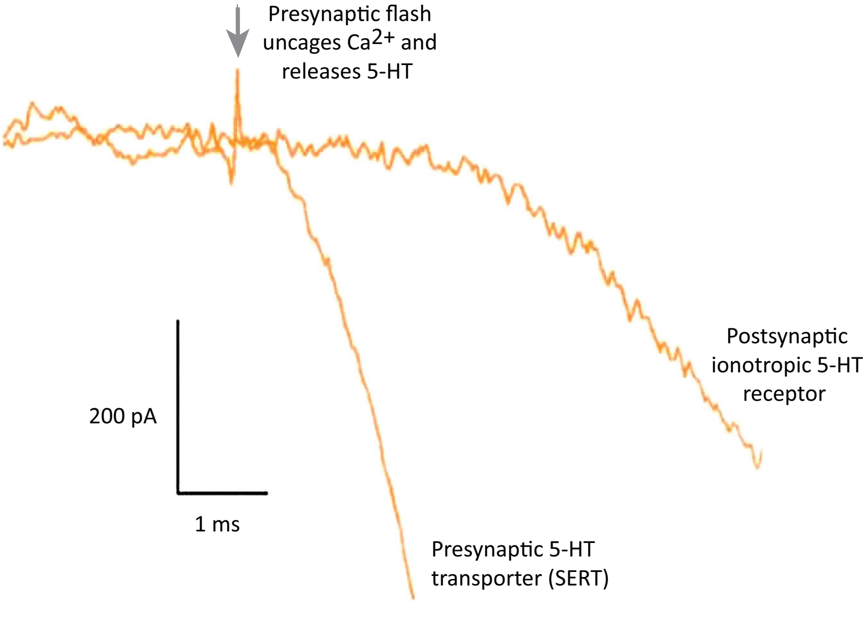

Trends in Neurosciences

Figure 2. Presynaptic Serotonin Transporter (SERT) and Postsynaptic 5-HT Ionotropic Receptors Responding to the Rapid Release of Presynaptic Ca^{2+} in the Leech Synapse. Adapted from [12].

conditions to authentic ionotropic receptors. In addition, drugs such as AMPH generate similar fast-acting currents. Thus, alongside its role as a DA transporter, DAT generates currents comparable to those generated by glutamatergic and GABAergic ionotropic receptors. The presynaptic dopaminergic terminal therefore contains both an inhibitory metabotropic DA receptor (D2) and an excitatory ionotropic DA receptor (DAT). Because DAT contains an endogenous leak current, drugs such as cocaine, which block the leak, are inhibitory. A similar story obtains for serotonin or norepinephrine. DAT, SERT, and NET act as excitatory or inhibitory ionotropic receptors depending on the ligand [9]. For many years, we have referred to the current-generating property of monoamine transporters as electrogenic or channel-like; recognizing monoamine transporters as ligand-modulated ion channels in addition to their traditional role may change this perspective.

In vivo and *in vitro* data already support glutamate and GABA transporters as ligand-gated ion channels, but this is a controversial concept for monoamine transporters. Perhaps this is because *in vivo* data for monoamine transporters acting as receptors are scarce. Nevertheless, Ingram *et al*. showed that DA and AMPH modulate the excitability of mammalian dopaminergic neurons [10]. Carvelli *et al.* documented DAT currents in *Caenorhabditis elegans* dopaminergic neurons [11], and Bruns *et al.* [12] compared 5-HT ionotropic receptor currents and 5-HT-induced SERT currents in the leech synapse (Figure 2). Viewing monoamine transporters as ionotropic receptors, where almost none exist, may stimulate new experiments to test this perspective.

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Forum

The Neuroethological Paradox of Animal Consciousness

Yoram Gutfreund[1,*]

The more advanced our understanding of the brain of an animal is, the less likely that this animal is a conscious being. This provocative logical paradox is explained and analyzed, leading to the conclusion that to advance understanding of animal consciousness it is necessary to resolve first how our consciousness is produced by our brain.

The Question of Animal Consciousness

Which of our fellow animals share with us the mysterious and nontrivial abilities to be aware of our experience or to have internal feelings, abilities that are also known as **phenomenal consciousness** (see Glossary), qualia, or sentiency? This question of animal consciousness has provoked the imagination of scholars and non-academics alike from ancient days until the present time. However, it is only in recent decades that the question of animal consciousness has been finding its way into mainstream neurobiology, with the emergence of an increasing number of studies promoting strong claims about consciousness in animals. Some examples include: a recent book concluding that consciousness evolved with the most ancient vertebrates [1], a paper suggesting origins of consciousness in insects [2], and a signed declaration by scientists declaring the scientific finding of consciousness in mammals and birds [3]. These and similar claims from the scientific community have been fueling the popular view that advances in neuroscience and animal research are providing accumulating evidence that all mammals and birds, and possibly all vertebrates and some invertebrates, are highly conscious beings, and furthermore that progress in neuroscience is advancing towards resolving the questions of not only which but also how animals have consciousness. My aim here is to evaluate this view and promote a discussion about the extent to which it is useful to address consciousness in animal studies.

