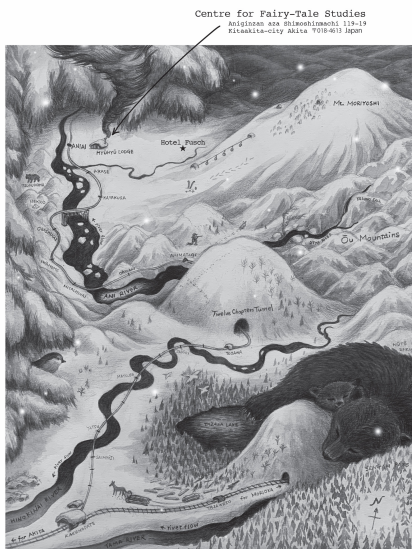


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Evidence and Inference: Blind Spots in the Neuroscience of Non-Human Minds

Matthew Kirkcaldie

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Evidence and Inference: Blind Spots in the Neuroscience of Non-Human Minds

Matthew T. K. Kirkcaldie

Abstract

Empathy, theory of mind and cognitive inference are used by humans to optimise our thinking and decision-making in social groups. Often, we extend this courtesy to nonhuman animals, acting as if they are conscious and experience the world in much the way that we do. Evidence from neuroscience suggests that nonhuman primates, at least, recognise us in a similar way. At the cellular level, comparative neuroanatomy demonstrates that all mammal brains are fundamentally similar and differ only in degree and proportion. If we believe that the physical structure of the brain is the seat of thought, then we have little basis for excluding animal consciousness. Nonetheless, the personal and institutional ethics which guide neuroscientists often make a categorical distinction between humans and other animals on this quality. Companion animals have been bred for their cognitive simpatico and nonverbal communication, but if science insists on a qualitative difference between human and animal minds, our view of dogs' personalities and intentions would be a delusion. There is a tension, manifested as descriptive blind spots, between our appreciation of animals as kindred spirits and our explanatory accounts of their brains. Should we face the implications of our common anatomy and behaviour, admit that nonhuman animals are conscious, and therefore acknowledge their rights? Can our instinctive recognition of intention and cognition in animals be reconciled with science? If so, neuroscience might help with 're-storying' the world by incorporating new perspectives to acknowledge animal minds.

Blind Spots in Neuroscience

The term *scotoma* refers to a gap in sensory information, of which the individual is unaware; the best-known example is the blind spot of the eye,

where the fibres of the optic nerve pass through the retina. When seeing, we are unaware of this blank area, and the brain fills the *scotoma* to make our mental image seamless (Zeki). To do this, the missing input is guessed at, and interpolated at a preconscious level. This description, familiar from any neuroscience textbook, hides a conceptual *scotoma* around consciousness. The perception of a flawless world occurs in a mind which we assume is the product of the brain's neural activity, whereas the substitution of damaged input is somehow 'pre-conscious,' despite involving the same neurons. If the visual cortex is the locus for conscious perception, and is also responsible for preconscious processing, how is the former experienced but the latter not? The conflict arises because neuroscience is unable to include consciousness in its framework, leading to descriptive discontinuities which we train ourselves to ignore.

In applying the scientific method to the brain, neuroscience has a unique epistemological problem: we do not know if consciousness can be explained using empirical evidence, because such evidence is evaluated by mental processes. We lack objective criteria for the presence, absence, or quality of conscious experience (Dung), so our 'causal' accounts rely on the so-called neural correlates of consciousness (NCCs), an explanation by proxy which feels more circumstantial than rigorous. Most neuroscientists acknowledge that subjective experience—how it 'feels to be'—is outside their purview, although many gravitate to these questions. The sharp irony is that the most compelling quality of the brain may be categorically inaccessible to neuroscience.

