Chapter 7: brain – a community of neurons

background reading

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Gee, H. (2021*), A (very) Short History of Life on Earth: 4.6 billion years in 12 chapters*, Picador, London.

Goodall, J. (1986), *The Chimpanzees of Gombe: patterns of behavior*, The Belknap Press of Harvard University Press, Cambridge, MA.

Roth, G. and Dicke, U. (2005), "Evolution of the brain and intelligence", *Trends in Cognitive Sciences*, vol. 9, pp. 250−257.

Savage-Rumbaugh, S. and Lewin, R. (1994), *Kanzi: the ape at the brink of the human mind*, Doubleday, London.

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de Waal, F. (1989), *Peacemaking among Primates*, Harvard University Press, Cambridge, MA.

de Waal, F. (2006), *Our Inner Ape*, Granta Books, London.

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notes

Constructive comments are welcome.

7.1 the brain's representation of its host organism

This section is based on Campbell 2008:section 49.3, Morris 2013:section 36.5, Purves 2013:114, Purves 2019:193-198, and Kandel 2021:84, 1231, and 1335.

7.1.1 the somatotopic neural map of the body

"**The brain is divided**", Morris 2013:36-18. In humans the outermost layer of the cortex is the neocortex, comprising 6 layers of neurons, lying parallel with brain's surface (Campbell 2008:1074, Purves 2019:593). The etymology of *cortex* is from Purves 2013:552.

Neurons are indeed "densely packed" in the cortex, to a degree that stretches the imagination. For example, a volume of 1 cubic millimetre of cortex – about the size of a pin-head – in the brain of a mouse, contains about 100,000 neurons, 100 million synapses, and a total length of about 4 kilometres of axons (Laughlin 2003:1873).

In **figure 7.1**, the side view of a human brain in **part (a)** is from "3D Brain", an online resource provided by the Cold Spring Harbor Laboratory, at http://www.g2conline.org/3dbrain/. The lobes are outlined with thick dashed lines, and they are consistent with Campbell 2015:figure 49.16 and Purves 2013:figure A.11. The primary cortex in each lobe is outlined, following Morris 2013:figure 36.23 and Purves 2019:figures 12.5 (visual), 13.16 (auditory), 17.5 (motor), and 27.1.

The transverse section of the somatosensory cortex, shown in **part (b),** is re-drawn from Purves 2019:figures 9.10 and 9.11. It comprises four regions, known as Brodman's areas 3a, 3b, 1, and 2. These aren't shown here, and I treat the somatosensory cortex as a single functional entity.

The somatotopic map, shown in **part (c),** is by Karen Gulliver, OpenStax College, part of Rice University, covered by license CC BY 3.0, and available at https://commons.wikimedia.org/wiki/File:1421_Sensory_Homunculus.jpg. The figure is consistent with Campbell 2015:figure 49.17, and Kandel 2021:figure 4-8.

The somatotopic map shown in figure 7.1 is simplistic in two respects. First, it shows little detail. Examples of more detailed neural maps are shown in Kandel 2021:figure 19-15, and Purves 2019:figure 9.13. Second, the body surface is represented in at least 10 different neural maps, each occupying a different region of cortex, which deal with different aspects of tactile sensation (Kandel 2021:452). For example, some regions deal with surface texture, while others deal with the size and shape of objects.

A 3-D model of the human brain, with its internal components, can be viewed at http://www.g2conline.org/3dbrain/.

"**The cortex is highly folded**", Morris 2013:36-18.

"**Figure 7.1(a) shows the four lobes**", Purves 2019:593, Morris 2013:36-18, and Campbell 2008:1075.

"**The size of the cortex in some mammals**", Campbell 2008:1075.

The neurons that carry sensory information to the central nervous system, and the motor neurons that carry information to the muscles are called peripheral neurons, because they lie outside the brain and spinal cord (Wills 1994:262). The overwhelming majority of neurons are within the brain and spinal cord; these are called inter-neurons, and they "*form the connecting links between the world we perceive and the world we act on*" (Wills 1994:262). Rats have about 20 inter-neurons for every peripheral neuron, but in humans, the ratio is about 20,000. The larger is the ratio, the greater is the ability to process and manipulate information and decision-making.

