Can Consciousness in Animals Be Assessed on the Basis of Their Behavior?

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The idea that animals have consciousness arose from studies of their behavior. However, behavioral studies are insufficient for assessing the existence of consciousness in animals. Following Gutfreund [2017], I am of the opinion that the answer to the question of consciousness in animals requires an understanding of the neural mechanisms of consciousness. The question here is that of whether it is possible to understand these mechanisms. There is a wide range of views on this question – from cartesian dualism, which denies the existence of any kind of neural mechanism for consciousness, to the diametrically opposite view, that consciousness is a cognitive function which can therefore theoretically be understood. I adhere to this latter point of view. However, as argued in this article, progress in studies of the mechanisms of cognitive functions, including consciousness, requires a paradigm shift in neurobiology from a purely connectionist approach towards cell biology.

Keywords: consciousness, behavior, sensory perception, language, microcephaly, concept cells.

In memory of my teachers Mark Victorovich Kirzon, Mikhail Georgievich Udel'nov, Aleksand Nikolaevich Kabanov, and Israel Moiseevich Gelfand.

 Consciousness in Humans and Animals. A relatively large number of articles has recently been published on the problem of the existence of consciousness in animals [Nikol'skaya, 2013; Butler, 2012; Dawkins, 2015; Gutfreund, 2017; Spence et al., 2017]. The idea that animals may have consciousness arose as a result of studies of their behavior in both natural and laboratory conditions. Animals display amazing innate forms of behavior and a surprising ability to adapt their behavior to changing environmental conditions. In addition, domestic pets learn to perceive the most minor changes in their owner's mood and, to some extent to copy their behavior (this latter is particularly characteristic of the great apes). It is therefore not surprising that investigators (and not only investigators) often describe the behavior of animals in purely anthropomorphic terms such as "sensible," "focused," "deliberate," etc. Everyone knows

the typical comment of an owner about his or her favorite dog: "She always understands everything, only she can't say so." From here it is just one step to the idea that animals, like humans, have consciousness. It has been suggested that the main elements of consciousness exist not only in mammals and birds [Butler, 2012; Butler and Cotterill, 2006; Fabbro et al., 2015; Harley, 2013; Spence et al., 2017], but even in insects [Barron and Klein, 2016] and cephalopod mollusks [Mather 2008]. I will not describe the results of fastidious behavioral experiments on whose results these conclusions are based, as I will separate the point of view of authors who believe that no study of external behavior can provide grounds for assessing the existence or absence of consciousness in animals. Furthermore, this not applies not only to animals, but also to humans. As stated convincingly in the books by Chailakhyan [1992] and Koch [2004], we cannot strictly speaking make judgments about the existence of consciousness in other people on the basis of their behavior, including their verbal utterances. I will provide a brief explanation of this point.

 What is consciousness? According to the most recent definitions given, that of Gutfreund [2017], consciousness is: "the subjective experience or feeling of any type." The

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author adds that "this is far from being a scientific definition, but is understood well by all who have subjective experiences."¹ In fact, despite the lack of a scientific definition of this phenomenon, all people intuitively understand what consciousness is, because every person is conscious of his or her own Personality (with a capital P), with his or her own thoughts, memories, sympathies and antipathies, emotions, etc. The only reliable fact which everyone knows about consciousness is that we have it while we are awake and, sometimes in a quite quirky way, during dreams. And it is this fact, not their behavior, that allows us to take the view that other people also have consciousness, as we are all of the same biological type. This can be illustrated by the following example. Current fantasy films often show human-like robots which provide ideal simulations of human behavior, including human cognitive functions such as the ability to carry out verbal communication, take decisions, etc. (which is not surprising, as robots are played by actors). Technological progress in this area is so great that these fantasies may be the truth of the very near future. However, regardless of how well robots simulate human behavior, it does not occur to anyone that robots have consciousness for the simple reason that, unlike animals, they are not biological entities and their human-like behavior is determined by mechanisms completely different from those underlying human behavior.

 The intuitive conviction of each human, that other people must also have consciousness, is to some extent reinforced by the fact that when we pronounce the word "consciousness," our companions do not ask "What's that?" – if they lacked consciousness, they would ask. And we would be unable to answer, in the same way that we cannot explain color to a person blind from birth.

