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Wiederorientierung in Bats and the Nature of Animal Consciousness

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Abstract: In 1974, Thomas Nagel wrote “What is it like to be a bat?”, a criticism of reductionist and materialist approaches to the mind-body problem. He used bat biosonar as an example of a sensory system with no similarity to any sense we possess. In this paper, we examine experimental and modelling research into bat auditory neuroethology over the thirty years since Nagel’s paper to assess whether his criticism remains valid. Is bat experience still fundamentally *alien* to us?

Keywords: bats, reductionism, materialism, neuroethology, biosonar.

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Introduction

In 1974, Thomas Nagel published “What is it like to be a bat?”, a criticism of reductionist and materialist approaches to the mind-body problem [1]. He took the position that consciousness made the problem intractable.

Nagel’s paper is actually a proposal for a phenomenology that is in some sense objective, permitting questions on the physical basis of existence to become more intelligible. By seeking an objective description of subjective experience, he felt that the resulting objective explanations might be improved. In making his argument, he used echolocating bats as examples of organisms with alien experience. He states, “Now we know that most bats...perceive the external world primarily by sonar, or echolocation, detecting the reflections, from objects within range, of their own rapid, subtly modulated, high-frequency shrieks.... But bat sonar, though clearly a form of perception, is not similar in its operation to any sense that we possess, and there is no reason to suppose that it is subjectively like anything we can experience or imagine....” He then suggests that we cannot extrapolate to the inner life of a bat from our own experience.

Microchiropteran bats are actually a good animal model for consciousness. They exhibit behaviour that suggests they may live primarily in their own simplified mental model of the external world. The *Wiederorientierung* phenomenon in bats provides insight into the emergence of mind in mammals [2]. Bats flying in a familiar area often seem to ignore sensory afference and instead depend almost exclusively on their memory of the area. This was reported by Möhres and Öttingen-Spielberg in 1949 [3], and reflected two types of behaviour:

Erstororientierung—when bats first encountered a novel situation.

Wiederorientierung—when bats flew in a familiar space.

This was first observed in the behaviour of a bat that was accustomed to roosting in a cage in a room. The researchers rotated the cage and eventually removed it, and noted that the bat continued to behave as if the cage were in its normal position until forced to reorient. This was evidence that a bat may use and maintain a world model that is only modified if circumstances force it to. Rawson and Griffin investigated this further. They asked whether the bats even cried at all. Their experiments involved placing and moving obstacles in a flight room. Their answer was that the bat still cried, but seemed to ignore the resulting returns [2, 4]. This led me to the following working hypothesis:

Bats seem to express intention.

But they also seem to use an internal model of the external world to control their behaviour.

Maintenance of congruence between the internal model and the environment is asynchronous, low-rate, effortful, and involves a ‘dialog’ (Griffin) between the animal and its environment (hypothesis testing). This led me to conclude that a model of target capture by bats must probably include cognitive states and processes [5], and later led me to suggest that bats plan into their immediate future [6].

Other experimental work since 1974 has clarified how the bat perceives its world [4, 7-18]. In particular, many ‘whispering’ bats have been identified that use passive echolocation to hunt insects. These and other studies have reduced the uniqueness of bat echolocation by showing that most mammals use passive techniques and that some are even capable of active echolocation. In particular, auditory localization in humans is termed ‘active vision’, and involves both passive and active echolocation [2].

So where is Nagel’s critique today?

We can no longer claim, as Nagel did, that bat sonar is fundamentally alien to us. True, the use of auditory localization techniques is effortful, and humans are restricted to low frequencies (below about 20-25 kHz), but the experience is available to us, and we can extrapolate from that to the experience of bats. *Wiederorientierung* is particularly interesting in this context—echolocating bats do not bother to

localize objects whose position is already known to them, which suggests that they also find it effortful. We can understand bats based on our own experience, and Nagel's criticism of reductionism in this context loses much of its power.

Note here that I am not claiming that reductionism is capable of explaining consciousness. Paul Davies's argument [19] pointing out that the computational resources of the universe since creation are insufficient to compute the shape of even medium sized proteins, is enough to show that computational techniques cannot predict the behaviour of biological systems for the foreseeable future. Higher level descriptions continue to be necessary. My criticism is rather that knowledge arguments [20]—claiming that materialism is false as otherwise someone possessing complete physical knowledge would have full knowledge of mental states that they had never experienced—assume infinite computational capabilities and so cannot apply to finite beings. Materialist accounts must fail because they are practically infeasible, not necessarily because they are theoretically inadequate. That they may be theoretically inadequate as well may be suggested by the work of Robert Rosen [21, 22], but it is already clear that they are inadequate to address consciousness in any practical sense.

