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Yuri I. Alexandrov

## How we fragment the world: the view from inside versus the view from outside

**Abstract.** *To construct an environment consisting of artificial objects it is helpful to use descriptions of how individuals behave. Implicitly, we do this on the basis that outward behavior reflects the dynamics of the subjective world and is a deployment of brain processes. But this is only partly correct: outwardly 'similar' behavioral acts or environmental patterns may correspond to very different neural activities (the view 'from inside' the subject). This is because behavior is the result of the history of behavioral development, such that the brain organizations that correspond to an 'object' are the ones that were constructed during the subject's past experience in the course of performing related activity. As the construction of brain organizations takes place in the context of a goal-oriented activity, the very nature of the neural organizations involved stays connected to this goal. Empirically, the goal aspect of the object seems more structuring than the pattern of the object itself. This article compares the view from outside and the view from inside for different kinds of specific experimental situations. We show that 'externally' similar objects may correspond to very different brain activations. Alternatively, behaviors and environmental events that seem different to an external observer may actually appear similar when viewed from inside the agent's brain. Experimental findings suggest that what is stable in an 'object' for a living organism is its subjective status: at the neural level, meaning for the agent is more important than 'objective' form. We also show that the nature of objects as seen from the inside depends on the way they were constructed through the organism's experience: behaviors or objects that may look similar from the outside are in this respect also different from the inside perspective. This has implications for the way we should construct objects in the digital world: building by mimicking the appearance of the physical world as seen from the outside may result in poor design.*

**Key words.** *Behavior – Brain – Goal – Individual development – Learning – Memory – Neuron – Subjective world – System*

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**Résumé.** *Pour construire un environnement composé d'objets artificiels, il est utile de se baser sur les descriptions du comportement de l'individu. C'est ce que nous faisons implicitement en nous fondant sur la croyance que le comportement extérieur reflète les dynamiques du monde subjectif et le déploiement de processus cérébraux. Mais cette croyance n'est que partiellement correcte: des comportements extérieurement semblables ou des schémas environnementaux peuvent correspondre à une activité cérébrale très différente (vue 'de l'intérieur' du sujet). Ceci est dû à ce que le comportement résulte de l'histoire du développement du comportement, de telle sorte que les organisations cérébrales qui correspondent à un 'objet' sont celles qui ont été construites au fur et à mesure de l'expérience du sujet lors de l'exécution de l'activité en question. Etant donné que l'organisation cérébrale se fait dans le contexte d'une activité orientée vers un but, la nature même des organisations neuronales concernées reste connectée à ce but. Empiriquement, l'aspect 'but' d'un objet donné semble plus structurant que le schéma de l'objet lui-même. Cet article compare la vue 'de l'extérieur' et la vue 'de l'intérieur' du sujet dans différentes situations expérimentales données. Nous montrons que des objets 'extérieurement' semblables peuvent correspondre à des activations cérébrales très différentes. A l'inverse, des comportements et des événements environnementaux qui semblent différents à un observateur peuvent paraître semblables s'ils sont vus de l'intérieur du cerveau de l'agent. Les résultats expérimentaux suggèrent que ce qui est stable dans un 'objet' pour un organisme vivant, c'est son statut subjectif: au niveau neuronal, la signification pour l'agent est plus importante que la forme 'objective'. Nous montrons aussi que la nature des objets vus 'de l'intérieur' dépend de la manière dont ils se sont construits au travers de l'expérience de l'organisme: les comportements ou les objets qui peuvent paraître semblables de l'extérieur sont aussi à cet égard différents dans la perspective de l'intérieur. Ceci a des implications potentielles sur la façon dont nous devrions construire les objets dans le monde numérique: les construire en répliquant l'apparence du monde physique tel que vu de l'extérieur peut résulter en une conception peu performante.*

**Mots-clés.** *Apprentissage – But – Cerveau – Comportement – Développement individuel – Mémoire – Monde subjectif – Neurone – Système*

## What you see is not what's inside

Should we design new systems based on the external appearance of the world or should we base them on the human-centered, subjective nature of the world as we experience it? Beyond philosophy and phenomenology, some general issues concerning the nature of objects have direct implications for the way we, as a society, decide to construct the world.

Considering the growing consensus in human-centered oriented design in the information and communication technology (ICT) research community, one could think that the choice is obvious: consider inside views and take into account the subject's goals and perceptions. But what is an inside view?

In order to construct an environment made of artifacts – artificial goal-objects of behavior – understanding the behavior of subjects is quite useful. Our usual and naïve understanding is based on the belief that outward behavior reflects the dynamics of processes in ‘black boxes’, that is in the subjective world and subject’s brain.

Within a reasonable margin, this is indeed true because behavior can be considered as an external display of this dynamic. However, patterns of subjects’ behavior that appear the same for an external observer (e.g. pressing a button) or similar changes of environment controlled by the observer (e.g. a flash of light, a display) can in fact be different when viewed from inside, at the neural level and as a subjective experience. And, conversely, events and behavior patterns that look different to an external observer may be identical or similar in the agent’s subjective world. Lahlou and colleagues were correct in claiming generally that ‘the goals and tasks define subjects’ viewpoint for perception of artifacts’ (Lahlou, Nosulenko & Samoyenko, 2002: 490); this is the perspective of activity theory (Nosulenko & Rabardel, 2007).

Nevertheless, I assume that the internal activity and the external display of its dynamics always *correspond*. This correspondence is sometimes not obvious, though, because several different internal activities may correspond to the same external display, and several external displays may correspond to the same internal activity. To show this, it is necessary to slip out of conventional paradigms and make explicit the parameters that appear to be the same for outwardly different acts, and different for outwardly similar ones.

This article investigates this issue by comparing ‘inside’ and ‘outside’ views of some simple behaviors. What are the parameters that appear to be the same for outwardly different acts, and different for outwardly similar ones? The search for the most important parameters and conditions would not be very effective if only speculative approaches were used. Defining these parameters requires special experiments. The tasks of these experiments can be defined through comparison of two views: the view from outside and the view from inside.

The latter view implies detailed objective recording of indexes of subjective experience dynamics. Its deployment into a research program depends on an understanding of the activity of single brain cells – neurons – and the structure of subjective experience. This understanding in turn depends essentially on theoretical positions that define the relation of mind and brain, as well as of brain and behavior.

## **The physical and phenomenal aspects of behavior: behavior as a systems-organization oriented by its future result**

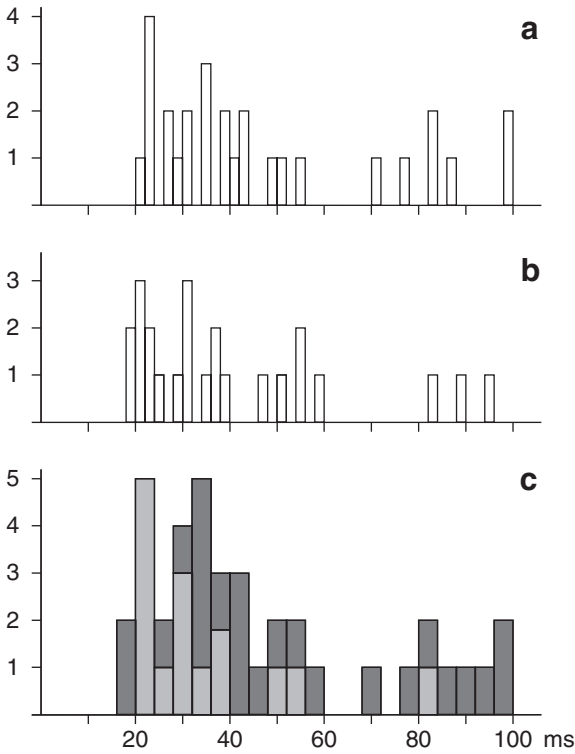
In order to describe the neuronal basis of subjective-experience dynamics, first of all we need to define its elements. The neural equivalent of an element of subjective experience, established during the formation of a new behavior and realized in behavior, is defined as an organization of a group of neurons composing the system. One well-developed systemic approach to the neuronal basis of behavior is based on P. K. Anokhin's theory of functional systems (for a review, see Anokhin, 1973).

The pivot of this theory is the definition of a *system-creating factor* – the *result* of a system – a desired relation between an organism and its environment achieved through the realization of that system. The principal determinant of a system is not a stimulus, an event in the past, but the *future result* of the behavior. Thus a system is understood as a *dynamic* organization of activity of components in different anatomical localizations, both in the brain and in the rest of the body. The interaction of components provides an adaptive result for an organism.

Within the framework of a systemic methodological approach, a wide range of experimental data has been analyzed, including the results of neuronal recordings *in vitro* and in normal and pathological animals performing both complex instrumental and simple behavioral acts when awake. Data from experiments with human subjects in tasks involving categorization of words, skilled performance, participation in game activity in groups, etc., were also included. On the basis of these analyses, qualitative and quantitative descriptions of the principles of formation and realization of subjective experience were suggested within the framework of a unified methodology (Alexandrov, 1989; Alexandrov & Järvillehto, 1993; Alexandrov et al., 2000; Alexandrov & Sams, 2005; Shvyrvkov, 1980, 1990).

One of the most important results is the following. The interaction of neurons while achieving a behavioral result is accomplished by synchronizing the activity of the neurons in different brain structures (Alexandrov & Shvyrvkov, 1974). The experimental results that led us to the above conclusion were obtained on awake, non-anesthetized rabbits. The activity of two neurons in the visual and somatosensory areas of the rabbit cortex in response to a conditioning flash was recorded simultaneously by two glass microelectrodes. The unconditioned stimulus, electrical stimulation of the skin, was applied 600 milliseconds (ms) after the flash through needle electrodes inserted under the skin.

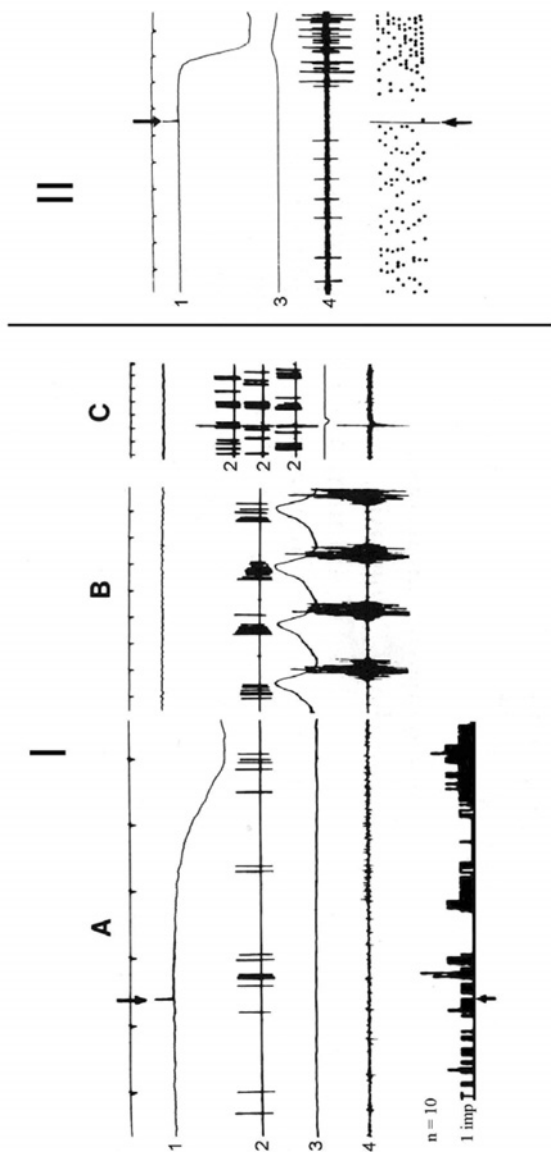
Histograms of distribution of neurons by response latency are illustrated in Figure 1. The maxima of the probabilities of responses in both areas lay