 These points show why I am in complete agreement with Gutfreund's original idea that solution of the problem of the existence of consciousness in animals requires an understanding of the neural mechanisms of human consciousness. Only in this case can we explain whether and to what extent analogous mechanisms function in animals. However, this way of putting the question inevitably leads to another no less difficult problem, that of how realistic our understanding of the neural mechanisms of consciousness is. I will discuss this question in more detail in the next section.

Do We Know the Mechanisms of Consciousness? There is a wide range of views on the question of the knowability of the neural mechanisms of consciousness – from cartesian dualism, which in principle denies the existence of any kind of neural mechanisms of consciousness, to the

diametrically opposite point of view, which holds that consciousness is among the cognitive functions of the brain, whose mechanisms will sooner or later be known. The current position on this point is that every point of view is more a matter of faith than something based in rational arguments. I am an adherent of the latter point of view, i.e., I recognize that the mechanisms of consciousness are fundamentally knowable. At the same time, I am aware that this point of view is not as much for scientific as esthetic considerations. As a natural scientist, it suits me to think that the capacities of science to know the manifestations of nature, which include consciousness, are unlimited. Meanwhile, all other points of view (naturally, we are considering only those points of view that accept that consciousness is a function of the brain) suggest, for various reasons, that we have and can have no methods for studying the mechanisms of consciousness and, thus, recognize the existence of some limit to our understanding of the operation of the brain. However, recognizing the fundamental knowability of the nature of consciousness, I suggest that further progress in studies of higher nervous activity is significantly dependent on the paradigm shift from the dominant purely connectionist approach towards cell biology.

The connectionist paradigm and its limitations. According to the dominant paradigm of contemporary neurobiology, higher nervous activity occurs as a result of interactions between neurons forming complex networks. The neurons themselves are regarded as simple elements whose functions are limited to generating electrical potentials and transmitting signals to other cells using neurotransmitters. This purely connectionist paradigm was clearly formulated in the last edition of a popular neurobiology textbook: "Mental processes are the end product of the interactions between elementary processing units" ([Kandel et al., 2013], p. 17). This paradigm led to the point of view that both the whole brain and its individual areas are computation systems consisting of binary elements, which are particularly reflected in the titles of many recently published articles, for example [Bornkessel-Schlesewsky et al., 2015; Hickok, 2012; Marcus et al., 2014; Priebe and Ferster, 2015]. The term "computation" is used in these articles not only as a metaphor; it also reflects the point of view noted above and clearly illustrated in Fig. 1, where the human brain smoothly merges with a computer board. However, this analogy, in which the brain is represented as a giant computer, is not so obvious if we recall how quickly information is processed in computers and that neurons are regarded as "elementary processing units." Even the slowest computer chips work with time characteristics measured in nanoseconds. By comparison, the time characteristics of neurons operating as elements of a cortical network (spike conduction times via the fine axons of cortical neurons, durations of interspike intervals and magnitudes of synaptic delays on signal transmission from cell to cell using chemical transmitters) are measured in milliseconds.

¹ It should be noted that other definitions of consciousness are also difficult to regard as scientific. An example: "The biological phenomenon of aware, subjective experience that is generated by the activity of neurons and includes present stimuli, thoughts and/or feelings or remembered, imagined, or anticipated ones" [Butler, 2012].

 The idea that the brain is a computing machine, like the whole connectionist paradigm, is to a significant extent confirmed by many attempts at mathematical (computer and analytical) modeling of the higher functions of the brain, such as memory, language generation and perception, decision-taking, emotions, and others, using artificial neural networks consisting of simple neuron-like elements (I will not present references here, as at least 10 articles on this theme are published every month, especially in journals such as *Neural Computation*, *PLoS Computational Biology*, *Biological Cybernetics*, *Journal of Mathematical Psychology*, etc.). It can be suggested that any of these models may help understand the mechanisms of operation of the real brain. Furthermore, some authors take the view that this kind of modeling may help understand the mechanisms of mental disorders [Deco and Kringelbach, 2014].

