History of Thought, Book 1

The Co-Evolution of Technology and Cognition in Primates

Chapter 5: New World Monkeys

The oldest river in America is widely accepted to be the New River.[1]

Similarly, the oldest branch of monkeys is that of the New World Monkeys.

With the New World Monkeys, we officially begin looking at Anthropoids, and we get one step closer to modern humans. As a recap, all of our species we've discussed so far are in the same taxonomic Order, called Primates, within the general classification from the Animal Kingdom -> Chordata (Vertebrate) -> Mammal -> Primate. The Lemurs are our "6th cousins", in that they represented for us the Suborder of "wet-nosed" primates -Strepsirrhini, and as we've discussed in Chapter 3, are widely referred to as "pro-simians". All of the rest of us are in the Suborder Haplorrhini, or dry-nose, aka simple nose.

Inside Haplorrhini are two sub-groups, or Infraorders - the newly (in the last 10-15 years) reclassified Tarsiiformes as well as the Simiiformes. We covered Tarsiiformes in Chapter 4 with our cuddly tarsiers, and you could consider the tarsier our 5th cousin.

Now, with the New World Monkeys, we have drilled down to the Simiiformes, aka the simians, aka the anthropoids- our parvorder. Within this, there are two general divisions: the older the Platyrrhini, containing only New World Monkeys (NWM), and the newer more crowded Catarrhines, which hold the Old World Monkeys (OWM), as well as the apes and humans. This chapter deals with the New World Monkeys, whom you might consider our 4th cousins.

The New World Monkeys/Platyrrhini are a diverse group of over 50 species spread across five taxonomy families, found in Central and South America. Thus, "New World" refers to the fact that these monkeys reside today in the Americas, colloquially known to early scientists as the "new world." "Monkey" generally refers to an anthropoid with a tail, as opposed to later primates such as the ape or gibbon who do not have tails. With all of these "rhini" names, you might have guessed that the distinction between NWM Platyrrhini and OWM Catarrhines has something to do with a nose, and if so, you are right. Platyrrhini means flat-nosed, as their noses are flatter than those of other simians, and their nostrils face to the side. Old World Monkeys and indeed us humans, not only have a dry nose (haplorrhine), but we have a "down-nose" – catarrhine.

Current evidence indicates that New World Monkeys broke off 40 million years ago, or the equivalent of 2 million human generations ago, from some Last Common Ancestor (LCA) with the "Old World Monkeys." This occurred in Africa.

Various theories account for the physical migration to South America, and in particular, the phenomena known as "rafting" gets a lot of attention in the scholarly literature. Here, rather than getting into the *how* the monkeys diverged by reviewing those various theories, (which include geological and geographic background on plate tectonics), for our purposes, it is enough to have a basic understanding of *when* and *where*.

For now, though, let's first do a quick overview New World Monkeys, with particular attention to our checklist of cognitive evolution factors:

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[1] Ward, Dylan J., et al. "New constraints on the late Cenozoic incision history of the New River, Virginia." *Geomorphology* 72.1 (2005): 54-72., See also: http://www.wvgs.wvnet.edu/www/geology/geoles01.htm, and Morgan, John T., and Michael W. Mayfield. "Research Note: The Second Oldest River in the World?." Southeastern Geographer 34.2 (1994): 138-144. Please note that a review of the literature does not show scientific consensus on this, as there is with the new world monkeys. However, the parallels in the naming ironies were too good to pass up as literary device. Certainly New River Gorge tourisms board believe this "fact" anyway: http://explorenewrivervalley.com/ accessed on 4.14.15, http://www.visitnc.com/rivers-lakes accessed on 4.14.15

Physical characteristics

New World Monkeys(NWM) are usually small, ranging in size from the pygmy marmoset, which at 4 -7 ounces is the world's smallest monkey, to wooly spider monkeys at 25-35 pounds. Body size is positively correlated to lifespan in primates, so we see that the lifespan of NWM, which ranges from 15-25+ years in the wild, averages just a bit more than the tarsiers.

In addition to the range of body sizes, there is also a wide range of sexual dimorphism displayed across the NWM species, from positive dimorphism (male larger than female), to no dimorphism, to negative dimorphism (females larger than the male). This range is attributed to variations in social structures, sexual selection and diet.[2] The females breasts of many NWM monkeys species are located near the armpits so that they can be reached by the young riding on the mother's back. NWM are widely regarded as not menstruating, (their OWM cousins do), but some species may menstruate, but have less visibly apparent menstruation cycles.

Their tails are typically longer than OWM, and unlike their African cousins, the larger Central and South American NWM have prehensile tails. The most advanced tail is that of the spider monkey, who can not only hold and carry but also catch things with their tail. Their prehensile tails also feature a small patch of bare skin (bare skin is also known as glabrous) under the last vertebrate that has nerve endings and surface structure like a fingertip, enabling delicate tasks such as peeling bananas.

NWM noses, in addition to being flatter than other anthropoids, also feature a wider septum. Their eyes are forward-looking and binocular, accompanied by flattening of the face and other changes to the skull to support the stereoscopic depth perception and overlapping fields of view,[3] along with numerous changes to the visual pathways[4] and processing capabilities.[5]

The ears of the NWM represent an intermediate form between the large mobile ears of earlier primates and the later smaller fixed ears of later primates.[6] Not only are there fewer muscles controlling the movement of the ears, but in general NWM have less expressive faces than is seen in later primates.

Ethology:

Like most of the tarsiers and the lemurs (both of whom also have long tails), NWM are primarily arboreal. Thus, we can see that the long tail (even when it is not prehensile) is a typical technological innovation in response to moving in trees, providing the benefit of stabilizing the body during running along the branches and while jumping between limbs.

Tree-dwelling species can be more difficult to observe in the wild, and like their prosimian cousins, the life of the NWM in the wild is less well understood and documented than the more terrestrial primates. One interesting characteristic of the NWM is that different species have adapted to different food sources that occur in various ecological niches within different heights of the forest. Therefore, multiple species can co-exist within the same territory without competing. For example, the large wooly spider and howler monkeys eat fruit and leaves primarily at the higher levels of a tree, while the tamarins and marmosets diet consists of tree sap, fruit, insects and other food usually found in the lower branches of a tree.

This specialization in diet can affect differences in behavioral and cognitive tendencies. For example, one of the defining aspects of humans is their ability to think through the consequences of particular actions, and to develop patience, sacrificing minor near-term gains for longer term greater gains. That's why we sit through school, for example, to be able to get more rewarding jobs in the future. Well, that's at least why our parents and school systems make us sit through school, anyway. However, all of us, including humans, discount future rewards. Our ability to correctly assess the probability of future rewards and patience and self-control correctly are key skills for advancement. Studies on two closely related species of NWM (marmosets and cotton-top tamarins) shows that they

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[2] Ford, Susan M. "Evolution of sexual dimorphism in body weight in platyrrhines." American Journal of Primatology 34.2 (1994): 221-244.
[3] Parker, 2007, Changizi and Shimojo, 2008
[4] Padberg, Jeffrey, Elizabeth Disbrow, and Leah Krubitzer. "The organization and connections of anterior and posterior parietal cortex in titi monkeys: do New World monkeys have an area 2?." Cerebral Cortex 15.12 (2005): 1938-1963.
[5] Mitchell, Jude F., and David A. Leopold. "The marmoset monkey as a model for visual neuroscience." Neuroscience research 93 (2015): 20-46.
[6] Cohen, Meyer Michael. Perspectives on the Face. Oxford University Press, 2006., p 31-32

have significantly different cognitive abilities on these kinds of tasks. This variation is not explained by body size, EQ, or social structure, but can be explained by diet: tree gum is a key source of nutrition for marmoset, and to get it, the marmoset must find or create a wound to the tree, then wait for the gum to come out slowly. The tamarins feed on insects and are more likely to make "bird-in-hand" decisions when faced with cognitive choices, shaped by the need to react quickly to fast-moving prey.[7]

All of the NWM are diurnal, except for the night (aka owl) monkey, which is the only nocturnal monkey.

Anatomy/locomotion:

NWM hands have non-opposable thumbs that are in line with their fingers, and to grip things they pinch their thumbs (which possess certain rotational capabilities as well) in a scissor-like motion against their palm/other fingers. These "fingers" or digits feature nails, rather than claws (except for the marmoset and tamarin). Their hands and fingertips are very well innervated and perceptive;[8] in some cases nearly as perceptive in detecting things with their hands as humans.[9]

Two specific aspects of this sensitivity contribute to NWM locomotion: Meissner's corpuscles and finger ridges. Meissner's corpuscles are highly sensitive structures that can detect minute differences in pressure, and are highly effective at gauging the friction or surface of an object (they also are the primary method for blind people sensing Braille).[10] These corpuscles are most developed in humans but have only been found otherwise in the animal world among primates, some unrelated tree-climbing marsupials such as the Queensland possums, and a few rodents.

Finger ridges are patterns of ridges on our fingertips which give us fingerprints.[11] These ridges serve to increase the friction or traction against something being touched. The fact that these ridges, particularly the whorls, serve primarily to aid in gripping can be illustrated in the bathtub. When you spend too much time in the tub, your fingertips get exaggerated whorls, in the form of large wrinkly "prunish" looking fingertips. Testing has shown this pruning greatly aids in gripping wet surfaces.[12] So, taken together, NWM are well adapted to grasping branches and moving around an arboreal environment with their long, strong fingers with finger whorls and Meissner's corpuscles, and grasping (but not fully opposable) thumbs. These same adaptions are precursors for effective tool use, which we will discuss later.