**FIGURE 1**  
**Latencies of responses to conditioning flashes in the somatosensory and in the visual cortex**

*Note:* Distribution of neurons by latencies of responses to conditioning flashes: (a) in the somatosensory (n = 30), (b) in the visual (n = 28) cortex; (c) in the somatosensory (light colouring) and visual (dark colouring) cortex. Abscissa, latent period, ms; ordinate, number of neurons.

in the interval between 20ms and 40ms and amounted to 0.58 and 0.57 for the visual and somatosensory areas respectively. The earliest responses in the visual area (Figure 1b) clearly preceded the earliest responses in the somatosensory area (Figure 1a, left fragment) by only 2ms, and if the latent periods were estimated with accuracy of not more than 4ms (Figure 1c), the maxima of the histograms coincided. Since fluctuations of the latencies of responses of the same neuron in both the visual and the somatosensory areas were usually more than 4ms, discharges even of those neurons whose mean response latencies differed considerably could be synchronized. These



**FIGURE 2**  
**Changes in the activity of the trigeminal-mesencephalic neuron (I) and an individual motor unit of m. masseter (II)**  
**in the latent period of a behavioral act**

*Notes:* (IA) top: Recording of a separate act; bottom: histogram of a TMS neuron activity, constructed from the time of the appearance of the feeder's starter click (arrow). The channel width is 1.25 ms. (IB) Connection between the neuron activity and individual chewing cycles: (IC) TMS neuron activity during the intramuscular stimulation. An inhibitory pause with postinhibitory activation, characteristic of spindle afferents, is observed. (II) top: Recording of the activity of two motor units of m. masseter in the act of taking food; bottom: rasters of impulse activity of a motor unit with low-amplitude potentials in sequential behavior acts. The rasters were constructed from the starting click (arrow) of the feeder device. Designations: (1) head movement recording; (2) neuronogram; (3) recording of lower jaw movements; (4) m. masseter EMG. The time marker is 100 ms.

observations suggested that the possibility of synchronization of different neurons is embodied in the instability of their response latencies, which compelled a search for the cause of the variability of the latencies.

Thus different neurons may work together because their activity is not rigid but labile, and they can adjust to each other depending on factors of behavioral organization, varying from trial to trial.

This raised the possibility that the variability of the response latencies might be the result of the different degree of involvement of the same neuron in the general integration when different synaptic inputs of the neuron are used. This hypothesis was tested by changing the reinforcing stimulus. With a change in any parameter (intensity, localization) of the reinforcing current, the response latencies to flashes with unchanged physical parameters in both cortical areas could vary significantly as regards both their mean amplitude and their stability. It was concluded that the response latency of the single neuron in the behavioral act is determined by the whole range of influences to which the neuron is subjected when included in the general integration of the behavioral act, and not by the number of synaptic relays or the length of the conducting fibers from receptors to recorded neurons.

This means that, although neurons in different brain areas are located at a different 'anatomical distance' from the receptor, they may discharge synchronously because the latency of neuronal activation depends on numerous influences that coordinate activity of different neurons into a unified system.

It is important to stress that reorganizations of *peripheral-units'* activity synchronous with central neurons' activations appear during the organizational processes of a behavioral act – afferent synthesis and decision-making (Alexandrov & Grinchenko, 1980). These processes deploy in the latent period of the actuating mechanism's involvement, that is in the latent period of muscles' EMG activation and movement, whose development corresponds to the realization processes – the action program (Shvyrkov, 1990). Short latency activations of 16–32ms were observed in three out of sixteen TMS (trigeminal mesencephalic) neurons – identified proprioceptive elements. These are the first-order sensory neurons that send out the peripheral process to the proprioceptors of the masticatory muscles.

Figure 2.I illustrates the activity of a TMS neuron that exhibited activation with a 32ms latent period after the click (a clicking sound served as the start signal for the food-acquisition behavioral act) and before the beginning of movement and EMG activation, and exhibited the properties of an afferent spindle during the tests. This is important in connection with the fact that the commonly accepted concept of proprioceptor function presumes that the activity is analyzed only in connection with the functioning of the actuating mechanisms.



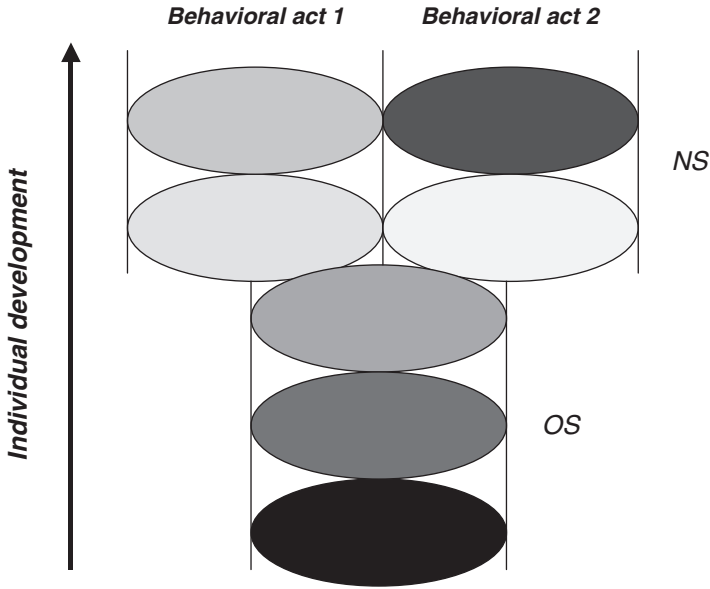
The appearance of early activations of TMS-neurons in the interval corresponding to the development of the organizational processes of the behavioral act confirms R. Granit's (1975) hypothesis on the connection between spindle activity that occurs before an arbitrary movement and the preparatory processes of the arbitrary act. The changes that occur in the alpha-skeletal motor activity which were identified in an analysis of individual motor unit activity (Figure 2.II) apparently should also be associated with those preparatory processes. Thus we can conclude that not only central neurons but peripheral elements too are *synchronously* active during preparation and realization of the behavioral act. The old view that the interpretation of the world is a succession of processes of perception → interpretation → movement subserved by successive propagation of activity from sensory to motor brain structures and from peripheral to central elements of the nervous system is not supported by experimental findings. Rather, these data suggest that relevant changes in the environment are associated with simultaneous reorganization of activity of all these elements, and that all of them are involved in all stages of organization and realization of a behavior.

Interestingly, a very similar conclusion about synchronous activity of the neurons in different brain structures, but related to the 'binding' problem, was developed later and has gained considerable experimental support (Roelfsema et al., 1997; see also Thatcher, 1997). Synchronization of neurons located in different brain areas has been suggested to be important in understanding consciousness (Engel et al., 1999; Thompson & Varela, 2001).

### *System development: how an object is constructed 'inside'*

Another key concept in the theory of functional systems is development. Both concepts, development and result of a system, are merged into the concept of systemogenesis. Systemogenesis refers to the idea that, during early ontogeny, those differently localized elements of the nervous system and body that are essential for achieving the results of the systems undergo selective and accelerated maturation, thus ensuring the survival of the organism at the early stages of individual development (Anokhin, 1973).

V. B. Shvyrykov (1986) suggested that systemogenesis takes place also during learning in adults because the formation of a new behavioral act is always a formation of a new system. The principal factor in understanding the role of different neurons in the organization of behavior is the history of behavioral development, that is the history of the successive systemogeneses



**FIGURE 3**  
**Systemic structure of behavior**

Note: 1 and 2 = different behavioral acts; OS = old systems; NS = new systems; arrow = course of individual development.

(Alexandrov, 1989; Alexandrov & Alexandrov, 1982). The system-selective concept of learning (Shvyrvkov, 1986) is in line with the idea of a selective, rather than an instructive, principle underlying learning (Edelman, 1987). This concept considers the formation of a new system to be a fixation of the stage of individual development – the formation of a new element of subjective experience during learning.

The neural basis of this process is the specialization of ‘reserve’ (‘silent’) neurons, but not a change in specialization of already specialized units. New neurons appearing in neurogenesis are also likely to be involved in this process (Shoers et al., 2001), in which new systems (NS, Figure 3) are added to the existing ones (OS, Figure 3) (Alexandrov et al., 2000; Shvyrvkov, 1986). They do not substitute for the previously formed systems, but instead are ‘superimposed’ on them (Figure 3).

Specializations of neurons in relation to systems of specific behavioral acts have been shown to occur in both humans and animals (see

Alexandrov, 1989; Alexandrov et al., 2000; Quiroga et al., 2005; Ranck, 1973; Shvyrkov, 1986; Svarnik et al., 2005; and others). New systems cannot be formed without relevance to the achievement of specific results. In this sense there is no difference between knowledge and the experience of action performance.

Neurophysiological studies have demonstrated that specialization of recently specialized neurons does not change during a single-unit recording lasting for weeks and even months, and that there are many silent neurons in different brain areas (Bradley et al., 1996; Brecht, Schneider & Manns, 2005; Chang et al., 1994; Gorkin & Shevchenko, 1991; Greenberg & Wilson, 2004; Jog et al., 1999; Nicolelis et al., 1997; Schmidt, Bak & McIntosh, 1976; Swadlow & Hicks, 1997; Thompson & Best, 1990; Williams, Rennaker & Kipke, 1999; Wilson & McNaughton, 1993; Woodward, Janak & Chang, 1998).

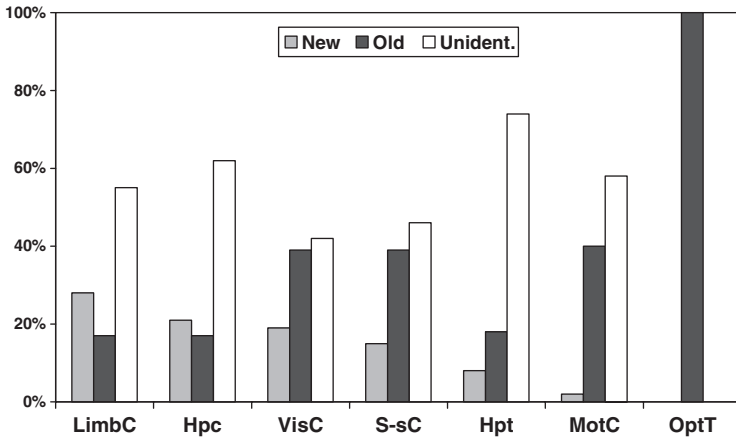
It has been shown (Alexandrov et al., 2000; Alexandrov & Sams, 2005; Shvyrkov, 1986) that complex instrumental behavior is realized by new systems formed during learning of the acts that go to make up this behavior and by the *simultaneous* realization of older systems formed at previous stages of individual development. The latter may be involved in many behavioral patterns, that is to say they may belong to elements of subjective experience that are common to various acts (see Figure 3).

Therefore, *behavior is the realization of the history of behavioral development*. Multiple systems, each fixing a certain stage of development of the given behavior, are involved.

Our single-unit recordings during instrumental behavior have demonstrated that, generally, neurons with new specializations are abundant in the cerebral cortex (though different cortical areas may vary with respect to this parameter; for instance, the motor cortex is dominated by neurons specialized with regard to systems formed at the early stages of individual development: so-called *old-system* neurons, for example ‘movement’ neurons or ‘food-taking’ neurons).

The limbic (cingulate) cortex is dominated by neurons specialized with regard to *new* systems formed when animals learn instrumental food-acquisition tasks in an experimental cage (e.g. ‘pedal-pressing’ neurons), whereas phylogenetically archaic and peripheral structures had very few of them, if any (Alexandrov et al., 2000; and see Figure 4).