See also the reference on inter-neurons in the note to section 6.3.1.

the primary somatosensory cortex

"**Lying along the front edge of the parietal lobe**", this section's purpose is to give a simple description of how an animal's brain holds a neural representation of its physical body. And so, I focus on the primary somatosensory cortex, and omit the primary motor cortex, which lies alongside, and is organised in a similar way (Campbell 2008:section 49.3, Kandel 2021:84).

There are also other cortical areas devoted to different senses. For example, there is an auditory cortex in the temporal lobe, which is organised by pitch, with neurons sensitive to low frequencies at one end, and neurons sensitive to high frequencies at the other (Morris 2013:13-19).

"***integrates tactile information***", Morris 2013:36-19.

"***importance to the sense of touch***", Kandel 2021:454.

"**We need fine discrimination**", Kandel 2021:84.

"**The somatotopic maps**", Purves 2013:194, Kandel 2021:456 and Box 19-2.

7.1.2 plasticity in the somatosensory cortex

"**An animal has a dynamic neural representation**", Kandel 2021:1230.

“**Each digit is mapped**”, Kandel 2021:1229.

“**One individual monkey**”, Purves 2019:197, Kandel 2021:1336.

“**An owl monkey’s middle digit**”, Purves 2013:196, Kandel 2021:1229 and figure 49-19.

“***functional remapping***”, Purves 2019:197.

“**The somatotopic map also adjusts reversibly**”, Purves 2013:197.

Figure 7.2(a) is re-drawn from Purves 2019:figure 9.13; **part (b)** is re-drawn from Purves 2019:figure 9.15; and **part (c)** is re-drawn from Purves 2019:figure 9.14. These show parts of the somatosensory cortices in owl monkeys.

A somatosensory cortex similar to the one shown in part (a) is in Kandel 2021:figure 19-15. The findings shown in (b) and (c) are also shown in Kandel 2021:figures 53-16 and 49-19, respectively.

7.2 how the brain represents its position in physical space

This section is based on Epstein 2017, Grieves 2017, Kandel 2021:chapter 54, Kiehn 2014, Lever 2009, Moser 2014, O’Keefe 2014, Purves 2019:Box 30D, Rowland 2016, and Schafer 2020.

“**Specific neurons**”, it’s actually the “hippocampal formation”, which also includes regions like the entorhinal cortex and the subiculum, but here I’ll treat it as just the hippocampus (O’Keefe 2014:figures 2 and 8, Grieves 2017:figure 2).

7.2.1 the hippocampus and physical space

“**The hippocampus is a structure**”, Thompson 2000:25 and 394.

“**The major types of nerve cells**”, these are the “big four” in O’Keefe 2014, while Grieves 2017 presented a “big three”, omitting the boundary cells. However, these cells are only the main players in a diverse suite of spatially modulated neurons (Grieves 2017, Schafer 2020, Rowland 2016, Kandel 2021:1360). Some of these cells deal with discrete objects in the environment, some deal with spatial goals and destinations, while others track speed and direction, and these functions clearly correlate with the physical world. Other cells are “conjunctive cells”, and these appear to bring together a number of environmental features.

“***collectively form the neural basis***”, Grieves 2017:113.

boundary cells

“**There is a class of cells**”, Grieves 2017. There are a number of types of boundary cell, and some take account of the animal’s orientation. Boundary cells have a complex relationship with place and grid cells that is not well understood (Grieves 2017:125).

“**A population of boundary cells**”, Lever 2009:figure 2.

head direction cells

“**Head direction cells fire**”, Grieves 2017:119.

“***appears to form a compass-like***”, O’Keefe 2014:294.

place cells

“**Place cells have been found**”, Grieves 2017:117.

“**Rats construct place fields**”, Grieves 2017:117.

“***represent higher order constructs***”, Grieves 2017:117.

“***collective activity of a few dozen place cells***”, Rowland 2016:21, and also see O’Keefe 2014:286.

“***can contain multiple maps***”, Kiehn 2014.

“**When an animal enters**”, Kandel 2021:1360, Thompson 2000:415.

“**This neural map is so reliable**”, Thompson 2000:414.

“***thus providing neural evidence***”, Epstein 2017:1509.

