To appear in *The Oxford Handbook of the Philosophy of Perception,* M. Matthen, ed., Oxford University Press, forthcoming (expected: 2013).

Date: Wednesday, July 3, 2013
Actual Word Count (including everything in this file): 10,133

Nonhuman Animal Senses

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ABSTRACT:

How ought we to determine the senses of nonhuman animals? To answer that question, we first need to determine the relationship between our understanding of nonhuman animal senses and those of humans; should the two accounts be continuous or discontinuous with one another? In this chapter, I argue that regardless of how we answer these questions, the understanding of nonhuman animal senses is philosophically interesting and should receive more attention than it has to date. Nonhuman animal senses such as infrared perception and magnetoreception pose some interesting conceptual challenges to attempts at understanding their operation.

KEYWORDS:

Aristotle, infrared perception, magnetoreception, sensory modalities, star-nosed mole

1. Introduction: A star-nosed mole problem redux

Aristotle is given credit for developing the earliest systematic account of the nature of the senses in the Western world. Famously, in works such as *De Anima* and *De Sensu,* he identifies five senses: Sight, hearing, smell, taste and touch (for more, see (Sorabji 1971; 1992; Keeley 2009)). What is less well appreciated is that Aristotle apparently thought these five senses were not only the complete list of senses in humans; he also thought they were the only possible senses—and hence the senses of all animals. (Although he discusses many other animals, he never discusses any different perceptual abilities in them; only suggesting that some animals have more powerful versions of the senses humans have.)

It is now commonly (but not universally[1]) proposed that Aristotle undercounted when it comes to humans. Now sensory scientists speak of a vestibular (balance) sense, a sense of the position of one's limbs (proprioception) and the sense of touch might better be thought of as separate senses, based on the different physiological mechanisms carrying out different neural processes (pressure, temperature, pain), to name only a few. However, there is no disagreement when it comes to Aristotle's count of the animal senses. We now believe that nonhuman animals have many more senses than he thought: *electrical* senses in a variety of fish, sharks and perhaps even the platypus

[1] See (Nudds 2004; Nudds 2011) for a recent discussion that takes a five-sense view of humans as its starting point.

(Scheich, Langmer et al. 1986; Keeley 1999; Pettigrew 1999),[2] *magnetic* senses in elasmobranch fishes (sharks, skates and rays (Kalmijn 1982)), and perhaps turtles (Putman, Endres et al. 2011) and migratory birds (Mouritsen and Ritz 2005).[3] Moreover, a number of animals can perceive stimuli well beyond what humans can, as in the famed *olfactory* abilities of bloodhounds, *ultrasound* perception in shad (Mann, Lu et al. 1998), *ultraviolet* perception in bees and *infrared* perception in vampire bats, snakes and boas. There is a strong scientific and lay consensus that nonhuman animals exhibit much more sensory variety than Aristotle dreamed.[4]

How ought we think about such nonhuman animal senses?

A number of years ago, I published a paper (Keeley 2002) that, in part, I hoped would rekindle interest among philosophers in this question: the question of how to individuate the sensory modalities. Related to this question are a number of others: What makes one sense (hearing, say) different from another (e.g., smell)? How many senses should neurotypical humans be said to have? How should we think of the senses of neuroatypical individuals, for instance as in synesthesia or blindsight? What evidence would be needed to establish the existence of a previously unknown sense—a “sixth sense”? Are senses natural

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[2] And just recently, evidence has been published that a placental mammal, a dolphin, has an electric sense (Czech-Damal, Liebschner et al. 2011).

[3] However, also see (Johnsen and Lohmann 2005) for a discussion of the difficulties scientists have had in definitively identifying the nature of magnetoreceptive mechanisms in many organisms.

[4] A good, general overview of animal senses can be found in (Hughes 1999). There is even reason to speak of the senses of plants, for example, in the case of the vibrisa of venus flytraps or the light and chemical sensitivity of vines (see (Milius 2009)). However, for reasons of space, plants won’t be discussed here.

kinds? If not, what are they? And so on.

In that paper, I identified two broad classes of questions in this area of interest. The first I called *Aristotle's Problem*: "How many modalities do humans have and how ought we decide the issue?" (Keeley 2002: 10). There has indeed been a resurgence of philosophical interest in the nature of human senses recently.[5] On the strength of that interest, as well as the litany of reasons I discuss in (Keeley 2002: 7-9), I will here be assuming the philosophical importance of Aristotle's problem.

Concerning the second class of questions I identified in my earlier paper, there has been considerably less uptake. Immediately after discussing Aristotle's problem, and describing a particular late-20th century scientific debate concerning what sense to assign to the striking, fleshy nose of one species of mole, I then observed that,

> The same problem arises again, in a slightly different guise, in animal sensory biology. … What I shall call the *star-nosed mole problem* is the general philosophical problem raised by this type of scientific controversy. On what philosophical grounds should we decide which organisms possess which modalities? When scientists claim to have discovered a new sensory modality, what is the theoretical content of this claim? (10-11)

I called this the *star-nosed mole problem* in celebration of the work of sensory biologists (most notably, Ken Catania—who has since been awarded a MacArthur Fellowship for his work) at determining that the nose of these moles is

