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Finding Hippocampus Minor

What makes us uniquely human?

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When Darwin showed how the living world was united through a single chain of history of descent, he threatened what had been an obvious scriptural answer to our understanding of ourselves. Even if humans were not the special creation of God, we might, we *must*, have something uniquely our own. But what is it? At the time, and even today, this is not a simple question, despite its simple appearance. Indeed, as phrased it may have no meaning, especially if there has ever been more than one "human" species.

The idea of multiple human species isn't new. Before Darwin, Linnaeus had accepted various "anthropomorpha" reported to exist somewhere south of *Terra incognita* (Fig. 1A). For much of the last century, the fossil record has spawned debates about how many "human" species there are or were. Do we share our 'unique' features with them? Were they endowed with consciousness or language...or souls?

The first prominent post-Darwinian attempt to address the nature of humans was Thomas Henry Huxley's *Man's Place in Nature,*[1] published in 1863, only four years after the evolution bombshell was dropped. Darwin tried to be coy about humans, but the issue was obvious. If life is a history rather than a chain of special creations, humans must have a place in rather than separate from nature. There should be roughly continuous variation among humans and our close animal relatives, if Darwin was right that species form by gradual divergence over time.

The frontispiece to Huxley's book was a figure comparing ape skeletons (Fig. 1B). This was morphed in the 1970s by Time-Life Books into a march of human evolution, and has been parodied countless times since, even by creationists.[2] Huxley systematically compared human morphology with that of other primates. Similarities were well known, but Huxley made them more cogent in the new evolutionary context. He was sympathetic to Linnaeus' rather fanciful parade, because he said Linnaeus had not seen great apes in person, but instead had relied on material provided by a student named Hoppius.

Huxley showed that in behavior, morphology, and embryology, as well as in the known fossils, apes are "blurred copies" of ourselves, which should lead to "profound mistrust of time-honoured theories and strongly-rooted prejudices" about our position in nature. The fact that 'every bone of a Gorilla bears marks by which it might be distinguished from the corresponding bone of a Man,' leads to the 'one immediate conclusion' that we and the 'Man-like apes' constitute different *families* 'separated by no greater structural barrier from the brutes than they are from one another'. But the data also vindicated the 'sagacious foresight' of Linnaeus, that we are in the same *order*. That assertion not only raised a problem with regard to the view that humans are unique among animals in some special way, but got Huxley into hot water, a place he loved to be.

"THE FIRST MONKEY THAT COMES TO HAND"

The prevailing view was and, to a great extent, still is that humans are unique creatures. The obvious seat of our uniqueness is the brain. Richard Owen, a leading scientist, founder of the British Museum of Natural History, and Darwin's antagonist, fed the hunger for gray matter that matters by claiming that the human brain does have a structure, the hippocampus minor (Fig. 2), that is absent in the apes.

Huxley found this assertion to be beyond ludicrous and, in vitriolic attacks over several years, pointed out the manifest falseness of Owen's assertion, as shown in Figure 2 from Huxley's book. In a long diatribe, he accused Owen of willful misrepresentation in persisting in his claim even though one could demonstrate that the claim was "contrary to the plainest facts.... on the first monkey that comes to hand."[1]

Huxley was making the point that species can differ in quantitative ways. There is no need for traits to be present in one but not the other. Basically, that idea is a leftover from pre-evolutionary creationist thinking in which humans simply had to be really different from the beasts. Today, it may be sport to laugh at the hapless Owen, who understandably resented being shown up by the new Darwinian guys on the block. But is it sporting? Could the spirit of Owen, yearning for a human-specific trait, be alive and thriving in our modern genetic age?

