The Theory of the Organism-Environment System: III. Role of Efferent Influences on Receptors in the Formation of Knowledge*

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Abstract—The present article is an attempt to give—in the frame of the theory of the organism-environment system (Jarvilehto, 1998a)—a new interpretation to the role of efferent influences on receptor activity and to the functions of senses in the formation of knowledge. It is argued, on the basis of experimental evidence and theoretical considerations, that the senses are not transmitters of environmental information, but create a direct connection between the organism and the environment, which makes the development of a dynamic living system, the organism-environment system, possible. In this connection process, the efferent influences on receptor activity are of particular significance because, with their help, the receptors may be adjusted in relation to the parts of the environment that are most important in achieving behavioral results. Perception is the process of joining of new parts of the environment to the organism-environment system; thus, the formation of knowledge by perception is based on reorganization (widening and differentiation) of the organism-environment system, and not on transmission of information from the environment. With the help of the efferent influences on receptors, each organism creates its own peculiar world that is simultaneously subjective and objective. The present considerations have far-reaching influences as well on experimental work in neurophysiology and psychology of perception as on philosophical considerations of knowledge formation.
Keywords: efferent, epistemology, influences, knowledge, movement, perception, receptors, senses, systems approach.

Introduction

DURING THE PRESENT century, several scientists have stressed the mutual dependence of the organism and its environment. Koffka (1935), for example, described an organism as a system that consists of both the body of the organism and its behavioral environment. Especially during the last decade, there have been several attempts to treat organisms as complex dynamic systems that have a very intimate connection with the environment (Freeman, 1995; Thelen, 1995; Tani and Nolfi, 1997) or that even include parts of the environment (Gibson, 1979; Maturana and Varela, 1987; Järvilehto, 1998a).

One of the basic problems in understanding the characteristics of such systems has been the question of formation of knowledge. From ancient times, the senses have been thought to have the role of channels through which knowledge arrives from the environment into the organism. The conception of the senses as "windows of knowledge" was so strong and irrefutable that usually attempts to treat organism and environment as one system broke down just here and the system had to be divided into two sub-systems. When dealing with

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perception Koffka (1935) divided the animal-environment system into two systems, the environmental stimuli being represented in the animal in the form of isomorphic fields, and Gibson (1979) used the metaphor of resonance implying that the animal and environment were resonating as two separate sub-systems.

The arguments of sensory physiologists seem indisputable: the eye responds to light and transmits a picture from the environment. Let the philosophers speculate otherwise—in any case, the light stimulus is outside and perception inside! Although in the history of philosophy and psychology there has always been some dispute on whether human knowledge is based directly on the functioning of the senses or whether it is, in some sense, constructed by thinking (empirism contra rationalism), there has been no question about the role of the senses as transmitters of at least some kinds of raw data or simple sensations from the environment.

The Role of Movement in Perception

The theory of the organism-environment system (Jarvilehto, 1994, 1998a,b) starts with the proposition that, in any functional sense, organism and environment are inseparable and form only one unitary system that is organized for useful behavioral results. Thus, the formation of knowledge cannot be based on any transfer process from the environment into the organism, because there are no two systems between which this transfer could occur. According to the theory, mental activity is activity of the whole organism-environment system, and the traditional psychological concepts (like perception) describe only different aspects of organisation of this system as a whole. Knowledge is the form of existence of the organism-environment system, and new knowledge is created by perception when new parts of environment join to the system while changing the structure of the system. An increase in knowledge would mean a widening and differentiation of the system, which would make new kinds of behavioral acts and new results of behavior possible. From this, it would follow that knowledge is not, as such, based on any direct action of the senses.

Such a conclusion may seem to be simply contrary to the facts. However, there are some earlier considerations that go in the same direction, namely those ideas in which the role of movement has been stressed in perceptual activity. Already in 1855, Alexander Bain proposed that sensory and motor action together constitute conscious perception. He stressed the role of eye movements and thought that they determine, to a large extent, what we see. If the eyes move in a circle, we see a circle and the perception of a straight line is based on linear movement of the eyes. He maintained that the content of perception was directly related to the character of the motor activity.