[5] Here's just a small sampling: (Noë 2002; Noë 2004; Nudds 2004; Ross 2008; Batty 2010; Fish 2010: Ch. 9; Gray and Tanesini 2010). Fiona Macpherson's (2011a) recent edited collection of papers both new and old represents an important contribution to these concerns. See also the Editor's contribution to this volume.

a sensory organ and that, further, the sensory modality of this organ is tactile in nature (and not electrical or chemical, as had previously been hypothesized).[6]

Star-nosed moles are striking but not unique and can be taken to represent the more general class of concerns about the nature of nonhuman animal senses. When confronted with a nonhuman animal, how ought we decide what sensory capacities it has, how those senses relate to other animals (including humans) and how any given nonhuman animal sense relates to its other senses and other non-sensory abilities? At the time, I noted that this set of problems had been almost completely ignored by philosophers and not much has changed since.[7]

What might be motivating this ongoing oversight? Is it mere philosophical prejudice? I think not. Although it is rarely explicitly discussed, there are *prima facie* reasons for ignoring nonhuman animal senses in the philosophy of perception. However, on deeper consideration, I believe those reasons do not hold up. This is an issue that has not received sufficient consideration and in this chapter I plan to explore the relationship between the human and nonhuman cases with an eye towards explaining why I believe philosophers should not ignore the nonhuman cases. In the section that follows, I will propose an explanation for this lacuna concerning nonhuman cases in the philosophical

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[6] See (Keeley 2002) for details and citations.

[7] Tom Nagel’s famous 1974 paper, “What is it like to be a bat?” was clearly inspired by the then recent discoveries concerning bat echolocation, but it wasn’t really *about* the sense of echolocation, so it isn’t a clear counter example to the point I’m making here. However, one philosopher that clearly *has* written about the issue of nonhuman senses is Richard Gray (2005; 2011) and I will be looking at his work in §4. Macpherson (2011b) also discusses senses outside of the human case. Finally, I applaud Mohan Matthen for including a chapter on this topic in the current volume.

discussion. Then, in §3, I will present my reasons for embracing the philosophical study of nonhuman animal senses, despite those unvoiced concerns. Before wrapping up this chapter, in §4, I will have a look at some nonhuman animal senses—infrared reception, but also a bit at magnetoreception—to leave us with examples to think about.

2. A Meta-question

If my proposal is correct concerning the existence of Aristotle's and the Star-nose Mole Problems, then there are two important sets of questions here, but if so, another question—a meta-question—arises: What is the relationship between these two questions? One's answer to this meta-question may have important consequences for the relationship between the *answers* to these two sets of questions. For example, it might be argued that because of a fundamental continuity of humans and other animals, these really ought to be treated as the same larger set of questions, but applied to different segments of a single domain: the world of animals.[8] On the other hand, one might argue that with respect to the senses, at least, the nonhuman animal and the human cases are discontinuous to such a degree that we can expect their answers to be discontinuous as well. On this view, the answers given to one problem may have little to do with answers to the other.

[8] To be honest, in my 2002 paper, I simply assumed this kind of connection between the human and nonhuman cases, in part relying on arguments I had presented earlier (Keeley 2000), although this earlier paper did not explicitly talk about the senses. Part of my goal here is to make that case more explicit.

Another way of characterizing these two answers to the meta-question is in terms of the strength of the proposals being made.[9] The latter approach to the question is a weaker proposition. On the discontinuity reading, there are two sets of questions—one concerning the senses of humans, the other concerning the senses of nonhuman animals—but the answers one develops for one set might nonetheless help in answering the questions of the other set by providing us with innovative ideas and hypotheses. On the continuous reading, we have a stronger thesis: answering one of these questions *just is* an answer to the other question. You *cannot* answer the questions of one set without answering the other. That strong connection is the alleged upshot of the biological continuity of human and nonhuman animals.[10]

Let's look at these two answers a little more closely: If one believes that there is a deep connection between the sensory abilities of humans and other animals, then this would imply that there ought to be a similar connection between the explanations of the senses in both cases. This view relates to why I am using the somewhat cumbersome phrase "nonhuman animal" instead of just "animal." In our post-Darwinian world, we now recognize (or *should* recognize) that humans are animals, too. Hence, in the case of traits that we share with our

[9] My thanks to Richard Gray for this way of characterizing the issue here.

[10] There is a third possibility here—arguably, the position that Aristotle himself takes—namely, that the two cases are discontinuous, but nonetheless the explanation in one domain is built on the answer in the other domain. On this account, although humans are importantly different from nonhuman animals, a full understanding of the human case will require an understanding of those nonhuman animals. In other words, humans are a *special* kind of animal, so that in an important sense humans are both continuous *and* discontinuous with these other creatures. I will not address this case specifically, but if I am correct in what I propose about both the continuous and discontinuous cases, I believe my conclusions will apply to this third, middle option, *mutatis mutandis*. (Thanks to Mohan Matthen for pointing out this third option to me.)

nonhuman evolutionary cousins, we should be wary of discontinuous explanations. If this is the case, then one test of a philosophical theory of the senses ought to be not just how well it captures human senses, but also how it captures those of nonhuman animals, whose senses were formed by the same processes of natural selection and ontogenetic development as were human senses. On such an approach, it is reasonable to conclude that *of course* the understandings of human and nonhuman senses ought to develop hand-in-hand with one another. On this view, Aristotle’s problem and the star-nosed mole problems are just opposite sides of the same coin. Let’s call this the *continuity thesis.*