NWM are usually quadrupedal, although some, like the spider monkeys, combine leaps and some swinging by the arms (known as "semi-brachiation") when moving through the treetops. We'll talk a bit more about brachiation when we get to our chapter on gibbons, but for now we'll just note that these larger NWM species begin to exhibit this form of locomotion, and to some degree show the physical characteristics of brachiators: long, muscular forearms, flexible shoulder joints, muscular chest and upper bodies, and hands adept at gripping. In the case of the NWM, this includes occasionally hanging by their prehensile tails, in concert with their grasping hands/limbs. Humans, with their grasping hands, long arms, flexible shoulder sockets and monkey bar playground equipment, by the way, show residual signs of brachiation. So what begins in NWM, peaks in gibbons, still shapes our own biomechanics in interesting ways today.

The spider and capuchin monkeys will often walk bipedally, though we should point out that accomplishing a 2-footed walking motion like the capuchin and trained poodles is different than "striding." Humans "stride," which is to say move primarily via a bipedal action which is a combination of posture and muscle use that provides for significant energy savings for an animal as it moves from point a to point B. We'll come back to the bipedalism discussion in more detail in the Chapter on Protohumans, and specifically when we talk about Australopithecines.

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[7] Stevens, Jeffrey R., Elizabeth V. Hallinan, and Marc D. Hauser. "The ecology and evolution of patience in two New World monkeys." Biology Letters 1.2 (2005): 223-226.
[8] Jones, Lynette A., and Susan J. Lederman. Human hand function. Oxford University Press, 2006. P 24-31
[9] Mountcastle, Vernon B. The sensory hand: neural mechanisms of somatic sensation. Harvard University Press, 2005.
[10] Hoffmann, Joscelyn N., Anthony G. Montag, and Nathaniel J. Dominy. "Meissner corpuscles and somatosensory acuity: the prehensile appendages of primates and elephants." The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 281.1 (2004): 1138-1147.
[11] Penrose, L. S., and P. T. Ohara. "The development of the epidermal ridges." Journal of medical genetics 10.3 (1973): 201.
[12] Kareklas, Kyriacos, Daniel Nettle, and Tom V. Smulders. "Water-induced finger wrinkles improve handling of wet objects." Biology letters 9.2 (2013): 20120999.

Language use

NWM vocal communications are more complex than nearly all other non-primates and non-avians, and in some ways, resemble the two most complicated animal vocal communications – human speech and birdsong.[13] NWM use a variety of vocalizations, including loud low sounds that carry well across distance (used for announcing and maintaining territories), as well as more subtle and nuanced communications, which, while varying by species, contain the signs of elementary syntax. It's useful to note that about 20% of alarm calls made by younger animals are made in response to inappropriate targets. This greatly improves as they mature; this is evidence that the complexity of the calls is learned, rather than innate.[14]

Visual displays, such as the use of postures (some of which include hair-raising, also known as piloerection) are common, as are facial expressions such as baring of the teeth. Returning again to the animal communications framework we introduced in the last chapter; we can consider the evolutionary roots of these displays. Specific postures reflect higher states of muscle activation or tone, and thus signal "Beware: I am not lazy and asleep, I am ready." This includes standing, and more upright postures, shoulders back, and tails raised. These mark alertness and locomotor readiness and signal a potentially aggressive tendency. (This is also probably the message a dog is sending when it is wagging its' tail at you). Bared teeth pull the lips back so that the teeth can be engaged without cutting the lips, and thus are first and foremost an implied threat. Sweating, too, indicates a preparation for action, since the body is beginning a preparatory cooling process.

Other postures are more protective. Crouching, lowering of the body and tail, and curling of the tail down under and between the legs are efforts to shield the body and vital areas from attack. The piloerection, raising of hairs, is commonly associated with an animal "trying to look bigger" but most likely originally evolved in an effort to stay cool. Taken together with the curled tail (another warming mechanism) and the body tremors that sometimes accompany frightening acts, and you can see a body working hard to warm itself, most likely as a result of shunting of the blood from the periphery to the core as a result of autonomic stress triggers – the opposite effect of what you would see in an animal preparing for rapid violent action, but exactly what one might see as it anticipates for massive limb damage or as it enters clinical shock conditions.

So the NWM communications are comprised of an endless variety of visual cues like these, along with scents which are occasionally used for marking of territories and during mating and dominance behaviors. These communications skills to navigate a social system in ways that are more sophisticated than previous primates. Capuchins monkeys, for example, have been observed making selective alliance choices during conflicts. When facing an opponent, a capuchin will not always seek out his "best friend", but rather appears to make assessments between his opponents' relationships with other monkeys before selecting allies. Instead, they solicit aid from individuals with whom they have a better friendship than their opponents. [15]

Senses: a growing dominance of vision

NWM exhibit less of a dependence on smell than the earlier primates, but still have an enhanced sense of smell relative to later primates. NWM, for example, occasionally use scent as a way to communicate dominance among the group,[16] particularly among the nocturnal night monkeys, but there is little evidence that NWM use scents to mark their territories.[17]

NWM appear to have a more sophisticated glandular structure in their skin than earlier primates such as the lemur, and this is likely to be a co-evolution along with changes to the sense of smell. The lemur had a simple glandular structure that had the "smelly" apocrine glands everywhere there was a hair. In NWM, the glands become more differentiated, so that "common" eccrine sweat glands are now at nearly every hair follicle, and apocrine (smelly) glands are distributed in key places around the body. Specifically, NWM tend to have concentrations of

[13] Snowdon, Charles T. "Vocal communication in New World monkeys." Journal of Human Evolution 18.7 (1989): 611-633.
[14] Perry and Manson 2008
[15] Perry et al 2004
[16] Heymann, Eckhard W. "Scent marking strategies of New World primates." American Journal of Primatology 68.6 (2006): 650-661.
[17] Miller, Kimran E., Katalin Laszlo, and James M. Dietz. "The role of scent marking in the social communication of wild golden lion tamarins, Leontopithecus rosalia." Animal Behaviour 65.4 (2003): 795-803.

apocrine glands in the chest area.[18] This would explain various chest rubbing behaviors found among adult NWM.[19] It has been suggested that this sweat gland specialization and distribution is strongly correlated with the gradual evolution of bipedalism in primates.[20]

What accounts for the mechanism in which smell plays a smaller role in the lives of new world monkeys, than, for example, in lemurs and tarsiers? Like the lemurs and tarsiers, but unlike humans, they still have a functional vomeronasal organ and thus two separate ways to smell (nasal and vomeronasal). However, unlike the lemurs and tarsiers, new world monkeys show a decline in the function of the vomeronasal. Where does this change in functionality come from? Is it encoded in and learned via the social group, like the lemur parenting or new world monkey vocalization? No, the current consensus is that mammals' sense of smell is encoded in genes.

In fact, there are more than 1,000 genes that together comprise the Olfactory Receptor (OR) gene superfamily,[21] and this is the largest superfamily of genes in the mammal genome. In humans, this superfamily is so pervasive that clusters of them are found on every chromosome save the 20^{th} and the Y on the 23^{rd}.[22] Together these gene clusters provide the basis for the sense of smell.[23]

The loss of the sense of smell in primates corresponds to a decline in the genetic material in this gene superfamily, much in the same way that copies of analog audio or videotapes contain errors that were not in the original. In humans, approximately 60% of the gene clusters contain errors, called coding disruptions or pseudogenes, and this corresponds to our greatly reduced sense of smell. In Great Apes and Old World Monkeys, there are errors in approximately 30% of the OR genes, and in New World Monkeys, with the one notable exception, about 18.9%.[24]

What is that notable exception? Howler monkeys, the ones whose color vision is very interesting, and that we'll talk more about shortly. Howlers have a relatively high percentage of OR gene errors, at just over 30%.

So here we see a clear line between the rise of one technology innovation – trichromatic vision, and the decline of another, a species' ability and reliance on smell. So, let's now turn to the vision of NWM, including that of the Howler.

<u>Vision:</u>

Primate evolution is not a straight line, and no place is that better represented than in the development of color vision among the NWM. Consider first that the vision of primates (and indeed mammals) is far more rudimentary or degraded than other animals such as birds and reptiles. Other non-mammalian animal species feature more complex lens, musculature, acuity, and can perceive a broader range and diversity of color discrimination. It is likely that the mammalian nocturnal heritage resulted in the loss of many of these characteristics. What they retained was the most fundamental structures necessary for seeing in low level light, such as the rods (detect light from dark) and basic color vision in the shorter wavelengths, which allow dichromatic primates to distinguish blue from yellow, which is helpful in dusk and dawn conditions. This is the vision that early primates like lemurs and the NWM (besides the Howler) retained.