In addition, the founder of experimental psychology, Wilhelm Wundt, saw the importance of motor activity when trying to explain visual illusions, for example. The horizontal-vertical illusion was, in his opinion, a typical example: here we have an illusory lengthening of the vertical line because the eyes must move upwards along the line and oppose gravity, and thus the energy needed for the eye movement is higher than with the horizontal movement of the eyes. Wundt (1897) writes: "The phenomena of seeing teach us that the idea of distance between two points depends on the motor energy of the eye used when the eye moves this distance (...) The motor energy becomes a component of the idea by combining with the sensation which we may perceive." (Wundt, 1897).

Wundt thus regarded sensation and motor energy as separate components of an idea. This would mean that, besides the sensory stimulation, movements have an essential significance for perception. Thus, perception would not be simple copying of the environmental stimuli.

Several researchers have recently developed "motor" theories of perception associated with these early ideas (for a review, see Coren, 1986), according to which perception is always a result of co-operation between the sensory organs and muscles. However, these theories usually preserve the traditional conception of the role of senses as transmitters of environmental information. The movements are thought only to modify the process of formation of knowledge; they are not considered as authentic parts of this process.

The Dynamic Character of Nervous Activity

The traditional conception of the senses as transmitters of knowledge is explicitely based on the idea of two systems (organism and environment) between which the transfer of knowledge occurs. This process has been formulated during the last decades with the help of the information theory. According to this theory, developed originally for the description of automata (Shannon, 1948), formation of knowledge is based on information transmission carried out by signals (stimuli), in which the information is stored with the help of a code. When applied to the description of the action of the senses, this means that the stimuli are transformed in the receptors into nervous activity according to a well-defined rule, the neural code, which may be later used by the central nervous system in the process of decoding, or reading the information from the neural signal (Somjen, 1972).

There have been several candidates for the neural codes: firing frequency in the neuron, intervals between the discharges, patterns of intervals, number of fibers or cells activated, location of the neurons, etc. Regardless of what the code is, the information processing approach presupposes that there must be a decoder in the organism system—a group of cells, some brain area, or homunculus—that can read the information from the signals. Such a decoding process is possible only if this decoder knows the code used in the modification of the signal in the periphery, and if this code stays constant or does not change suddenly without advance warning. Basically, the decoding process is possible only if the relations between the cells in the periphery and in the central nervous system stay constant under different action situations. However, the experimental findings during the last decade have questioned precisely this basic assumption.

Many neurophysiological studies have recently shown that neural responses do not simply follow the given stimuli, but often have a dynamic character, showing no simple dependence on the stimulus parameters. For example, if the same stimulus is repeated or presented under different conditions the responses may vary considerably. This is true of both specific cells in the central nervous system and of receptor cells in the periphery (Freeman, 1995).

Until recently, it has been an undisputed fact that the peripheral nervous system acts as a kind of passive transducer coding the environmental stimuli for use in the central nervous system. However, receptor cells do not have connections to the central nervous system only through afferent fibers. There are also efferent fibers from the central nervous system that may influence the activity of the sensory neurons. During the last years, research has indicated that such connections may be shown at least for audition, vision, the sense of balance and skin senses (Biondi and Grandori, 1976; Liberman et al., 1990; Highstein, 1991; Mikkelsen, 1992; Alexandrov and Jarvilehto, 1993).

Two Experiments: Efferent Influences on Touch and Vision

Recent experimental results show that the efferent connections may influence the sensory organs' dependence on the behavioral situation and goals of behavior of the experimental subject (animal/man). In our research, we found such results when investigating responses of cutaneous peripheral neural units in experimental situations while the subject performed a variety of tasks (Astrand et al., 1986).

In the first situation, the subject attended to tactile pulses of varying intensity that were applied to the receptive field of a mechanoreceptive unit, and reported numerically the intensity of the touch sensations elicited. In the other situation, the identical pulses were applied to the receptive field of the same unit, but the subject's task was to count deviant tones in a rapidly presented series of standard tones. Thus, this task had nothing to do with the presented tactile stimuli. In both situations, peripheral responses of the single mechanoreceptive units were recorded by microelectodes from the radial nerve at the wrist level (for the recording technique, see Jarvilehto, 1976).