If, on the other hand, one takes the two cases to be importantly discontinuous—that is, if one denies the continuity thesis—then one will not be bothered that the account of human senses relies upon features that are missing or inaccessible in the case of nonhuman animals. In fact, the importance of such a feature might be a big part of what motivates the belief in the discontinuity in the first place. Let’s call this the *discontinuity thesis.*

Among philosophers of perception who discuss the senses, I am aware of no significant discussion of this relationship or arguments concerning what answer to the meta-question we should endorse. I would like to suggest that the fact philosophers have largely ignored the star-nosed mole problem indicates an implicit belief in the discontinuity of the human and nonhuman cases. They have not addressed the issue of nonhuman senses, I suggest, because when they speak of the senses, they take themselves to be tackling a different set of questions. Alternatively, they may simply be assuming a strong version of the continuity thesis and therefore believe that because of the deep connection between human and other species that any account of the senses in human *just is* an account of the senses in other animals. But there is a problem with both assumptions, in that on either account more needs to be said to give a full account.

Historically, the notion of a discontinuity between humans and nonhuman animals with respect to the senses is a modern idea. As Heller-Roazen (2009: ch. 5) describes it, prior to Descartes and the Modern turn in philosophy, sentience was a trait that humans and nonhuman animals were taken to share. Further, with that sentience came a shared sense of self awareness (a view that Heller-Roazen dubs “*Sentio ergo sum*”). What separated humans and nonhumans, instead, is our rationality, our capacity to reason. But this close connection of humans and animals was lost in the move to Cartesianism, which reserved “real” sensation, along with self-awareness & consciousness, to humans (and at the same time stripping the animals of their sentient status, or at least putting humans and nonhuman animals into importantly different categories when it came to the senses).

In the background here is what might be called the “specialness” of human conscious experience, of which perceptual experience is clearly a significant part. If human consciousness has an importantly different status from that of other animals, then it should only be expected that the senses of humans and nonhuman animals would be treated differently. Why think of human consciousness as especially different from that of other animals? Well, for starters, due to our capacity for language and categorization, we are able to report on the nature of our phenomenology in a way that other animals seem incapable of. It is, for example, open to humans and arguably humans alone to undertake to refine our introspective reports on the basis of careful practice and training, as psychologist Edward Titchener (1901-1905) proposed.[11]

Second, in addition to the ability to report verbally on them, there is also the obvious fact that we possess human senses and as a result, stand in a relationship to them that is importantly different from our relationship to the senses of other animals. The intuition here is that the peculiar phenomenal experiences associated with the operation of humans senses can be understood to be "obvious" to a neurotypical human in a way that the senses of animals are not—especially those senses that are not shared by humans. I believe that this intuition plays an important role in the most famous philosophical discussion of animal senses: Thomas Nagel's 1974 "What is it like to be a bat?" That paper raises the titular question about the senses of bats as a question distinct from the hoary problem of other minds; it is not the same question of asking what it is like to be another human being. This is presumably because, by virtue of being

[11] For a contemporary critical discussion of introspective techniques, see Chapter 5 of (Schwitzgebel 2011). Also, in stressing the essential importance of the "special introspective quality" of the different senses, I suggest that the view presented in (Grice 1962/1989) is a representative of the position I describe in this paragraph.

human and possessing human senses, you know what it is like to sense the world as I do, in a way importantly different from how either of us can know what it’s like to sense the world via echolocation.

On both of these accounts, we should expect the understanding of human senses to be importantly different from our understanding of nonhuman animal ones. This is because they purport to understand the senses in ways that aren’t applicable in the nonhuman cases: The former deals with senses-as-introspectively-reportable, the latter with senses-as-possessed-and-experienced-by-humans. If it is the senses understood in these ways that motivates and interests you, then it might seem that nonhuman animal senses—which share neither of these defining features—are just irrelevant. At least, if I am correct in proposing that something like this line of reasoning is cogent, it would give us a plausible hypothesis to explain why, to date, philosophers have simply not been all that interested in thinking about nonhuman animal senses.

1. The importance of nonhuman cases

With the potential answers to the meta-question on the table—answers stressing either the continuity or discontinuity of human and nonhuman sensory abilities—I now want to turn my attention to reasons why there is philosophical and theoretical value to understanding nonhuman animal senses in light of those answers. I hope to show that no matter how one answers the meta-question, there are nonetheless good reasons for philosophers to pay attention to the nonhuman senses.

If the continuity thesis is correct, then as noted above, it is hard to see how nonhuman animal senses will *not* be relevant to addressing Aristotle's problem. After all, the continuity thesis supporter will note, we have no sensory organs not shared by other organisms, which is why we routinely do things such as use the macaque (a genus of old world monkey) as the workhorse of visual neurophysiology. The reason we've been able to learn so much about *human* vision from studying monkeys is that, in a real sense, much of what we think of as "human vision" is not correctly thought of as *human* at all, but rather *primate* or *mammalian* or even *vertebrate*. Indeed, when we don't recognize this, we are committing a form of anthropocentrism; that is, we are taking as specifically human a trait that is more correctly thought as belonging more broadly to other organisms, additional to us.[12]

The role of nonhuman senses for the understanding of human senses is not merely theoretical; it has historical precedent. Consider the case of what some argue is the first sense besides Aristotle's five to be scientifically established: The sense of balance. As psychologist-turned-historian-of-neuroscience, Nicholas Wade (2003) describes, a sense of balance was a phenomenon in search of an organ by the 19th century. Even the ancients were familiar with the experience of vertigo and wondered what underlay it. At the same time, the semicircular canals of the inner ear were organs in search of a function. There was an idea that they were part of our auditory system,

[12] I explore this idea more fully in (Keeley 2004), "Anthropomorphism, Primatomorphism, Mammalomorphism: Understanding cross-species comparisons." See also (Matthen 2007).

specifically responsible for the perception of noise; after all, these organs are located adjacent to our cochlea and are even physically connected to the ear canal. They are all part of the bony labyrinth.