Since our own mind is the only one we can directly experience, in seeking to explain consciousness we study the actions of others, assuming them to be the product of similar mental states to our own. This 'theory of mind' is used to infer internal states; we assume that behaviour is guided by thoughts and intentions to which we are not privy (Premack and Woodruff). Neuropsychologists apply this principle to conjecture about the cognitive state of people who experience damage or other impairments of the brain. Changes in behaviour or self-report are taken as evidence of altered mental experience, implying that their injuries indicate where the affected mental faculties arise in the brain (Berlucchi and Marzi). These inferences are cross-correlated with other data to give circumstantial explanations for how the brain makes a mind, or at least which parts of it are important for doing so.

The main source of such confirmatory data—animal-based research—has a different, but related *scotoma*: neuroscience also dodges the question of whether nonhuman animals have minds and subjective experiences like our

own. We accept them as valid analogues and models for the human brain but deny their sentience and agency when making comparisons with humans, or ethical decisions. Lab work in neuroscience routinely skates around this gap, which manifests as mutable views of animals' agency and subjectivity. When science requires killing and dissection, researchers transition from lab interactions with 'naturalistic' animals to extracting scientific data from 'analytic' animals, reflected in the language they use (Lynch).

Neuroscience and the Mind

To understand these gaps, it is useful to examine the roots of our mechanistic and physical paradigms of brain function. Neuroscience is a young discipline, whose ground zero is usually placed in the meticulous anatomical surveys made by Santiago Ramón y Cajal and other European scientists in the late 19th century (Llinás). New techniques in microscopy and tissue staining opened a window to the intricate structure of the nervous system (Jones), raising many questions which persist over a century later. 'Mind' was the subject of theology and philosophy for millennia before our current model of science emerged, but a few years before Ramón y Cajal's studies, neuropsychologists such as Paul Broca and Carl Wernicke drew it into the descriptive frameworks of neurology and neuroscience by correlating brain damage with mental functions such as speech, memory, and recognition (Berlucchi and Marzi). The *scotoma* has been with us from the outset: Ramón y Cajal made free reference to consciousness, perception and the soul when speculating about function in his cellular studies but reconciling these two modes of description has remained an existential, painfully unsolved problem for neuroscience, a form of 'baked in' Cartesian dualism (Arshavsky).

These cavils were set aside in the explosion of data and insight offered by new techniques in anatomical tracing, histology, biochemistry, behaviour and especially electrophysiology in the first half of the 20th century (see Chudler for highlights). Discovery of the action potential in neurons suggested a close (and partly false) analogy with the on/off logic of digital computers emerging around the same time (Buzsaki), leading to pervasive and unhelpful metaphors of the brain as a computer focused on the representation and processing of information (Allman; see Cobb for a history of brain paradigms). Neuroscience converged on functional descriptions tied closely to measurable attributes, which have been invaluable in finding treatments for diseases and uncovering much of the fine detail of these systems but have little to say about subjectivity or consciousness.

The primary epistemological barrier is an inability to frame questions linking subjectivity to neural activity—an impasse famously dubbed the ‘hard problem’ by philosopher David Chalmers (“Facing Up”), the easy problem being NCCs. Despite the dismissive terminology, close observation of NCCs in humans and animals during experience and behaviour has been a notable success of recent neuroscience and represents our best hope for insight. It remains an article of faith among neuroscientists that through patience and inference, it may be possible to identify the most important NCCs and thereby new paradigms for investigation (e.g., Kitchener and Hales)—or instead we may shade the boundaries of the hard problem with ever-greater precision. Chalmers has even suggested that the experiential aspect of mind may need to be taken as axiomatic: a property similar to energy, which is the subject of theory but is not reductively explained (“Conscious Mind” 111).

Although neuroscience has acquired a degree of authority and cachet in the last few decades and is popularly viewed as deeper or somehow more credible than psychology and sociology (O’Connor and Joffe), it is truer to say that these disciplines use different, mutually incompatible perspectives to address common questions. Neuroscience should not be viewed as somehow more fundamental in explaining consciousness: its more quantitative basis is hardly an advantage in a domain where we don’t know what to measure. Rather than deciding the proposition, this article is intended to explore whether the question of animal minds can be reconciled with the basis of neuroscience.