It is reasonable to assume that the specificity of subjective experience ‘projection’ to cerebral structures is determined by the particular characteristics of neurons composing these structures. These characteristics determine the involvement of neurons of the given structure in the formation of



**FIGURE 4**  
**Patterns of neurons' behavioral specialization in different brain structures**

*Notes:* A pattern of specialization of neurons (within the given structure) is defined according to the set of systems with respect to which units of this structure are specialized, and also according to the quantitative relation among neurons belonging to different systems. Relative numbers of neurons belonging to 'new' and 'old' systems (see text for explanation) as well as of neurons, whose specialization was not identified (unident.; they do not show consistent activation during behavioral cycles of instrumental behavior), in limbic (posterior cingulate) cortex (LimbC), hippocampus (Hpc), visual cortex (VisC), somatosensory cortex (S-sC), hypothalamus (Hpt), motor cortex (MotC), and optic tract (OptT).

the particular behavior. The neurons participating in a functional system are located in different anatomical areas.

*Mind-body problem: systemic solution*

The ideas presented above are fundamental to systemic cognitive neuroscience (systemic psychophysiology), which suggests a systemic solution to the mind-body problem (Shvyrkov, 1990). In this solution, the organizing of physiological processes into a system is based on specific systemic processes. Their substrate is physiological activity, whereas their informational content is mental. The mental processes that characterize an organism and behavioral act as a whole and the physiological processes that take place at the level of separate elements cannot be related directly, but only through

the informational systemic processes. *Mental events cannot be related directly to the localized elementary physiological events, but rather to the systemic processes of their organization.*

Psychological and physiological descriptions are partial descriptions of the same systemic processes. We stress that systemic processes involve not only the brain but the whole body (this is also the position defended by ‘embodied cognition’; Hutchins, 1995). Thus, the term ‘mental’ characterizes the organization of activity not only in neurons but also in other anatomical structures of the organism.

This solution to the mind–body problem resembles Hegel’s ‘neutral monism’ (see Priest, 1991), which argues that mental and physical are two aspects of united reality. D. J. Chalmers (1995: 215) formulated a double-aspect principle: ‘Information (or at least some information) has two basic aspects, a physical aspect and a phenomenal aspect’. We would replace ‘some information’ with ‘informational systemic processes’, that is to say processes that organize elementary mechanisms into a functional system: afferent synthesis and decision-making, program of action and acceptor of action result (Anokhin, 1973).

From this point of view, mind may be considered a subjective reflection of the objective relation of an individual to the environment. That is, mind is considered to be a structure represented by systems accumulated in the course of evolutionary and individual development. Relations between these systems (intersystem relations) may be described qualitatively as well as quantitatively.

Considering these notions and relying on ‘the view from inside’ (monitoring the neuron activity occurring during a behavior), we can define specific research problems that include the relationship of this view to ‘the view from outside’. Hopefully, the results of such research will be useful for both theoretical and applied explorations.

Thus, returning to the above issue of the relationship between activity of separate brain cells – the neurons – and the structure of subjective experience, we can conclude the following: *When describing the formation of neuronal specializations and activity of specialized neurons, we simultaneously describe the structure and dynamics of the subjective world.*

### **A summary of findings on the nature of the neural activity underlying behavior and tasks for future investigation of human behavior following from these findings**

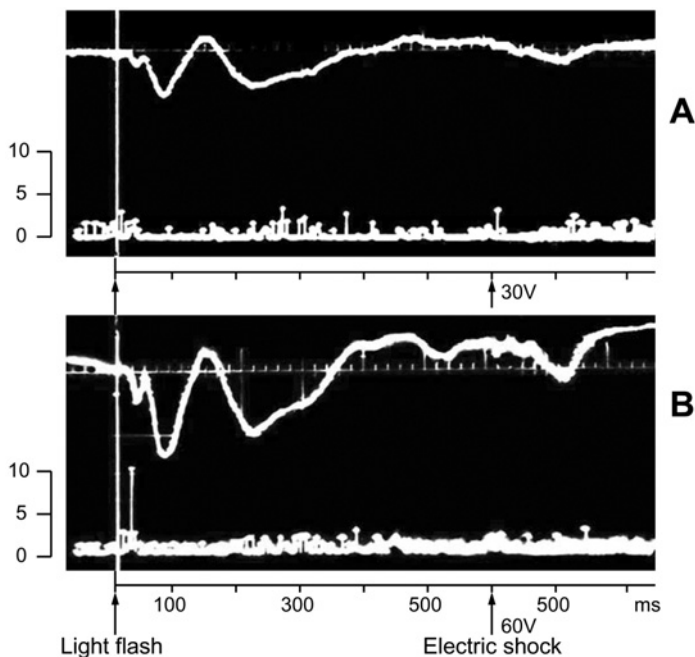
The following section may appear cumbersome to social scientists; it is indeed more neuroscience than social science. Nevertheless, as we know

that behavior has neural bases, it is interesting, for a social scientist, to know what actually happens in the brain when the subject behaves. At least our theories of human behavior should take into account what we learn at this neural level. Some experiments described in this section concern comparatively simple artificial passive stimulations of body surface or regularities of brain subserving of elementary behavioral acts, while others deal with active environmental stimulation taking place during the active agent's behavior or with brain mechanisms underlying complex instrumental behavior; but the point they all make has general applications for understanding the very nature of what behavior is from a subjective perspective. Considering the simple stimulation and elementary behavioral acts, we are using the same approach here as Lenay (2008): by doing experiments on very simple, easy-to-understand cases, we seek to highlight some fundamental issues concerning the phenomenological nature of behavior.

The experiments described here shed some light on the nature of behavior and its construction, in simple and more complex cases. They give food for thought to those interested in understanding what activity is for the subject, from the inside perspective. As we shall see, some of these findings provide a different perspective on some classic issues, such as having intentions, making sense of, learning. For the sake of simplicity, the findings discussed here are formulated as section titles expressed in a simple sentence, followed by a description of the experimental investigations that led to these conclusions.

*1. Depending on the goal of the subject's behavior; similar variations of the environment, in terms of physical parameters, can be differently reflected in the activity of central and peripheral neurons.*

Send flashes of light to a rabbit and measure the activity of sensory neurons. One might think that the stimulus produces a brain activation which depends on the physical parameters of the flash, whatever this flash signals: food or electric-shock presentation. If these parameters are the same, then the characteristics of an activation are the same. Experimental data show that this is not the case. The activation of neurons prompted by the flash depends on what behavior deploys after this flash: food acquisition or avoidance. This may be derived from N. A. Shvyrkova and V. B. Shvyrkov's (1975) experiments, which showed that the sets of neurons activated in the visual cortex are different during presentation of *identical* flashes which induce different types of behavior (food-acquisition and defense). Dependence of the sets of rabbits' visual-cortex neurons activated after presentation of *identical*



**FIGURE 5**

**Appearance of short-latency activation in visual cortex evoked by light flash as a result of increase of magnitude of electric shock reinforcement**

*Notes:* In (A) some ‘inhibition’ of discharges can be seen after presentation of light flash (left arrow) reinforced by contralateral forepaw electric shock stimulation (right arrow; 30V). (B) shows the appearance of short latency activation after presentation of light flash reinforced by stronger (60V) contralateral forepaw electric shock stimulation. (A, B) upper sector: averaged EEG-evoked potential recorded from primary visual cortex; lower sector: histogram of unit activity; bin width – 4 ms,  $n = 25$ ; *abscissa*, time; *ordinate*, number of impulses in the bin.

flashes, followed by electric shock from the varying parameters of this shock, was also shown. The changes in parameters of the reinforcing shock led to changed activation properties of most cells in response to the light flashes and the electrical stimulation (Figure 5; Alexandrov, 1975).

So there is no *perception* of a stimulus pattern *per se*. There is no ‘objective’ coding of physical parameters of stimulus which, at the *subsequent* processing stages, becomes ‘subjective’, as many have suggested. Perception is subjective from the first millisecond of its deployment. Perception is always *interpretation* in terms of needs, and the vocabulary of these terms is formed during individual development with respect to the peculiarities of given development occurring in a given society.

The activation characteristics of a central 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 receptive field) of the neuron and *in the set of the neurons activated* (disappearance or appearance of receptive field) when applying similar stimulation in behavioral acts characterized by *different goals*.

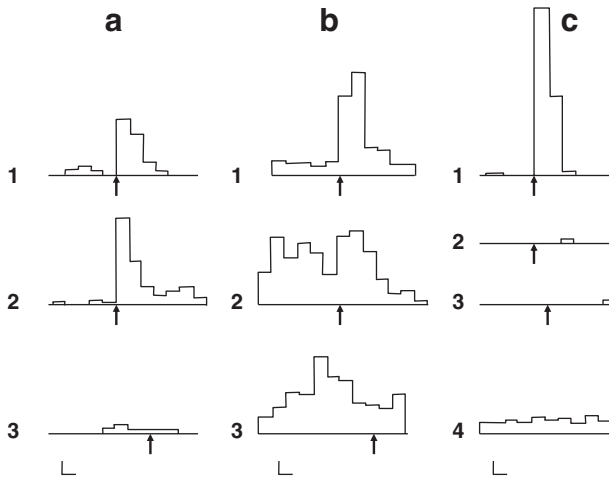
A relatively long time ago it was shown, in experiments with recording single neurons from the somatosensory and visual cortex in rabbits (Alexandrov & Grinchenko, 1984) and rats (Chapin & Woodward, 1982), that, while the parameters of the neuron-receptive field stimulation are the same, neuron-activation characteristics and the presence of activation *per se* depend on the goal of behavior, which includes contact with objects in the environment.

Somatosensory and visual cortical unit activity was compared in experiments on unrestrained rabbits during receptive field testing and natural 'self-stimulation' of the receptive surfaces of surrounding objects in the course of food-acquisition behavior. Unit activity evoked by receptive field testing may correspond completely (Figure 6a), partially (Figure 6b) or not at all (Figure 6c) to its activity during food-acquisition behavior, that is to say neurons demonstrating connection during testing with particular receptive fields (parts of the body or retina) may preserve, modify or lose it during food-acquisition behavior. Consequently, on the basis of the activity of a neuron evoked by testing, it is impossible to predict reliably its activity during realization of food-acquisition behavior, for even neurons with identical receptive fields may have different activity in a food-acquisition situation.

Receptive field testing in an alert animal is not simply stimulation of a certain part of the body surface or visual field, it is alteration of the environment which causes the realization of passive-defensive or orienting-investigative behavior. From our viewpoint, activity of the neuron in a given situation can be regarded not as a response to a definite afferent volley but as activity subserving the corresponding behavior: in a 'passive' behavioral situation (receptive field testing) and/or in the situation where active goal-directed behavior is realized.