How did we come to our contemporary view that there is a vestibular sense and that the semicircular canals is the organ that mediates that sense? Largely through comparative evidence. After all, humans are not unique in having these structures, so to figure out the role of these organs in humans, physiologists probed their role in these other animals. For example, in the 1820s Flourens lesioned these organs in doves, pigeons and rabbits and observed the effects on their movements ("...but which [Flourens] preferred to interpret, from his bias to the acoustic theory of the labyrinth, as the expression of painful auditive disturbances" (Mach 1898: 290)). Later in the century, Ernst Mach did ingenious work on the vestibular sense in humans, using a specially built spinning chair. However, according to Mach, the "most remarkable, most beautiful, and most convincing experiment" was conducted by Austrian physiologist Alois Kreidl on *crustaceans*:

> According to Hansen, certain Crustacea on sloughing spontaneous-ly introduce fine grains of sand as auditive stones into their otolith vesicle. At the ingenious suggestion of S. Exner, Dr. Kreidl constrained some of these animals to put up with iron filings (*ferrum limatum*). If the pole of an electromagnet be brought near the animal, it will at once turn its back away from the pole accompany-ing the movement with appropriate reflex motions of the eye the moment the current is closed, exactly as if gravity had been brought to bear upon the animal in the same direction as the magnetic force. This, in fact, is what should be expected from the function ascribed to the otoliths. If the eyes be covered with asphalt varnish, and the auditive sacs removed, the crustaceans lose their sense of direction utterly, tumble head over heels, lie on their side or back indifferently. This

does not happen when the eyes only are covered. (302-303)

According to Mach then, it was work on crustaceans along with work like his own on humans that established the sensory function of the semicircular canals and convinced sensory scientists that there was a sixth sense of balance.[13] This is not a unique case. As I discuss in Keeley (2002), the decisive evidence in Catania’s case that the nose of the star-nosed mole was primarily a tactile sensory organ—and not an olfactory or electrosensory one, as had been proposed by others—was the comparative evidence he was able to present showing that the sensory end organs and cortical wiring of the star-nosed mole were homologous to the organs in other species of mole; organs commonly agreed to be tactile in nature. Comparative evidence often lets us answer questions related to one species by comparing that species to others; humans are no exception.

Yet another issue that points to the importance of understanding nonhuman animal senses has to do with the evolution of sensory systems. Today we are confronted with the sensory skills of extant species, including ourselves. But all of these extant species, including us, are the product of evolution from many, many extinct species. The further back in history we go, the less like us these organisms were in terms of the sensory systems they had. Our sensory systems have evolved from other systems just as much as any of our other traits.

[13] Something that is just common sense to the Anlo-Ewe of West Africa, who count a sense of balance among their set of basic senses, alongside vision, hearing, etc. (See (Geurts 2002).) This only goes to show that what common sense purportedly tells us may not be so “common” after all.

There was a time in the history of this planet when the first creatures evolved the ability to sense light and we are likely the descendants of those creatures (or some others that convergently evolved the same ability) (Parker 2003). How our current sensory systems have come to have the form they currently have—how they process information, how sensory representations have changed over time, what the nature of our evolutionary niche is—informs our understanding of our current senses. For example, the proposal that primate color vision originally evolved to enhance our ancestors' ability to spot ripe fruit within a cluttered visual environment can inform our understanding of the nature of color perception (Regan, Julliot et al. 2001).

To sum up the argument of the last few pages, a proponent of the continuity thesis will argue that the senses of humans are senses that we share with other, nonhuman animals. As such, they are better thought of as traits of some larger taxonomic grouping than simply humans—they are, for example, vertebrate or mammalian traits. This being the case, then humans are just one instance of the trait in this larger set. Regardless, when one learns about a shared sense in one of these organisms one *ipso facto* learns about that sense in the human case.

But if one denies the continuity thesis, what then? To deny this is to deny the claim that humans share important features with nonhumans. Or rather, it is to deny that humans and nonhumans *fully* share what it is to have a sense—there are uniquely human aspects to the human possession of senses, such as reportability or the fact that we humans possess those senses. On the second point, we already can see reasons for calling it into question. The charge of anthropocentrism—that it is incorrect to speak of human senses as purely *human* senses and to do so is to assign a trait to humans that properly belongs to a broader taxonomic category—takes on that claim directly. Yet, setting that aside what if there are unique aspects to human senses? Would not that imply that it is misguided to pay too much attention to nonhuman animal senses?