Neuroscience and the Easy Problem

The most obvious approach to this question is via reductive explanation, i.e., the NCCs, although Chalmers himself considers the hard problem irreducible (“Conscious Mind”). However, we may be able to define the scope of our interest: if a form of conscious experience can be tied to a specific substrate, it becomes possible to test whether animals have it as well (e.g., Low et al.). Sleep, for example, is a reasonably well understood alteration in consciousness, linked to complex systems shared by most vertebrates (Scammell, Arrigoni, and Lipton), although these systems *regulate* consciousness rather than creating it, and sleep itself varies considerably between species (Siegel). Other structures have been posited as drivers of consciousness, notably the claustrum (Crick and Koch), linked to startling subjective experiences such as stopping time when stimulated during surgery (Koubeissi et al.). However, the most widely accepted NCC is cellular activity

in the cerebral cortex, whose pink folded surface represents ‘the brain’ in popular culture.

Centuries of observations, including surgical treatises from pharaonic Egypt (Breasted) and Galen observing brain injuries in gladiators and animals (Bem et al.), support the notion that conscious minds are created by regions of the cerebral cortex. Damage to small areas of the cortex can cause highly specific dysfunctions such as blindness, paralysis or mutism, or more elusive changes in personality, judgement, or insight. Audacious studies using stimulation during surgery on awake people—notably by Wilder Penfield and colleagues (Costandi)—have demonstrated that cortical activity can generate mental experiences, sensation, and movement.

Cortex uses a lot of energy, so its blood flow is rationed to active areas, which can be detected by functional magnetic resonance imaging (fMRI; Carter and Shieh). fMRI is regrettably popularised as the brain ‘lighting up’, whereas in fact it measures tiny magnetic fluctuations with significant uncertainty. Although fMRI studies are often underpowered and difficult to replicate (Marek et al.), the probability plots use vivid colours and crisp boundaries to ‘show’ cognitive processes in the cortex. As a result, the relationship between cortical regions and putative ‘elements of cognition’ is quite circular. Neuropsychology and neurology test functions we believe are tied to specific anatomical areas, based on studies of people with well-localised strokes or injuries (Bem et al.). Over time, the set of abilities we call ‘cognition’ has converged on things attributable to a physical substrate; in a way, neuroscience, neurology, and neuropsychology are co-conspirators in shaping a consensus view of ‘mind’ as the conscious correlates of neural activity, in a neat inversion.

Under the microscope, the cellular structure of the cortex is quite uniform, despite the variety of functions attributed to its regions. In most areas, six layers of neurons are visible, interlinked to combine inputs and send activity to other brain structures (DeFelipe). Functionally, the cortex is associative and interpretive: much of the essential work done by the nervous system happens in other structures, but cortex groups those activities within a larger context such as an overall goal, or a considered response to a complex situation. Knowledge and memory are key to identifying the context of actions, so the ability of the cortex to physically capture these experiences is arguably its most important function. Roughly 85% of the volume of cortical tissue is occupied by physical connections which preserve this memory across decades, persisting through sleep, coma, and anaesthesia (Braitenberg and Schüz).

Cortical activity is thought to combine sensory input into complex experiences and ‘descriptions’ of the world and use them to inform decisions and create behaviour (Watson, Kirkcaldie, and Paxinos). The language used to describe these functions is predictably dualistic: to say sensory regions ‘represent’ the external world implies an entity to whom representations are addressed, making decisions-in-abstract which are set as goals for responding, passed down to the frontal lobe. Such metacognitive elements cannot be localised to brain structures in ways which satisfy the criteria for evidence and reproducibility and are often handwaved away with weak arguments appealing to ‘emergence’.