“**It has also been observed**“, Kandel 2021:1365, Thompson 2000:415.

grid cells

“**In contrast to a place cell**”, Grieves 2017:120, Schafer 2020. Place cells are located in the hippocampus, while grid cells are found in the entorhinal cortex, lying just behind the hippocampus (Schafer 2020, Grieves 2017:figure 2).

“**Grid cells are found**“, Rowland 2016:22.

“***grid of regularly tessellating triangles***”, Hafting 2005:801 and figure 1. Tessellating equilateral triangles form tessellating hexagons, and the grid cell firing field is also described as a hexagonal array.

“***helps the animal compute***”, quote from Schafer 2020, and also see O’Keefe 2014:305, and Kiehn 2014.

“**Grid cells generate**”, Moser 2014:467, Rowland 2016:29.

“**While all grid cells**”, Moser 2014:467, Rowland 2016:22, Kandel 2021:1361 and figure 54-13.

“**Thus, each location**”, Kandel 2021:1361.

“**It’s possible to reconstruct**”, Moser 2008:1144.

“**Grid cells and place cells**”, Moser 2014:471. Grid cells are “*one synapse upstream*” (Moser 2014:467) from the place cells, and it appears that the signals from the grid cells are transformed within the hippocampus into the specific locations associated with space cells, but it’s not yet understood how this is done (Kandel 2021:1361).

“***map of space in general***” and “***a large number of maps***”, both quotes from Moser 2014:471, and also see Kandel 2021:1365.

The four images in **figure 7.3** are from Grieves 2017:figure 8, with the addition of labels and the hexagonal grid in part (d).

Citation: Grieves RM, Jeffery KJ. The representation of space in the brain. Behav Processes. 2017 Feb;135:113-131. DOI: 10.1016/j.beproc.2016.12.012. Epub 2016 Dec 26. PMID: 28034697.

7.2.2 human studies

“**For example, the right hippocampus**”, O’Keefe 2014:304 and figure 29.

“**Furthermore, it has been found**”, O’Keefe 2014:304 and figure 30.

7.2.3 neural representation of the external world

“***activity patterns referred to as neural representations***”, Moser 2014:466.

“**We’ve seen how individual neuron types**”, Schafer 2020.

7.3 the brain’s representation of social space

This section is based on Eichenbaum 2015, Epstein 2017, Montagrin 2017, Schafer 2018 and 2020, and Tavares 2015.

7.3.1 maps of physical space

“**The traditional map of physical space**”, Kandel 2021:1361.

mapping space with vectors

7.3.2 maps of social space

“**It’s well established**”, Tavares 2015:232, Montagrin 2017:3, Schafer 2018:482.

“***status affects resource allocation***”, Schafer 2018:482.

“**Just as we can map physical space**”, Eichenbaum 2015:9.

“**Figure 7.4(b) depicts the social world**”, power is on a linear scale, but affiliation is referenced to the individual, and so it could be depicted as a polar plot (as in Eichenbaum 2015:figure 1). However, it’s not easy to combine these two views in a clear, unambiguous way, and so I’ve plotted social space as a straightforward cartesian plot with two linear orthogonal axes.

“**We talk of knowing**”, Schafer 2020, Lakoff 2003.

“***she’ll rise to the top***”, “***he’s climbing the ladder***”, and “***the bottom of the social hierarchy***”, are all from Lakoff 2003:16.

social vectors

“**The vector angle**”, the vector angle depends on both power difference and affiliation, and Tavares describes the vector angle as representing “*the normalized function of power modulated by affiliation*” (Tavares 2015:235).

“***social distance***”, both Schafer 2020 and Tavares 2015:235 use this phrase.

Figure 7.4 is based on Schafer 2018:figures 1 and 2, Schafer 2020, and Tavares 2015.

“**Therefore, social maps**”, Eichenbaum 2015.

“**Fourth, just as we navigate**”, Schafer 2018:figure 2 shows an example of a simple social navigation.

7.3.3 the hippocampus and social space

“**This question was addressed**”, Tavares 2015, and the findings are summarised and discussed in Eichenbaum 2015, Epstein 2017, Montagrin 2017, and Schafer 2018 and 2020.