`(Note that when we use the term "color" to apply to color vision, we mean it in the primary sense. Blue, for example, when used in the primary sense refers generally to a reflected light with any wavelength of between 450-495 nanometers (nm). Color is, after all, is just a range in the electromagnetic spectrum that is perceivable to the human eye, and that visible human spectrum ranges from about 380-750 nm, with no discrete boundaries between colors.[25] And these distinctions are fairly arbitrary, as Sir Isaac Newton, who created the naming scheme for the colors taught to most school children, wasn't, in his own word, very good at distinguishing colors. He initially created a palette of 5 primary colors, then upgraded it to 7 (adding orange and indigo) for reasons that are

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[18] Machida, H., E. Perkins, and F. Hu. "The skin of primates. XXXV. The skin of the squirrel monkey (Saimiri sciurea)." American Journal of Physical Anthropology 26.1 (1967): 45-53.
[19] White, Brent C., et al. "Chest-rubbing in captive woolly monkeys (Lagothrix lagotricha)." Primates 41.2 (2000): 185-188.
[20] Folk Jr, G. Edgar, and A. Semken Jr. "The evolution of sweat glands." International journal of biometeorology 35.3 (1991): 180-186.
[21] Glusman et al. 2001; Zozulya et al. 2001; Young and Trask 2002; Zhang and Firestein 2002; Olender et al. 2003).
[22] Glusman et al. 2001; Zozulya et al. 2001
[23] Buck and Axel 1991
[24] Gilad, Yoav, et al. "Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates." PLoS Biol 2.1 (2004): e5.
[25] Thomas J. Bruno, Paris D. N. Svoronos. CRC Handbook of Fundamental Spectroscopic Correlation Charts. CRC Press, 2005.

not completely understood, but rumored to related to mystical reasons, and or consistency with the 7 notes in the musical scale.[26] Within those primary colors are an infinite variety of hues. For now, I don't distinguish between, say, Benjamin Moore's Palladian Blue as distinct from Sherwin Williams Tiffany Blue; these are both just shades within the primary Blue color. The primary colors are red, green, blue, and are those color families which can be mixed to make up virtually an unlimited number of other colors.[27] Also remember – color is not an intrinsic property of something. Color is a function of how it is examined. If you illuminate something, say, for example, by shining a bright white light on an apple, that object, or more properly the surface of that object, has certain intrinsic properties to reflect or absorb energy. In the case of the apple and the white light, many photons would be reflected in the range of 620nm-750nm, so our brains would perceive it as "red". However, if you illuminate an apple with a red light, or a green light, or examine it with something other than a normal human eye, it will appear differently. For now, we'll just simplify the color ranges into simple references to the primary or basic color range categories, with an understanding that in the real world color is something we perceive as a result of a blend of reflected light photons across the electromagnetic spectrum.)

Not all non-Howler New World Monkeys are dichromatic. Also, if you'll excuse the pun, the situation is not as black and white as being di-chromatic or tri-chromatic. Di-chromatic just means that animals can't distinguish the full range of red-green-blue colors that humans typically think of as "color-vision", but within the di-chromatic category there are a number of different variations. To understand that, remember that vision is composed of rods and cones. Rods are best at sensing levels of light, (as well as our mechanism for detecting motion)[28] and are predominant in the nocturnal monochromatic vision of our tarsier cousins and in the eyes of the night monkey. Cones sense color, through variations in visual pigments known as opsin, which is a protein molecule that wraps itself around retinal, which itself derived from vitamin A. Each type of cone contains opsin molecules tuned to just one color wavelength frequency. Different amino acid sequences in the opsin account for this tuning.[29] When photons of that specific wavelength hit the cell, they cause a change in the shape of the retinal, which cause a change in the shape of the opsin, which triggers a chemical reaction that causes the nearby nerve cells to send a signal that the color has been detected.[30]

Cones in the animal kingdom usually come in four different types – two shortwave (ultraviolet and blue) and two medium/long wave (red and green). To see in 3 colors, then, an animal would need rods and at least 3 different types of cones.

Ultraviolet is one of the low light wave colors that at 100nm-400nm is longer than x-rays but shorter than our primary color range "blue" (which would include colors we'd describe as violet, but that does NOT include ultraviolet). Primates, unlike other animals, are not able to perceive ultraviolet, and this is likely one of those characteristics that we lost over time. It is probable that this particular trade-off was made in exchange for increased visual acuity in daylight.[31] However, primates all share the other short wave sensitivity - blues. The genetic encoding for this blue vision is found on chromosome 7.[32] You could consider this capability to be a separate primordial subsystem that we primates all have in common and retained from our pre-nocturnal days.

Each of these discriminations would serve a different evolutionary purpose. So it is fair to say that all primates can distinguish light from dark. Among New World Monkeys, all, except for the nocturnal and monochromatic owl monkey, can see yellow from blue.

The question now becomes - which other colors can they see? Di-chromatic NWM have rods, and cones that can sense blue and one other color. However, they are remarkable in the range of which *__other__* color they can see. This variety is referred to as polymorphic di-chromacy. Simply put, while most NWM can only sense 2

[26] Topper, David. "Newton on the number of colours in the spectrum." Studies in History and Philosophy of Science Part A 21.2 (1990): 269-279.
[27] Shevell, Steven K., ed. The science of color. Elsevier, 2003.
[28] Land, Edwin H. The retinex theory of color vision. Scientific America., 1977.
[29] http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/V/Vision.html
[30] http://www.brainpickings.org/2013/06/13/how-our-vision-works/
[31] Douglas, R. H., and G. Jeffery. "The spectral transmission of ocular media suggests ultraviolet sensitivity is widespread among mammals." Proceedings of the Royal Society B: Biological Sciences 281.1780 (2014): 20132995.
[32] Nathans, J., and D Thomas (1986). "Molecular genetics of human color vision: the genes encoding blue, green and red pigments". Science 232 (4747): 193–203. doi:10.1126/science.2937147. PMID 2937147.

primary colors, which two varies considerably.[33] This is because the medium/long wave cones (reds and greens) in NWM are generated from one particular area on the X chromosome,[34] and this one spot only has room for one color gene. This single gene area can be occupied by 3 or more different gene sequences which are known to be stable and available to this one position within a given population of monkeys.

A small percentage of female NWM are tri-chromatic. To understand those few females, it is key to consider that males, with their XY chromosomes configuration at their 23rd pair, have just the one X chromosome, and thus the one single medium/long gene, and just the one color (in addition to blue which is stored on the 7th chromosome). Females have 2 Xs on their 23rd pair of chromosomes, but since most females are homozygotic (both of their X genes are similar), they are still di-chromatic. However, if the female has different X chromosomes, and is thus heterozygotic, she may have two different medium/long wavelength cones (say a red and a green) on her 23rd chromosome. Together with the blue (on her 7th chromosome) she would now be able to distinguish the three colors – reds, green and blues/violet. Thus the wide range of color vision types in non-howler new world monkeys is enabled not only by different allele combination on the one X chromosome among the di-chromates but also by the trichromatic heterozygotic females.

How is the Howler different? The Howler Monkey, unlike humans and other primate trichromates, has not one but two different sections (specifically two different exon five sequences) on the same X chromosome, allowing them to produce multiple cones sensing different wavelengths.[35]

So what we see in New World Monkeys is the emergence of color vision in a range of forms, and through a variety of different mechanisms, from monochromatic, to dichromatic to trichromatic. Even among the dichromates, within the same species and family you can have individuals that see six different ways.[36] And fully expressed tri-chromatic color vision, as in the Howler monkey, has a different blueprint than that which eventually evolved separately in later primates. Thus, New World Monkeys represents an intermediate stage of color vision, not fully mature, in a variety of contemporary "prototypes". One could describe the state of color vision across these American Monkeys as a stable polymorphism, or cross-section of animal innovation in action.

Now that we've discussed the how, let's talk about why – why is this such an important advancement? . A typical discussion for this variability goes like this:

> *"Why would good colour vision be so important that trichromacy evolved independently in New and Old World monkeys? A favoured suggestion is that it has to do with eating fruit. In a predominantly green forest, fruits stand out by their colours. This, in turn, is probably no accident. Fruits have probably evolved bright colours to attract frugivores, such as monkeys, who play the vital role of spreading and manuring their seeds. Trichromatic vision also assists in the detection of younger, more succulent leaves (often pale green, sometimes even red), against a background of darker green — but that is presumably not to the advantage of the plants."*

Dawkins explanation comes right out of a school of thought known as the "angiosperm radiation hypothesis." First proposed by Robert Sussman, this hypothesis makes the case that the central driving force of primate evolution was the co-evolution of flowering plants with color vision in animals like monkeys.[37] Color vision by itself is not an advantage in a world full of multi-hued greens. As flowers developed, an ecosystem developed around them, including primates, bats, and those birds that feed off of plants, who spread the seeds of the fruit that accompanied the flowers. In this hypothesis, primate traits were shaped by the drive of the earliest primates to reach food that grew on the ends of branches—flowers, fruits, and the insects feeding off of the vegetation. Sussman contends that primates operating in low light conditions needed enhanced visual and manipulation skills. This co-evolution is thought to have occurred between the Paleocene era (65.5 mya to 60 mya) and the Eocene (60 mya to 34 mya).

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[33] Mollon, J. D., J. K. Bowmaker, and G. H. Jacobs. "Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments." Proceedings of the Royal society of London. Series B. Biological sciences 222.1228 (1984): 373-399.
[34] Jacobs, Gerald H., et al. "New World monkeys." Nature 382 (1996): 11.
[35] Jacobs, Gerald H., et al. "New World monkeys." Nature 382 (1996): 11.
[36] http://news.nationalgeographic.com/news/2003/11/1125_031126_tvmonkeyvision.html
[37] 5. Robert W. Sussman, "Primate origins and the evolution of angiosperms" in American Journal of Primatology, Vol. 23, 1991. Article first published online 2 May 2005; Conroy, pp. 41-43 and Sussman, Robert W., D. Tab Rasmussen, and Peter H. Raven. "Rethinking primate origins again." American Journal of Primatology 75.2 (2013): 95-106.