The handwaving indicates another *scotoma*: acceptably causal descriptions can be made of networks with a few dozen to a few thousand neurons, but that is five orders of magnitude less than the level at which we try to describe cognitive function. Thus, the neuroscience of the mind consists of descriptions at the conceptual level, and at the cellular level, with an enormous gulf between; few neuroscientists are willing to contemplate this void, let alone navigate across it (but see Buzsáki). Instead, recent large scale neuroscience funding is based on the simple faith that if we collect *all* the data at the cellular scale, massive simulations will reveal in detail how the brain works (e.g., Markram, Muller et al.). This approach is borrowed from engineering, where simulation is used to tackle awkward scales in fluid and solid properties. However, unlike molecules, complex and self-regulating neurons and glia are not homogeneous in bulk and cannot be reductively approximated for the sake of simulation (e.g., Mitra). Taking their cue from the Human Genome Project (Gates et al.), such approaches forego novel ideas or hypotheses in favour of ‘shotgun’ data collection at the prestige scale of science (e.g., the US Brain Initiative and European Human Brain Project), and have yielded few insights despite profligate funding (Yong; Mullin; Naddaf).

At the cellular level, human and other mammal brains are suggestively similar, and scale approximately with body size; to what extent humans may be exceptional has been debated for decades (see Herculano-Houzel, Manger, and Kaas for a quantitative perspective). All mammals have a cerebral cortex, divided into the same basic functions in most species (Krubitzer), but characterising their similarity is confounded by two issues. One is that much of our knowledge of cortex comes from experimental studies in nonhuman animals, which could not be performed on humans. For example, the canonical view of visual processing derives largely from cats (Zeki), since at the time, the use of cats was routine in neuroscience and their excellent vision afforded a plausible model. Corroborating data has been found in primates

and experimental visual prostheses for blind humans, but the paradigm of cortical vision derives from the feline brain. Similarly, for other systems we accept mammal (frequently mouse) brains as valid analogues and extrapolate their data to our own, unless contradicted by human findings.¹ Comparing cortical function across species is thus also self-referential.

Outside of the mammal-specific cortex, the elements and organisation of the rest of the nervous system are highly similar across fish, amphibians, reptiles, and birds. The genetic regulators which shape this common *bauplan* (Swanson) are very old, and also govern segmental organisation in invertebrates (Krumlauf), clear evidence of genetic and structural continuity across all animals. This universal foundation doesn't imply that its derivatives are equivalent, and in fact there have been many duplications and alterations of function across evolutionary timescales; these genes can have quite different roles in different species (Singh and Krumlauf). However, it illustrates the deep homology between species across evolutionary timescales, and that brains have acquired complexity incrementally rather than through abrupt changes or new beginnings² (Allman; but see Woych et al.).

Despite our close kinship, we might imagine that there are special qualities of the human brain by which we can draw a distinction from other mammals. However, the cellular structure of the cortex appears so similar between species that it takes a specialist to appreciate the distinctions (DeFelipe). Elements thought to be specifically human (e.g., von Economo neurons; Banovac et al.) have subsequently been found in other mammals, so that there appears to be nothing categorically unique to the human cortex. Human neurons are more structurally complex than all other species (DeFelipe; Loomba et al.) but thus far we have failed to identify any human-specific types or properties. Indeed, the conservation and commonality of genetic regulators, signalling systems and guided connectivity demonstrates the smooth lineage of evolution from ancestors we share with animals we now regard as 'others'; we were once literally the same, so drawing a line requires a transition across it to have occurred. Many studies have sought to identify a catalyst for our becoming human—e.g., genes regulating brain growth or connectivity, or the adoption of agriculture and cooking—but the lack of consensus, and the wide variety of candidates for a supposedly transformative change, suggests that there may not be a discontinuity after all (Herculano-Houzel, Manger, and Kaas).

The other issue confounding neuroanatomy as a clue to animal minds, is that we don't know which aspects of cortical structure are significant and which are mere detail. In my own field, there are several mutually

incompatible ways to describe and group neurons of the mouse cortex (Kirkcaldie), despite its comparative simplicity (DeFelipe). Elaborate multidimensional classifications (e.g., Markram, Toledo-Rodriguez et al.; Ascoli et al.) attempt to capture all possible descriptive data but offer few functional clues. It may be more helpful to approach the problem by turning it around, assuming that cognition is a common trait and asking what aspects of cortical structure are most consistent across species (e.g., Bucher et al.).