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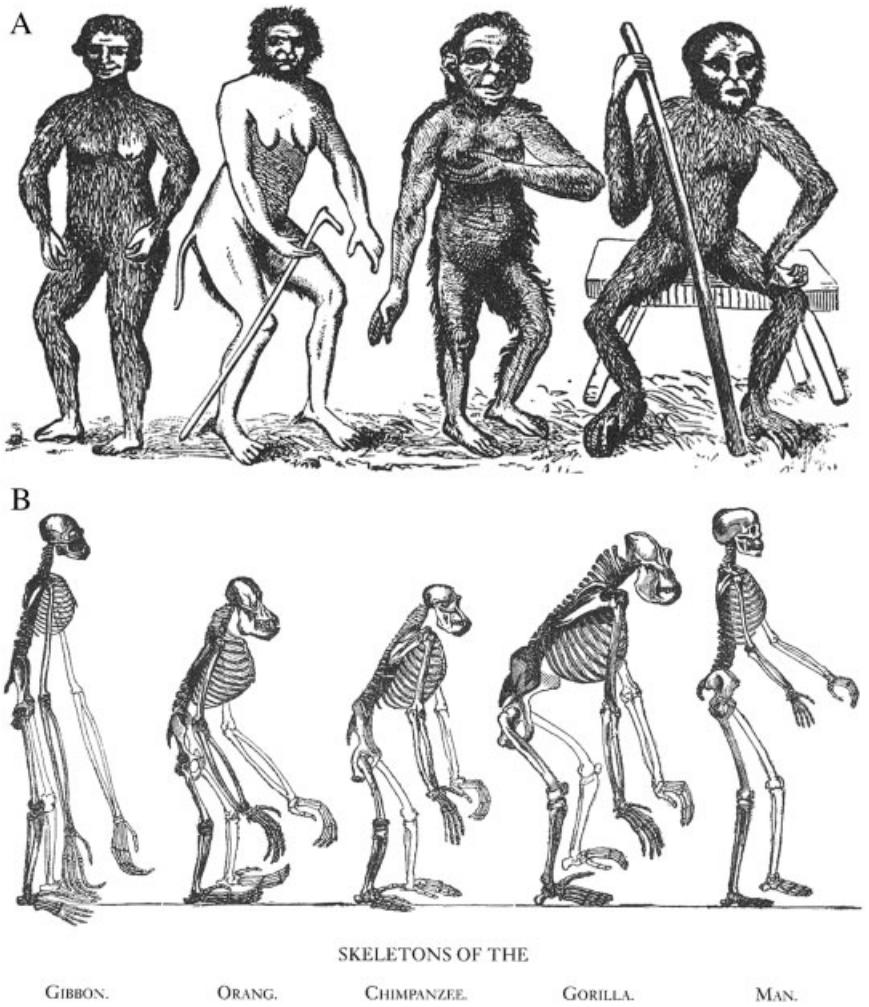

Figure 1. March of the primates. A. Linnaeus' idea of the Anthropomorpha, attributed to a Linnaeus student, Hoppius, who provided previously published figures for Linnaeus to use. B. Skeletons of apes and human. Both From Huxley.[1]

WHAT GENOMES SAY

Let's take a global look first. The availability of a chimpanzee whole-genome sequence makes it possible to see how we differ from them in our DNA, but forces us to consider a gradation of similarities-with-differences similar to those Huxley dealt with. Primate genomes contain more than three billion nucleotides. DNA replication is good, but not perfect, and a given nucleotide is hit by mutation about once every hundred million gametes. That suggests that there may hardly be any of the three billion nucleotides that don't vary in somebody. Among the 6.5 billion humans, each with two genome copies, an average nucleotide position contains around 130 new mutant changes every generation; the exception would be nucleotides that are always lethal when mutant. At every position in the genome, each of the four nucleotides (A, C, G, and T) is probably found in someone. On average, any two copies of a human genome, including your two, differ at about three million nucleotides. In fact, this greatly understates the amount of variation because some areas of the genome, such as short repeat elements called microsatellites, mutate many times more often.

Chimpanzees have a similar pattern of variation, but because of their vastly smaller species size a much higher fraction of their nucleotides probably do not vary today. There are millions upon millions of nucleotides that, in the vast majority of humans, differ from the corresponding nucleotide found in any living chimp. A widely quoted figure is that humans are 95%–98% genetically identical to chimpanzees. That means that if you align a single copy of each genome, somewhere around 100 million of the nucleotides will differ, a mere five of which are shown in a randomly chosen bit of comparison in Figure 3. You can make as much or as little of these millions as you please, depending on your perspective.[3] By count it's a large number, and perhaps a rich mine for a cladist; even considering how much human-chimp genomic overlap there is, it takes comparison of only a small amount of randomly chosen sequence to determine, with all the statistical precision you could possibly want, what species you belong to.