If a neuron of a sensory structure can be activated by stimulation of a certain receptive surface in one behavior (during receptive field testing the organism also behaves as we have already mentioned above) 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 receptive field testing. This proposition is supported by the data reported by H. Sakata and Y. Iwamura (1978). They found units in the primary somatosensory cortex of the monkey that had no receptive field on the palm





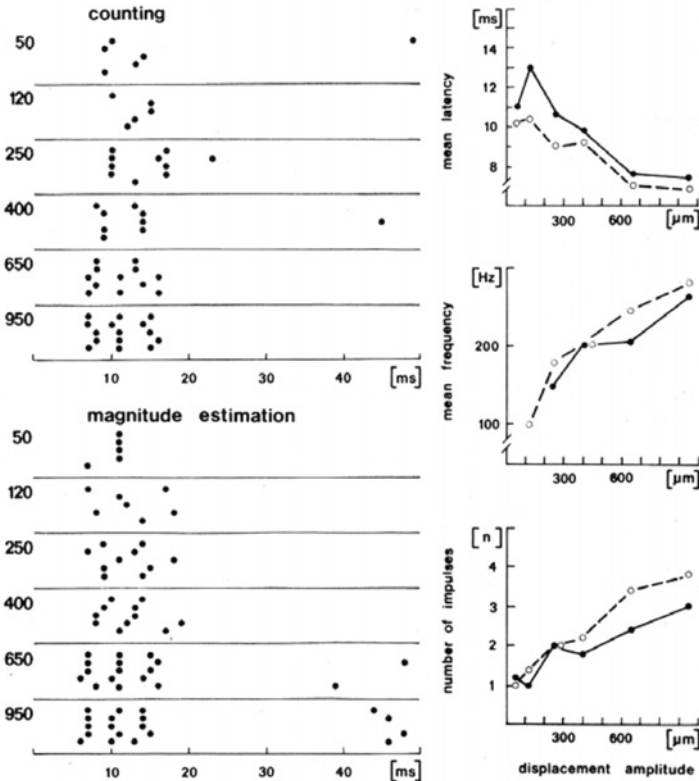
**FIGURE 6**

**Comparison of activity of three somatosensory cortical neurons (a–c) during testing of their skin-receptive fields and during food-acquisition behavior**

*Notes:* (1) Histograms of unit activity during testing, drawn relative to times of contact with receptive surface of skin of nose (in a, b) and corner of the mouth (in c); (2) histograms of unit activity drawn relative to time of pressing lever; (3) time when nose crosses plane of opening into feeding bowl. (4) Histogram of unit activity while animal sits quietly; calibration (below): 5 impulses, 200 msec; instants relative to which histograms were constructed are marked by arrows,  $n = 10$ . Neurons whose activity is shown in the histograms in a, b were located 100  $\mu\text{m}$  apart and had the same receptive field on the contralateral side of the nose i.e. activation due to contact of the object with this zone during testing was observed in both neurons (a1, b1). However, during realization of food-acquisition behavior they showed different patterns of activity. One neuron (a) in this state was activated in full agreement with its activity during receptive-field testing, only as a result of contact of the nose with the feeding bowl (a2, on right of arrow); activation was absent at times other than during contact of the receptive zone with objects during approach to the feeding bowl (a2, on left of arrow), during approach to the lever and pressing it (a3), and also while taking food, either from the hand or from the cage floor. Activity of the other neuron corresponded only partially to activity during receptive-field testing: Activation on contact of the nose with the feeding bowl was observed in this cell, just as in the previous one (b2, on right of arrow). This neuron, however, was also activated during approach to the feeding bowl and lever (b2, b3, on left of arrow), when the receptive zone was not in contact with any environmental objects. Analysis of activity of a third neuron (c) showed no agreement between activities in situations of receptive-field testing and food-acquisition behavior realization. On palpation and displacement of a contralateral area of skin between the nose and corner of the mouth, marked activation was observed (c1). However, during realization of food-acquisition behavior, neither when food was taken from the feeding bowl (c2), when both contact between receptive zone and feeding bowl and food and displacement of the skin inevitably took place, nor during pressing the lever (c3) was activation observed. It is interesting to note that differences in the characteristics of activity of this neuron were discovered not only on comparing two behavioral situations (receptive-field testing and realization of food-acquisition behavior), but also during analysis of a third situation – when with the animal sitting quietly (c, 4) and in the absence of any contact between receptive zone and environmental objects, increased (compared with the testing situation) activity appeared (compare c4 and c1, on left of arrow – the interval in which again there was no contact between receptive surface and object).

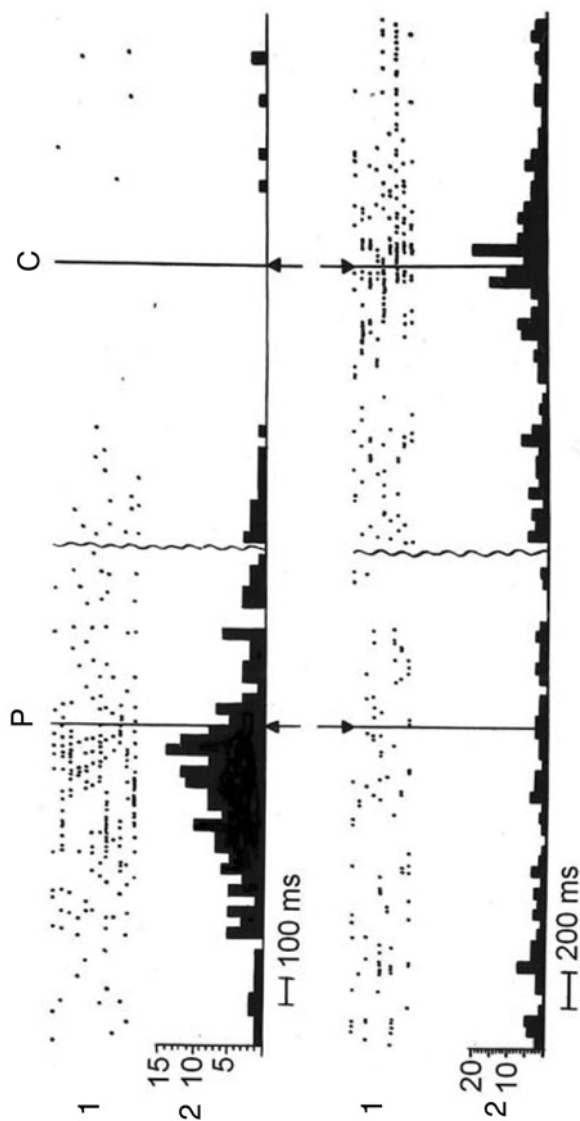
during receptive field testing and were not activated with passive hand displacement. They were, however, activated during grasping of certain objects.

We obtained similar results in collaboration with Finnish colleagues at the level of *peripheral* elements (Åstrand et al., 1986). The characteristics of responses of 23 peripheral mechanoreceptive units of the arm to tactile pulses of varying amplitude (50–950 microns) were studied by means of human



**FIGURE 7**  
**An example of the task effects on the unit activation**

*Note:* Slowly adapting unit Y14M5. The counting task presented as the first one: on the left are the responses to stimuli of different amplitudes, each dot representing one impulse and each line one response, during counting and magnitude estimation task (the stimulus amplitude in μm given on the left); on the right are the average latency, mean frequency and number of impulses for each stimulus amplitude, counting task (black dots, continuous lines) and magnitude estimation (open dots, broken lines).



**FIGURE 8**  
**Examples of neurons of the motor cortex activated in only one of the acts**

*Notes:* (1) rasters and (2) histograms of neuronal activity plotted from the start of lifting the head from the feeder (*upper*;  $n = 12$ ) and from the phasic burst of the EMG correspond to grasping the object with the teeth (*lower*;  $n = 9$ ). The neuron represented at the top of the figure is activated when grasping food with the teeth and at the start of lifting the head from the feeder in the act of grasping the plastic (P) piece (left of the wavy line); in the act of grasping the carrot (C) piece (right of the wavy line) pronounced 'inhibition' of activity is noted for this neuron. The second (lower) neuron is activated when grasping the C piece with teeth (right of the wavy line) but not the P piece (left of the wavy line).

microneurography during two different tasks: counting deviant auditory signals or defining the amplitude of tactile stimuli. For 18 units, differences were obtained between the two task situations when thresholds, latency of the first impulse, mean frequency of impulses or number of impulses in responses to identical tactile stimuli were compared (Figure 7). The sensitivity of the units was higher during the magnitude estimation than during the counting task. The dependence of the activity characteristics of the peripheral units 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 neuron activity discussed in the preceding paragraph (Alexandrov & Järvilehto, 1993).

The results show that the reorganization of the neural processes according to the task of the subject is not limited to the central nervous system but involves the periphery as well. The characteristics and even the thresholds of activations of *peripheral elements* during identical tactile stimuli presentation are *dependent on the subjects' goals*.

Recent results also demonstrate that the activity of neurons in projectional sensory areas strongly depends on the behavioral context (auditory cortex: Brosch, Selezneva & Schech, 2005; visual cortex: Shuler & Bear, 2006).

So there are no objects *per se* (as sensory patterns) for the inner view but rather objects-in-the-perspective-of-a-goal: objects of activity.

## *2. Outwardly similar behavioral acts that provide different goals have different brain bases*

Observe rabbits that take objects of identical shape out of their feeding cup. One could think that the same motor behavior would always correspond to the same neuron activity, at least in the motor areas of the brain. In fact, although the movement is the same, depending on whether the objects are real carrots or plastic carrots, the activity of the neurons is different. In other words, from the inner view, there are no motor movements *per se* but only movements-with-a-goal: movements not as a block that may be inserted in this or that behavior but as a special characteristic of entire goal-directed activity. It was shown that the seizure of food objects and visually similar non-food objects is subserved by different sets of active neurons in the motor and visual cortex (Alexandrov & Korpusova, 1987).

In experiments on alert rabbits, neuronal activity of the motor and visual cortical areas was studied in behavioral acts of seizing a piece of plastic or a carrot from consequently presented cups of the feeder; the animal had an opportunity to seize a piece of carrot after grasping and taking out of the previous cup the piece of plastic. The 'visual environment' in which the behavioral acts were realized was identical; plastic and carrot pieces were identical in form and visual characteristics. Behavioral acts of plastic and carrot-piece grasping were similar in electromio- and actographic characteristics; the motor composition of these acts did not differ.

In both behavioral acts 61 neurons were activated, 5 in the act of plastic-piece grasping, 22 in the act of carrot-piece grasping; in other words 30% of neurons were activated only in one of the compared behavioral acts (Figure 8). Characteristics of the activations appearing in both acts could be significantly different: different frequency, and connected with different stages of the compared behavioral acts.

Thus, in different behavioral acts (grasping a carrot and grasping a piece of plastic), which can be characterized as the same movements in the same environment, the compositions of the activated neurons of the motor and visual cortical areas differ. We may conclude that the appearance of cortical neuron activations in behavior depends on the goal of the behavioral acts and is not strictly determined by the parameters of the movements and environment.

Essentially different sets of the rabbits' cingulate cortex neurons are involved in outwardly similar instrumental acts of pedal pressing (or pulling the ring) that lead to food acquisition if the pedals (or the rings) are placed along two opposite walls of the experimental cage (Alexandrov et al., 1990, 1993, 2001; Alexandrov, 2006; and see Figure 9).

It is noteworthy that outwardly different forms of behavior may have more similar brain bases than outwardly identical ones. Sets of the cingulate cortex neurons activated in seemingly very different instrumental acts (pressing the pedal and pulling the ring in the same corner of the experimental cage) with the same behavioral result (taking food from the feeder located on the same wall of the cage as the given pedal and ring) overlap much more (Averkin et al., 2004).

Different neurons of a monkey's cingulate cortex are active while pressing the same pedal if these acts are involved in different forms of behavior: approach versus withdrawal; in other words if they subserve food acquisition or avoidance of electric shock to the skin, respectively (Koyama et al., 2001; Nishijo et al., 1997). J. J. Paton and colleagues (2006) have shown that different neuron sets in primate amygdala are active during presentation of visual stimuli with positive and negative values.