 It should, however, be emphasized that far from all mathematicians adhere to the use of a simplified connectionist approach and such a simplified model for understanding the cognitive functions of the brain. In the preceding publication, I provided a detailed description of mathematician Gel'fand's view, who holds that existing mathematical approaches generally reduce the complex organization of the brain to the level of simple engineering systems [Arshavsky, 2010].2 Here I cite another well-known mathematician, Manin. In his book *Mathematics as Metaphor* [Manin, 2008] he discussed the processes underlying the operation of the brain and presented the following question:

Do we already have the correct language to describe these processes, as we talk only about the construction of ever more detailed views, or whether this is a complete change in the main paradigm before us? (page 374).

 To explain the reasons for doubting the adequacy of existing "cybernetic" approaches to studies of the operation of the brain, Manin gave the example of people's verbal communication ability:

 "We know how large the database containing the dictionary and grammar is and how diffi cult it is to organise searches of it taking account of both semantics and grammar at all levels and to write programs simulating the production and understanding of speech. Parallelism here is very poor. The time parameters of the elementary processes in the nervous system are on the scale of milliseconds. Synchronization is objectionable. How can language algorithms be maintained in natural time in such 'wetware'? It is simpler to suggest that there is something very important that we still do not understand" (page 375).

 In a recent article, Manin and Manin came to the conclusion that the brain can correctly be compared with the internet (World Wide Web), where the role of computers is played by individual neurons and specialized groups of neu-

Fig. 1. Illustration of the concept that neural networks in the brain are computation building blocks analogous to microprocessors in computers [Marcus et al., 2014].

rons [Manin and Manin, 2017]. Below I will provide two physiological examples showing how difficult it is, if even possible, to explain the mechanisms of cognitive functions both in animals and humans in the framework of the purely connectionist concept proposing that real neural networks are made up of simple binary elements (this question is discussed in more detail in [Arshavsky, 2011; Arshavsky 2009, 2017]). In addition, an experimental observation will be presented supporting the view that, at least indirectly, cognitive functions can be mediated at the cellular level.

Qualitatively different sensory sensations. This example, inspired by Hawkins' book [2014], comes from sensory physiology. Why do signals arriving in the brain from different sensory organs induce qualitatively different sensations? It is surprising that this question receives almost no discussion in the physiology literature and is mainly left to the mercy of philosophers.³ Here I formulate this as a purely physiological question. Why do signals arriving from receptors in the retina to the occipital part of the brain via fibers from neurons in the lateral geniculate body induce visual sensations, while signals arriving from the organ of Corti into the temporal area of the cortex via fibers from neurons in the medial geniculate body induce auditory sensations? It is not at all easy to answer this question staying within the framework of a purely connectionist paradigm. The occipital and temporal areas of the cortex are made up of identical types of neurons and have a similar layered organization in the horizontal plane and columnar organization in the vertical plane. The neurons generate identical action potentials and use identical transmitters to propagate their signals. The

² This article is preceded by an Annotation. I would like to take this opportunity to advise readers that I had nothing to do with its authorship.

 3 I have examined the neurobiology book mentioned above [Kandel et al., 2013] and a specialist book on the physiology of the sensory systems [Smith, 2005]. Neither notes the problem of the mechanisms of the different qualities of sensations.

Fig. 2. MRI images of a normal brain (left) and the brain of a patient with primary microcephaly due to a mutation in the *ASPM* gene, which is important for the functioning of the mitotic spindle in neuroblasts [http:/dx.doi.org.10.1371/journal.pbio.0020134.g001].

same can be said of the lateral and medial geniculocortical pathways. They have similar organization and their fibers terminate in the cortex on the same types of neurons. The different perception of signals arriving from the retina and the organ of Corti can hardly be explained in terms of the quantitative morphological differences between the occipital and temporal areas of the cortex. Although these differences vary significantly in different species depending on their modus vivendi (for example, diurnal and nocturnal animals), the occipital and temporal areas always function as visual and auditory centers respectively. Finally, there are no grounds for proposing that the differences in the functions of the occipital and temporal areas of the cortex are formed by learning, as precocial animals (such as ungulates) see and hear virtually from the moment of birth.