Social Cognition and Mirroring

Communication, and collective knowledge such as books, are often cited as key enablers of human cognitive superiority. History, and the explosive growth of social media, are testament to our hunger for community and interaction with others, a trait common to many social mammals (Barrett and Henzi). Why is this such a fundamental? Having a brain which usefully understands and predicts the world becomes even more useful if we can draw on others' knowledge: the wisdom of the crowd magnifies the capabilities of the individual, and if we know others' skills and experience, we can ask their advice. This 'extended self' is enabled by social cognition, in which nuanced interactions with others are used to improve our own situations. Understanding others as individuals, inferring their internal states, and modelling their likely reactions to new situations, may also allow us to turn the lens inward, creating a sense of self by predicting one's own future actions (Falk and Miller; Barrett and Henzi; Kirkcaldie and Kitchener; Bonaiuto and Arbib).

Predicting another's behaviour invites a paradox: how could we model a whole brain using only part of our own? If possible, it would be more efficient to mimic the other's state of mind. In the early 1990s, a chance discovery about the control of movement offered a glimpse of how we might understand others' actions. Recordings from the frontal lobe of a macaque monkey during movements intended to grasp objects, confirmed that actions were preceded by activity in a pre-motor planning area of the cortex (di Pellegrino et al.). However, as the experimenters set up the task for the monkey, they found that this pre-motor activity was also triggered by seeing another individual making the same movement, as if 'mirroring' the action in order to understand it. Further investigation showed that these 'mirror neurons' also responded to the *intention* of making the movement, even out of sight (e.g., reaching for a hidden cup; Rizzolatti and Craighero). This implies that on some level, monkeys can infer intention in another individual—even a human. Two

implications are profound: that mammal brains may interpret others' actions by a kind of internal mimicry, and that the inference of intention can cross species boundaries. These exciting concepts triggered a wave of speculations far beyond the original scope of understanding motor control (Iacoboni and Dapretto; Bonini et al.) many of which have weathered three decades of scepticism to persist as useful explanations for interactions and empathy.

The notion of cortex adapted for a mimetic understanding of others is seductive, and mirror neurons were rapidly co-opted to explain human cognition and disorders such as autism (Iacoboni and Dapretto; Bonini et al.), despite being observed only in primates at the time. Of course, any human trait they may explain must also apply to the animals under study, but this is often overlooked; monkeys' mirror neurons recognise human intentions, but reciprocal acknowledgement is grudging (e.g., Kaplan). It may be that the door is opened too wide for comfort: explicit searches for mirror neurons have uncovered similar systems in primates, bats, rodents and even songbirds (Bonini et al.; Prather), which suggests that understanding and modelling others' actions may be universal in mammal and bird brains. Birds have an analogous but structurally different brain component, pallium, instead of cortex (Stacho et al.; Güntürkün et al.); these structures are comparable in capacity, and parrots and corvids (Baciadonna et al.), have similar or greater numbers of neurons in their pallium than the cortex of similarly sized primates, along with appropriately complex behaviours (Olkowicz et al.). Although direct evidence is currently lacking, we may also eventually add octopuses and other cephalopods to this club (Mather; Godfrey-Smith, "Cephalopods"; Ponte et al.).

Mirror neurons' cross-species responses imply a commonality of embodied cognition, at least among primates (Iacoboni and Dapretto), which can also be seen in human interactions with animals and our beliefs about their minds. If anthropomorphism has a biological mechanism, the vicarious experience of behaviours by unconsciously embodying them is a strong candidate. In understanding intentionality to predict actions, the recognition of other minds is implied. Of necessity, this would cross species boundaries, otherwise animal intentions would be a mystery, whereas anticipating them is key to survival in many situations (Heyes). Evolution would also foster kinship: in the process of divergence from common ancestors, there would be no line to draw between 'us' and 'them' until hundreds of generations had passed (Allman; Preston and de Waal).

Behavioural studies and many other animal interactions (e.g., Haraway) document non-human animals acknowledging humans as

counterparts, and the existence of mirror neurons in companion animals has been inferred on the basis of physical *simpatico*, such as dogs catching yawns from humans (Joly-Mascheroni, Senju, and Shepherd). These suggest a direct mechanism for social interaction, but, more importantly, a neural correlate for interspecies kinship. Animals, lacking our philosophical and cultural baggage, are free to recognise fellow sentient beings via their equivalent of anthropomorphism.