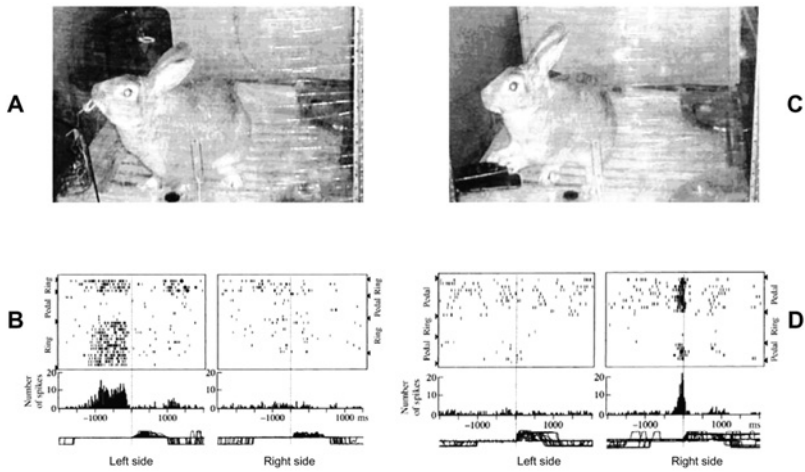


FIGURE 9

**Activation of neurons in the rabbit cingulate and anterolateral motor cortex appearing in one but not in another outwardly similar act of instrumental food-acquisition behavior**

*Notes:* The experimental cage (A, C) in which instrumental food-acquisition behavior is performed by the animal pulling obliquely on a ring (A) or pressing a pedal (C) is fitted with paired feeders that automatically deliver a reward when the corresponding pedal (located on the same wall of the cage as the feeder) is pushed or the corresponding ring is pulled. Beneath are shown raster plots of spike activity and histograms of neuron activity in the anterolateral (D) and cingulate (B) areas of the cortex. In B, a neuron in the cingulate cortex is activated on seizing the left but not the right ring; there is no activation on approach to or pressing of the pedals. In D, a neuron in the anterolateral cortex is activated on contact with the right but not the left pedal; there is no activation on approach to and seizing of the ring. In B and D, raster plots and histograms are constructed in relation to the start of pulling the ring and the start of pressing the pedal respectively. The vertical lines passing through all components in fragments B, D identify the time-point at which raster plots and histograms were constructed. Vertical bars on raster plots show individual neuron spikes, and horizontal bars show sequences of spikes in an individual cycle of the food-acquisition behavior. Cumulative histograms with a channel width of 20 ms are shown beneath the raster plots. The lowest plots are behavior actograms for all cycles of the food-acquisition behavior performed by the animals during recording of spike activity from the corresponding neuron. Upward displacements of lines on the actograms show pulling of the ring or pressing of the pedal; downward displacements show lowering of the animal's snout to the feeder. In B, diamonds show repeat pulls.

Outwardly similar behavior of identical auditory signal detection is subserved by different brain activity in a positive emotional situation (earning money) and in a negative one (avoiding money loss). The dynamics of perceptual learning are also different in these situations (Alexandrov, Klucharev

& Sams, 2007). In this study the valence of condition had a significant influence on the amplitude of auditory N100. The amplitude was larger in a punishment than in a reward condition. The effect of emotional context revealed in our experiments is consistent with the idea that the brain represents sensory-specific information in accordance with a current task goal (Wheeler, Petersen & Buckner, 2000). Our results indicate that the brain mechanisms involved in the processing of identical auditory stimuli differ quite early on in the processing stage depending on the emotional context.

Our study, as well as those cited above, has shown that different sets of central neurons are active during outwardly similar acts when they are performed to achieve different goals. Thus it is possible that auditory-cortex neurons coordinate their activity with different sets of activated neurons in approach and avoidance trials.

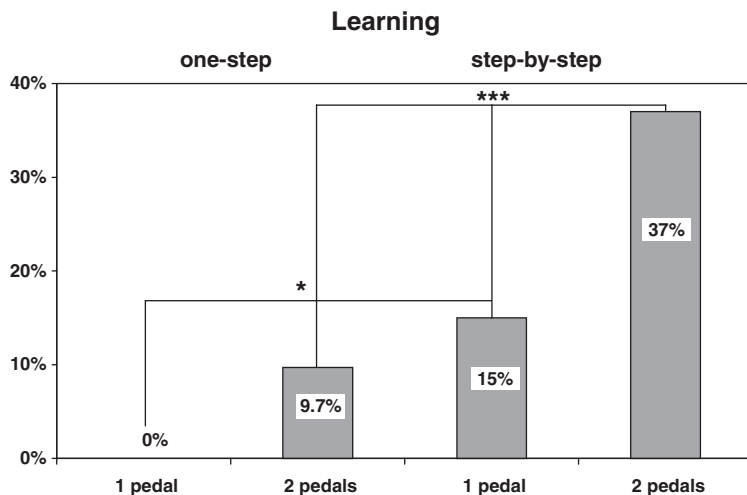
The above data make relevant the *task* of comparing motor characteristics of behavior and facial expressions during realization of ‘similar’ behavioral acts aimed at different goals, including the goals of emotionally positive approach and negative withdrawal behaviors.

Let us take another example. Suppose somebody is learning how to use Excel in order to get a salary increase or in order to process their own data more effectively. In both cases they master the program, but in all probability, the systemic organization of this ‘Excel behavior’ is different. As mentioned above, outwardly similar behavior aimed at different results has different brain bases. We can assume that, when the behavior is formed to perform the task of learning this behavior, then an individual also learns to achieve some result, for instance to show good results, to conform to certain requirements, etc. But the organization of this behavior will be different if an individual learns to achieve the result that this behavior is usually aimed at: for example, learning to handle a device so as to pass an exam, and learning to use it in practice.

In this case the *task* of defining similar and different characteristics of behavior, formed under assignment and ‘for real business’, becomes relevant.

*3. Brain subserving of behavior reflects the history of its formation; hence the activation characteristics and sets of active neurons are different in outwardly similar forms of behavior with different histories of formation*

Let us teach some rabbits how to get a piece of carrot by pressing a pedal. One might think that, once the rabbit knows how to do this, the neurons activated

**FIGURE 10**

**Relation between the number of learning stages and the number of neurons specialized in relation to newly learned behavior**

*Note:* Relative number of neurons specialized in relation to acts acquired during learning the instrumental food-acquisition behavior near one wall of the experimental cage (1 pedal) or at both walls (2 pedals). Rats were trained using 'one-step' or 'step-by-step' paradigms (see text for details).

\*  $p < 0.01$ ; \*\*\*  $p < 0.0001$ , Wilcoxon's criterion.

will be the same, no matter how the rabbit learned the task. But this is not the case. Step-by-step learning produces different neural networks and activation than learning in one step. What is apparently the same 'know-how' viewed from the outside may correspond to different systemic structures, depending on the way it was constructed.

It was shown in our laboratory that there were significant differences of neuronal activations in what seemed to be the same instrumental food-acquisition behavior of animals taught to perform the successive acts of this behavior in various orders (Alexandrov et al., 2000; Gorkin & Shevchenko, 1996). It has also been found in our laboratory that the number of neurons active in what was apparently the same behavior depends on the number of steps required to learn this behavior (Gavrilov et al., 2007). After step-by-step attainment of instrumental food-acquisition behavior, neurons were found in the posterior cingulate cortex that were selectively and invariably (in 100% of cases) activated during realization



of certain definitive acts of the behavior, which were the stages of learning. These stages were: approaching the feeder → turning away from the feeder towards the pedal → approaching the pedal → pressing the pedal. It was suggested that specializations of such neurons (manifested by their ‘act-specific’ activations; see Figures 8, 9 and 13) were established during learning of the respective behavioral acts.

Transformation of learning stages into acts of learned behavior (see ‘System development’ and Figure 2) implies that the history of behavior formation is embodied in its systemic structure. If this is true, the number of neurons specialized in relation to the newly learned behavior should correlate positively with the number of learning stages. To test this assumption, we compared *patterns of specialized neurons* (diversity of neuronal specializations in the given brain area and proportion of neurons with different specializations) in the posterior cingulate cortex in two groups of rats, which learned what was outwardly the same behavior either step-by-step or in one step.

Rats from the ‘one-step’ learning group were placed in the experimental cage for 30–40 minutes. During this time they had the opportunity to learn to press the pedal to get a piece of cheese from the feeder. Most animals found the solution after 3–4 days of exploration. Rats from the ‘step-by-step’ learning group were taught first to approach the feeder, then to go away from the feeder, then to approach the pedal and finally to press the pedal. Every stage of learning took one day. So step-by-step learning also took 4 days. Similarly, both groups of animals were taught to press a second pedal to obtain food (the second pedal and feeder were situated on the opposite wall of the experimental cage). The main difference between training strategies is that in the step-by-step group, food reward was used to elaborate each of the consecutive acts (approaching the feeder, turning away from the feeder towards the pedal, approaching the pedal, pressing the pedal), while in the one-step group only one act (pressing the pedal) was rewarded.

From 196 cingulate neurons recorded in rats having undergone step-by-step learning (Gavrilov, Grinchenko & Alexandrov, 2002; Svarnik et al., 2005), 72 units (37%) in animals able to press two pedals (‘2 pedals’ in Figure 10) had specific activations during realization of *new* acts (see above) acquired during learning in the experimental cage. There were only 7 such neurons (9.7%) out of 72 recorded in the one-step learning group. The difference was significant ( $p < 0.0001$ ,  $\chi^2$ ; Figure 10). The same regularity was discovered when the numbers of neurons specialized in relation to new acts were compared in animals able to press only one pedal (out of two mounted in the experimental cage; ‘1 pedal’ in Figure 10). From 52 cingulate neurons

recorded in rats having undergone step-by-step learning, 8 (15.4%) had specific activations during realization of the above-mentioned new acts. There were no such neurons (0 out of 57 recorded) in the one-step learning group ( $p < 0.01$ ,  $\chi^2$ ).

Thus, in accordance with our proposition, we found a positive correlation between the number of learning steps and the number of neurons specialized in relation to newly acquired behavior: the more steps there are, the more activated neurons subserve this behavior.

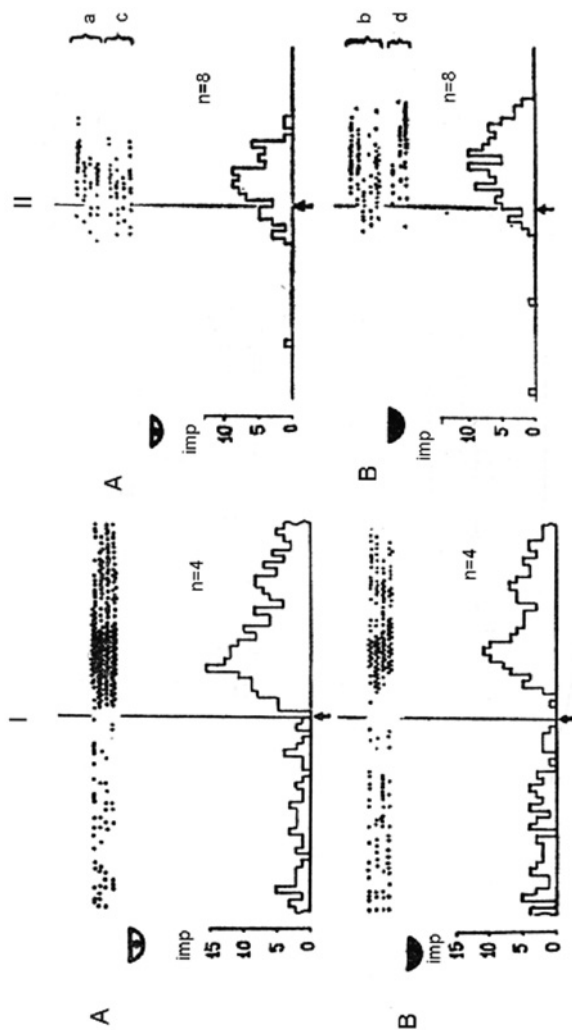
The above results lend sense to the *task* of comparing characteristics of ‘the same’ behavior with the different histories of its formation. For instance, how different are the number of errors, speed parameters, etc., of the behavior formed via different numbers of steps. This of course has many potential implications for teaching, but also for writing user manuals, etc.