 Experiments on rats and mice have shown that although neurons in different parts of the cortex, including the occipital and temporal, mainly express the same genes, they also express a number of area-specific genes [Ersland] et al., 2012, 2013; Leamey et al., 2008; Stansberg et al., 2011]. The authors themselves are inclined to interpret these results in the framework of the widely accepted connectionist paradigm. In other words, they suggest that these genes determine the specific organization of the neural networks making up the different sensory areas. However, it is entirely unclear what specific characteristics of the networks of uniformly organized cortex they have in mind.4 It is also unclear which specific characteristics of the network could determine such radical functional differences between different sensory areas. Is it irrational to suggest that the cerebral neurons involved in the perception of different sensory signals have more complex functions than merely generating electrical potentials, and that they are qualitatively different from each other? This hypothesis requires the area-specific genes expressed by neurons in the occipital and temporal areas of the cortex to determine some unknown

internal property allowing these cells to function as "visual" and "auditory" cells respectively.

 The human ability to communicate with language. The second example is from neurolinguistics. Language – oral and written, and also the sign-based language among deaf people – is a uniquely human ability to create an essentially infinite number of meaningful communications using a finite number of lexical elements and a set of grammatical rules. Even great apes, which communicate using a complex system of sounds, gestures, and expressions, are unable to create even the simplest of sentences. Like any species-specific characteristic, the human ability to communicate using language is determined by genetic factors [Fisher et al., 2003; Li and Bartlett, 2012; Reader et al., 2014]. A natural question is that of which phenotypic aspects of the organization of the human brain are determined by language-related genes. As the purely connectionist concept regards neurons as simple elements generating electrical potentials, it does not propose any radical differences between cerebral neurons involved in performing cognitive functions in humans and animals. This unavoidably leads to the conclusion that the decisive cause of the unique abilities (including linguistic capacities) of the human brain is the enormous number of neurons and synaptic connections allowing a much more complex network to be formed than in animals (for example, [Dicke and Roth, 2016; Hofman, 2014]). Thus, the location of the language centers in the left hemisphere is often linked with the greater size of the left frontotemporal area than the right [Dorsaint-Pierre et al., 2006; Geschwind and Levitsky, 1968].

 The point of view that the intellectual capacity of the human brain is mainly determined by the numbers of neurons and their connections is rebutted by data obtained from studies of the mental capacities of patients with microcephaly. Microcephaly patients include individuals whose frontooccipital circumference is three or more standard deviations below the mean. The commonest cause of congenital microcephaly is impairments to the final stages of the division of the precursors of the cells involved in forming the cerebral cortex ([Faheem et al., 2015; Trimborn et al., 2005; Woods et al., 2005]; Fig. 2). Here I will discuss only types of

⁴ I note that in the laboratory rodents the cortex is organized more uniformly than in humans, where it is divided into 52 cytoarchitectonic zones with different layer thicknesses, neuron sizes, and other mostly quantitative characteristics.

Fig. 3. Concept cells. *a*) Responses of a neuron in the entorhinal cortex to presentation to the patient of 76 different stimuli, including photographs and names (pronounced or written on the computer monitor) of familiar people, as well as photographs of animals and famous architectural monuments. The neuron responded to different photographs of Luke Skywalker, a character in the film *Star Wars* (stimuli Nos. 7, 38, and 39), as well as to his name, both written (stimulus 58) and pronounced by synthesized male and female voices (stimuli 71 and 72). The neuron did not respond to other photographs or names, with the exception of a photograph of Yoda, another character from *Star Wars* (stimulus 63). The horizontal line shows five standard deviations above the mean baseline activity level [Quian Quiroga, 2012]. (b) Responses of two concept neurons recorded with the same microelectrode in the amygdala. The upper neuron selectively responded to photographs (stimuli 24–26), the written name (stimulus 27), and the pronounced name (stimulus 90) of one of the researchers running the experiment; this person was previously unknown to the patient. The second neuron selectively responded to photographs of the actor Michael Douglas (stimuli 56–58). In contrast to the upper neuron, this neuron did not respond to Douglas' written name (stimulus 59) and responded weakly to pronunciation of his name (stimulus 96) [Quian Quiroga, 2009].

microcephaly with head circumference three, but not four, standard deviations below the mean. Brain weight in these individuals is 430–600 g [McCreary, 1996; Seemenová, 1985], which is about 2.5 times below the normal (1300– 1400 g) and is close to brain weight in the great apes (420 g in chimpanzees, 500 g in gorillas).