Although we tend to view recorded neural activity as fundamental, more ‘hardware’ than the ‘software’ of culture, society and life experience, there is also evidence that mirror neurons acquire their function during the process of learning motor skills (Cook). Rather than a genetically determined function, mirroring may be a skill learned in tandem with movement, which is plausible since cortical control is shaped by feedback (e.g., Avanzino et al.). This opens the intriguing idea that depending on how we learn, we may be able to shape our recognition of intentionality, and what creatures we consider as having intentions.

Experiencing ‘reflex empathy’ in the process of understanding others’ actions most likely includes an appreciation of the motivations behind them: even in monkeys, intention is clearly being recognised by some mirror neuron responses (Rizzolatti and Craighero). Humans routinely infer cognition from behaviour and attribute others’ actions to hidden mental states, an ability known as theory of mind (ToM; Premack and Woodruff; Nissani): essentially, the realisation that other people have different minds to our own and may feel differently or have different knowledge. As a cognitive tool for enabling social integration, a brain capable of ToM may have been a selectable trait during evolution, since understanding others in order to cooperate and coordinate is a compelling advantage in complex environments (Premack and Woodruff; Preston and de Waal; Barrett and Henzi; Krachun et al.). Behaviours apparently requiring ToM have been documented in several species, including chimpanzees (Premack and Woodruff; but see Povinelli and Eddy; Nissani) and some corvid birds (Dally, Emery, and Clayton), all of which exhibit complex social structures and interactions.

If animals model and understand others, how do they perceive themselves? Animals’ internal mental states have been studied using the mirror test (unrelated to mirror neurons): do animals, confronted with a mirror and allowed to explore it, realise that the reflection they see is their own face and not another animal? Misidentification of the image as a stranger is taken as the absence of a sense of self, but the range of animals which have passed the mirror test is impressive: chimpanzees (Gallup; Krachun et al.),

gorillas (Murray, Anderson, and Gallup) but probably not monkeys (de Waal et al.; but see Chang et al.), elephants (Plotnik, de Waal, and Reiss), dolphins (Reiss and Marino) and magpies (Prior, Schwarz, and Güntürkün).

Humans are not born with ToM, and its emergence is acknowledged as a key developmental milestone (Poulin-Dubois); it is also critical to the development of language, since realising that others have separate minds is the motivation to communicate. There is evidence that ToM is culturally plastic in emergence (Shahaeian et al.), and we might speculate that our willingness to recognise other minds could be trained: individual belief in animal minds may depend on the stories and folklore we hear as children (Haraway). Discourse and narrative have been argued as catalysts for ToM by referencing the embodiment of experience (Rokotnitz)—i.e., the commonality of intentions and actions between individuals—by portraying movements and activities we would typically recognise using mirror neurons (Willems, Nastase, and Milivojevic).³ It may be that stories and literature exist to build and reinforce our social selves by scaffolding the development of ToM; if so, the popularity of anthropomorphic animals in children’s literature may explain (and be employed to foster) our acceptance of nonhuman consciousness (e.g., Conrad, Marcovitch, and Boseovski).

One famous anthropomorphic story is that of Hachi-kō, a dog so beloved in Japan that the details of his life are blurred by fictionalised accounts; a recent source based on extensive research is used here (Itoh). Bred in Akita Prefecture and given to Professor Ueno Hidesaburō, Hachi accompanied his devoted owner to Shibuya station or the nearby Agricultural College each morning and returned to meet him at day’s end. However, after two years, Hidesaburō died of an aneurysm at the College, and never returned from his workday. At the subsequent wake, a confused Hachi lay under Hidesaburō’s coffin as he had under his bed, then walked to the station to wait (Itoh). Was this habit, or did he ‘believe’ his master would eventually return?