We use a procedure called functional magnetic resonance imaging, commonly called fMRI, to identify activity in different regions of the brain (Purves 2019:27, Kandel 2021:112−115 and figure 6-1). Neural activity requires oxygen, and when a brain region is activated by a particular task, it is quickly supplied with oxygen-rich blood. fMRI makes use of the fact that blood has different magnetic properties, depending on its oxygen content, and this makes it possible to follow the functioning of different regions of the brain in real time. fMRI can monitor neural activity in regions as small as a 3x3x3 mm cube, and over a timescale of a few seconds. This small brain region is known as a voxel.

“**In each interaction**”, the following examples, with quotes, are from Tavares 2015:Supplemental table S1.

“**Each subject’s brain was monitored**”, Schafer 2018. Two other regions correlated with the vector angle: the left inferior parietal lobule and the left dorsolateral pre-frontal cortex, but the rôles of these regions are not as clear as for the hippocampus (Schafer 2018:483). Only one region of the brain correlated with social vector length, and this was the posterior cingulate cortex (PCC), which lies close to the hippocampus, and is functionally related to it (Schafer 2018:483). Tavares 2015 found that “*the PCC tracked the social vector length at each decision point*” (Schafer 2018:484). In this section I’m focussing on the simple and clear involvement of the hippocampus in basic social navigation, and so I’m ignoring other regions of the brain.

Functional imaging of healthy humans shows that activity increases in the left hippocampus when words, objects or people are recalled, and in the right hippocampus when spatial information is recalled (Kandel 2021:1300).

“***identified each character’s position***”, Eichenbaum 2015:10.

“***the hippocampus tracks relationships***”, Tavares 2015:239.

“***a crucial player***”, Schafer 2018:483.

Figure 7.5 is based on Tavares 2015:supplemental table S1 and figure S1.

7.4 the cognitive dimension of social living

7.4.1 brain and body size

“**A human brain**”, Roth 2005.

“**However, if we compare brain size with body size**”, the classic study is by Jerison 1973, and see also Dunbar 1997:57, Roth 2005, Dawkins 2005:80, and Bonner 2006.

Figure 7.6 is based on Dunbar 1997:figure 1, Bonner 2006:figure 15, Roth 2005:figure 2, Purves 2013:figure 15.7, and Schoenemann 2006:figure 1, with data for selected primates from Schoenemann 2013:table 8.2. Graphs are plotted for averages of brain and body sizes, and different authors give slightly different figures for these, and hence slightly different graphs, although they are all fairly consistent.

The best-fit lines for reptiles and bony fish are estimated by eye from Bonner; the best-fit lines for birds and mammals are very close, so I’ve put them on one best-fit line; the best-fit line and selected examples of mammals are from Roth 2005, whose best-fit line is slightly lower than that given by Schoenemann 2006; the best-fit line and selected examples of primates are from Schoeneman 2006 and 2013. I’ve given a single best-fit line for all primates, but the prosimians, monkeys and hominids have slightly different best-fit lines (Schoenemann 2006:figure 1).

If brain mass was proportional to body mass, then the log-log plot would have a slope of 1, so a 10-fold increase in body size would require a 10-times bigger brain. However, the brain deals with sensory inputs from nerves which are mostly in the body’s surface, and on this basis one would expect the brain size to scale with the body’s surface area and this would give a log-log plot with a slope of 2/3 (Dawkins 2005:81, Schoenemann 2013:137).

To understand why this should be so, think of a 1 cm cube of something that has a mass of 1 gram. The surface area of the 6 faces of this cube will be 6 cm^2. Now pack 1,000 of these cubes together to make a bigger cube that is 10x10x10 cm, which has a surface area of 600 cm^2 and a mass of 1,000 grams. The surface area has increased by a factor of 100, while the mass has increased by a factor of 1,000. The log of 100 = 2, and the log of 1,000 = 3, so on a log-log plot the slope will be 2/3.

But the slope of the plot of log brain size against log body size is consistently 3/4, which is close to 2/3, but sufficiently different from this figure that we can infer that the brain-body relation is not down to the body's surface area.