 Despite the approximately threefold decrease in the number of cortical neurons, these microcephaly patients are capable of verbal communication, at least at the level of a five-year-old child [Trimborn et al., 2005; Woods et al., 2005]. Furthermore, more than a dozen articles have been published with titles of the type *Microcephaly with normal intelligence* [Chacon-Camacho et al., 2015; Evans, 1991; Hennekam et al., 1992; Ramírez et al., 1983; Rizzo and Pavone, 1995; Rossi et al., 1987; Seemanová, 1985; Wilder, 1911]. Some of these individuals have finished school and have then received specialist education. Among them are people in professions such as postmen [Wilder, 1911], qualified secretaries [Rossi et al., 1987], kindergarten assistant

[Evans, 1991], bank employees [Rizzo and Pavone, 1995], and even doctors [Ramírez et al., 1983]. As the authors of these studies focused on describing the general intellectual abilities of people with microcephaly, I reverted to some of them to request more detailed descriptions of the linguistic abilities of their patients. I have previously quoted the response of well-known neurologist Professor R. Hennekam of Amsterdam University and would like to quote him again:

 "They were completely normal human beings, attending normal primary and secondary school, and had all the abilities that normal educated persons have. Several of the younger generation were taught three languages, as is the case for many people in the Netherlands, and their abilities in using these (oral and written) were certainly no less than those of their peers."

It is clear how difficult it is to explain the normal linguistic capacities of people with microcephaly and their reduced neural networks purely from the point of view of the connectionist concept. It might be more correct to suggest that the language genes determine not only the number of neurons and the architecture of their connections, but also some unknown internal properties of neurons, allowing them to carry out specific language functions. In fact, this is the same suggestion made to explain different sensory sensations, i.e., that they are cognitive functions, in this case linguistic, mediated primarily at the intracellular level. Network mechanisms support the cooperative and coordinated activity of specialized neurons.

Concept cells. The idea that cognitive functions might be mediated at the intracellular level has received experimental support as a result of the discovery of the so-called "concept cells" [Quian Quiroga, 2012; Quian Quiroga et al., 2005; 2009; 2013]. In patients suffering from frequent (from several times a day to once a month) epileptic seizures and receiving no treatment other than surgical, activity were recorded from individual neurons using an apparatus used for locating the focus of epileptogenic activity. The medial temporal lobe (hippocampus, parahippocampal cortex, entorhinal cortex, and amygdala⁵), where foci of epileptogenic activity was most frequently located, were found to contain neurons responding selectively to images of a familiar person, for example, a family member, politician, popular actor, or film star (Fig. 3). The responses were independent of the concrete characteristics of the images, such as the size of the face on the photograph, the turn of the head (profile, half face, or full face), clothing, or whether the image was a color photograph or a diagram. Some of these neurons responded not only to images of the person concerned, but also to the person's name said aloud and/or written on a computer screen (Fig. 3, *a*, *b*, upper part). These concept cells were found to form quite quickly, as a neuron selectively responding to the photograph and name of one of the members of the research group with whom the patient had not previously been familiar was found (Fig. 3, *b*, upper part). Neurons selectively responding to different photographs of architectural monuments (the leaning tower of Pisa, the Taj Mahal, Sydney Opera House) or an animal (dog, squirrel, hare) were also found.

 Results obtained by Quian Quiroga et al. showed that the ability of the brain to create abstract representations ("concepts") of individual persons, animals, or objects could be recorded at the level of single neurons. Each concrete object appeared not to be represented in the brain by one or just a few neurons (the proverbial "my grandmother" neuron). If this were so, the probability of recording concept cells in relatively short tests would be approximately zero. In the authors' view, the number of neurons representing

5 Although the authors of the studies cited included the amygdala as part of the medial temporal lobe, this structure, in contrast to the other three, is essentially not a cortical, but rather a nuclear formation. It would probably be more correct to say that all these structures are parts of the limbic system. However, this is a purely terminological problem with a complex history.

each concept is around 20000. These neurons do not form a compact group. Rather, they are disseminated in the medial temporal lobe, as when a single electrode records two concept cells, they always respond to the image not of one specific person, but to the images of different people (Fig. 3, *b*).