The results showed that the thresholds and response characteristics of the recorded mechanoreceptive units changed with the task the subject was given. When the subject attended to the touch stimuli the thresholds of the units were lower, more impulses were elicited with identical stimuli, and the latencies of the responses were shorter than during the counting task. From the point of view of the "coding", this would mean that the nervous system could not identify the identical stimuli from one situation to another. Therefore, the central nervous system would not receive unequivocal information from identical events in the environment during the two tasks.

However, such results could also be interpreted as showing only that the dynamic changes in the receptors are not related to the tactile stimuli as such, but would rather indicate a general sensitization of the receptors while attending to certain kinds of stimuli. It could be furthermore assumed that this state is somehow indicated to the central decoder that would then correspondingly correct the incoming signals. But, even with such an interpretation, we should admit that unequivocal neural coding in the peripheral nervous system is questionable, and that the peripheral neural system is not an automatic or mechanical transducer of the physical parameters of environmental stimuli.

However, in our research with freely moving rabbits (Alexandrov et al., 1986) we obtained results that indicate that the attention of the subject does not have a decisive role in this process. The results showed that the dynamic changes at the receptor level are not simply due to attention or to the use of a certain receptor field that would be sensitized in a certain task. Such changes are, rather, related to the whole behavioral situation.

In our experiments, we had a freely moving rabbit that acquired food in a cage by pressing a pedal and we recorded unit activity directly from the optic nerve at a point before the nerve enters into the lateral geniculate body. When the rabbit was performing the food-acquisition task, we could observe activations of the units in the optic nerve that had a constant relation to certain phases of the rabbit's behavior. The units were always activated, for example, when the rabbit was approaching the pedal or when it was moving to the automatic feeder. Apparently, such activations could be interpreted as responses of the optic nerve units to the visual stimulation by the pedal or the feeder.

Before starting the recordings, we had taught the rabbit to also perform the task when its eyes were covered with non-transparent cups, preventing the use of any visual information. When, during the experimental session, we closed the eyes of the rabbit so that no visual stimulus could influence the retina, we found that the optic nerve unit which we recorded continued to show activations as the rabbit approached the pedal, for example. Thus, such activation could not be related to any direct visual effects from the environment, and, for many units, the activation seemed to be independent of visual stimulation. Consequently, such activations could not be due to the effects of stimuli, but had to be mediated over the efferent influences upon the retina. On the basis of their latencies to direct visual stimulation, we could also show that the unit discharges were not from efferent fibers, but reflected activations of the ganglion cells.

Such results question the attention hypothesis, because when the eyes of the rabbit are closed, there is nothing to be attended to in the visual modality. Thus, there should be no reason to either modulate the peripheral activity or to sensitize the receptors. The results should, rather, be interpreted as showing that at all levels of the nervous system unequivocal coding of environmental information is difficult, if not impossible.

The finding that there is no simple coding of environmental stimulus information by the receptors has far-reaching consequences. First, we must conclude that the application of the information theory is problematic in the description of the functioning of the senses. Second, this finding means that knowledge about environmental features and events is not simply based on the assumed transduction in the sensory systems.

But if the receptors do not code environmental information and transmit it to the central nervous system, how, then, is knowledge formed and why do organisms have receptors? The idea of the transfer of knowledge from the environment into the organism is a cogent hypothesis, because it is based on our everyday experience and on the common sense explanation of causal factors in behavior. If the hypothesis does not hold, are there any other possibilities for the formation of knowledge? Why are there efferent influences at all? If, during evolution, receptors developed in organs responsible for exact coding of environmental stimuli, it is difficult to conceive why their action should be distorted by the central nervous system in the form of the efferent influences. Of course, we could suppose, as indicated by the attention hypothesis, that the influences on receptors are controlled in such a way that a model of influences is stored in the central nervous system when such influence is exerted in the periphery and this model would then be used in the correction of the incoming information.

But even then we have the question of how the central nervous system would "know" how much the receptors should be influenced? Furthermore, if the knowledge comes through receptors, how could anything about the behavioral situation be known before the information from the receptors was received? Moreover, if this situation was already known, then it would no longer be necessary to modify the action of the receptors.