Not necessarily. To see a reason why not, consider a concept drawn from the science of neuroethology—the biological science that studies the neural basis of naturally occurring behavior: Champion species. We begin with the observation that humans are unique in many ways, perhaps even in ways related to our senses. Arguably, we have a unique capacity to report on the nature of our sensory experiences. OK, but also observe that all evolved organisms are unique (Foley 1987). That is to say that while humans are unique, they are not *uniquely unique*. Neuroethology has traditionally taken as its paradigm cases, unique and extraordinary animal systems which are arguably the best at some capacity. So, because bats and owls have the most developed auditory systems, neuroethologists have chosen to study these animals as a way to understand the nature of audition. Neuroethologist Walter Heiligenberg explicitly endorses this approach and enumerates its rationale, noting that some animal species are *champions* in particular aspects of sensory or motor performance and,

> ... such superior capabilities are linked to highly specialized neuronal structures. Such structures incorporate and optimize particular neuronal

> designs that may be less conspicuous in organisms lacking these superior capabilities. Moreover, the behavioral repertoire of such "champion" species readily offers paradigms for testing the performance of their special designs at the level of the intact animal. Electric fish and echolocating bats, for example, are masters in the processing of temporal information and show an abundance of mechanisms devoted to the analysis of temporal signal characteristics. Therefore, these animals provide powerful model systems for behavioral as well as cellular studies of a wide scope of neural mechanisms dedicated to temporal information processing. Their exploration will reveal the diversity and limitations of these mechanisms and should ultimately facilitate our understanding of temporal information processing in other systems, for example, speech perception in humans. ((1991: 2), see also (Carr 1993; Keeley 2000))

Seen in this light, humans can be seen as champion species when it comes to reportability.[14] We can (and have) done psychophysics on nonhuman animals. For example, we can present sensory discrimination tasks to dogs to determine the nature of canine color vision (Coile, Pollitz et al. 1989; Neitz, Geist et al. 1989). But due to our capacity for language we can report *a lot* about what we experience through our senses, more so than other species. By studying humans we can learn about the ability of other animals to report on their senses; similarly, as Heiligenberg notes, we can learn about the senses of humans by studying champions species who share our senses.

The argument of this section so far has a straightforward structure. I begin by taking it for granted that there is philosophical and theoretical interest in understanding the nature of human senses, i.e., Aristotle's problem. I then present a number of reasons and lines of argument to show how the study of nonhuman animal senses is important for a full understanding of human senses.

[14] Perhaps, as well as what we humans can do with those reports (see Mohan Matthen's contribution to this volume).

This is to treat nonhuman senses instrumentally, as a tool for understanding their human counterpart. I now want to end this section by arguing that, all that aside, nonhuman animal senses are intrinsically interesting. Independent of what they can tell us about our own senses, they are philosophically and theoretically interesting all on their own.

One reason is perhaps the most banal and the least likely to sway the unconvinced: philosophers ought to be interested in nonhuman animal senses for one of the same reasons scientists are, namely that these organisms are part of the same world that we occupy. Hence, to the extent that we wish to understand our world—a goal that scientists and philosophers share, one hopes—then the senses of animals, especially the list of senses not shared by humans, ought to be something that philosophers ought to help us understand. Part of the motivation here is the simultaneous recognition that (1) one goal of philosophy is to understand the world as it is experienced and that (2) nonhuman animals inhabit different worlds than we do, in part as a result of their different senses.

In claiming that animals occupy "different worlds" than humans, I am invoking Jakob Johann von Uexküll's (1934/2010) venerable notion of the *Ümwelt* here. Translated literally, *ümwelt* just means "environment" or "surroundings," but in the technical sense von Uexküll employs it is closer to the environment of the organism as it senses and interacts with that world, such that two different species of organisms that inhabit the same physical environment would occupy different (but, perhaps overlapping) *ümwelten* as a function of their respective sensory systems and means of interacting with that physical environment. In a famous example, von Uexküll describes the role of butyric acid in the *ümwelt* of the tick. (Butyric acid, which is released from the sebaceous follicles of mammals, is the sensory cue that a tick uses to determine when to drop from its perch on a branch in the hopes of landing on a mammal below.) By way of analogy, he compares butyric-acid-for-the-tick with raisins-for-a-human-gourmet:

> Just as a gourmet picks only the raisons out of the cake, the tick only distinguishes butyric acid from among the things in its surroundings. We are not interested in what taste sensations the raisins produce in the gourmet but only in the fact that they become perception marks of his environment [*ümwelt*] because they are of special biological significance for him; we also do not ask how the butyric acid tastes or smells to the tick, but rather, we only register the fact that butyric acid, as biologically significant, becomes the perception mark for the tick.
>
> We content ourselves with the observation that perception cells must be present in the perception organ of the tick that send out their perception signs, just as we assume the same for the perception organs of the gourmet. The only difference is that the tick's perception signs transform the butyric acid stimulus into a perception mark of its environment, whereas the gourmet’s perception signs in his environment transform the raisin stimulus into a perception mark.
>
> Every subject spins out, like the spider’s threads, its relations to certain qualities of things and weaves them into a solid web, which carries its existence. (von Uexküll 1934/2010: 52)

The “solid web” of this metaphor can be thought of as the *phenomenology* of the tick.[15] Although I will not argue for it here, I contend that philosophers should not be exclusively interested in the phenomenological worlds of neurotypical humans; we should also explore and seek to understand those of

[15] (Buchanan 2008) explores the connections between von Uexküll’s work and the philosophical movement of phenomenology.

the autism spectrum disorder, synesthesia, schizophrenia, “human echolocators” (such as Daniel Kish (2009)), and so on. By the same token, what I am arguing in this chapter is that we should be similarly interested in the phenomenological worlds—the *ümwelten*—of bats, electric fish and star-nosed moles.