Life, however, is more interesting than nucleotide counts. For most purposes it's not the number alone that matters: A single nucleotide difference

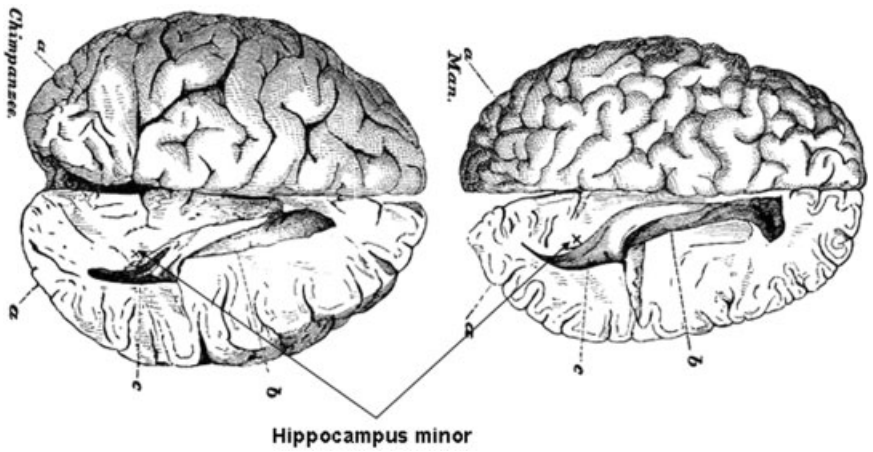

Figure 2. Hippocampus minor, chimpanzee and human. From Huxley[1] with the Hippocampus minor label added.

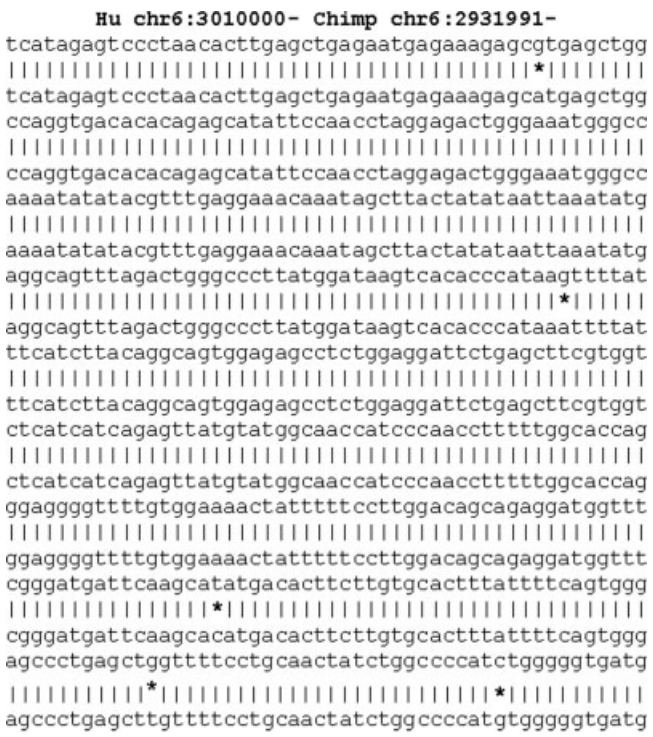

Figure 3. Comparison of a short bit of 450 base pairs near the end of chromosome 6 between ``the'' human (top of each paired row) and chimp (bottom of each row) genome sequences. Asterisks show the five differing nucleotides in this short region; the top line gives the nucleotide starting position along the respective chromosomes. Source: UCSC genome browser http://genome.usc.edu.

can be devastating, as victims of many serious diseases clearly show. We're also learning that genomes are remarkably fluid constructs in unexpected ways. For example, recent sequencing has revealed extensive evidence of unsuspected duplication events. Perhaps 12% of the genome (360 million base-pairs) consists of copy-number variants. These are differences in the numbers of copies of chunks of sequence scattered across the genome and containing hundreds of known functional elements.[4–6] that vary between humans and chimps or that are even polymorphic within our own species.[7] Olfactory genes provide but one example, showing the implications of this type of variation.[8] A high fraction of our thousand olfactory receptor genes are defunct; mutations have made them no longer usable. Some of these mutations are still polymorphic, so the gene works in some people but not others. What you can smell, and how it smells, is different from my experience. The same is true of chimpanzees. Neither all of us nor all of them have the same number of functional genes, much less the same sequence. Overall, while genomic approaches can definitively determine whether you're a human or a chimp, that doesn't answer the question of our uniqueness in a satisfying way. What if we try to be more genetically specific?