This theory competes with two other older theories trying to explain color vision. The first speculated that primate evolution was driven by visual predation (picture the tarsier and new world monkeys needing novel sight innovations to improve their hunting). The second, called the arboreal hypothesis, contended that life in the trees was responsible for the changes in primate adaptions. This second one placed a good deal of weight on the decline of smell (dominant in a terrestrial environment) and the increase in visual changes (such as more forward-looking stereoscopic eyes and the introduction of color vision) and changes in musculature (such as prehensile tail and the semi-brachiated tree swinging).

One final note on these visual innovations comes again from Dawkins – he points out that innovations in and of themselves are useless if an organism doesn't adapt to use it. As he puts it,

> *"I have talked as though the acquisition, by mutation, of a new opsin automatically confers enhanced colour vision. But of course differences between the colour-sensitivities of cones are no earthly use unless the brain has some means of knowing which kind of cone is sending it messages. If it were achieved by genetic hard wiring —this brain cell is hooked up to a red cone, that nerve cell is hooked up to a green cone — the system would work, but it couldn't cope with mutations in the retina.*
>
> *How could it? How could brain cells be expected to 'know' that a new opsin, sensitive to a different colour, has suddenly become available and that a particular set of cones, in the huge population of cones in the retina, have turned on the gene for making the new opsin?*
>
> *It seems that the only plausible answer is that the brain learns. Presumably it compares the firing rates that originate in the population of cone cells in the retina and "notices' that one sub-population of cells fires strongly when tomatoes and strawberries are seen; another sub-population when looking at the sky; another when looking at grass.*

To understand how this statement will be relevant to us later, picture the soldier returning home from war with a missing arm, trying on a new carbon fiber prosthetic. Though the arm has a hand that can fully articulate, complete with sophisticated electronics and sensors, it takes a while for that soldier to train the various remaining muscles in his arm, chest and other parts of his body, to learn how to activate and control the arm effectively. This learning is unique to each individual, based on their unique musculature, bone structure, scar tissue and innervation, and I'd say that this education process is not unlike the process by which the body begins to sense and adapt to new capabilities it didn't evolve around, such as a novel perception of color. Yes, the former occurs mid-life, and the latter occurs from birth, but I think, given the lack of other exemplars to inform how an organism adapts its cognition to innovative new sensory and motor capabilities, that the precedent here is worth us noting for later use.

So, speaking of humans, why are we spending so much time talking about monkey vision, and how are these genetic and other factors affecting the emergence of color vision, millions of years ago, relevant to our questions about how the co-evolution of technology and cognition of the past inform modern human interactions with technology today?

As we hinted about in the prosthetic arm example, it's not about color vision at all, but about cognition. Human brains are dominated by visual input,[38] and color vision is arguably one of the most defining attributes of this sense. Looking at how this attribute first evolved in primates gives us the chance to see how an innovation manifests through various pre-cursors and in various forms. It also allows us to examine the alternate theories regarding how color vision co-evolved with our environment and our adaptions to it, over millions of years.

Yes, going from being able to see two primary color families to three is an exponential jump, since a dichromatic organism might perceive something like 10,000 separate individual colors (presumably including both Palladian Blue as well as Tiffany Blue), and a trichromate perhaps a million. This material is not setting us up for another exponential step forward, however. Tetrachromacy – the presence of four different cones in one individual, and therefore the ability to something on the order of 99 million colors, is already said to exist in humans, albeit extremely rare. No, we are discussing something much bigger than the next stage in the evolution of color vision. The visual changes facing the human species now and in the near future are far larger than jumps between di-, tri- and tetra-chromacy. And we are going to go through them in decades, not in millions or 10s of millions of years.

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[38] McBride, Dennis K. "The quantification of human information processing." Quantifying human information processing (2005): p 33

How so? Picture a fighter pilot flying along in a modern jet fighter, say the new F-35 Joint Strike Fighter. As she looks ahead and sees the real world through her windshield in normal full natural color, inside her visor has a digital display of all of the information she needs to accomplish her mission – speed, heading, height, targets, warnings, etc. As her eyes move from her windshield down towards her feet, she "sees" through the plane, as feeds from various cameras around the plane now display on her visor, giving her the ability to see under, all around and through the plane.[39] And this vision isn't just ordinary light and standard color wavelengths; she can toggle infrared or night vision, and ostensibly upgrade or change out those cameras to see in any other necessary frequency in the electromagnetic spectrum.

OK, what does this have to do with color-vision in monkeys?

I think we can all agree that the $400,000 Rockwell Collins Gen III augmented reality capabilities I just described are a quantum leap forward over having two, three or even four kinds of cones in our eyes.[40] Is it a fantastic over-reach, then, to consider this technology innovation as having the potential for broad impact on cognition of the ordinary human brain? I don't think it's too radical an example at all.

Consider radar. In World War II, the US spent $17,756 in 1943 (about $240,000 in today's money) to install the SCS-520 airborne radar on some of its aircraft.[41] Like the Rockwell Collins helmet, the SCS-520 radar was state of the art, ultra-top secret technology, and expensive. Within 10 years, however, this radar technology was used in the civilian sector to heat food in commercial settings; in 20 years it was available for use in homes across America; this technology, known as a RadarRange when it first came out, is today's ubiquitous microwave oven.

Later, we'll discuss how we don't have to wait 20 years to begin to see huge innovations in how we literally 'see the world'. Today, hundreds of millions of Americans use their smartphones to navigate using realtime GPS maps, complete with "streetview"; millions of others use their smartphones cameras and displays to overlay the names of constellations in the sky (Star Chart), or find out the names of people standing around them (NameTag),[42] play augmented reality games like Pokemon Go,[43] translate printed words,[44] or arrange 'hookups'.[45] Looking just slightly forward, we see that Land Rover has already demonstrated a "see-through" hood in its concept car,[46] Continental has announced availability of Augmented Reality Heads Up Displays for cars starting 2017,[47] and companies like Magic Leap challenge our imagination by blending the real and virtual world.[48]

When we get to those technologies, I'll make the case that they are examples of polymorphisms; multiple technologies attempting to break into or take advantage of the same environmental niche or opportunity, using different tactics. The classic precedent for that argument is set here, as numerous species of New World Monkeys attempt to varying degrees of success to develop color vision, thousands of miles from and millions of years earlier than the color vision that eventually evolves completely independently in Old World Monkeys and the later primates (including us) on the African continent. In its own way, Google Glass is a bit like that heterozygotic female capuchin monkey that somehow puts together the right mix of alleles to distinguish between red, green and blue. It works, but if it doesn't offer significant environmental advantages, and/or the surrounding social system doesn't develop around it enough to lock it in, it will come and go. Here we set the stage for that conversation by laying the historical, evolutionary and conceptual framework.

What – you think that a better product will always beat out an inferior pre-cursor? Without bringing up Betamax and VHS, it is useful to remind readers that the QWERTY keyboard is the default standard in the US because it was optimized for preventing jamming in early typewriter designs (by forcing people to type slower), not

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[39]https://www.rockwellcollins.com/~/media/Files/Unsecure/Products/Product%20Brochures/Displays/Soldier%20Displays/F-35%20Gen%20III%20Helmet%20data%20sheet.aspx
[40] http://www.washingtonpost.com/news/checkpoint/wp/2015/04/01/meet-the-most-fascinating-part-of-the-f-35-the-400000-helmet/
[41] http://www.ibiblio.org/hyperwar/USN/ref/NightFighterRadars/index.html
[42] http://www.cnet.com/news/facial-recognition-app-matches-strangers-to-online-profiles/
[43] http://www.dailymail.co.uk/sciencetech/article-3063974/Be-AR-fraid-afraid-Augmented-reality-game-turns-home-horror-story-zombies-demons-stalk-you.html
[44] http://en.wikipedia.org/wiki/Word_Lens
[45] https://play.google.com/store/apps/details?id=com.singlesaroundme.android&hl=en
[46] http://www.landroverusa.com/our-story/news/virtual-imaging.html
[47] http://www.pcmag.com/article2/0,2817,2461037,00.asp
[48] http://www.engadget.com/2015/02/25/magic-leap-explainer/

because it was the fastest most comfortable typing pattern.[49] When jamming was no longer an issue, faster typing patterns were proposed by Dvorak and others, but they faced an impossibly uphill battle changing the lock-in of QWERTY.[50]

So to wrap up our discussion of vision, NWM exhibit an intermediate transitional stage between earlier primates' reliance on smell, and the later primates' reliance on vision. As a result of the increased role of vision, the brains of these animals are physically different from earlier animals, as the visual cortex increased in size,[51] and olfactory bulb and related brain morphology is noticeably reduced.[52] The enhanced vision lead to better and more differentiated diet, which lead to even greater opportunities for encephalization and ecological niche stability. Before we can conclude our NWM visit by discussing EQ, we still have a few more factors to consider from our cognitive factors checklist, and we find that the NWM has even more insights to offer us.