The upshot of this section should be that there are two answers to the meta-question and on both answers, there is still philosophical & theoretical value in the question of nonhuman animal senses. If the two questions are indeed deeply related due to the continuity of biology, then the understanding of nonhuman animal senses is necessary to understand human senses. If there is a significant discontinuity between nonhuman and human senses, the understanding of nonhuman senses is *still* philosophically and theoretically important because (1) not everything about human senses are discontinuous, (2) the champion species argument, and (3) they are intrinsically interesting.

4. The case of infrared reception

I want to end by taking a look at an example of a nonhuman animal sense in order to leave the reader with a feel for how they might be interesting examples to explore. It has the property of challenging us to think about the sensory possibilities in ways that commonsense reflection on our own human sense perhaps does not. It represents a sense that Aristotle, with his Ancient Greek physics and philosophy of mind, would have had a hard time getting his head around. He was, for example, familiar with the existence of strongly electric fish, such as the Mediterranean *Torpedo*, but lacking any concept of electricity, he was at a loss what to make of these creatures beyond that they were extremely odd in their ability to make a fisher's arms feel leaden as a net was pulled in.[16] While we now have a much firmer grasp on the phenomenon of electricity, the perception of the world via electroreception is still rather mysterious. Something similar can be said of the infrared case to which I will now turn. I propose that these cases are interesting both in themselves and for what they can tell us about our own senses.

The ability of some animals to perceive infrared wavelength light creates some interesting difficulties in thinking about the senses. Some animals can directly perceived electromagnetic radiation in the infrared portion of the light spectrum. The modifier "directly" is important here, because if one thinks about it, in a sense humans can come to know about the existence of infrared radiation in a variety of *indirect* ways. For example, it makes some sense to say that, even from a good distance, you can *see* that the red, glowing iron bar that the blacksmith has just pulled from the furnace with her tongs *is hot*. As another example, most of us are familiar with the night vision goggles that are now commonly used by advanced militaries; these electronic optical devices rely, in part, on infrared sensitivity to enable their users to operate visually in low-light conditions. However, in both of these cases, perception of the thermal energy properties of the world are brought about by the eyes operating in the normal—

[16] Hence, our modern English words "torpor" and "torpid" share a common root with the *Torpedo*. Plato, too, was familiar with this electric fish. There is a humorous passage in the *Meno* where the effect of Socrates' speech on his listeners is likened to the paralyzing effects of the *Torpedo* (and his flat forehead also unfavorably compared to the head of this unattractive fish).

non-infrared—range of the electromagnetic spectrum. In the case of the iron bar, what we are seeing is a particular red colored glow in a specific context and are calling on our learned knowledge to infer or judge that it must be hot. In the case of the night vision goggles, this equipment operates by taking infrared information and systematically converting it into light within the range that human eyes can see.

To distinguish such cases of direct from indirect cases of perception, neuroethologists find it important to distinguish between cases of *reception* from *detection*.[17] The suffix *-detection* is applied in cases where an organism is capable of responding, *by any means,* to the presence of a particular type of stimulation in the environment. The suffix *-reception* is reserved for those organisms that carry out such sensory discriminations through the use of a dedicated anatomical system of structures. [18] So, as described above, humans are infrared-detecting their environment. This is different from the cases I am about to describe where organisms have specially evolved organs for direct perception of light in the infrared range.[19]

A number of animals have been described that are commonly believed to be infrared receptors, most famously pit vipers who along with some other snakes, boas and pythons possess a morphologically distinct organ near the

[17] I discuss this distinction further in (Keeley 1999: 404 (textbox)).

[18] The concept of evolutionary and developmental "dedication" is discussed in (Keeley 2002: 17-19).

[19] Although, as I will discuss below, it might make sense to speak of an infrared receptive sense in humans mediated by thermoreceptors in the skin, as when one *feels* the warmth of the sun on a bright and sunny day. But even so, this would be a different sensory activity than the two examples of infrared detection described above.

eyes known as a *pit organ*.[20]

As established by neuroethologist Theodore Bullock and biologist Raymond Cowles in the 1950s—see (Bullock and Cowles 1952; Bullock and Diecke 1956)—these pit organs enable their possessors to thermally image their environment, a useful ability for an animal that preys upon warm-blooded animals often in low-to-no-(visible)-light situations, such as in underground dens. These animals also possess separate organs (what we would naturally think of as "eyes") that operate in visible ranges.[21] The importance of the pit organs is illustrated by experiments in which snakes with intact pit organs but occluded or destroyed eyes can nonetheless hunt and strike accurately (De Cock Buning 1983).

While the photoreceptors of human and snake retinae reliably respond to the impact of photons in the visible range of electromagnetic radiation, the thermoreceptors of the pit organ are different. Richard Gray (2005) aptly summarizes it,

> Although the mechanisms underlying thermal imaging are still not fully known, behavioural and physiological studies have provided a good deal

[20] Infrared reception has also been investigated in a number of insect species, such as in "fire-beetles" that seek out recent forest fire areas for breeding (Schmitz, Schmitz et al. 2000). See (Campbell, Naik et al. 2002) for a review.