Thought Experiment: Knowledge Formation without Senses

Could we even imagine that knowledge formation to be possible without the help of receptors? Let's make a thought experiment: Let us assume there exists an imaginary organism having no receptors, but only motor organs. Such an organism is, of course, impossible, because a receptor is simply a cell that is connected both to the organism and to the environment. As no organism may develop without an environment, it necessarily would have such cells and could not live without them. But let us imagine such an organism only for the purposes of our thought experiment.

Could such an organism have knowledge from its environment, from the structures outside its surface boundary, or would it be closed into its inner life only? Now, we must understand the concept of knowledge broadly, as the possibility of acting in the environment appropriately. Could such an organism learn something about the environment to which it would have no direct access through the senses?

Let us put our organism into an environment consisting of a cube with smooth walls. The cube is filled with a homogenous energy field (like water) and the organism is able to swim in the field by using two pairs of fins which move the organism in two dimensions: forwards-backwards or right-left. The pairs of fins are connected by a sensitive and dynamic set of interneurons which join the pairs of fins so that only one pair may be used at once. The muscles of the fins and the interneurons feed off some mysterious inner energy that the organism may obtain from the energy field in the form of induction when its body is moving in relation to the field. If the movement of the organism stops, the amount of inner energy for one pair of fins goes down and is finally exhausted. The other fins still have, however, their own energy storage that they may use when the first pair is no longer working, and therefore the movement of the organism is restored in some other direction. These fins then work as long as the movement continues and, simultaneously, the energy potential of the other fins is restored. If the movement of the organism stops completely, it cannot restore the inner energy and it dies.

Now the organism moves in one direction inside the cube by moving one pair of fins. This movement inhibits through interneurons the movements of the other pair. During the movement, the organism may induce more inner energy from the homogenous energy field and thus it would move indefinitely if the walls did not exist. When it hits the wall preventing its movement forward, the original pair of fins still move, until their energy store is depleted. Then they stops, the inhibition on the other pair disappears, and they start to move, giving the organism movement in some other direction. This movement continues again until the organism hits another wall, stops and the other fins again start to move.

Let us now further suppose that the connections of the interneurons between the pairs of fins are such that they may be dynamically changed. The continuous movement of the organism within the cube indifferent directions therefore starts to change these connections so that the use of energy by the fins and the induction of energy from the energy field becomes optimal. Therefore, the organism starts to turn already before it hits the wall, and develops continuous movement even with the walled space.

Thus, it seems that the organism learns the structure of its environment in the sense that it may anticipate the walls and the instant of hitting them. The walls and the organism start to form one system, the result of which is the continuous movement of the organism. The walls of the cube are elements of this system in the sense that their existence partly explains the action of the organism (turning). Essential in the functioning of such system, is the number of interneurons, their dynamics, and the constancy of the environment. In a randomly changing environment, constant connections between the interneuron could not be formed.

Probably, it would not be too difficult to build a computer simulation demonstrating the actions of this kind of organism (Tanji and Nolfi, 1997). In any case, the result of the thought experiment so far seems to show that an organism may be connected to its environment in a reasonable, functional way even in the absence of any receptors: even in the absence of senses it may learn to know its environment. Then what do we need receptors for?

The thought experiment is untenable since there are no organisms without some kind of receptor. Even the idea of induction of energy from the energy field means the assumption of some sort of general receptor. However, all organisms have cells that may use environmental energy (such as photoreceptors) or whose function may be distorted by energy gradients (such as mechanoreceptors).

The significance of receptors may be seen when the conditions of our thought experiment are changed by adding one hole (a receptor) to the surface of the organism through which it may directly use certain kinds of energy foci (concentrated spots) in the field. The environment of the organism is, thus, no longer homogenous, but consists of energy gradients. Here, the walls no longer exist. The receptor hole has a certain size, making possible the direct use of only certain spots. Let us further suppose that the main energy for the movement must come from such spots; the induction from the energy field is no longer a sufficient energy source. Therefore, the organism must, every now and then, hit such energy spots with the receptor to have enough energy for its life process. Let us further assume that the spots stay in certain places and are restored at once when they are used; so far the environment is constant. We may also assume that there are now many pairs of fins making the movements of the organism possible in any direction. However, these fins also have reciprocal innervation so that movement in one direction inhibits the fins working in the opposite direction.