It's been found that the plot of log metabolic rate (in Joules/hour) against the log of organism mass also has a slope of 3/4, and this holds for single-celled organisms, and cold-blooded and also warm-blooded organisms, and is known as Kleiber's law (Dawkins 2005:523, West 2005, Campbell 2008:figure 40.19, Morris 2013:figure 40.4, Milo 2016:204). Each group of organisms lies on its own best-fit line, and each line has a slope very close to 3/4. If we consider the warm-blooded organisms, then both the mouse and the elephant lie on the same line, with a slope of 3/4. So an organism that is 10,000 times heavier, with roughly 10,000 times as many cells, only produces 1,000 times as much energy in metabolising. So, the cells in the elephant each produce less metabolic energy than the cells in a mouse. This seems odd, for one would think that cells in these warm-blooded mammals should metabolise at the same rate. If the cells in the elephant metabolised at a faster rate, then they would generate more heat, and the animal would be warmer. It's been estimated that "*if an elephant had the metabolic rate of a mouse then you could fry an egg on its back*" (Tudge 1996:125).

The answer lies, not in the cells, but in the system of transport, that supplies these cells with nutrients, and takes away their waste products. This plumbing system takes up its own space within the animal's body, and this is optimised at a fixed percentage of the body volume, and for mammals this is about 6−7% of body volume. The consequence is that as body size increases, the transport system doesn't quite keep up with the increase in the number of cells, and so the cells' metabolic rate goes down. It turns out that Kleiber's law, with its distinctive 3/4 slope, "*can be derived from the physics and geometry of supply networks*" (Dawkins 2005:526). It seems likely that the relation between brain and body size, with its 3/4 power scaling, is also due to metabolic limitations (Schoenemann 2013:138).

Mass-specific metabolic rates, that is in Watts/kilogram of wet mass, have a consistent range of values, between ~0.3 and ~9 W/kg for a wide range of organisms, spanning over 20 orders of magnitude in mass (Milo 2016:204). Within the groups of similar species there could be a 100-fold range in mass-specific metabolic rate, which casts doubt on Kleiber's law.

The relation between brain and body size is only one of several scaling relationships for living things – see Bonner 2006:60 and West 2005.

The density of brain tissue is about 0.99 g/cm^3, which is so close to 1.0 that brain mass in grams and brain volume in cm^3 (cc) are numerically identical (Beckmann 1999).

log-log graphs

"**This tells us that a body**", this 3/4 scaling relation appears to arise from the limitations of transport processes, which provide nutrients to, and remove wastes from, the body's cells (Schoenemann 2013, Dawkins 2005:81 and 522).

"***with increasing body size***", Roth 2005:252.

encephalisation quotients

"**Broadly speaking**", Bonner 2006:figure 15.

"**Birds have brains**", Font 2019 on brain size and Emery 2004 on cognitive abilities.

"**Among the mammals**", Roth 2005.

"**This suggests that intelligence**", Roth 2005, Emery 2004.

"**Intelligence is adaptive**", Griffin 1994.

"**So, a human brain**", Aiello 1995. Different authors give slightly different figures, for example, Dawkins 2005:86 gives 6, and Roth 2005 gives about 7.5.

"**However, we need to be careful**", Roth 2005, and Eccles 1991:42 on preferential enlargement.

the brain is an energetically expensive organ

"**First, of the 20,000 or so genes**", Purves 2019:1.

"**Second, the brain**", Attwell 2001.

"**Thus, the brain**", Aiello 1995.

"**So, overall**", Thompson 2000:122, Roth 2005.

"***need brains that are so much larger***", Dunbar 2007b:1344.

"**Evolution is an economical process**", Dunbar 2007b. Unless the lifestyle of an animal enables it to make use of its intelligence, a big brain is an encumbrance rather than an advantage. Colin Tudge (2005:125) gives the example of a catfish that wakes up one morning with the brain of Albert Einstein, but then finds that its brilliant intellect is wasted on its fellow catfish, and the pond it is in can't provide enough nutrients its new brain needs.

"***evolution is the outcome***", Dunbar 1998a:179.

7.4.2 a cooperative response to predation

"***create functional***", Dunbar 2017a:5.

"***the single most important cause***", Cheney 2007:48.

"**Typically, almost all deaths**", Cheney 2007:41, Silk 2009.

"**Even the survivors suffer**", Cheney 2007:48.

"**A lone animal makes decisions**", this is a bit simplistic, for every decision an animal makes about how to act has implications for the other individuals in the local population, and their responses will act back on that animal (Dunbar 2010).