The Neuroethological Paradox of Animal Consciousness

In the following, 'animals' refers to non-human animals. I would like to begin by presenting what I call the neuroethological paradox of animal consciousness. Let us consider the following three postulates:

(i) The brain of species X produces consciousness.
(ii) We understand how the brain of species X works.
(iii) We do not understand how any brain produces consciousness.

For logical reasons, the above three postulates cannot coexist – that is, at least one must be wrong. I believe we can agree that postulate (iii) is correct, and thus we are left with two postulates, at least one of which must be wrong. If we understand how the brain of species X works, its brain cannot produce consciousness. Based on the assumption that consciousness is a product of the brain, species X cannot have consciousness. The conclusion is therefore that the more we understand the brain of a given species, the less likely it is that this species is conscious, or, it might be better to say, the less justified we are in ascribing consciousness to this species. In some ways, discussed below, this conclusion is evident, but to common thinking it is highly paradoxical. The brain is considered to be the organ of the mind and, if so, its understanding should intuitively lead, if anything, to a better understanding of consciousness. The resolution of this paradox must therefore lie in what it means to understand the brain. The goal of **neuroethology** is to explain animal **behavior** by the action of its nervous system. Thus, for a neuroethologist such as myself, understanding the brain is to find a neurophysiological explanation for the behavior of the animal.

Theodore Bullock, a leading neuroethologist, initiated in the late 1960s, together with Walter Heiligenberg, a large-scale research program aimed at unraveling the neural basis of the **jamming avoidance response** in the weakly electric fish [4]. At about the same time, Mark Konishi, together with Eric Knudsen, pioneered the study of sound localization in barn owls [5]. Today, the jamming avoidance response in weakly electric fish and sound localization behavior in barn owls are considered to be the first complex vertebrate behaviors that science has solved. That is, we know in sufficient detail how the brains of these animals produce these behaviors. Following this pioneering work, research moved on to explore other more complex behaviors in these and other animals. Nobody stops to ask questions such as: how the fish subjectively feels the interaction with the other fish or how the owl subjectively experiences the sound objects. Everything needed to be explained has been explained, and consciousness did not play a part in it. Nowadays, researchers are uncovering the neural basis of **cognitive behaviors** in animals, including but not limited to attention, multisensory integration, and decision making [6,7]. There is no reason to think that the explanation of these phenomena will be any different in this respect from the example of jamming avoidance behavior or the barn owl head-turning response: consciousness remains unnecessary. More generally, brain research is progressing rapidly while the understanding of

Glossary

Behavior: all bodily responses and actions, including muscle movements, neural activity, and hormone secretion.

Cognition: a subgroup of behaviors that are expressed mostly by the neural activity of the brain and not by muscle movements, and are therefore sometimes called covert behaviors. Examples are: attention, problem solving, decision making, binding, integrating, number sensing, categorizing, and more. These are objective behaviors of the brain carried by neural circuits to allow versatile interactions of the organism with its environment. There are no real philosophical issues regarding the study of cognition: the challenge concerns the difficulty of studying behaviors that are hidden deeply in the brain. Cognition can be accompanied by consciousness or not.

Consciousness: this article addresses phenomenal consciousness, which is the subjective experience or feeling of any type. This is far from being a scientific definition, but is understood well by all who have subjective experiences.

Jamming avoidance response: an adaptive behavior exhibited by some species of weakly electric fish. When two nearby fish generate oscillating electrical fields at the same frequency, each fish will alter their discharge frequency to ensure they do not 'jam' each other's electrolocation sense.

Neuroethology: a subfield of neuroscience studying the comparative neural basis of animal behavior.

consciousness is at a long-standing halt. This growing gap between our advanced understanding of animal brains and our lack of understanding of consciousness in animals should, in line with the above paradox, reduce our confidence in the idea of widespread consciousness across animal species. If one day we obtain a full explanation of how human consciousness emerges from the action of our neurons, then postulate (iii) becomes the incorrect and the paradox disappears. Until this happens, I argue, it is too early to assert strong scientific conclusions about consciousness in animals.