Now the organism moves in this heterogeneous environment. If it does not hit any energy spots, it dies. Eventually, one of the organisms (we may also assume that there are now many of them) encounters a spot that gives it energy to move further in this direction. Slowly, the energy for this direction is depleted and some other fins start working, turning the organism in another direction. Again, one spot is found and then, later, the direction of movement is changed again. If there are enough dynamic interneurons connecting the fins, the organism starts to move from one energy spot to another, optimising its energy consumption in the same way as the organism within four walls. Such an organism would then live forever. The life process of the organism is, however, very sensitive to any change in the structure of the environment.

We then go to the last part of our thought experiment and assume a heterogeneous environment that is continuously changing. The place and size of the energy spot is continuously changing. Furthermore, we add efferent fibers to the receptors that may regulate the size and the quality of the receptor hole. The organism may now use different kinds of energy spots of varying sizes. What happens now?

First of all, most organisms with fixed receptors disappear and the new organisms with efferent control of receptors start to show behavior that differs in principle from the behavior of the earlier organisms. When the organism does not get an energy supply with one size or quality of receptor, it changes the receptor hole so that it may also fit the energy spots of other sizes and qualities. Thus, the organism starts to search, to investigate its environment. There is no longer random movement that brings the organism to a fixed energy spot by chance, but the organism may locate spots of different sizes and qualities. It may also search for other spots if the original ones disappear. Through this fitting process, the organism starts to be a functional whole with its environment to which it may join in many qualitatively different places. The organism starts to "perceive" its environment.

Concluding Discussion

On the basis of the results of our thought experiment, we may better see why receptors exist even if they are not transmitters of information, and why efferent influences are important for all receptors. The receptors give the possibility of direct contact to the parts of the environment necessary for successful behavior, and the efferent influences help in the search for new useful aspects of the environment. The properties of the receptors are continuously modified, and such receptor patterns are created, which fit to useful energy configurations of the environment, making new results of behavior possible (Freeman, 1997). Perception is the process in which certain parts of the environment that are defined by dynamically changing receptors are joined into the structure of the organism-environment system. Perception is a process involving the whole organism-environment system.

The earlier researchers presenting motor theories of perception were right insofar as they saw the significance of both movement and sensory processes as the basis of perception. From the point of view of the theory of the organism-environment system, these theories were, however, incomplete in the sense that they were still based on the idea of information transmission from the environment; the movement was seen only as a component modifying the sensation coming through the senses. However, if perception is a process involving the whole organism-environment system, there is no causal relation between the movement and perception. The movements of the organism are an expression of the reorganization of the system; they are as much parts of the perceptual process as the events in the receptors or in the environment.

Perception is not a linear process proceeding from the stimulus to the percept, but, rather, a circle involving both the sensory and motor organs as well as the events in the environment. A perceptual process does not start with the stimulus, rather the stimulus is an end of this process. The stimulus is like the last piece in a jig saw puzzle. The last piece of the puzzle fits in its place only because all other pieces of the puzzle have been placed in a particular way. It is just this joining of the other pieces, their co-ordinated organization, which leaves a certain kind of hole into which this last piece can be fitted. Thus, it is just the organization of the other pieces that defines a possible last piece with which we may finish the puzzle. Exactly in the same way, a stimulus is present only if there is an organisation into which this stimulus may be fitted. Thus, the stimulus is as little in a causal relation to the percept as the last piece of the puzzle to the constructed picture. The stimulus is a part of the process of reorganization of the structure of the organism-environment system, which forms the basis of new knowledge.

It is, however, necessary to consider briefly what kind of knowledge was created in our thought experiment. Most thinking mistakes associated with "knowing" are connected to the idea that "knowledge" is only that which may be reported, told to another person, or to oneself. Such a way of thinking neglects all knowledge that is not shared with other people. However, every living organism must necessarily know something insofar as it can act in its world. It is precisely the structure of the organism-environment system that makes the behavior and behavioral results possible, and it is just this structure that is knowledge in a broad sense. Therefore, knowledge is the form of existence of the organism-environment system.