Tool use

Tool use is still considered by many people to be that distinguishing characteristic of human intelligence. Usually, that kind of statement provokes a response that includes references to otters who use stones to cracks open clams, chimpanzees and crows who use sticks to extract insects, and even dolphins who use sea sponges to protect their sensitive snouts.[53] A classic popular reference that also comes up is the "organ grinder monkey", such as Dexter, the monkey in *Night at the Museum*, where he (actually a she, as Dexter is played by a 21-year-old monkey by the name of Crystal) can apparently manipulate keys to open locks, use cell phones or work a remote control. This monkey is a capuchin monkey, and is a New World Monkey.

The "organ grinder" name refers to a common use of capuchins as a trained pet/assistant for itinerant street musicians who played barrel organs. In addition to being a simple draw or additional attraction, these monkeys were often trained to hold cups and work the crowd for money. Capuchins have even been trained as human assistants for disabled people, there being a distinct slow-down in the organ grinder trade these days.

Despite trained feats like these well-known tricks, and the observations of tool use done in captivity or under more clinical and research conditions, no capuchins or other NWM has ever been observed using tools in the wild, other than the occasional use of a rock to break open a nut.[54] So it's fair that say that the capuchin, widely regarded as the most intelligent of the NWM, has the potential to learn how to use tools, but only with significant training by humans. One reason that tool use may not be adopted and passed on within wild monkey populations is the lack of imitation. Basically, the old proverb, "monkey see, monkey do" does not hold up in the research,[55] and this is relevant to our discussion on cognition.

The basis of imitation in the animal kingdom seems to lie in a relatively recently discovered type of neuron called a "mirror neuron". This neuron fires during voluntary motor control. It also fires in the same way when you see someone doing the same motor activity. Research continues to develop around how this works exactly, and the implications for this, but in the meantime, there is strong evidence that mirror neurons are one of the main ways that humans come to understand and imitate (learn) to perform actions.[56] How? Every time an animal sees an action done, its mirror neurons fire, stimulating connections in the observer's prefrontal cortex, in areas that corresponds and connect to areas stimulated when the observers themselves performs this action. This bridges information from direct experience into observed experience, creating knowledge and understanding.[57] These neurons have been

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[49] Arthur, W. Brian. "Competing technologies, increasing returns, and lock-in by historical events." The economic journal (1989): 116-131.
[50] http://www.howtogeek.com/189270/alternative-keyboard-layouts-explained-dvorak-colemak-and-whether-you-should-care/
[51] Kaas, Jon H., ed. Evolutionary neuroscience. Academic Press, 2009, p 807-809
[52] Meisami, Esmail, and Kunwar P. Bhatnagar. "Structure and diversity in mammalian accessory olfactory bulb." Microscopy research and technique 43.6 (1998): 476-499.
[53] http://www.theatlantic.com/technology/archive/2014/04/these-genius-dolphins-are-using-sea-sponges-as-tools/361168/
[54] elizabetta visalberghi and Ottoni 2005
[55] Visalberghi, E., and D. Fragaszy. "Do monkeys ape? Ten years after. Imitation in Animals and Artifacts, K Dautenhahn, C Nehaniv." (2001). P 471-496
[56] (see Rizzolatti et al. 2001).
[57] Rizzolatti et al. 2001)."

widely found in the human nervous system, and to a lesser extent in apes, and to an even lesser extent in OWM.[58] But, it appears that our friend the NWM have even less mirror neurons.

So, assuming new actions (novelty) occurs from time to time among NWM, one reason that it does not diffuse may simply be that neurological basis for imitating other NWM isn't as developed. We can test that theory out as we move into OWM, apes and humans who show more advanced mirror neuron systems. Since we know there is compelling evidence on the lack of motor neurons in NWM, and we see exhaustive work trying – and failing- to show learning through imitation within NWM, the mirror neurons provide us with a critical area for further inquiry as we look into the cognitive processes of later primates.[59]

Of course, imitation isn't the only way to learn among animals. It's most useful for learning new procedural tasks or movements when the opportunities for practice are low, or when the costs of error are high. Tool use certainly meets these criteria in most cases, so if imitation is not available, that would be a blow to the diffusion of tool use in the natural world. Social learning, however, is another powerful force influencing how animals behave. If capuchins are smart, and can be taught how to do complicated things, why don't we see populations, even if they lack imitative traits, using social learning to pass on behaviorally adaptions between members?

After all, as the leading researcher on capuchins says,

> *"If prevalence of learning is related to potential opportunities for, and benefit of, learning socially, if manipulative propensity is indicative of an underlying cognitive sophistication, and/or if learning abilities are modular in some sense, one could reasonably predict that capuchins should possess stronger social learning propensities than other primate species that do no display equivalent tolerance, interest in each others' activities and innovations in manual activities."*

But they don't. Yes, there are a few instances where monkeys in captivity will learn to use a door from others who do it better, and others will copy that one, and so on.[60] And observations of animals in the wild who were more likely to watch the individuals who were most proficient at getting food.[61] These instances represent the potential for cultural transmission, but the NWM only do this rarely.

Why? Well, it turns out that while capuchins are pretty smart in some areas, they lack certain areas that leading human educational researchers like Piaget say are pre-requisites from effective learning from others, including attentional, memory and conceptual capacities, which we'll talk about shortly.

The good news for NWMs is that their cultural style is conducive to learning. Dutch primatologist Carel van Schaik has argued that social tolerance is a prerequisite for socially-transmitted tool use. He points out that you can't learn from other animals if you aren't close to them, and you can't get close to them if you are afraid of them. Tool use is more commonly observed in primate societies which are "laid back," and dominant individuals are more tolerant of subordinates, and reconciliation occurs after conflicts, and juveniles are allowed to get close and observe what they are doing.[62]

Understanding that NWM are smart enough to learn tools, and are culturally oriented to pass along the lessons of tool use, but ultimately lack the ability to influence each other's ability to learn tools, let's look closer at their social structure.

<u>Social structure/Parenting/Rearing/learning/cultural factors</u>

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[58] (see Byrne 1995, Galef 1988, Tomasello & Call 1997, Visalberghi & Fragaszy 2001, Whiten & Ham 1992, Ferrari, Pier Francesco, et al. "Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex." European Journal of Neuroscience 17.8 (2003): 1703-1714.
[59] Visalberghi, Elisabetta, and Dorothy Fragaszy. "f 8" Do Monkeys Ape?"-Ten Years After." Imitation in Animals and Artifacts (2002): 471.
[60] Dindo et al 2007
[61] Ottoni 2005
[62] van Schaik et al 1999

NWM social structures are typically described as fission/fusion organization. Multiple animals are closely bonded in small groups, which are less strongly bonded to other small groups to form a large tribe. In these groups, the members regularly engage in grooming, play and other prosocial activities. NWM like capuchins are known to share food,[63] and usually engage in a more cooperative style than will be seen among the more aggressive OWMs like baboons.

Like the tarsier, but unlike most Old World Monkeys, some New World Monkeys form monogamous pair bonds. Since monogamy is not the common reproductive pattern in primates (and indeed is found in less than 20% of mammal species), but is common to both our advanced human societies and NWM, this is probably a good time to review the theories behind monogamy. Why? Monogamy is correlated to extended childhood, and extended childhood is correlated to advanced human cognition. Understanding the factors that bring about the social innovation of monogamy can help to us to understand the underlying prerequisite conditions for current and future cognition.

Monogamous bonds tend to form in response to some of the same factors that affect sexual dimorphism, which we discussed in the last chapter. This includes non-economic gender-specific factors, such as parental investments, as well as economic factors, including resource availability such as access to food, mate selection, and territory.

Primate females typically feature longer gestation and lactation periods (also correlated to increased intelligence) during which they are not able to reproduce. Males in a monogamous relationship, therefore, can't increase their chances of reproductive success by having more offspring. The two male strategies that would co-evolve with longer gestation and lactation would then be to either a) seek more mates for more offspring, or b) increase their own parental investment to increase the odds that their existing offspring live long enough to reproduce.[64]

Primates pursuing 'option a' become polygamous, and the male seeks more mates. Social structures where this occurs feature competition and sexual selection pressure, and less male parental involvement.[65]

The strategy that prevails in a given species can be a function of distribution of resources. Primates, and thus females, are more likely to live where there is plenty of food. Females tend to congregate (as opposed to disperse and spread out) when there are advantages to do so, such as group detection of predators, and/or around a resource supply when resources are scarce elsewhere. Environments in which females are congregated in close physical proximity are more conducive to polygyny, assuming the male can defend his females. This defense is done either by controlling access to the females directly (physically driving away males who attempt to mate with a member of his harem), or by controlling them indirectly by controlling the critical resources through territoriality (driving all males away from his territory). The measurement of an environment's concentration of food and females has been referred to as Environmental Polygamy Potential, or EPP for short). It's worth noting that when highly prized resources like food, water and shelter are highly clumped, in that they are abundant in certain small areas and not abundant elsewhere, then individuals tend to clump, and a small percentage of the species population has a chance to have a large genetic effect on the future of the species. If resources are fairly abundant over a wide distribution, and there is a lack of predatory pressure or group defense to predators, then individuals disperse, and the likelihood of having and successfully defending multiple mates goes down.

However, close proximity can work both ways on polygyny - if the females synchronize their estrus cycles (which some species will do when in close physical proximity) and thus come into sexual receptivity at the same time, it is harder for one male to defend multiple females and successfully maintain this genetic strategy.