#### *4. ‘Visual’ structures of the brain are involved in behavior without the individual having visual contact with the environment*

If we close our eyes tightly and carefully walk between a chair and a table using palpation, we can think that our vision doesn’t help us and that the visual cortex as well as retinal activity does not subserve this ‘blind’ behavior. However, this is not the case.

It was shown that activity of visual cortex neurons (Figure 11) and even ganglion retinal cells (their axons form the visual nerve along with the efferent fibers; Figure 12) is organized in accordance with the stages of food-acquisition behavior realized by an animal with eyes covered by non-transparent caps (Alexandrov, 1989; Alexandrov & Alexandrov, 1982; Alexandrov et al., 1986; Alexandrov & Järvillehto, 1993). Nevertheless, the set of activating neurons and the activation characteristics change when compared to an open-eye situation for the same behavior. Based on the available data (see Alexandrov & Sams, 2005; Kolbeneva et al., 2006), we can propose that the extent of differentiation in organism–environment relations decreases with eyes closed, in part at least because of increased contribution to the behavior organization by other modalities which provide less differentiated interaction.

These results point to the *task* of comparing motor characteristics of ‘the same’ behavior performed under normal conditions and under limited contact with the environment. It is also important to find out how these characteristics change with modifications of the environment as reported by different modalities, and how different the performance errors are in these two situations.



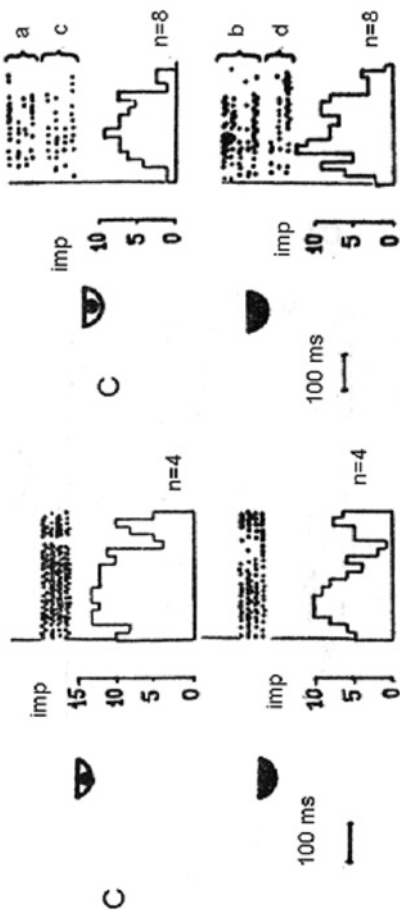
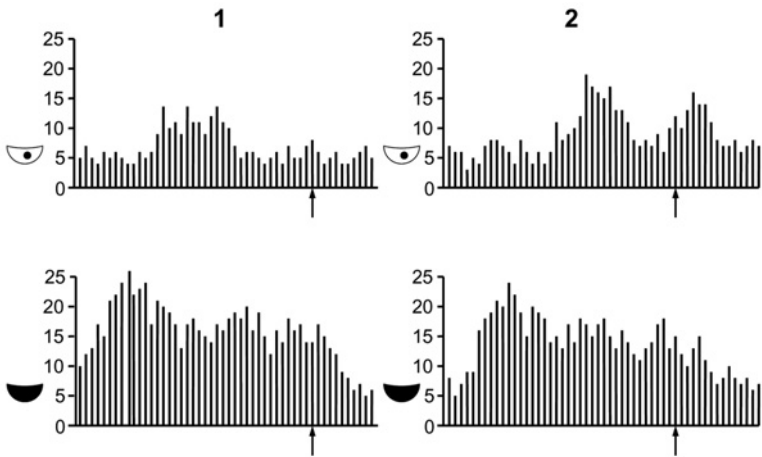


FIGURE 11

Activations of (I) visual- and (II) motor-cortex neurons are not extinguished by the non-transparent caps being put on

Notes: A and C (upper) show unit activity in the behavioral act with the eyes open, B and C (lower), with the non-transparent caps on. The onset of head movement towards food is marked with an arrow; *abscissa*, time; *ordinate*, number of impulses in the bin (*imp*); *n* = number of successive realizations of the behavioral act in which the neuron activity was analyzed. Lower-case letters indicate the succession of the non-transparent caps being put on and taken off. In C, histograms and rasters are plotted with the first spike in activation for a zero. Activations of the presented neurons appear at the same stage of the behavioral act, whether the eyes are open or have been closed by the caps. An averaging (from the first spike in the activation for both neurons) (C) clearly demonstrated that even the structure of activation is not changed by putting on the non-transparent caps.



**FIGURE 12**

**Strengthening of activation of optic tract fiber in 'closed-eye' behavior**

*Notes:* The upper section shows unit activity in the instrumental food-acquisition behavior with the eyes opened; the lower section shows activity of the same unit in the behavior with the eyes closed; (1) is a pair of histograms plotted from the end point (marked with an arrow) of the rabbit's approach to the pedal; the activation corresponding to movement from the feeder to the pedal; (2) is a pair of histograms plotted from the end point of the animal's approach to the feeder, and here the activation corresponds to movement from the pedal to the feeder. Bin width = 20 ms,  $n = 10$ . It can be seen, in both cases, that after the non-transparent caps are put on, activation is not only greater in amplitude, but also starts earlier and ends later.

*5. Brain organization of a behavioral act depends on its position in the behavioral continuum*

One may think that, if we have learned several actions, we can retrieve them from our 'memory warehouse' separately and put them together as they are into this or that behavioral pattern, just as children build different constructions using the same set of bricks. However, our actions are much more plastic than bricks. Actions change their properties when they are included in different constructions. To play with such bricks, isn't it a dream! We do it our whole life long.

It was shown that the characteristics of neuronal activations during switching from one act to the next in a sequence both reflect the parameters of the previous act and predict the parameters of the following act (Dorris, Pare & Munoz, 2000; Prut & Fetz, 1999). This dual dependence is due to assessment of the result of the performed behavior and, connected to it, organization of the following act. Consequently, the successive acts appear to be linked. It was

also found that sets of neurons subserving 'the same' behavioral act occupying different positions in a sequence are different (Shima & Tanji, 2000).

Hence, the *task* of comparing motor and other characteristics of 'the same' behavior included within various sequences is important.

#### *6. Systems formed at different stages of individual development have different properties*

It is known that recently formed skills are the first to suffer in pathology (Th. Ribot's law; Ribot, 1901). It has been shown that acute alcohol delivery has greater influence on the activity of neurons that belong to earlier-formed systems (Alexandrov et al., 1990, 1993).

These results outline the *task* of comparing motor characteristics of behavioral acts, subserved by the realization of systems of different ages.

#### *7. Previously formed behavior is modified by forming a new behavior*

You will recall from the above that specialized neurons do not change their specialization in relation to 'their' act, and that to form a new action other ('reserve') units must be recruited. It therefore might be concluded that, if we put some memory in our 'memory warehouse' and do not use it for some time, it stays on a shelf in the form it had when we put it there. However, this conclusion is wrong.

Behavioral data obtained in I. P. Pavlov's lab (1952) led him to conclude that adding new conditional reflexes immediately influences the state of the previous ones. We consider learning to be the specialization of a new group of neurons in relation to a formed system and the 'addition' of the latter to previously formed systems. It is logical that this addition should require mutual coordination of a new element with the ones previously formed and lead to reconsolidation modification of the latter. The molecular-biological characteristics of reconsolidation of memory and underlying modification occurring after repeated actualization have now been identified (see, e.g., Sara, 2000). Activation of a memory, like its formation, requires protein synthesis for reconsolidation processes. Thus protein-dependent consolidation processes can be linked not only with 'new' memories but, more generally, with 'active' memories (Nader, 2003).

The concept of reconsolidation modification does not contradict the position presented above regarding the permanence of the system's specialization

of neurons. Reconsolidation does not alter the modifications leading to the formation of long-term memory (Nader, Schafe & LeDoux, 2000). According to the aforementioned data, neurons that belong to a given system, and which are involved in one behavior, do not change their systemic specialization when the system provides for another behavior, but they do reorganize their activity.

Based on the data from experiments with investigation of systemic neuronal specialization, it has been concluded recently that earlier formed systems change after learning the next act (Alexandrov et al., 2001). The reconsolidation modification undergone by the earlier-formed 'old' system when a new related system appears was termed 'accommodation' reconsolidation (Alexandrov, 2006; Alexandrov et al., 2001). However, for the above conclusion, we used experimental data obtained during recordings of neuron activity *after* learning in earlier acquired definitive behavior for a hypothetical reconstruction of events taking place during the learning of this behavior. The way accommodation reconsolidation manifests itself *during* learning has been recently demonstrated in our laboratory by A. G. Gorkin, who used chronic tetrodes to record the activity of cingulate cortex neurons in rats.

Animals learned the above-mentioned instrumental food-acquisition behavior. At the start, they learn to press the first pedal to get a piece of food from the feeder located at the same wall of the experimental cage. After that they learn to press the second pedal located at the opposite wall of the cage. 'Non-specific' activity of some neurons appearing in behavior learned first was modified after the behavior near the opposite wall had been established. An example of such modifications of activity in neuron 40103–1, which was specialized in relation to the act learned second (near the opposite wall) can be seen in Figure 13.

In the activity of the specialized neuron a 'specific' phase can be distinguished – expressed activation; it appears during that behavioral act, in relation to a system in which this neuron was specialized. This activation usually greatly exceeds the 'non-specific' activity of the same neuron recorded during other behavioral acts; furthermore, 'non-specific' activity is more variable and does not appear in 100% of cases, as 'specific' activations did. The behavioral specialization of a neuron is its permanent characteristic. That is why neuronal activity can serve as an index for the actualization of a specific system, and the 'non-specific' activity of a neuron may indicate retrieval of the specific system from memory during performance of other

behavioral acts. Thus we consider 'non-specific' activity as an indicator of a relation between the system to which a given neuron belongs and other related systems.

The neuron presented in Figure 13 originally (after first learning; acts 1–6) showed 'non-specific' activation during turning the head to a pedal (act 1) and approaching a pedal (act 2). After the establishment of the second behavior (acts 11–16), 'specific' activation of this neuron during approaching the feeder (act 15) and seizing food in the feeder (act 16) appeared. At the same time, a significant increase ( $p < 0.01$ ; Wilcoxon's criterion; compare 1 and 2 in upper and lower graphs) of mean frequency of 'non-specific' activation (acts 1, 2 in lower graph of Figure 13) was revealed, evidencing 'accommodation' reconsolidation.

Hence the *task* of defining the dynamics of earlier formed behavior characteristics (both motor and effectiveness) at the introduction of a new skill into the structure of preexisting memory is of relevance.

#### *8. The brain activity of an observer while watching the behavior of a demonstrator depends on the observer's own experience with the same behavior*

Numerous reports show the influence of observation of a behavior on learning this behavior. We propose that the observation contributes to the process of neuronal specialization. Consequently the brain activity of an observer will be different when s/he has neurons specialized in relation to the observed behavior (then the activity of these neurons in observation will produce the 'mirror cells' phenomenon), and when there are no such neurons.

Accordingly, brain mapping of subjects who observe dancing shows that the patterns of brain activity depend on the observer's own skill in that particular dance (Calvo-Merino et al., 2005). In animal experiments, we obtained results that demonstrate the dependence of the observer's brain activity characteristics on own experience in the observed behavior (Ashumova et al., 2004).