"**So, group living demands higher cognitive abilities**", this is the essence of the social brain hypothesis (Humphrey 1984:chapters 1 and 2, Dunbar 1998a, 2005:chapter 7, 2007b, 2014:chapter 3 and 2017a). A diversity of explanations have been proposed for the evolution of large brains in primates, and while each one explains some of the facts, only the social brain hypothesis appears to explain them all (Dunbar 2017a). So, there's no need to weigh the different hypotheses, or even specifically mention the social brain hypothesis, and in the following sections I'll look at the dependence of a social lifestyle on cognitive skills.

"***individuals living in stable social groups***", Dunbar 2007b:1345.

"***the grand dawn***", Morowitz 2002:138.

the benefits and costs of group living

"**The benefits of living**", Silk 2007, Dunbar 2007b and 2017a, Morowitz 2002:chapter 24.

"**However, there are distinct disadvantages**", Silk 2007, Dunbar 2005:91 and 2017a.

"**In addition, the social hierarchy**", Dunbar 2017a.

Mark Moffett notes that there “shy” chimpanzees who may disappear from observation for months at a time. These are often “*beaten-down females who are members of the community but keep to themselves in a private corner of its territory*” (Moffett 2019:50).

“***implicit social contract***” and “***Fitness payoffs***”, Dunbar 2007b:1346.

“***sensitivity to others***”, de Waal 2007:218.

a social terrain

“***intense social interaction***”, Lewin 1999:67.

“***calculate the consequences***”, Humphrey 1984:21.

“***knows all the others personally***”, Tudge 2009:129.

selection pressures to evolve bigger brains

“***individuals living in larger social units***”, Dunbar 2017a:5.

“**An individual’s breeding competitors**”, Lewin 1999:193.

“***any heritable trait***”, Humphrey 1984:22.

7.4.3 the cognitive demands of social living

“**These cognitive demands**”, Dunbar 2007a, and 2014:59.

the mathematics of social relationships

“**The number of relationships**”, Tudge, 2009:129.

“**If we add another member**”, the number of social relationships is the sum of an arithmetical series, which starts at 1 and ends at the number of members in the group. In general, the sum of an arithmetic series is $S = n(a_1 + a_n)/2$, where n is the number of terms, a_1 is the first term, and a_n is the last term. So, the number of relationships in a group of n individuals is $n(1 + n)/2$. For 3 members, $S = 3(1 + 3)/2 = 6$; for 4 members, $S = 4(1 + 4)/2 = 10$; for 5 members $S = 15$; for 10 members, $S = 55$, and for 20 members, $S = 210$. The number of relationships increases hugely as the group gets bigger.

“***the complexities of group living***”, Tudge 2009:130.

correlations between neocortex size and group size and social complexity

“**To minimise the predation risk**”, Dunbar 2003:169 and 2017a:5.

“**So, the “quality” and “quantity”**”, Dunbar 2017a:5.

“**This is found to be the case**”, Dunbar 2017a:5, Dunbar 1998a:box 1.

“**… but only the neocortex …**”, most of the cortex that covers the cerebral hemispheres (as shown in figure 7.1) is neocortex, which is defined as cortex that has 6 cellular layers (Purves 2019:593). The six-layered neocortex is the most recently evolved part of the forebrain, and is found only in mammalian brains (Purves 2013:517).

“**The neocortex**”, Purves 2013:517. See also Dunbar 1998a:180 on neocortex, and Dunbar 2007a on the high level of cognition.

“**The fact that the groups**“, Dunbar 2005:94.

Figure 7.7 is taken from Dunbar 1998a:figure 3 (which names all species of the three types), Dunbar 2003:figure 1 (which gives simians and apes, and also the point for humans), and Dunbar 2007b:figure 1 (which gives simians and apes, but no point for humans). The best-fit lines have been positioned by eye, and so are only indicative.

These three graphs are in good agreement with each other, but don’t match Dunbar 2014:figure 3.1(a), in which the log scales are incorrect on both axes. The preferred sizes of primate and human social groups are taken from Dunbar 2014:80 and Dunbar 2017b. The data in Dunbar 2014:figure 3.1 is interpreted as showing different socio-cognitive grades within the monkey species, but I’ve kept to a single monkey grade, to keep things simple.