 There are two possible explanations for the formation of abstract concepts represented by the corresponding neurons. One is based on the connectionist point of view. This proposes that abstract concepts are formed at the level of the neural network, such that the responses of concept cells reflect the activity of the whole network. The alternative explanation holds that concepts are formed at the level of individual neurons, while synaptic connections support the interaction of cells representing different concepts. It should be noted that these two explanations are equally hypothetical, as there are no data showing that neurons representing the same concept interact and form a network. They have the same probability of being connected to neurons representing other concepts. Below, I present two arguments in favor of the second explanation.

 1. The responses of concept cells to images of a given person recorded in different structures of the medial temporal lobe differed in terms of latency and various other characteristics (for example, the proportion of neurons responding to both an image of the person and the person's name was lower in the amygdala than the entorhinal cortex and hippocampus; this type of cell was completely absent from the parahippocampal cortex). If we accept that the response of a concept cell reflects not its properties, but the activity of the neural network, this means that each of these structures forms its own concept network rather than there being a single network common to the whole of the medial temporal lobe. However, in this case we come to the paradoxical conclusion that the ability of neural networks to form abstract concepts does not depend on their actual cytoarchitectonics (to see this it is enough to compare the cytoarchitectonic organization of the amygdala and entorhinal cortex or hippocampus).

 2. According to the connectionist concept, the mechanism of formation of neural networks representing abstract concepts may be based exclusively on synaptic plasticity, i.e., on changes in the strengths of existing and the formation of new interneuronal connections. However, there are serious difficulties with this explanation. We should recall that that concept cells were found in patients suffering from frequent epileptic seizures, in most cases originating directly within the medial temporal lobe. This type of seizure is due to high-frequency, synchronous discharges of neurons in extensive areas of the cerebral cortex [Weiss et al., 2016; Wyllie, 2006]. If plasticity is an immanent property of synapses, then such spike discharges, regardless of their origin, must induce significant changes in the strength of interneuronal connections. This means that every epileptic seizure in studies of patients must lead to destruction of neural networks formed not only in the medial temporal lobe, but also

 These arguments, especially the latter, suggest that the ability of the human brain to create abstract concepts can hardly be based on purely network mechanisms. It has to be suggested that this ability is based on other, apparently intracellular, mechanisms, protected from ongoing synaptic activity.

Conclusions. In conclusion, I would like to draw attention to a number of theoretical studies whose authors linked the mechanism of cognitive functions, including the mechanism of consciousness, to quantum processes occurring within brain cells [Liberman et al., 1987; Hagan et al., 2016; Hameroff, 2001, 2014; Korf, 2015; Liberman et al., 1989; Penrose, 2001]. In contrast to studies addressing theoretical analysis of neural networks, these studies have not received wide recognition in the literature. However, it remains possible that the situation could change in the visible future, and that these or similar ideas relating to studies of intracellular processes will play the leading role in the physiology of higher brain functions. Otherwise, how could we explain cases of microcephaly with normal intellect and the existence of concept cells in patients with epilepsy, and particularly the paradoxical contradiction between the high rate of mental processes and the slow rate of the operation of neurons as elements of neural networks? (I note parenthetically that one of the clearest examples of this paradoxical contradiction is the result of the two matches between Garry Kasparov and the Deep Blue supercomputer. Although the computer could analyze 2·108 positions per second, Kasparov successfully confronted the computer and the final match score was $6.5:5.5$ in his favor.

 We might think that the shift in the basic paradigm from pure connectionism to intracellular neurobiology would not only allow us to understand the mechanism of cognitive functions, but also provide a solution to the problem of the existence of consciousness in animals. In contrast to studies of behavior, where it is virtually impossible to overcome anthropomorphism in assessing results, this type of approach can, as rightly noted by Gutfreund [2017], be strictly objective.

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