So, females go where the food is, and males go where the females are. This is a good rule of thumb not just for Ladies Night at your corner pub, for situations when primate male parental investment is relatively small. Social structure and ecology interact further to create situations where males defend access to their harem by keeping other males away (harem or territory defense), or live communally in larger groups (often due to resources, predator defense and/or other social characteristics), and defend their rights to mate through dominance rituals.

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[63] Burkart and van Schaik 2012; Sabbatini et al 2012

[64] J Theor Biol. 1983 Sep 7;104(1):93-112. The evolution of monogamy in primates. Rutberg AT.

[65] Emlen, Stephen T., and Lewis W. Oring. "Ecology, sexual selection, and the evolution of mating systems." Science 197.4300 (1977): 215-223.

Thus, two conditions are usually met in polygamous social structures: first -it's economically feasible for a male to defend multiple females, and second – males can capitalize on having access to multiple females by minimizing their resource investment in parenting. It's not enough to have many babies, if they all starve or die from predation.

This contrasts sharply, then with the characteristics of monogamous species, which according to Devra Kleiman of the Smithsonian, tend to arise where there are limited mating opportunities, male investment in the offspring is high, and there is high confidence in paternity. Interestingly, he also notes that monogamy is often associated with low mating frequency, so these social structures are not maintained by purely by sexual attraction.[66] In these situations, there is also often less sexual dimorphism, as we discussed in the last chapter.[67]

Note that so far, we have focused on the male of a species. In fact, many biologists tend to agree that for a male, all other things being equal, a polygynous strategy is the most effective one. Reversing this, one could examine female strategies. After all, they will need to innovate either to develop rearing strategies in the absence of a male, or come up with tactics for securing the male to perform the parental duties.[68] Several strategies develop in the first case, and in non-monogamous primates the most common one is allo-rearing, where the females of a group share in mothering tasks. Strategies for engaging the male into parenting (which also maximize females chance of reproducing her own genes) include social dispersion and anti-social behavior towards other females (making it more difficult for a male to defend multiple females due to the energy costs associated with larger territories) as well as by having offspring that require more food and care, such as larger children, or multiple offspring at once, whose rearing is so resource intensive that it requires male parental involvement, and thus makes it uneconomical for the male to have multiple young from different females at the same time.

So, how do these factors play out in our NWM? Several smaller monkeys, notably the titi, night and the golden lion tamarin are monogamous. Their social structures typically feature much smaller family units of 2-11, with an average of 5 members.[69] Like most animal populations, to avoid inbreeding NWM have mobility between families. Characteristically, each species will have gender-specific mobility, where either the males or the females leave their home family. NWM species vary, but in most species, it is often the female that leaves, and the males that are known to stay.[70] The tendency for an animal (of either gender) to stay in the area they were born and raised is referred to as "philopatry." Social structures are influenced by the gender that is philopatric; in the case of NWM, since most females tend to live most of their reproductive life in troops with unrelated females, their social structures tend to have weaker female-female bonds and less tolerance than is found in OWM, which feature more female philopatry.[71] Gestation is typically about five months, and the 1-2 offspring in each litter, and children that are precocious, in that they are relatively large, fully furred, and able to move around on their own. Typically, the dominant male and female breed, and the reproductive drive in the subordinate adults is suppressed, thought to be done by smell and hormonal mechanisms. Often these pairings are for life. During a long-term study of multiple families of monogamous night monkeys, most pairings stayed intact for the life of the animals. Those existing pairs that were "disrupted" by "floaters" (unattached males that pursue a female already in an existing relationship), often resulted in the eventual death of the exiled male, and a lower level of offspring by the new couples.[72]

NMW offspring are weaned within about five months, and these smaller new world monkey species display cooperative rearing, where all of the adults contribute to raising the young. This behavior is uncommon in primates. These monkeys become sexually mature at 15-20 months, but due to social structure may not actually reproduce until 30 months.[73]

Of course, not all NWM are monogamous. Group size and behavior vary by species, ranging in size from squirrel monkey large groups of up to 500 down to night monkeys' small nuclear family units. Among the larger-bodied NWM, such as the wooly spider and the howlers, animals generally live in larger groups of 10-25 members, and within these groups, the females do the majority of the parenting. Mating tends to be polygamous, with one

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[66] Kleiman, Devra G. "Monogamy in mammals." Quarterly Review of Biology (1977): 39-69.
[67] Kleiman, Devra G. "Monogamy in mammals." Quarterly Review of Biology (1977): 39-69.
and twinning." Animal Behaviour 50.4 (1995): 1057-1070.
[69] Dietz & Baker 1993
[70] Strier, 1994, Strier 2000
[71] Strier, 1999, Di Fiore and Campbell 2007
[72] http://news.nationalgeographic.com/news/2013/02/130213-valentines-day-owl-monkeys-animals-love-science/
[73] (Kleiman et al. 1988.

dominant male defending access to a harem of 2-4 females while they are sexually receptive. Gestation is 6-8 months, and births, usually of single offspring, can be three years apart.

In between are capuchins (the organ grinder monkeys), whose adult size is 3-9 pounds, and group size is 10-20, with an equal split in genders. These monkeys typically exhibit pure polygamy, with adult males engaging in sexual activity with all of the adult females, and vice versa. The other interesting aspect of their reproduction is that courtship in capuchins is initiated by females. Pregnancies occur during the dry season, last 5-6 months. Offspring are born singly, weigh only about 7 ounces, and are dependent on their mother for food for the first two months of life. Parenting is done exclusively by the mother for the few weeks of life, in which they child does not normally move around independent of the mother (not precocious); after the first few weeks the group collaborates in allorearing.

How do social innovations such as allorearing benefit the group? When a father and other group members help to parent, they do things like carry the infant. If a group invests shared energy in carrying infants, the troop is more mobile, and thus has greater ability to adapt to changes in climate and food ability. Therefore, one could say that the increase in monogamy and increase in parental investments by the males gives the troop advantages not available to say, prosimians such as lemurs who do not often carry the young.[74] Later we'll talk about how human hunter-gatherers typically have fewer children, because of the challenges in moving them, and agricultural societies, which don't move, have more.

Certain other behavioral characteristics might also develop alongside allorearing that could lead to increased cognitive performances in certain situations. For example, callitrichids, a NWM species which is allo-reared, performs significantly better on socio-cognitive skills than other NWM who are reared independently, or with less allorearing. Specifically, alloreared species have much higher attentional bias towards monitoring others, and ability to coordinate with others across space and time, increased social tolerance, increased responsiveness to others' signals, and are much more likely to be spontaneously prosocial. In tasks that require these skills, then certain NWM may outperform other species, though there is not necessarily an increase in executive function or increase in other areas of cognitive awareness.[75] Hopefully, the reader will see the connections between these factors and the modern American trend of dual-income households, supported by day-care, and the cognitive implications of attentional biases and executive function.

So, there are two hypotheses or conditions associated with animal monogamy: the economics of food, territory and females makes it impossible to efficiently manage multiple females, or greater parental involvement conveys significant advantage to the gene pool. Which is it for our New World Monkeys? It appears that they exhibit monogamy not so much because of food scarcity and distribution of available females, but because male parental investment provides significant advantages to the gene pool, giving them greater care to a slower maturing offspring, while still allowing the group to maximize mobility and resilience.

One last note on monogamy – monogamy presumes the obvious: males and females coming together for sex. I think it bears considering that this is but one genetic "strategy", and that monogamy is a reproductive strategy nested within a sexual reproductive strategy. We should not just accept that as a given until we've briefly considered the alternatives.

The options for asexually continuing your genes include a) not dying, b) cloning oneself with little or no genetic change, and c) reproducing in such a way that genetic material is refreshed or changed around in some ways that don't include sex.

Not dying is, in fact, a strategy in nature, albeit that success is extremely rare. In the future section of this book, we will examine the prospects for greatly extending human life. However, for now, long life in the terrestrial animal world equates to 100-200 years, something some humans and tortoises have been known to do. As a life, that's pretty good, but as a stand-alone genetic strategy it has some shortcomings. In the aquatic world these feats are reached by some whales and sharks, but is minor in comparison to the arctic crustaceans who have lived up to 500 years.[76] Individual trees of course, can live a long time. It's quite common to find trees several hundred years

[74] J Theor Biol. 1983 Sep 7;104(1):93-112. The evolution of monogamy in primates. Rutberg AT.
[75] Burkart, Judith Maria, and Carel P. van Schaik. "Cognitive consequences of cooperative breeding in primates?." Animal cognition 13.1 (2010): 1-19. (?)
[76] http://www.usatoday.com/story/tech/2013/11/15/newser-worlds-oldest-animal/3574863/

old, with species of pines, junipers, redwoods and sequoias having members living over 1,000 years, and several individual specimens of bristlecone pines are reported to be at or near 5,000 years old.