[21] It is difficult to talk about infrared perception in non-question-begging ways because of the anthropocentrism that is built into our ordinary language about light. After all *infra*red, as well as *ultra*violet, are defined entirely in terms of our normal human capacities. Beyond what our species-typical eyes are capable of, there is nothing else that separates the wavelengths we call "red" and "violet" from "infrared" and "ultraviolet." Yes, they differ by wavelength, but so do green and yellow. As Gray (2005) puts it "According to physics, electromagnetic radiation forms a continuous spectrum with no intrinsic divisions" (466). Further, "Photons have discrete energy values; nevertheless, there are no more general ways of distinguishing them by means of their intrinsic properties. Those divisions that are made in the electromagnetic spectrum arise from the relational properties of electromagnetic radiation, viz. the way it interacts with objects" (474).

> of information. What is apparent is that the sensory endings of the receptors are receptive to specific wavelengths of electromagnetic radiation (photons of specific energy level). Sensitivity is maximized at the middle region of the infra-red range (about 10 µm). Significantly, the sensory endings are insensitive under conditions of stimulation similar to their natural environments to other ranges of electromagnetic radiation, for example visible light, to other forms of heat transference, for example conduction (making them independent of fluctuations in the body temperature of the snake), and to other forms of physical stimuli, for example sounds, odours and vibrations. Their sensitivity to radiant energy enables pit vipers to distinguish objects within their perceptual range from the differences in their temperatures from a background level which can be as small as 0.01°C. (466)

This case is interesting because two commonly used and commonsense criteria for dividing up the senses pull us in different directions in the case of the perception of infrared stimulation, as discussed (in more detail than I can here) by Gray (2005). For example, one very important criterion when talking of the senses is the presence of an identifiable organ. This was clearly important to Aristotle, for example, and it seems plausible to point to the importance of organs to our commonsense way of talking about the senses. Using this criterion, when confronted with pit vipers, we ought to talk about two separate senses. After all, there are many anatomical differences between the organs for perceiving visible and infrared light. Additional to the physically distinct locations of the two organs, one of them (the eye) has a lens for focusing its photonic stimuli whereas the pit organ lacks a lens.

However, as I (2002) and others have argued, another important criterion is "...the differing general features of the external physical conditions on which the various modes of perceiving depend[; …] differences in the 'stimuli' connected with different senses," as Paul Grice (1962/1989: 250) puts it. As I have already noted, there is no non-arbitrary difference between the range of physical stimuli perceived by these two different organs. In terms of the physics, there are no grounds for distinguishing between two senses here. There is but one sense distributed over two anatomical structures. Therefore two criteria here—organs and physics—contradict one another.

Further, this is not simply a difficulty for pit vipers. After all, humans also have thermoreceptors. Ours are in our skin as part of our capacity to detect temperature. As Gray notes, there is evidence that these cells respond to stimulation in the infrared range (Greffrath, Nemenov et al. 2002). Perhaps, as I suggest in a footnote above, these thermoreceptors are responsible for the feeling we have as the sun beats down upon us or when we react to the radiant energy of a fire from a distance. If so, then relying on the physics criterion would lump this skin-temperature sense in with the eyes, both as part of the same sense. On the organs criterion, we clearly are presented with two senses.

There is a further complication. In the discussion above, I have sometimes slipped between speaking of "infrared perception" and "heat perception," as if they were synonymous. They're not. Our commonsense notion of "heat," in fact, covers two different, but related, physical situations. Some of what we commonly think of as heat is *radiant heat*. This is electromagnetic energy *à la* infrared radiation. However, part of what we think of as heat is *kinetic energy*; it is the vibration of particles that make up a substance. So, heat can be transferred in two ways: (1) it can be radiated as infrared (and other frequencies) of light and (2) it can be conducted by contact as the kinetic energy of a hotter source is *conducted* to a cooler target. Further, the thermoreceptors in the skin are normally thought of detecting conductive heat. You submerge your hand into water warmer than the skin of your hand. The kinetic energy of the water is conducted into your skin, stimulating your thermoreceptors and you perceive the warmth.

Gray uses this distinction between radiant and conductive heat energy to propose another problem for thinking about the temperature senses. He calls it the Vampire Bat Problem[22] and it is this: “Vampire bats are so-called because of their exclusive diet of blood. What is less well-known is that they locate the capillaries that are close to the skin surface of their prey by means of heat sensors in their noseleafs” (469). He continues:

> The possibility thus arises of the heat sensors of the vampire bat being receptive, i.e. sensitive as part of the bat’s natural environment, to both radiant energy (when it is at a distance from its prey) and kinetic energy (when it is in contact with its prey). So the following question naturally arises: would it possess two senses or just one sense? The vampire bat problem is the converse of the pit viper problem: the vampire bat problem arises where one sensory organ is an appropriately wired up sensory organ that is historically dedicated to facilitating behaviour with respect [to] two identifiable physical classes of energy. (469-470)

One response to this conflict is to bring in additional criteria to arbitrate the conflict between these first two criteria. As Gray (2005) observes, …[W]hy should

[22] Gray notes that while he bases his account on work in neuroethology (Altringham 1996), many of the details of this sensory system are still unknown. Therefore, he stresses that his account should be taken as a “thought experiment” (469) or a proposal for how this system might turn out to function. It hits me as a plausible account.

we expect distinct forms of energy, as characterized by physics, to correspond neatly (one to one) with distinct sensory systems, as characterized by neurobiology?... Nature and the evolutionary process which acts on what nature supplies are more complex" (472).