HOW MANY GENES CAN DANCE IN THE HEAD OF A *PAN*?

As in Owen's time, attention stays mainly on the brain, but genes have replaced anatomical structures on the human uniqueness dissecting table. Human mental capabilities are clearly different from or, if we allow ourselves a bit of hubris, better than those of other species. (Really, we're just better for what we do or we do what our brains are better at.) Genes that are differentially expressed in the brain or that, when mutated, lead to anomalies like small brains or language deficiencies, have attracted particular interest. However, thousands of genes are expressed in the brain and we know of tens, if not hundreds of them that, when mutated, affect mental function. So perhaps an additional criterion is needed to qualify a gene for the human uniqueness sweepstakes. The criterion that's currently preferred is the adaptive one, that a brain-related gene should also show evidence of a selective history in the human lineage compared to the chimp.

Based on coding changes, several genes have been identified that appear to satisfy this criterion.[9–16] But major functional effects can also result from changes in the timing or level of gene expression. In 1975, before much was even known about gene regulation, King and Wilson[17] speculated that the rapid evolution of humans might mainly be due to changes in gene regulation rather than gene structure. A recent test has been developed to search genome sequence for evidence in the human lineage of natural selection applied to noncoding, presumably regulatory regions of the genome.[18] This is new work, but a interesting areas have already been found, providing at least tantalizing evidence. One may affect *FOXP2*, a gene already touted as a major factor in the evolution of human language. However, many if not all of the candidate "brain-evolution" genes are also expressed in other tissues, like the heart, so we can't automatically assume that the detected selective pressure was related to brain function.

A poorly understood issue in evolutionary genetics is the degree to which traits like our smart brains, which are affected by many genes, evolve via major mutations in a small number of genes or by minor changes in many of them. Few if any geneticists claim, when pressed, that they have found "the" gene rather than one of a number of relevant genes that account for our brain evolution. But simple, unitary images of selection are widespread in the public eye. In our profession, too, they can take on an uncritical life of their own.

A problem is that we're so closely related to chimpanzees that there hasn't been time for too many changes to have accumulated. Although single changes in regulatory nucleotides or amino acids can have major effects on

traits, including the brain, selection based on single changes is difficult to detect from sequence data unless it has been recent and intense. The trace of selection can be weak in traits that are molded by many genes or that evolved slowly or early in our separation from chimps, as did the adaptation to bipedalism. And that brings up another point.

The focus on, if not obsession with, the brain as our figurative hippocampus minor is a choice we make. A good case can be made that the signal human characteristics, as unique in their ways as language, are the anatomical rather than mathematical digits. What about our humble thumbs; hairless, sweaty skin; upright posture, with all its skeletal rearrangements; wide birth canal to accommodate altricial young; various metabolic features; and poor teeth, hearing, smell, and vision? If the fossil record is any guide, it was anatomical features other than the brain that both preceded and enabled the evolution of our talk-generating, tool-envisioning brain. Some brain enlargement was already under way in cercopithecines before there were any hominids. But if brains were of primary adaptive importance, why is it that chimps remain so chimpish? Or, indeed, are the distinctions blurring, if chimps turn out to make spears for hunting[19] or have been making tools for thousands of years.[20] or, for that matter, if spider monkeys form raiding parties?[21] Let's at least acknowledge a value judgment when we see it. It might seem a good idea to propose a search for the origin of our uniqueness in genes for arched feet, an idea that could interest Dr. Scholl, but the Discovery Channel won't return your calls, and good luck selling it to NSF!

IF FOSSILS COULD TALK

Dead men usually tell no tales, but we're getting at least genetic tales from our long-dead ancestors. For nearly a decade, sequences from mitochondrial DNA (mtDNA), the maternally inherited particles, have been available from European Neandertal fossils roughly 40,000 years old, and from archaic anatomically modern humans about 25,000 years old. mtDNA sequence variation helps us date evolutionary events, but our biological functions are mainly coded in nuclear DNA (our chromosomes). Fossil nuclear DNA has been hard to obtain in sufficient quantity to sequence, but advances in technology have changed this. More than a million base pairs of sequence have recently been reported from a 38,000 Croatian Neandertal leg-bone fragment.[4,22]