We posit that the mechanisms of learning which start with observation and the trial-and-error mechanisms of 'independent' learning are different. Hence the task of comparing parameters of movements, effectiveness and stability of behavior acts formed with and without prior observation becomes relevant.



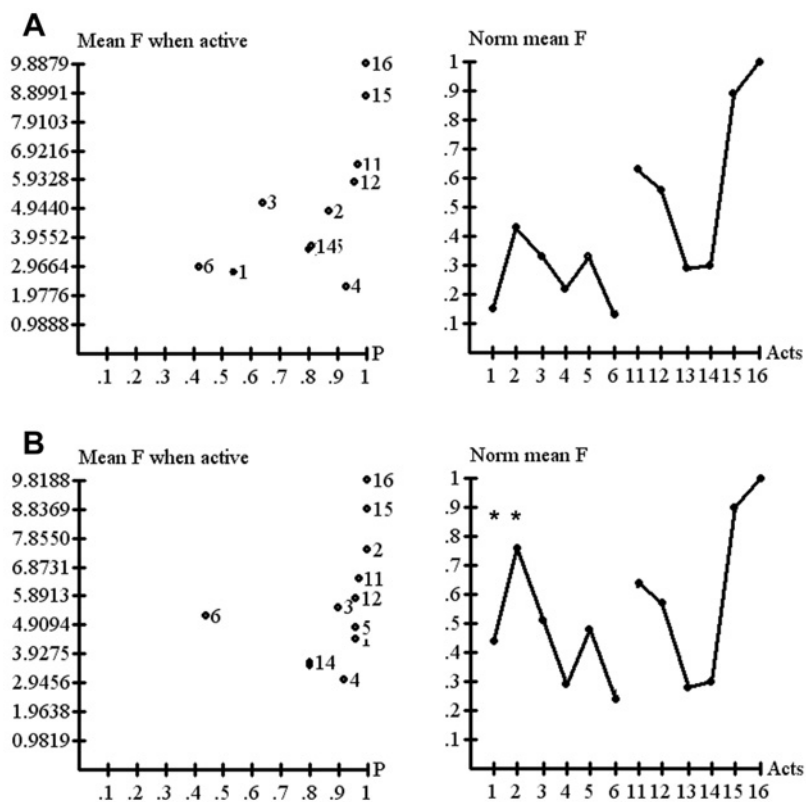


FIGURE 13

Change in the activity of cingulate cortex neuron in the previously learned (first) behavior after the establishment of the new (second) behavior

*Notes:* The upper pair of graphs demonstrates activity of the neuron in the first realizations of previously learned acts (acts 1–6) and in the first realizations of newly formed acts (acts 11–16). The lower pair of graphs demonstrates activity of this neuron in the first realizations of newly formed acts and in the previously formed behavior after the establishment of the new one.

Left graphs (*upper* and *lower*): *abscissa*, the probability of the presence of activation in the corresponding acts; *ordinate*, mean frequency in acts marked with the corresponding numbers (1–16). Right graphs (*upper* and *lower*): *abscissa*, the numeric labels of the corresponding behavioral acts (1, 11, turning a head to a pedal; 2, 12, approaching a pedal; 3, 13, stay in pedal corner of a cage; 4, 14, pressing a pedal; 5, 15, approaching a feeder; 6, 16, seizing food in a feeder); *ordinate*, the normalized average frequency of activity in the corresponding acts.

*Upper:* 1, n = 33; 2, n = 33; 3, n = 34; 4, n = 45; 5, n = 33; 6, n = 33; 11–16, n = 29–31. *Lower:* 1–6, n = 29–31.

\*  $p < 0.01$ ; Wilcoxon's criterion.

## Conclusion

We have shown that:

- Brain subserving of behavior reflects the history of its formation. Hence the activation characteristics and sets of active neurons are different in outwardly similar forms of behavior with different *histories* of formation. Environment similar in physical parameters is differently reflected in the activity of central and peripheral neurons depending on the *goal* of behavior.
- The brain organization of a behavioral act depends on its position in the behavioral continuum.
- The construction of systemic neuronal structures underlying behavior is continuous: brain subserving of previously formed behavior is modified by forming a new behavior.

What can we conclude for the construction of future augmented environments?

First, we can conclude that it is compulsory to take into account subjects' goals, and not rely on visible behavior alone. This has obvious implications for user research. It also has implications for design: the user's goals should be central to the system's specifications.

Second, we conclude that the way behavior is learned or a representation of an object is constructed through experience will have a deep impact on behavior. The phase in which subjects are first exposed to a new system requires specific attention in its design. Depending on the context, goal and type of learning, future behavior in relation to that system will be different.

At present, the way we design an augmented environment is often naïve, and we try to specify a system for what *it* should do. A new line of research would be to try to describe the system as lived by the user, from a subjective and goal-oriented perspective. While it may be too early to recreate a completely new approach to system design (a daunting task), at least a second iteration in the system design could be to review the system from this subjective perspective and to adapt the specifications of the system when their characteristics introduce too important a gap in the fluid execution of activity from a subjective user's perspective. For example, 'objects' or 'behaviors' which seem identical through operation of the system may in fact correspond to different 'objects' or 'behaviors' for the user as encountered in different steps of an operation, for instance if they refer to objects learned in completely different goal-contexts; and this may provoke usability problems, action slips or misunderstandings.

We consider the systems approach to be a theoretical bridge between studies of animal and of human behavior. It may help us use data obtained from experiments on animals to understand the brain bases of behavior in humans without oversimplification. For example, we have shown in animals that a moderate dose of alcohol (1 ml of ethanol per kg of body weight) suppressed the activity of neurons belonging to newer systems significantly more than of those belonging to older, earlier-formed ones (Alexandrov et al., 1990, 1993). From this we posited that in humans the same amount of alcohol (1 ml/kg) will suppress more brain subserving of comparatively ‘younger’ systems. Indeed, we showed that alcohol more significantly suppressed brain activity underlying categorization of later-learned foreign words than words of the native language (Alexandrov et al., 1998). Of course we cannot advocate anything like the technique of constructing an environment consisting of artificial objects with the same techniques we used for rabbits or rats; but there are some psychological techniques (cf. perceived quality: Nosulenko, 2008) which are a practical step in that direction.

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## References

- Alexandrov, Yu. I. (1975) 'Changes of patterns of the visual unit responses due to changes in the reinforcement parameters', *Journal of higher nervous activity* 25(4): 760–68. (in Russian)
- Alexandrov, Yu. I. (1989) *Psychophysiological significance of the activity of central and peripheral neurons in behavior*. Moscow: Science. (in Russian)
- Alexandrov, Yu. I. (2006) 'Learning and memory: traditional and systems approaches', *Neuroscience and behavioral physiology* 36: 969–85.
- Alexandrov, Yu. I. & Alexandrov, I. O. (1982) 'Specificity of visual and motor cortex neurons activity in behavior', *Acta neurobiologiae experimentalis* 42: 457–68.
- Alexandrov, Yu. I. & Grinchenko, Yu. V. (1980) 'Hierarchical organization of physiological subsystems in elementary food-acquisition behaviour', in R. F. Thompson, L. H. Hicks & V. B. Shvyrkov (eds) *Neural mechanisms of goal-directed behaviour*, pp. 177–89. New York: Academic Press.
- Alexandrov, Yu. I. & Grinchenko, Yu. V. (1984) 'Somatosensory and visual cortical unit activity in rabbits during receptive field testing and food-getting behavior', *Neurophysiology* 16: 212–19.
- Alexandrov, Yu. I. & Järvilehto, T. (1993) 'Activity versus reactivity in psychology and neurophysiology', *Ecological psychology* 5: 85–103.
- Alexandrov, Yu. I. & Korpusova, A. V. (1987) 'Role of goal in the determination of the activity of neurons in the visual and motor cortical areas of the rabbit', *Neuroscience and behavioral physiology* 17: 437–79.
- Alexandrov, Yu. I. & Sams, M. E. (2005) 'Emotion and consciousness: ends of a continuum', *Cognitive brain research* 25: 387–405.
- Alexandrov, Yu. I. & Shvyrkov, V. B. (1974) 'Latent periods and synchronization of unit discharges of the visual and somatosensory cortex in response to conditioning flashes', *Neurophysiology* 6: 437–9.
- Alexandrov, Yu. I., Grechenko, T. N., Gavrilov, V. V., Gorkin, A. G., Shevchenko, D. G., Grinchenko, Yu. V., Aleksandrov, I. O., Maksimova, N. E., Bezdenezhnych, B. N. & Bodunov, M. V. (2000) 'Formation and realization of individual experience: a psychophysiological approach', in R. Miller, A. M. Ivanitsky & P. V. Balaban (eds) *Conceptual advances in brain research*, vol. 2. *Conceptual advances in Russian neuroscience: complex brain functions*, pp. 181–200. Amsterdam: Harwood Academic.
- Alexandrov, Yu. I., Grinchenko, Yu. V., Järvilehto, T., Laukka, S., Maz, V. N. & Korpusova, A. V. (1993) 'Effect of ethanol on hippocampal neurons depends on their behavioral specialization', *Acta physiologica scandinavica* 149: 105–15.
- Alexandrov, Yu. I., Grinchenko, Yu. V., Järvilehto, T., Laukka, S., Maz, V. N. & Svetlayev, I. A. (1990) 'Acute effect of ethanol on the pattern of behavioral specialization of neurons in the limbic cortex of the freely moving rabbit', *Acta physiologica scandinavica* 140: 257–68.
- Alexandrov, Yu. I., Grinchenko, Yu. V., Shevchenko, D. G., Averkin, R. G., Matz, V. N., Laukka, S. & Korpusova, A. V. (2001) 'A subset of cingulate cortical neurons is specifically activated during alcohol-acquisition behaviour', *Acta physiologica scandinavica* 171: 87–97.
- Alexandrov, Yu. I., Grinchenko, Yu. V., Shvyrkov, V. B., Järvilehto, T. & Soininen, K. (1986) 'System-specific activity of optic tract fibres in open- and closed-eye behavior', *The Soviet journal of psychology* 7(2): 299–308.
- Alexandrov, Yu. I., Klucharev, V. & Sams, M. (2007) 'Effect of emotional context in auditory-cortex processing', *International journal of psychophysiology* 65: 261–71.