We can call upon a criterion based upon the behaviors used in association with putative senses to help understand how they ought to be grouped or separated.[23] For example, in the case of the pit viper, that the two organs are used differently in separate situations as part of the normal life of the animal (hunting outdoors in daylight versus underground and at night, say) help us to see these as separate senses, regardless of the similarity implied by the physics criterion. Something related can be said in the human case—I am not aware of species-typical behavior in humans that use the infrared perception of the skin in conjunction with the eyes in normal lighting, so it does not make sense to speak of skin thermoreception and vision as parts of the same electromagnetic sense.

The vampire bat problem poses a more intriguing problem. If it is correct to think of kinetic heat and radiant heat as two different identifiable physical classes of energy, as Gray argues, it is unclear how one can avoid the conflict between the physics criterion and the organ criterion (which points to two modalities in a single organ). Given the close association between these two forms of energy—radiant energy hitting a substance is converted into kinetic energy and perhaps both can be better thought of as forms of a unitary concept of thermal energy—

[23] Compare the similar role of behavior in differentiating the senses proposed in Mohan Matthen's contribution to this volume.

perhaps the physics criterion can be thought of as *not* calling for a division here. However, even if something along these lines could be made to work, a very similar problem arises in another case: magnetoreception.

The perception of magnetic fields is currently a very exciting area in the study of the senses. As mentioned in my introduction, a variety of animals have been discovered with behavior that certainly seems to be magnetic in nature, but in many of these animals, the mechanism that mediates this behavior is currently a hot topic of debate. Identifying the mechanism is relevant in order to determine which animals have genuine magneto*reception* and which are carrying out magneto*detection* via some other sense. Therefore, what needs to be discovered are magnetoreceptive organs and this poses special challenges, as Johnsen & Lohmann (2005) observe:

> Several factors have made locating magnetoreceptors unusually difficult. One is that magnetic fields pass freely through biological tissue. So, whereas receptors for sensory modalities such as vision and olfaction must contact the external environment to detect stimuli, this restriction does not apply to magnetoreceptors, which might plausibly be located almost anywhere in an animal’s body. In addition, magnetoreceptors might be tiny and dispersed throughout a large volume of tissue, or the transduction process might occur as a set of chemical reactions, so that there is not necessarily any obvious organ or structure devoted to magnetoreception. Finally, humans either lack magnetoreception or are not consciously aware of it, so our own sensory experiences provide little intuitive insight into where magnetoreceptors might be found.[24] (703)

Yet another possibility is that magnetoreception is occurring in a sensory

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[24] Hughes (1999) echoes this point: “It is worth noting that the bodies of animals are completely transparent to magnetic fields (if that were not the case, magnetic resonance images of the inside of the body would not be possible). This means that the magnetoreceptor would work no matter where in the body it was located—the search has focused in the head, but the magnetoreceptor could be *anywhere”* (158, emphasis in original).

organ we normally think of as dedicated to another modality, hence invoking the Vampire Bat Problem. One currently intriguing avenue of research into a possible magnetoreceptor mechanism derives from a 1977 *Nature* paper by M. J. R. Leask. Leask proposes that magnetic energy could effect the way that photons are absorbed by photoreceptors. That is, as an organism visually senses the world, information about the ambient magnetic environment is revealed. The details of this cryptochrome hypothesis—as it has come to be known, referring to the blue light photoprotein implicated by the proposal—involve quantum mechanics and would take us too far astray to get into here.[25] (However, I will note that, intriguingly, a relevant cryptochrome has been identified in the human retina (Foley, Gegear et al. 2011).) Regardless, the point here is that *if* this mechanism is established as mediating magnetoreception in some organism, then we will again be faced with Gray's Vampire Bat problem, as in these creatures it could be said that they "see" magnetic fields. Does this mean that as they turn from looking Westward to look to the North that the overall color of the scene that they are peering at changes in a systematic way? This an intriguing possibility and one that would cause us to rethink the way we understand the relationship between sensory modalities and their organs.

The upshot of this section and this chapter as a whole has been to demonstrate current areas of interest and philosophical controversy within the study of nonhuman animal senses. There are a number of open questions here.

[25] See (Hughes 1999: 162-170; Phillips, Jorge et al. 2010; Ritz, Ahmad et al. 2010) for more information.

Whether we are talking about electroreception, infrared reception or magnetoreception, we have active areas of scientific investigation that pose a number of conceptual difficulties that can reward deeper philosophical exploration. The scientists working on such nonhuman animal systems are regularly grasping with conceptual, theoretical and philosophical difficulties involving cases that force us to rethink the nature of our own senses. Further, these researchers daily grapple with trying to move beyond the human realm of sensory experience to grasp other ways of interacting with the physical world.

Acknowledgements

I would like to thank Richard Gray for insightful discussions of this chapter and to Mohan Matthen for comments. I also thank the members of the Champalimaud Centre for the Unknown in Lisbon for providing me an excellent environment during the writing of this chapter. Finally, I thank Pitzer College for a Research & Awards Grant for financial support.

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