Here we will briefly point out that living a long time, if it is measured in hundreds of years, or even a thousand years, pales in comparison to genetic lines that are millions or 10s of millions of years old. Of course, developing an ability to live a long time doesn't mean you are immortal, it simply means you've developed some defenses against senescence - the deterioration that usually comes with aging. Individuals which have developed anti-senescence capabilities may still die from a whole host of traditional causes, such as being physically destroyed by fire or being eaten. Typically, long life tactics include innovations against cellular damage traditionally associated with chronological aging, wherein DNA damage prevents further replication. Only two species on earth may have solved this. The first is the Turritopsis nutricula, a very small jellyfish, which essentially replenishes its cells, and, after it becomes sexually mature, can revert back into its immature stage through cell transdifferentiation.[77] Theoretically, this animal could live forever, if it is not eaten or otherwise destroyed (would a stake through its heart work, or am I mixing that up with something else?). The second species is the Hydra.a small fresh water organism which may have evolved the ability to have its cells replenish themselves.[78]

Given those unique exceptions then, and withholding any discussion on the prospects of greatly extended human life, we turn to asexual reproduction, such as cloning. Here we see greater prospects for genetic furtherance. In trees, for example, we go from the thousands of years to the tens of thousands, as evidenced by a colony of Aspen trees in Canada that are reportedly 80,000 years old, whose life is maintained through a process of self-cloning. Dozens of other species have been documented as being able to reproduce asexually, including Komodo dragons and hammerhead sharks. Females from both of these species can reproduce in the absence of any mates whatsoever.

The problem with cloning strategies are, that the more they reproduce asexually, the less able they are to reproduce sexually. The 80,000-year-old aspen grove is a great example: they've evolved so specifically, that they are very poor at reproducing sexually, and thus their genetic makeup rarely changes. Why is that important?

It turns out that a constantly changing gene pool is one of the key determinants of survivable. One reason? The static gene pool is not static, since mutations tend to build up and erode fitness.[79] Also, while the gene pool of a cloning species is relatively dormant, its environment isn't, and predators and competitors will be evolving to exploit characteristics of a species that doesn't evolve.

Again, there is a known rare exception to the gene pool stagnation which occurs through asexual "cloning" strategies- a few species of whiptail lizard in which the males have become extinct. How do they cope with the problem above? They evolved a duplicate set of chromosomes in each cell, and develop genetic diversity by exchanging chromosomes in each generation. This recombinatorial process provides a genetic diversity that so far has allowed the species to continue on with robust genetic diversity, in the absence of males.

Horizontal Gene Transfer(HGT) is left off this list, because it is not yet very well understood. But since future research might come out that determines it is a factor, let's review it. HGT is the process by which you absorb DNA from the species living around you, rather than from your ancestors.[80] Yep, that happens. Yep, it happens in humans. This alternative mechanism for gene transfer is well studied in simple single-celled organisms, but was doubted in more complex organisms like humans. Alistair Crisp and colleagues performed detailed analyses of the genomes of 26 animal species, 10 of which were primates (including humans), and compared gene sequences between related species to find sequences which did not develop and pass down from common ancestors.[81] They identified 145 human genes that originated outside of the traditional ancestral mechanism that we know as traditional evolution. These genes include 17 that were identified when the human genome was sequenced, plus 128 new ones.[82] And these are not just garbage or dormant genes; many of them are operational; in fact, foreign HGT-acquired genes are more likely to be operational than traditionally acquired genes. Their specific function, like most human genes, are not exactly known, but they've been shown to influence enzyme production in various processes such as immune

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[77] Piraino, Stefano, et al. "Reversing the life cycle: medusae transforming into polyps and cell transdifferentiation in Turritopsis nutricula (Cnidaria, Hydrozoa)." Biological Bulletin (1996): 302-312.
[78] https://www.sciencedirect.com/science/article/pii/S0531556597001137
[79] http://news.discovery.com/earth/cloning-aspens-natural-selection.htm
[80] Syvanen, M. "Horizontal gene transfer: evidence and possible consequences." Annual review of genetics 28.1 (1994): 237-261.
[81] Crisp, Alastair, et al. "Expression of multiple horizontally acquired genes is a hallmark of both vertebrate and invertebrate genomes." Genome biology 16.1 (2015): 50.
[82] Crisp et al, p 5

system, metabolism, anti-microbial responses. Where do these genes come from? About half of the foreign genes in human DNA come from bacteria and protists, and the other half come from fungi and viruses. In humans, much of this HGT appears to have happened millions of years ago, in some last common ancestor to primates, long before the K-Pg barrier and our lemurs, but has been shown to be an ongoing activity in many other species at a slow and steady pace. The question that always comes up with HGT is- how does it happen? We still don't know, but in most of the cases the standard mechanism for gene transfer in bacteria seems to account for the HGT we see in other species: DNA transformation (uptake of free DNA in solution), plasmid-mediated transfer (conjugation), and bacterial virus–mediated transfer (phage transduction).[83] But there is evidence that other mechanisms like introgression, involved in the process of pollination of plants, has occurred in the animal kingdom as well, such as among species of ducks[84] and between humans and Neanderthals.[85]

But in humans this process may just be an ancient part of our ancestors, or perhaps an ongoing process that moves very slowly, and with a low impact on each generation. What's clear is that it exists, it has affected humans, but it is poorly understood. Therefore, we note it here as an appreciable but not significant force for asexual reproductive genetic diversification.

Which brings us back to sexual reproduction. If the four prior strategies above are so poor or so rarely effectively pursued, what advantages does sexual reproduction bestow? It turns out that the sexual selection process itself provides an evolving influence not only on the fitness of a species, but also gives the genetic pool chances to refresh and adapt to changing environments.

This is illustrated recently in a study of flour beetles, of all things. After seven years and fifty generations scientists compared the resilience of fitness of generations where males had to compete intensely with 10 other males for females against populations where monogamous pairing was done. Their findings? The populations where competition existed were far more fit and more resilient to inbreeding.[86] This effect provides a robust effect separate from the generally accepted "survival of the fittest," which is generally accepted to mean the adaptions of and competitions between *new* characteristics, and the fitness of those characteristics to a given environment.

So, males exist to promote genetic diversity, and when males compete for females, this benefit is even greater. Yet monogamy poses certain cognitive advantages to a species. As species evolve and adapt to changing environments, we'll see these forces express themselves in various ways (innovations) to achieve lasting effect on the human cognitive ability and thus gene pool. Some of these ways are rapidly evolving in the modern era, driven by new technologies.

<u>EQ</u>

So, how do the New World Monkeys score on encephelisation quotient (EQ), as a result of all of these various biological and behavioral traits?

Like body weight and mating styles, there is significant variation among NWM EQ, but as a whole, they average a very respectable 1.8, ranging from the tamarins at about 1.3 and up to the "brightest"- capuchins which score at 2.8.[87] And Executive Brain Ratio? It jumps up significantly over the prosimians, ranging from 7-23. Interestingly, the highest EBRs were for the spider monkey (23), with the vaunted capuchin coming in at about 17.[88]

Of course, EQ is a gross measure and is the only measure that can be used for extinct species. For extant species like our NWM, we can examine other specialized aspects of cognitive development.

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[83] Syvanen, Michael. "Evolutionary implications of horizontal gene transfer." Annual review of genetics 46 (2012): 341-358.
[84] Kraus RH, Kerstens HH, van Hooft P, Megens HJ, Elmberg J, et al. 2012. Widespread horizontal genomic exchange does not erode species barriers among sympatric ducks. BMC Evol. Biol. 2:45
[85] Currat M, Excoffier L. 2011. Strong reproductive isolation between humans and Neanderthals inferred from observed patterns of introgression. Proc. Natl. Acad. Sci. USA 108:15129–34
[86] Lumley, Alyson J., et al. "Sexual selection protects against extinction." Nature (2015).
[87] Relative Brain Size, Gut Size, and Evolution in New World Monkeys, Walter Hartwig1,*, Alfred L. Rosenberger2,3,4,5, Marilyn A. Norconk6 andMarcus Young Owl, Article first published online: 1 NOV 2011 DOI: 10.1002/ar.21515 http://onlinelibrary.wiley.com/doi/10.1002/ar.21515/full
[88] Reader and Laland, 2003, p 104-105

One such aspect of specialized development we can see in NWM is the beginning in a preference for which hand they use to manipulate things. This preference is a key part of the specialization that comes with more specialized tasks.[89]

Prosimians offer only a limited amount of hand specialization. Most individuals show some occasional preference in use for one hand over another, but this preference is incomplete, in that they don't use that hand exclusively. In those animals that do show stronger preferences for one hand over another, the weighting is split between left and right, with slightly more showing a preference for left.[90]

New World Monkeys, owing in part to the wide range of animals in the family, again display a range of manual lateral specializations. Like the prosimians, most populations contain a mix of left and right-handed, but this specialization is not complete, in that animals will occasionally be ambidextrous. Interestingly, for those species with higher EQ, there is more specialization, and more complete specialization (exclusively one hand preference when doing complex tasks). Among these species the hand preference slightly favors the right.[91]

Why should we care about this nuance? Hand specialization is a pre-requisite for more advanced skills such as tool use, and for activities in which humans' opposable thumbs come into play, so it's useful to begin to note the emergence of that specialization at this point in primate development. Moreover, manual lateralization is accompanied by changes to the brain, specifically by asymmetrical specialization between the two hemispheres of the brain. As one half of the brain adapts to a higher level of specialization, say the left hemisphere develops to accommodate a more robust right handed set of capabilities, it might offload function from the other hemisphere, freeing it up to specialize in some other way.[92] In the case of humans, who are predominantly right-handed, and thus left hemisphere dominant in manipulating things, have a higher reliance on parts of the left hemisphere for language, specifically Wernecke's areas (located about halfway between the visual and auditory cortexes), and Broca's area.[93] In left-handed people, there is a slightly higher tendency for these functions to occur on the right hemisphere.[94]

Note that there are serious methodological concerns with making certain statements about which hands primates use, since most of the experiments developing our evidence are constructed using tasks not naturally done in the wild. Likewise, what evidence we do have on prosimians and NWM is mixed. Also, there is not yet a clear and 100% linkage between manual specialization and language. That said, speech and ability to perform complex tasks with our hands are the hallmarks of advanced human cognition, and both have a proven lateral specialization. Coincidentally, we see both more advanced vocalizations as well as manual specialization beginning at the same time here in NWM.