Donald Griffin's Pragmatic Working Definition of Consciousness

The neuroethological paradox of animal consciousness and its conclusions strongly contrast with the common view, mentioned above, that neurophysiological findings, together with behavioral evidence and evolutionary concerns, support the hypothesis that consciousness is common in the animal kingdom. What is the origin of this view, what is the evidence for it, and what does this evidence really support? In 1976, Donald Griffin, a well-known neuroethologist, published the book *The Question of Animal Awareness* in which he argued that, owing to evolutionary continuity, (i) traces of human-like consciousness should be found in animals, (ii) it is the task of ethologists to identify and characterize these traces, and, subsequent to their identification, (iii) it is the task of neuroethologists to uncover their neural basis [8]. Many see the publication of this book as representative of a change in our scientific thinking about animals from behavioristic and reflexive views to cognitive and subjective views [9].

On the cover of the book, E.O. Wilson wrote 'We will owe him a debt for breaking the taboo. The taboo Wilson was referring to was not the idea that animals can have consciousness. The possibility of animal consciousness has been expressed by many before Griffin, including Darwin himself [10]. The breaking of the taboo is the controversial claim that consciousness in animals can and should be studied using neuroethological and behavioral tools. Griffin was well aware of the philosophical problems hindering his ambitious attempt. He understood that, to fund a scientific study of animal consciousness, the first and most crucial task is to neutralize these problems by phrasing a set of objective criteria for consciousness in animals. Here are Griffin's requirements for consciousness, freely phrased from his book:

(i) Having the internal representation of objects and events in the world not limited to time and place (mental images).
(ii) Having the ability to understand the relationships between different mental images (awareness).
(iii) Having the ability to orient towards a specific mental image (intention).
(iv) Having the ability to plan how to achieve the intention.
(v) Having the ability to report the internal image (if an ability to communicate exists).

It is nowadays easy to see how these criteria fail to discriminate consciousness from lack of consciousness; any navigational application running on a smartphone easily passes the test. Although insights from smartphones were not available at the time, Griffin acknowledged the weaknesses of his criteria, referring to them as '. . . some rough-and-ready unsophisticated definitions which I believe will suffice at this preliminary stage . . . ', and 'mental images and their use by an animal to regulate behavior provide a pragmatic working definition of consciousness.' Here, I believe, lies Griffin's mistake, a mistake that has been repeated in many studies since. Specifically, defining complex cognitive behaviors as pragmatic working definitions of consciousness, as did Griffin, is now the common way that biologists bypass (and ignore) the philosophical obstacles [11,12]. But is this practice justified?

Anatomical and physiological evidence supports the notion that complex cognitive behaviors evolved early in evolution and are widespread in animals. However, this is not the question of animal consciousness. The question of animal consciousness is: which animals are also capable of feeling that they are behaving? Selective attention, for example, can be traced to insects [13] and is likely a fundamental property in the brains of active food-seeking organisms. But this does not answer the question when in evolution did the first organism become consciously aware of its selections. There is no reason to expect that this subjective awareness must co-occur with selective attention merely because it sometimes does for us [14]. Consciousness is probably the last biological phenomenon about which we have no idea why it should appear in evolution. Why does an antelope being chased by a lioness need to suffer terrible fear while its body is responding so efficiently to the threat? Therefore, there is no basis to suggest where consciousness should appear on the phylogenetic tree between worms and humans.

The crucial question then concerns what cognitive behavior (or brain structure) is both necessary and sufficient for consciousness. The paradox above highlights the difficulty of answering this question. Neuroethologists are now exposing the underlying neural basis of cognitive behaviors, making them appear less complex, less mysterious, and more automatic-like. Once a cognitive behavior in an animal is explained by the physical dynamics of its underlying neural circuitry, a rigorous scientist must follow the principle of Occam's razor and reject the consciousness hypothesis.

Concluding Remarks

The analysis above leads me to conclude that the question of animal consciousness is, in theory, tractable, but that a full understanding of the neural basis of human consciousness must first be obtained. I believe it is time to admit that until then we cannot answer the question of animal consciousness. Some colleagues will surely disagree, but any rebuttal must face the question – what do we now know about animal consciousness (not cognition) that we did not know 40 years ago when Griffin published his famous book on animal awareness?

Some readers of this article will be alarmed that my criticism of scientific claims for widespread sentiency in the animal kingdom can lead to unethical objectification of animals. I argue the contrary, it is the scientific attempts to divide animals into those that are conscious and those that are not that can lead to objectification of animals. My claim is that any such attempt is premature, including theories that assign consciousness exclusively to great apes [15]. Animals should be treated with respect and compassion because this is the most sensible and humane thing to do, irrespective of findings emerging from laboratories studying animal brains and behaviors.

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