Consequently, we should not think that the organism in our experiment knows something about its environment in the usual sense of the word, that it has knowledge of its own existence or that it knows that it is confined to a space of certain form. This sort of knowledge presupposes the existence of consciousness that is based on co-operation of many organism-environment systems (Jarvilehto, 1994). Consciousness means the appearance of a social environment, shared activity, and the possibility for the description of the own action and its objects. Consciousness is not a property of the brain or even an individual, but always presupposes the existence of several individuals joining their action for common result. Such a system is created by communication; thus language, for example, is not a means of information transmission, but a way to produce common organisation and common results. The knowledge that may be communicated is only part of all knowledge that exists in the social system. The organism in our thought experiment therefore "knows" the cube or parts of its environment only in the sense that it may join specific parts of the environment to its structure, in order to obtain useful behavioral results; but it is not conscious of its world.

As the character of the efferent influences on the receptor activity is determined by the behavioral situation and the structure of the organism-environment system, an organism has its specific environment even if it has similar receptors as another organism of the same species. This "behavioral environment" (Koffka, 1935) or "Umwelt" (v. Uexkull and Kriszat, 1932) is subjective, because those forms of energy used by one organism cannot be simultaneously used by another. It is, however, at the same time, also objective in the sense that it consists of real parts of the environment—not of subjective interpretations or representations of the surrounding world.

It is precisely the development of sensitivity of the receptor to different types of energy and its efferent control that makes the widening and differentiation of the behavioral environment possible. If the sensitivity of the receptor increases, there is a corresponding increase in the behavioral environment and if it decreases, this will lead to the disappearance of the parts of the environment that earlier belonged to the system. Mead (1934) already pointed this out beautifully in the 1930s, probably without knowing anything about the possibility of efferent influences: "We have seen that the individual organism determines in some sense its own environment by its sensitivity. The only environment to which the organism can react is one that its sensitivity reveals. The sort of environment that can exist for the organism, then, is one that the organism in some sense determines. If in the development of the form there is an increase in the diversity of sensitivity there will be an increase in the responses of the organism to its environment, that is the organism will have a correspondingly larger environment. (. . .) In this sense it selects and picks out what constitutes its environment. It selects that to which it responds and makes use of it for its own purposes, purposes involved in its life-processes. It utilises the earth on which it treads and through which it burrows, and the trees that it climbs; but only when it is sensitive to them." (Mead, 1934)

Consequently, the senses do not act as "windows of knowledge", but they make the formation of knowledge possible by acting as "holes" which are filled by specific parts of the environment (Freeman, 1997). Knowledge is not "out there" in the form of stimuli to be transferred into or constructed inside the organism. The stimulus exists as a stimulus because there is a preorganized system defining some environmental change as a stimulus. Every organism "assumes" something about its environment in the sense that it has a structure into which only certain parts of the environment may be fitted. This idea was expressed already several hundred years ago by Spinoza (1677/1985), who stated that perception is a truer reflection of the structure of our body than any outer object as such.

The present considerations have profound consequences for the experimental work in the sensory physiology and the psychology of perception as for the foundations of philosophy as well. As to the experimental work, one example may be mentioned: the event appearing after the stimulus (response) in the brain or in behavior is the result of organization preceding the behavior; it does not reflect processing of the stimulus, nor does it indicate processes started by the stimulus *per se*. Thus, "lawful" relations between the stimulus and the response are seriously flawed and their spurious constancy is mostly due to the fixed experimental situations.

In philosophy, the present conception of the formation of knowledge unites the empiricist and rationalist concepts. Knowledge is created empirically through experience, in the sense that formation of knowledge presupposes the reorganization of the organism-environment system and the joining of new elements into the system. Knowledge is not, however, based on the functioning of the senses, but on the structure of the organism-environment system and on its modifications in the process of differentiation and widening of the system with new results of behavior (Popper, 1962). Therefore, we may as well say that knowledge is formed rationally.

The separation of ontology and epistemology is based on the separation of man and environment. If the environment exists with all its properties without a human being, it is quite reasonable to ask separate questions about the existence of man and matter, and about knowing the world. If man is born into a ready environment, it is, of course, completely logical to ask how he may get knowledge from the surrounding environment what the ultimate parts of this environment really are, and how we may be sure that we have correct knowledge about these properties. All such problems disappear if we see that man and environment belong to the same system. Then the question "what exists?" is identical with the question "what can we know?"

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