The data consist of many short sequence fragments scattered randomly across the genome. Human and Neandertal sequence differs by only about 0.5% (99.5% identity), much closer than we are to chimps, consistent with the two lineages having diverged roughly 500,000 years ago. That's if they did separate. Even as fragmentary as they currently are, the Neandertal sequences have already energized lusty arguments about whether Neandertals and early modern humans interacted in more than a platonic way: Were they one species or two, and how can we tell?[23]

The current data are too fragmentary to provide a look at any complete gene we might choose, but much more data will soon be available. The obvious targets of interest will be genes claimed to have been key to our uniqueness. If it turns out that Neandertals carried alleles that comparison with chimps has suggested are our "advanced" genetic elements, such as our uniquely human brain gene sequences, will that undermine our sense of uniqueness? Will this finally confirm that Neandertals, and maybe even Australopithecines, did "sing?"[24]

We should be careful with our answers, to keep the debate on a higher plane than those our benighted forebears held about whether all races were fully human. Certain points of delicacy hinged on the answers, such as whether an earlier form of market globalization, known as the slave trade, could be morally rationalized. Seventy years ago the leading anthropologist Carleton Coon noted that a Neandertal in a business suit would hardly look remarkable to us.[25] That makes Coon appear to have an inclusive view of humanity, but we should recall that he thought that different races had different histories of reaching "full" humanity (if they'd even done it yet), which may be why he opposed school integration in the United States.[26,27] That's not so far removed from some of the genetic poking around going on today as to whether all human races bear the uniquely human brain-gene alleles or whether some may be more adapted for physical than intellectual skills.

A HUMAN AVERAGE, BUT NO AVERAGE HUMAN

When we ask what makes us human, we should pose the question clearly. There are human genomes, but "the" human genome doesn't exist. The human genome sequence on deposit (ncbi.nlm.nih.gov) is not a dictionary of the human. It's an assemblage of different DNA segments obtained from different people. No person has this sequence, much less two copies of it. "The" genome is a molecular abstraction, a kind of Platonic ideal, just as Plato asserted that each actual chair, say, is but an imperfect manifestation of some real but immaterial idea of "chair." But what we want to understand is the uniqueness of real chimps and humans, not imaginary stereotypes.

There are human averages, but there is no average human. There are real human beings and, for a while longer at least, real chimpanzees, but we're each different and nobody is average for every trait. The human genome sequence is not an average of many sequences, but a fragmentary pot-luck sample of single sequence subsets. So when we discuss what makes us human, a single DNA sequence, even a complete one, isn't exactly it.

It may be useful to envision what actually exists in the world at any given time, as a multidimensional cloud of individuals, traits, or copies of DNA, like a cloud of midges hovering over a sunlit spot on a summer's day (Fig. 4). We can describe the average or pick type specimens and draw phylogenies (who would you pick as the human type specimen?). But these are constructs that we impose on reality. The representation in Figure 4 shows considerable overlap between

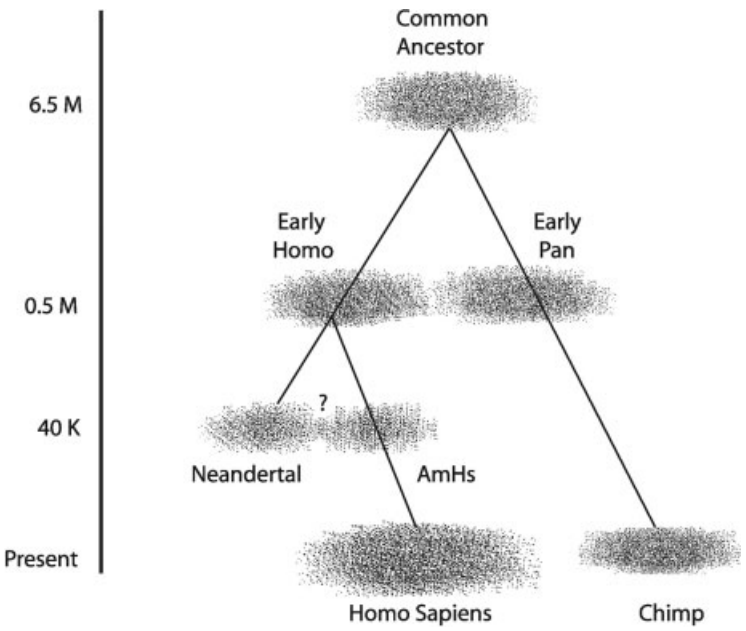

Figure 4. Variation and speciation. A schematic representation of the individual traits, genome sequences, or what-you-will that make up the real world (shown as dots). Concepts like type specimens or ''the'' genome sequence for a species are like the centroids of these distributions, connected phylogenetically here by lines; these are constructs that we define rather than find in nature. This figure shows a conception of the human chimp split, with a ''Neandertal'' side branch. Vertical scale is time in millions (M) or thousands (K) of years; AmHs: anatomically modern *Homo sapiens*. Drawn by A. V. Buchanan.