“**From prosimians to simians to apes**”, Dunbar 2005:95.

comparing the “quality” of the social systems of lemurs, baboons and chimpanzees

“***socio-cognitive complexity***”, Dunbar 2014:66.

“**We can easily count**”, Dunbar 2010.

“**Lemur social systems**”, van Schaik 1993.

“**While conflicts between females**”, Dunbar 1997:22, Kudo 2001.

“**Lemurs are omnivores**”, see https://en.wikipedia.org/wiki/Lemur and also the University of Wisconsin primate factsheet on the Ring-tailed lemur, at http://pin.primate.wisc.edu/factsheets/entry/ring-tailed_lemur/taxon.

“**A baboon group**”, Cheney 2007:278.

“**There is often some form of reconciliation**”, Cheney 2007:83.

“**Baboons will sometimes look out**”, Harding 1974.

“**Chimpanzee social groups**”, Goodall 1986:chapter 7.

“**There is a well-defined**”, Dunbar 1988:11.

“**Hunting practices**”, Wilson 1975:543, Goodall 1986:286, Boesch 1989.

a fractal hierarchy of friendship groups

“**In figure 7.7**”, Dunbar 2014:67 and figure 3.1.

“**It has been found**”, Zhou 2005, Dunbar 2005:97, 2014:75−84.

“**We see the people**”, Dunbar 2014:figure 3.5.

“***demarcates the limits***”, Dunbar 2014:77.

“***people we know as individuals***”, Dunbar 2014:77.

“**Those within the 150-layer**”, Dunbar 2005:98.

“***may well be one-way***”, Dunbar 2011:347.

“**A diversity of human social communities**”, Dunbar 2014:table 3.1, Hamilton 2007 on hunter-gatherer societies, Zhou 2005 on military groupings, Hill 2003 on Christmas cards, and Dunbar 2015 on Twitter and Facebook communities. Dunbar (2014:386) notes that Hamilton’s conclusion that the scaling ratio was about 4 was because the series of groupings started with the individual, a group size of 1. Hamilton’s first four groups had mean sizes of about 5, 16, 54 and 165, with a scaling ratio of about 3.3.

“**Twitter communities**”, Dunbar 2014:69.

“***specifically identifies the 150 layer***”, Dunbar 2014:77.

“**The preferred sizes**”, Zhou 2005, Dunbar 2014:79, Dunbar 2015.

“**This is sometimes called self-similar**”, Dunbar 2014:78, Hamilton 2007.

“**Fractal scaling of community sizes**”, Dunbar 2014:79, Hill 2008, Dunbar 2017b.

“**Primates have preferred group sizes**”, the core group size of 5 is found in human social networks and in primate grooming networks, and we’ll see in chapter 8 how 4−5 is also the limiting size of a human conversation clique.

“***ubiquitous feature***”, Hill 2008:749.

“***a group of 15 consists***”, Dunbar 2017b.

“**Complex hierarchical systems**”, Hamilton 2007, Barabási 2003.

“***may have evolved***”, Hamilton 2007:2196, and Dunbar 2011 suggests that “*specific group sizes are more efficient for certain activities than for others*”.

behavioral indicators of a big neocortex

“**However, there are a number**”, Dunbar 1998a:185, Dunbar 2007a, Dunbar 2014:61.

“**First, primate species**”, Byrne 2004.

“**Second, primate species**”, Lewis 2000.

“**A third example**”, Pawlowski 1998.

“***reduce the power differentials***”, Pawlowski 1998:364.

coalitions and the structure of primate social groups

“**Primate individuals**”, Dunbar 1997:chapter 3, 2014:39 and 293.

“***achieves a state of dynamic equilibrium***”, Dunbar 1997:44.

“**Members of a coalition**”, Dunbar 1997:chapter 3.

“**Primates in larger social groups**”, Dunbar 2014:figure 2.1.

“**Social grooming**”, Kudo 2001:712.

“**The overall pattern**”, Kudo 2001:719.

“**With a lifestyle out in the open**”, Dunbar 1997:39.

Figure 7.8 is taken from Kudo 2001:figure 3. The best-fit lines are positioned by eye, and are only indicative.