- Alexandrov, Yu. I., Sams, M., Lavikainen, J., Näätänen, R. & Reinikainen, K. (1998) 'Differential effects of alcohol on the cortical processing of foreign and native language', *International journal of psychophysiology* 28: 1–10.
- Anokhin, P. K. (1973) *Biology and neurophysiology of conditioned reflex and its role in adaptive behavior*. Oxford: Pergamon Press.
- Ashumova, I. V., Kamyshova, O. N., Gavrilov, V. V. & Alexandrov, Yu. I. (2004) 'Actualization of elements of individual experience without behavior realization: EEG analysis', in K. V. Sudakov (ed.) *Proceedings of Scientific Council on Experimental and Applied Physiology*, vol. 12. *Systems approach in physiology*, pp. 371–2. Moscow: P. K. Anokhin Institute of Normal Physiology / Russian Academy of Medical Sciences.
- Averkin, R. G., Sozinov, A. A., Grinchenko, Yu. V. & Alexandrov, Yu. I. (2004) 'Rabbit's posterior cingulate (PCC) single unit activity in instrumental food-acquisition behavior performed by one way or two alternative ways', in *FENS (Federation of European Neuroscience Societies) Forum 2004, FENS Abstracts, A042.3*, vol. 2. (available at: [http://fensforum.neurosciences.asso.fr/posters/R2/A042\\_3.html](http://fensforum.neurosciences.asso.fr/posters/R2/A042_3.html))
- Åstrand, K., Hämäläinen, H., Alexandrov, Yu. I. & Järvillehto, T. (1986) 'Response characteristics of the peripheral mechanoreceptive units in man: relation to the sensation magnitude and to the task of the subject', *Electroencephalography and clinical neurophysiology* 6: 438–46.
- Bradley, P. M., Burns, B. D., King, T. M. & Webb, A. C. (1996) 'Electrophysiological correlates of prior training: an in vitro study of an area of the avian brain which is essential for early learning', *Brain research* 708: 100–108.
- Brecht, M., Schneider, M. & Manns, I. D. (2005) 'Silent neurons in sensorimotor cortices: implication for cortical plasticity', in F. F. Ebner (ed.) *Neural plasticity in adult somatic sensory-motor systems*, pp. 1–19. Boca Raton: Taylor & Francis Group, LLC.
- Brosch, M., Selezneva, E. & Schech, H. (2005) 'Nonauditory events of a behavioral procedure activate auditory cortex of highly trained monkeys', *The journal of neuroscience* 25: 6797–806.
- Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E. & Haggard, P. (2005) 'Action observation and acquired motor skills: an fMRI study with expert dancers', *Cerebral cortex* 15: 1243–9.
- Chalmers, D. J. (1995) 'Facing up to the problem of consciousness', *Journal of consciousness studies* 2: 200–19.
- Chang, J.-Yu., Sawyer, S. F., Lee, R.-S. & Woodward, D. J. (1994) 'Electrophysiological and pharmacological evidence for the role of the nucleus accumbens in cocaine self-administration in freely moving rats', *The journal of neuroscience* 14: 1224–44.
- Chapin, J. K. & Woodward, D. J. (1982) 'Somatic sensory transmission to the cortex during movement: phasic modulation over the locomotor step cycle', *Experimental neurology* 78: 670–84.
- Dorris, M. C., Pare, M. & Munoz, D. P. (2000) 'Immediate neural plasticity shapes motor performance', *The journal of neuroscience* 20 (RC52): 1–5.
- Edelman, G. M. (1987) *Neural Darwinism: the theory of neuronal group selection*. New York: Basic Books.
- Engel, A. K., Fries, P., König, P., Brecht, M. & Singer, W. (1999) 'Temporal binding, binocular rivalry, and consciousness', *Consciousness and cognition* 8: 128–51.
- Gavrilov, V. V., Grinchenko, Yu. V. & Alexandrov, Yu. I. (2002) 'Do neurons in homologous cortical areas of rabbits and rats have similar behavioral specialization?', in *FENS (Federation of European Neuroscience Societies) Forum 2002, FENS Abstracts, A040.8*, vol. 1. (available at: [http://fens2002.neurosciences.asso.fr/pages/posters/R2/A040\\_8.html](http://fens2002.neurosciences.asso.fr/pages/posters/R2/A040_8.html))
- Gavrilov, V. V., Kuzina, E. A., Kamyshova, O. N., Arutyunova, K. R., Grinchenko, Yu. V. & Alexandrov, Yu. I. (2007) 'Peculiarities of individual experience structure resulting from

- learning the same task by different ways', in *Proceedings of meeting IV of the Russian psychological society*, vol. 1, Rostov-na-Donu.
- Gorkin, A. G. & Shevchenko, D. G. (1991) 'The stability of units' behavioral specialization', *Neuroscience and behavioral physiology* 21: 222–9.
- Gorkin, A. G. & Shevchenko, D. G. (1996) 'Distinctions in the neuronal activity of the rabbit limbic cortex under different training strategies', *Neuroscience and behavioral physiology* 26: 103–12.
- Granit, R. (1975) 'The functional role of muscle spindles – facts and hypotheses', *Brain* 98: 531–56.
- Greenberg, P. A. & Wilson, F. A. W. (2004) 'Functional stability of dorsolateral prefrontal neurons', *Journal of neurophysiology* 92: 1042–55.
- Hutchins, E. (1995) *Cognition in the wild*. Cambridge, MA: MIT Press.
- Jog, M. S., Kubota, K., Connolly, C. I., Hillegaart, V. & Graybiel, A. M. (1999) 'Building neural representations of habits', *Science* 286: 1745–9.
- Kolbeneva, M., Petrenko, V., Bezdenezhnyh, B. & Alexandrov, Yu. I. (2006) 'Emotionality of Russian adjectives associated with different sensory modalities', in *Text processing and cognitive technologies*, Paper Collection 11, pp. 378–87, The 8th international conference on Cognitive Modeling in Linguistics, Proceedings, vol. 1. Moscow-Varna: Kazanx.
- Koyama, T., Kato, K., Tanaka, Z. & Mikami, T. (2001) 'Anterior cingulate activity during pain-avoidance and reward tasks in monkeys', *Neuroscience research* 39: 421–30.
- Lahlou, S., Nosulenko, V. & Samoilenko, E. (2002) 'Un cadre méthodologique pour le design des environnements augmentés', *Social science information sur les sciences sociales* 41(4): 471–530.
- Lenay, C. (2008) 'Médiations techniques des interactions perceptives: rencontres tactiles dans les environnements numériques partagés' [Technical mediation of perceptive interactions: tactile encounters in shared digital environments], *Social science information sur les sciences sociales* 47(3): 333–54.
- Nader, K. (2003) 'Response to Arshavsky: challenging the old views', *Trends in neuroscience* 26: 466–8.
- Nader, K., Schafe, G. E. & Le Doux, J. E. (2000) 'Fear memories require protein synthesis in the amygdala for reconsolidation after retrieval', *Nature* 406: 722–6.
- Nicolelis, M. A. L., Ghazanafar, A. A., Faggin, B. M., Votaw, S. & Oliveria, L. M. O. (1997) 'Reconstructing the engram: simultaneous, multisite, many single neuron recordings', *Neuron* 18: 529–37.
- Nishijo, H., Yamamoto, Y., Ono, T., Uwano, T., Yamashita, J. & Yamashita, T. (1997) 'Single neuron responses in the monkey anterior cingulate cortex during visual discrimination', *Neuroscience letters* 227: 79–82.
- Nosulenko, V. (2008) 'Mesurer les activités numérisées par leur qualité perçue' [Measuring activities in digital space by their subjective quality], *Social science information sur les sciences sociales* 47(3): 393–419.
- Nosulenko, V. & Rabardel, P., eds (2007) *Rubinstein aujourd'hui. Nouvelles figures de l'activité humaine*. Toulouse/Paris: Octarès/Maison des Sciences de l'Homme.
- Paton, J. J., Belova, M. A., Morrison, S. E., & Salzman, C. D. (2006) 'The primate amygdale represents the positive and negative value of visual stimuli during learning', *Nature* 439: 865–70.
- Pavlov, I. P. (1952) *Lectures about work of cerebral hemispheres*. Moscow: Academy of Medical Sciences of the USSR.
- Priest, S. (1991) *Theories of the mind*. London: Penguin.
- Prut, Y. & Fetzi, E. E. (1999) 'Primate spinal interneurons show pre-movement instructed delay activity', *Nature* 401: 590–4.

- Quiroga, R. Q., Reddy, L., Kreiman, G., Koch, C. & Fried, I. (2005) 'Invariant visual representation by single neurons in the human brain', *Nature* 435: 1102–7.
- Ranck, J. B. (1973) 'Studies on single neurons in dorsal hippocampal formation and septum in unrestrained rats, I: behavioral correlates and firing repertoires', *Experimental neurology* 41: 461–555.
- Ribot, Th. (1901) *Les maladies de la mémoire*. Paris: Félix Alcan.
- Roelfsema, P. R., Engel, A. K., Konig, P. & Singer, W. (1997) 'Visuomotor integration is associated with zero time-lag synchronization among cortical areas', *Nature* 385: 157–61.
- Sakata, H. & Iwamura, Y. (1978) 'Cortical processing of tactile information in first somatosensory and parietal association areas in the monkey', in G. Gordon (ed.) *Active touch*, pp. 55–72. Oxford: Pergamon.
- Sara, S. J. (2000) 'Retrieval and reconsolidation: toward a neurobiology of remembering', *Learning and memory* 7: 73–84.
- Schmidt, E. M., Bak, M. J. & McIntosh, J. S. (1976) 'Long-term chronic recordings from cortical neurons', *Experimental neurology* 52: 496–506.
- Shima, K. & Tanji, J. (2000) 'Neuronal activity in the supplementary and presupplementary motor areas for temporal organization of multiple movements', *Journal of neurophysiology* 84: 2148–60.
- Shoers, T. J., Miesegaes, G., Beylin, A., Zhao, M., Rydel, T. & Gould, E. (2001) 'Neurogenesis is involved in the formation of trace memories', *Nature* 410: 372–5.
- Shuler, M. G. & Bear, M. F. (2006) 'Reward timing in the primary visual cortex', *Science* 311: 1606–9.
- Shvyrkov, V. B. (1980) 'Goal as a system-forming factor in behavior and learning', in R. F. Thompson, L. H. Hicks & V. B. Shvyrkov (eds) *Neural mechanisms of goal-directed behavior and learning*, pp. 199–220. New York, London, Toronto, Sydney, San Francisco: Academic Press.
- Shvyrkov, V. B. (1986) 'Behavioral specializations of neurons and system-selection hypothesis of learning', in F. Klix & H. Hagendorf (eds) *Human memory and cognitive capabilities*, pp. 599–611. Amsterdam: Elsevier.
- Shvyrkov, V. B. (1990) *Neurophysiological study of systemic mechanisms of behavior*. New Delhi: Oxonian Press.
- Shvyrkova, N. A. & Shvyrkov, V. B. (1975) 'Visual cortical unit activity during feeding and avoidance behavior', *Neurophysiology* 7: 82–3.
- Svornik, O. E., Alexandrov, Yu. I., Gavrilov, V. V., Grinchenko, Yu. V. & Anokhin, K. V. (2005) 'Fos expression and task-related neuronal activity in rat cerebral cortex after instrumental learning', *Neuroscience* 136: 33–42.
- Swadlow, H. A. & Hicks, T. P. (1997) 'Subthreshold receptive fields and baseline excitability of "silent" S1 callosal neurons in awake rabbits: contributions of AMPA/kainate and NMDA receptors', *Experimental brain research* 115: 403–9.
- Thatcher, R. W. (1997) 'Neural coherence and the content of consciousness', *Consciousness and cognition* 6: 42–9.
- Thompson, E. & Varela, F. J. (2001) 'Radical embodiment: neural dynamics and consciousness', *Trends in cognitive sciences* 5: 418–25.
- Thompson, L. T. & Best, P. J. (1990) 'Long-term stability of the place-field activity of single units recorded from the dorsal hippocampus of freely behaving rats', *Brain research* 509: 299–308.
- Wheeler, M. E., Petersen, S. E. & Buckner, R. L. (2000) 'Memory's echo: vivid remembering reactivates sensory specific cortex', *Proceedings of the National Academy of Sciences USA* 97: 11125–9.

- Williams, J. C., Rennaker, R. L. & Kipke, D. R. (1999) 'Stability of chronic multichannel neural recordings: implications for a long-term neural interface', *Neurocomputing* 26: 1069–76.
- Wilson, M. A. & McNaughton, B. L. (1993) 'Dynamics of the hippocampal ensemble code for space', *Science* 261: 1055–8.
- Woodward, D. J., Janak, P. H. & Chang, J.-Yu. (1998) 'Ethanol action on neuronal networks studied with multineuron recording in freely moving animals', *Alcohol: clinical and experimental research* 22: 10–22.