chimps and humans in one dimension (Y axis), but none in the other (X-axis). However, both groups vary on both axes, so each comparison between one individual from each species would differ by different amounts on each axis. On the genomic level, which is widely assumed to be what defines life, there are billions of axes. So species themselves are basically quantitative and statistical concepts. We have to estimate species differences from samples, which means making often probabilistic decisions about what to count. Even that is a bit circular since we define the species first to guide the sampling.

In this sense, the difference between humans and chimpanzees may not be nothing, but it may be no thing. It's the classical challenge of trying to categorize variation. Human uniqueness is not well accounted for by a specific gene or by genes per se, nor by an enumeration of millions of individual, mostly trivial differences in DNA sequence. In a sense that perhaps is abstract to the point of metaphor, what makes us human is the interaction of these countless variable parts, differing in each individual but, jointly, placing them within their respective, ultimately unambiguously differing, multidimensional spheres.

Thinking this way may be less appealing than simplified media folklore, but it's better anthropology because it's closer to the truth. Perhaps a *reductio ad absurdum* can help make the point. If, as many would say, it's mental function that makes us uniquely human, are people with mutations in the responsible genes not fully human? Is there an IQ cutoff for fully human status and, if so, who is the Decider—and what about those who fall short?

The question of human uniqueness is an old one. In 1784, in a situation similar to Huxley's, Johann von Goethe showed that humans have premaxillary bones, removing a skeletal distinction that had been claimed contentiously at the time (de.wikipedia.org/wiki/Johann_Wolfgang_von_Goethe). In 1794, Charles Darwin's grandfather Erasmus anticipated Huxley's other point: "our fellow animals. . .are supported with bones, covered with skins, moved by muscles; that they possess the same senses, acknowledge the same appetites, and are nourished by the same aliment with ourselves; and we should hence conclude from the strongest analogy, that their internal faculties were also in some measure similar to our own."[28]

Our devotion to the head has always been more than anatomical. As Darwin the Elder put it, "the acquiring of languages, the making of tools, and the labouring for money; which are all only the means of procuring pleasure; and the praying to the Deity, as another means to procure happiness, are characteristic of human nature."[28] After Charles Darwin, when the obviousness of the Diety became markedly less, a focus on the head became more markedly a choice we make to define ourselves. As in a dictionary, definitions are arbitrary.

We should be used to the statistical nature of differences between species,

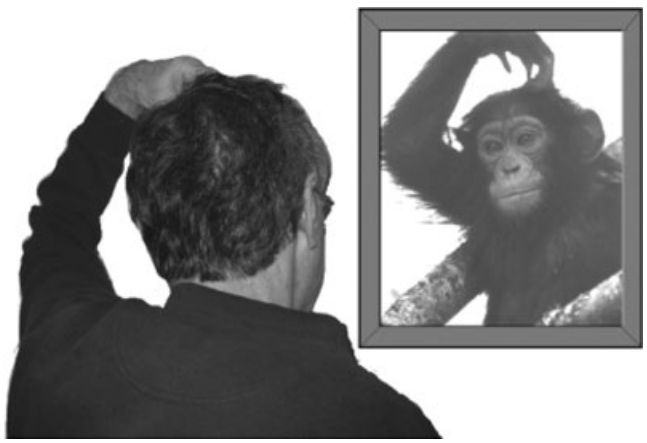

Figure 5. A mirror on one's own ideas? (Chimp courtesy Alan Walker)

but a hunger for simple distinctions persists. A common quip in response to the question "What is anthropology?" is "Anthropology is what anthropologists do." That isn't much of an answer, but it may be the best answer. To paraphrase Huxley, you can easily tell the difference between a chimp and the 'first human that comes to hand' (Fig. 5). But in practice, we each see what we choose to see.

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