As we examine the range of variability in NWM across body size, social structures EQ and other factors, it seems logical to ask what accounts for this variation. Of course, we've talked about the extrinsic factors influencing variability in cognition: diet, sexual and predatory selection, ethology, etc. However, are there cognitive factors that accounts for the innovations themselves?

Three factors seem to account for innovations we've been discussing here: individual experience, changes to cultural/social structures and changes to genes.

Individual experience seems pretty straightforward - for example, some monkey had to be the first to eat tree gum, certain insects and various leaves. But what causes that monkey to try it? And what are the factors affecting whether the monkey will try it, and more importantly survive it and perhaps gain some advantage that is passed on in some way to promote his or her genes? This is governed by factors such as novelty seeking, as well as by sheer chance.

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[89] Fagot, Joel, and Jacques Vauclair. "Manual laterality in nonhuman primates: a distinction between handedness and manual specialization." Psychological bulletin 109.1 (1991): 76.
[90] McGrew, W. C., and L. F. Marchant. "On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates." American journal of physical anthropology 104.s 25 (1997): p 217-219
[91] McGrew, Marchant, p 219-221.
[92] Hopkins, William D., and Monica Cantero. "From hand to mouth in the evolution of language: The influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (Pan troglodytes)." Developmental Science 6.1 (2003): 55-61.
[93] Corballis, Michael C. "From mouth to hand: gesture, speech, and the evolution of right-handedness." Behavioral and Brain Sciences 26.02 (2003): 199-208.
[94] Taylor, I. & Taylor, M. M. (1990). Psycholinguistics: Learning and using Language. Pearson. ISBN 978-0-13-733817-7. p. 367

Novelty seeking can be defined as the "reaction to novel or risk situations and objects, and by the global disposition to explore such stimuli."[95] Why does chance play a role? Animal environments, before man, were relatively stable for millions of years. New food sources, predators, threats and stimuli often took significant time to develop. So, the monkeys predisposed to novel things need chance to favor them to encounter novel things. Granted, in today's world, novel is everywhere, and perhaps our sensitivity to it seems high today due to the fact that our brains evolved in the past when novelty was relatively rare.

Novelty-seeking includes aspects of both risk-taking as well as curiosity. This is not the time or place for an extensive treatment of this multi-faceted trait across the broad number of NWM species. Instead, we bring this up to introduce the concept and illustrate it with some NWM examples. For example, in a study that compared novelty seeking across NWM (spider monkeys) and OWM (macaques), the results showed that the spider monkeys were more novelty seeking than macaques, males were more novelty-seeking than females, and that dominant macaques were more novelty seeking than non-dominant. This study's authors attributed differences in social structure as the primary driver of these differences.[96]

On its surface, innovation is often viewed as a good thing, but it has its limits. After all, who wants to be the first "friend who jumped off a bridge"? Research so far shows that animals who tend to innovate are those who are under pressure for resources, such as the smaller animals in a species with limited food[97] But animals who could innovate frequently don't, even if it not doing so means their death. Why? Brosnan and Hopper point to 5 limitations on animal innovation:

(1) neophobia: a hesitancy to approach a novel object, locale or food item
(2) conservatism - the disinclination to explore/ adopt new possibilities or opportunities
(3) conformity: the tendency to do what your peers do
(4) functional fixedness: the disinclination to use familiar objects in novel ways
(5) the endowment effect: the bias towards preferring an existing option over a new one

Basically, these various theories share the common basis that most individuals prefer the known over the unknown, even when the known is intolerable. Bottom line, individual innovation would appear to be an exception to standard animal behavior.

Individual novelty can also be brought about not just by circumstances or chance, but through cultural or social influences. For example, experiments done on NWM squirrel monkeys showed that increases in early life experiences and trauma increased later life novelty seeking. These results showed up even when these early life traumas were mild. Other separate research on squirrel monkeys showed that when innovations were performed by higher-ranking individuals, they were more likely to be copied, and thus effectively transmitted from the individual experience into the social structure.[98] Here we see an interplay that works in both directions between the social structure and the individual innovator.

So, we introduce all of these factors here to summarize the different ways that innovations can bubble up across animal species, in part because of the variability of the New World Monkey species calls our attention to diverse response to similar environments. Of course, all of these factors are influenced by the evolving environment, some of which co-evolved with NWM.

<u>The dog that didn't bark</u>

One final note on NWM cognition relates to a topic we will be discussing later called "Theory of Mind" (ToM). Theory of Mind, first put forth by Premack and Woodruff in 1978, is essentially the ability to put yourself in someone else's shoes, and consider the world from the available evidence as they might perceive it. It's related to,

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[95] Santillán-Doherty, Ana María, et al. "Novelty-seeking temperament in captive stumptail macaques (macaca arctoides) and spider monkeys (ateles geoffroyi)." Journal of Comparative Psychology 124.2 (2010): 211.
[96] Santillán-Doherty, Ana María, et al. "Novelty-seeking temperament in captive stumptail macaques (macaca arctoides) and spider monkeys (ateles geoffroyi)." Journal of Comparative Psychology 124.2 (2010): 211.
[97] Laland and Reader (1999a) f
[98] Claidiere, Nicolas, et al. "Diffusion dynamics of socially learned foraging techniques in squirrel monkeys." Current Biology 23.13 (2013): 1251-1255.

but probably independent from autonoetic consciousness[99] – the ability to mentally time-travel *yourself* into past memories or consider *yourself* in future scenarios.[100] Here's an example of Theory of Mind:

> *"Maxi eats half his chocolate bar and puts the rest away in the kitchen cupboard. Then he goes out to play in the sun. Meanwhile Maxi's mother comes into the kitchen, opens the cupboard and sees the chocolate bar. She puts it in the fridge. When Maxi comes back into the kitchen, where will he look for his chocolate bar? The answer to this question will seem obvious. First, Maxi doesn't know that his mother has moved the chocolate. Second, Maxi still believes, falsely, that his chocolate is in the cupboard. That is why he looks in the cupboard. If this is how you answered the question then you have a 'theory of mind'. We naturally explain people's behavior on the basis of their minds: their knowledge, their beliefs and their desires, and we know that when there is a conflict between belief and reality it is the persons' belief, not the reality that will determine their behavior. Explaining behavior in this way is called 'having a theory of mind' or 'having an intentional stance.'"*[101]

Why is Theory of Mind relevant to our questions? Because ToM is a key attribute of human cognition and social learning, and reaching it is a critical step in our early childhood development. Knowing when it begins is therefore very interesting to scientists. It has even been suggested that Theory of Mind is a key milestone in the development of effective artificial intelligence.[102][103]

That is why so many scientists have searched for it across the animal kingdom, including numerous research efforts on NWM. The NWM ToM result? Inconclusive at best. Even among the tests on the highest EQ capuchins, Theory of Mind has not been conclusively identified.[104] My personal conjecture is that the NWM lack the ability to build the abstract concepts of other self and motivations, and lack the ability to anticipate sufficiently to model what another actor might do, beyond that which they can directly observe and react to.[105] But I'm not an expert, and I didn't even stay in a Holiday Inn Express last night. Regardless, none of the experts have conclusively found ToM in NWM, yet.

So why bring it up here? Lack of evidence can be evidence, as in the classic example of Sherlock Holmes deductions about the "dog that didn't bark". Consider again that with the NWM we are examining a living creature that can give us insight into the stages of human evolution 40 mya. As we approach early hominoids we find that, through forces such as natural selection or genetic drift, those species are extinct, and we have to resort to crude measures such as EQ derived from bone fragments. Therefore, as we examine our living specimens, it's useful not only to note the traits that they exhibit, but also those they don't, to provide us with a baseline for comparison as we move on to both extant later primates, such as the next chapter's OWM, as well as the extinct anthropoids.

<Short conclusion, summarizing chapter and sequeing to next chapter. TBD>

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[99] Rosenbaum, R. Shayna, et al. "Theory of mind is independent of episodic memory." Science 318.5854 (2007): 1257-1257.
[100] Tulving, E. (2002) Episodic memory: from mind to brain. Annu. Rev. Psychol. 53, 1–25
[101] Frith, Chris, and Uta Frith. "Theory of mind." Current Biology 15.17 (2005): R644-R645.
[102] Scassellati, Brian. "Theory of mind for a humanoid robot." Autonomous Robots 12.1 (2002): 13-24.
[103] <author working note: Bring in De Waal: http://www.pnas.org/content/102/32/11140.long; introduce superstimuli (↵ Gallup, G. G., Jr. (1975) in Socio-Ecology and Psychology of Primates, ed. Tuttle, R. H. (Mouton, The Hague), pp. 309–342.) >

[104] (Kuroshima et al. 2002).
[105] https://youtu.be/axrywDP9Ii0