After several moves Hachi ended up living near Shibuya station again and resumed the habit of waiting for his long-dead master each day. At the time, he was regarded as a nuisance and chased from the station, and his health deteriorated. Near his end, a series of newspaper accounts and fictionalisations of his story established him as an embodiment of loyalty, and on that basis, he remains a national icon a century after his owner’s death. Curiously, the treatment of his remains reasserted his animal status: although his bones were buried with his master’s, his skin was stuffed and remains on display at the National Science Museum in Tokyo (Itoh).

Setting aside the mythic elements, how should we view Hachi's behaviour? A strict behaviourist might call it a failure to extinguish a pattern despite a lack of reward. Similarly, in cognitive testing of a laboratory animal, this might be viewed as a lack of behavioural plasticity, retaining a fixed habit which no longer achieves its purpose. Of course, Hachi's fame is evidence that most prefer to see his persistence as a devotion few humans could match; they would regard such views as perverse or churlishly academic. Shaped by culture, the empathetic narrative becomes in turn a fable to instruct children's views of animal minds.

Declaring Ambiguity

These strawman views of Hachi are provocations, but they betray the friction between the tenets of orthodox neuroscience and popular views of animal minds. To many neuroscientists, the lack of a causal explanation for 'mind' makes it more rigorous to exclude animals for which we have (arguably) no direct report of consciousness. It may also be more ethically comfortable to deny the subjectivity of animals, so as to sanction research we would not perform on humans, although this sits uneasily alongside the assumption of sentience which guides research ethics. We might ask *who* experiences distress if vertebrates are sentient but not conscious. Although the assumption is unexamined in ethical guidelines (e.g., National Health and Medical Research Council), it is loosely thought better to err on the side of caution, aligning with Kant's view that our treatment of humans is shaped by our treatment of animals, whether or not they are morally equivalent (Camenzind).

Despite this pragmatism, many scientists prefer to shed their Cartesian baggage and acknowledge the possibility of animal consciousness, seen prominently in the "Cambridge Declaration on Consciousness" (Low et al.). This published statement by a group of eminent neuroscientists expresses their consensus that "the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness ... all mammals and birds, and many other creatures, including octopuses, also possess [them]" (2) and that the major NCCs are most likely universal in complex brains. The authors stop short of addressing the 'hard question' of whether animals *are* conscious, on the basis that they are unable to communicate their internal states. It is noteworthy that this declaration persuasively summarises the evidence for animal minds but backs away from the implications of those arguments.

This curious mix of assertion and reticence illustrates the bind in which neuroscience finds itself, when trying to evaluate the prospect of animal consciousness. Our constructed evidentiary frameworks for deciding scientific belief are mismatched to our intuition and experience of animal minds, but in trying to resolve this difficulty, we realise that science itself is inadequate in this category of enquiry. We fall back on personal experience and belief in the agency and subjectivity of animals, readily supplied by our intrinsic (or learned) predisposition to understand action through intention, and the extent to which we generalise our theory of mind to other species (Nissani). It seems likely that these qualities have been shaped by learning and cultural transmission, at a level more fundamental than the adoption of scientific methods through later education. Ultimately, we maintain these received beliefs, and shape our arguments accordingly, tacitly accepting the *scotomas* which arise in consequence. For neuroscience, animal minds remain a potentially undecidable proposition, but as humans we remain free to recognise these “other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth” (Beston 25).

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Notes

- ¹ Wilder Penfield’s maps, in which the functional arrangement of cortical regions reflects the physical arrangement of body parts, are a rare example of extrapolating properties from human brains to nonhuman brains.
- ² This view applies mostly to the vertebrates, but an ancient divergence led to an independent invertebrate lineage of complex nervous systems in cephalopods, which exhibit many of the same behavioural qualities including sentience and perhaps consciousness (Godfrey-Smith, “Cephalopods”, “Other Minds”).
- ³ In the original studies identifying mirror neurons, these functions were observed in neurons located in regions equivalent to speech centres of the human cortex (di Pellegrino et al.). Speech and language derive from a human specialisation of higher-level movement control systems present in most primates and many other mammals.

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