts of the nervous system in relation to the realization of behavior?

3. Is the behavioral role of different neural structures fixed, or can it be changed in normal (e.g., during learning) or pathological cases?

Answers to such questions are the task of future work, but we have in our recent studies developed them on the basis of the *historical approach* to neural functioning. In this frame, the separate behavioral acts are considered as a simultaneous realization of numerous functional systems, formed at the consecutive phases of the development of the behavior of the organism. Functional differences between the different parts of the nervous system are related to the differences between the patterns of *behavioral specialization* (Alexandrov, Grinchenko, & Jarvilehto, 1990) of the units in these structures. Behavioral specialization means participation of the units in the realization of certain functional systems of different "ages" which are formed during early or late phases of individual development (Alexandrov, 1989; Alexandrov & Alexandrov, 1982; Shvyrvkov, 1986). For example, in the limbic cortex, more units belong to systems formed in the later phases of individual development, whereas in the motor cortex, most neural units belong to systems formed earlier in ontogeny. Furthermore, the pattern of behavioral specialization of units of the given structure has been shown to change in pathological conditions (Alexandrov, Grinchenko, & Jarvilehto, 1990; Alexandrov, Grinchenko, Laukka, et al., 1990) as well as during learning (Gorkin, 1988). During recovery of behavior after brain lesions and during learning, the number of units belonging to the newest systems increased, but during the acute influence of alcohol the number of these units decreased.

This approach to analyzing the activity of the nervous system may form the basis for a new, methodologically consistent systemic psychophysiology which does not aim at correlations of phenomena in psychology and neurophysiology, but at their methodologically consistent unification by understanding the organization of different levels of the organism–environment system.

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