But it is also clear that Nagel is also right. The variation in sensory systems among normal humans is greater than usually imagined. Human colour sensitivity reflects opponent processing between retinal cone cells that are most sensitive to red, green, or blue [23]. A simple experimental procedure can be used to see the individual variation—a candidate is presented with a series of colour bars, some varying a small amount in hue and some with constant hue, and is then asked to identify those that vary noticeably. This produces scores for the candidate's red, green, and blue sensitivity. Individual performance varies, with a few candidates having almost perfect colour sensitivity and some insensitive to variation in one or more colours. Studies like these have shown that some individuals are monochromates or dichromates, insensitive to one or more colours, most are trichromates, with varying sensitivity to all three, and even a few are tetrachromates, sensitive to two different green hues in addition to the red and blue. It is unusual for two people to have the same pattern of colour sensitivity, and women tend to have significantly better sensitivity than men.

The point is that there is marked variation in colour perception, and it is rare for two people to have the same sensitivity. Yet people can communicate intelligently about their experience of colour, and even many legally blind persons have colour sensitivity. Why doesn't this variation block their communication as Nagel's analysis might suggest?

There are recent results in neuroscience that suggest people are preadapted to communicate. That is, neural circuits play a role in communication that is robust to the normal variation in perception. The first of these results is the discovery of mirror neurons [24].

Mirror neurons are cortical neurons that spike when a primate performs an action leading to a reward, but also when it observes another primate taking that action or when it is cued to do that action. These have been found in monkey in Area F5, the premotor area, and recently in the insula [25]. The mirror neurons of the insula function somewhat differently from those in the other areas, firing actively when a monkey experiences emotional sensations and also when the monkey observes the same emotions. Area F5 is important in humans, because it is Broca's area, which plays a role in human speech and communication. This indicates mirror neurons are relevant for action understanding and imitation and are also linked to emotions. The areas they are found in signal a second region of the mammalian brain, the basal ganglia.

The basal ganglia consist of two major subsystems [26]. The first of these, the neostriatum, consists principally of neurons that detect synchronized spiking in functionally related but distributed areas of the cerebral cortex, while the second subsystem consists of a number of output nuclei using various

neurotransmitters to control the cerebral cortex, dopamine and GABA being particularly important. These neurotransmitters appear to function in opposition to provide a reward error signal that can be used to assess and learn the value of situations. In addition, there is evidence that these neurotransmitters also control switching between attending to external stimuli or holding those stimuli in short term memory [27], providing a reward-related mechanism for *Wiederorientierung* in bats. The basal ganglia are suspected of forming an ‘actor-critic’ system for the control and selection of behaviour [28-30]. This model was proposed as a mechanism for learning the rewards associated with possible actions and simultaneously the reward value of situations [28, 31]. An actor-critic model consists of two elements: a set of ‘actors’ that select actions in response to a situation using a current value function, and a ‘critic’ that learns the current value function of the situation based on future rewards. The rewards themselves are initially innate, but can also be learned.

It might be speculated that mirror neurons are specifically the inputs to the basal ganglia that report the observation of rewarding actions, whether performed by the self or by others. Basic appetites appear to be innate, although they can be modified through learning, and reflect neural circuits established very early in development [32]. It is not clear whether mirror neurons are also innate, but the neural circuits they use almost certainly are. Infants learn that certain action/state combinations lead to a reward, and these neural circuits allow them to recognize the occurrence of similar opportunities with respect to others. We see the emergence of early forms of interaction such as shared gaze, where the infant is cued to look at an object by the parent’s direction of gaze. More complex communication then evolves from this actor-independent perception of rewards. Consequently, the human brain is evolutionarily preadapted to understand moderately ‘alien’ minds by being innately wired to perceive the rewards and motivations of other humans.

To summarize, communication involves an ‘understanding’ of the reward system of the other mind and is based on the operation of neural circuits involving mirror neurons and the basal ganglia, brain areas which appear to be broadly distributed among mammals. Hence communication is a robust skill, as low-level rewards are generally similar for most mammals, implying that we can realistically learn to understand ‘alien’ minds of other species (and vice versa). The implication of this for the mind-body problem is that it suggests an ability to understand other minds—even other ‘alien’ minds—has been selected for evolutionarily. We cannot ‘understand’ another as they understand themselves, but we certainly can understand them well enough to predict their reward system and likely behaviour. This understanding cannot be feasibly based on a low-level reductionist analysis of the brain system, but must be based on higher-level, but still simplified, models of how minds respond to rewards and perceptions. Bat experience is not fundamentally *alien* to us, and an objective theory of mind is possible.

References cited:

1. Nagel, T., *What is it like to be a bat?* The Philosophical Review, 1974. **83**(4): p. 435-450.
2. Griffin, D.R., *Listening in the Dark*. 1958, Ithaca, New York: Comstock Publishing Associates.
3. Möhres, F.P. and T. Öttingen-Spielberg, *Versuche über die Nahorientierung und das Heimfindvermögen der Fledermäuse*, in *Verhandlungen der deutschen Zoologen in Mainz*. 1949. p. 248-252.
4. Griffin, D.R., *Cognitive aspects of echolocation*, in *Animal Sonar: Processes and Performance*, P.E. Nachtigall and P.W. Moore, Editors. 1988, Plenum Press: New York. p. 683-690.
5. Erwin, H.R., W.W. Wilson, and C.F. Moss, *A computational sensorimotor model of bat echolocation*. Journal of the Acoustical Society of America, 2001. **110**(2): p. 1176—1187.
6. Erwin, H.R. *Algorithms for Sonar Tracking in Biomimetic Robotics*. in *RASC-04*. 2004. Nottingham.
7. Fenton, M.B., *Natural History and Biosonar Signals*, in *Hearing by Bats*, A.N. Popper and R.R. Fay, Editors. 1995, Springer-Verlag: New York, New York. p. 37-86.
8. Kick, S.A., *Target detection by the echolocating bat, Eptesicus fuscus*. Journal of Comparative

- Physiology A, 1982. **145**: p. 431-435.
9. Koay, G., et al., *Passive sound-localization ability of the big brown bat (Eptesicus fuscus)*. Hearing Research, 1998. **119**: p. 37–48.
 10. Møhl, B., *Target Detection by Echolocating Bats*, in *Animal Sonar: Processes and Performance*, P.E. Nachtigall and P.W. Moore, Editors. 1988, Plenum Press. p. 435-450.
 11. Moss, C.F. and A. Surlykke, *Auditory scene analysis by echolocation in bats*. Journal of the Acoustical Society of America, 2001. **110**(4): p. 2207–2228.
 12. Pollak, G.D. and J.H. Casseday, *The Neural Basis of Echolocation in Bats*. 1989, Berlin: Springer-Verlag.
 13. Schnitzler, H.-U. and E.K.V. Kalko, *How Echolocating Bats Search and Find Food*, in *Bat Biology and Conservation*, T.H. Kunz and P.A. Racey, Editors. 1998, Smithsonian Institution Press: Washington and London. p. 183-196.
 14. Simmons, J.A., *Acoustic-imaging computations by echolocating bats: unification of diversely-represented stimulus features into whole images*, in *Advances in Neural Information Processing Systems 2*, D.S. Touretzky, Editor. 1990, Morgan Kaufmann: San Mateo, California. p. 2-9.
 15. Simmons, J.A. and R.A. Stein, *Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation*. Journal of Comparative Physiology A, 1980. **135**: p. 61-84.
 16. Suga, N., *Biosonar and neural computation in bats*. Scientific American, 1990. **262**: p. 60-66.
 17. Surlykke, A., *Interaction between echolocating bats and their prey*, in *Animal Sonar: Processes and Performance*, P.E. Nachtigall and P.W. Moore, Editors. 1988, Plenum Press. p. 551-566.
 18. Valentine, D.E. and C.F. Moss, *Sensorimotor Integration in Bat Sonar*, in *Bat Biology and Conservation*, T.H. Kunz and P.A. Racey, Editors. 1998, Smithsonian Institution Press: Washington and London. p. 220-230.
 19. Davies, P., *Emergent biological principles and the computational resources of the universe*. Complexity, 2004. **10**(2): p. 1.
 20. Pereboom, D., *Bats, Brain Scientists, and the Limitations of Introspection*. Philosophy and Phenomenological Research, 1994. **54**: p. 315-329.
 21. Rosen, R., *Life Itself: A Comprehensive Inquiry Into the Nature, Origin, and Fabrication of Life*. 1985, New York: Columbia University Press.
 22. Rosen, R., *Are our modelling paradigms non-generic?*, in *Time, Process and Structured Transformation in Archaeology*, S.E. van der Leeuw and J. McGlade, Editors. 1997, Routledge. p. 383-395.
 23. de Valois, R.L., et al., *Hue Scaling of Isoluminant and Cone-specific Lights*. Vision Research, 1997. **39**: p. 1823ff.
 24. Rizzolatti, G. and M. Arbib, *Language within our grasp*. Trends in Neurosciences, 1998. **21**: p. 188-194.
 25. Gallese, V., C. Keysers, and G. Rizzolatti, *A unifying view of the basis of social cognition*. Trends in Cognitive Sciences, 2004. **8**: p. 396-403.
 26. Wilson, C.J., *Basal Ganglia*, in *The Synaptic Organization of the Brain*, G.M. Shepherd, Editor. 2003, Oxford University Press: Oxford.
 27. Durstewitz, D., J.K. Seamans, and T.J. Sejnowski, *Neurocomputational models of working memory*. Nature Neuroscience, 2000. **3**: p. 1184-1191.
 28. Houk, J.C., J.L. Adams, and A.G. Barto, *A model of how the basal ganglia generate and use neural signals that predict reinforcement*, in *Models of Information Processing in the Basal Ganglia*, J.C. Houk, Davis, and Beiser, Editors. 1994, MIT Press: Cambridge, MA.
 29. Montague, P.R., S.E. Hyman, and J.D. Cohen, *Computational roles for dopamine in behavioural control*. Nature, 2004. **431**: p. 760-767.
 30. Schultz, W., *Reward signaling by dopamine neurons*. Neuroscientist, 2001. **7**(4): p. 293-302.
 31. Sutton, R. and A.G. Barto, *Reinforcement Learning*. 1998, Cambridge, MA: MIT Press.
 32. Pribram, K.H., *languages of the brain: experimental paradoxes and principles in neuropsychology*. 1971, New York: Brandon House, Inc. 309.