“**So, we can view**“, Kudo 2001:718.

7.5 baboons and the mental construct of a social group

“**Baboons live in social groups**”, Cheney 2007:51. This section is based on Cheney’s field studies of a group of chacma baboons living in the Moremi Game Reserve in the Okavango Delta of Botswana.

“**The females form the core**”, Cheney 2007:62.

“**Grooming strengthens**”, Cheney 2007:63.

“**The mortality rate**”, Silk 2009.

“**Female reproductive success**”, Cheney 2007:83.

“**The mother’s stronger social bonds**”, Silk 2009.

7.5.1 two female hierarchies

“**Female baboon society**”, the figure (based on Cheney 2007:figure 23, page 107 and Seyfarth 2017:figure 1) shows a typical dual hierarchy for female baboons in a social group (Cheney 2007:chapters 5 and 6, Seyfarth 2017).

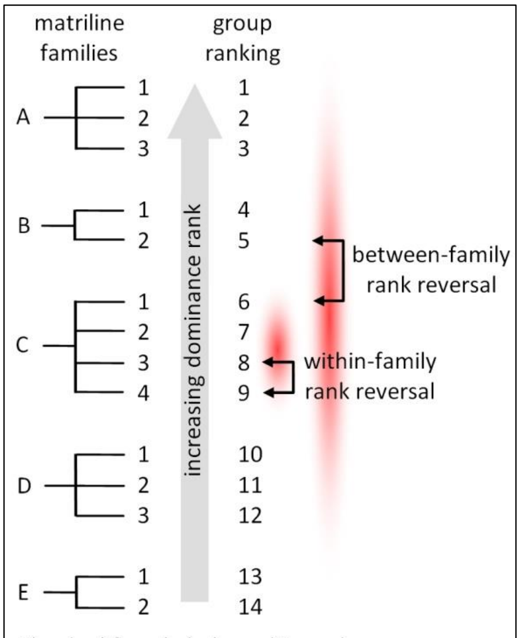
First, individual baboons have a ranking within their own matriline family, for example, C1–C4.

Second, every matriline has its own ranking within the whole social group, so all members of matriline B are outranked by matriline A, but in turn outrank matriline C.

Rank reversals within a matriline, for example, C4 and C3, affect only that matriline, as shown by the small shaded red shape.

However, rank reversals between members of different matrilines, for example, C1 and B2, are much more serious matters (Cheney 2007:108, Seyfarth 2017:80).

In this case, most members of the lower-ranking matriline rise in rank above all the members of the previously higher-ranking matriline, and furthermore, “*many members of multiple matrilines may lose or gain rank*”, as shown by the much bigger shaded red shape (Cheney 2007:108).



The dual female baboon hierarchy

“**Experiments in the field**”, Bergman 2003.

“**A dispute between different families**”, for a description of one such conflict, see Cheney 2007:69.

“**Each female baboon**”, the baboon group’s complex social structure means that even a single vocal interaction carries a large amount of information. For example, “*To recognise that the call sequence “Shashe grunts and Beth fear-barks” violates the existing dominance hierarchy, the listener must recognize the type of call given, consider the rules that govern the use of each call type (fear barks are only given to higher-ranking females, while grunts may be directed to either higher-ranking or lower-ranking females), identify both signalers, and recall their respective dominance ranks. And to recognize that the sequence “Champagne threat-grunts and Luxe screams” is more portentous than “Champagne threat-grunts and Hannah screams” – even though both sequences violate the dominance hierarchy – the listener must add matrilineal membership to her calculations*” Cheney 2007:109). Female baboons take only a very short time to respond to vocal exchanges, and so they must be able to make complex social computations very quickly.

7.5.2 a current social account

"**An adult baboon**", Cheney 2007:chapters 5 and 6, Smuts 2009.

"**For example, an individual female baboon**", Cheney 2007:chapter 5.

"**Social skills are very important**", Archie 2014, and Cheney 2007:110 on rates of infant survival.

"**Careful experiments**", Cheney 2007:chapters 5 and 6.

"**In addition**", Seyfarth 2012.

7.5.3 a mental construct of baboon social life

"**Baboons seem to have a theory**", Cheney 2007:117.

For example, baboons "*recognize rank, family, and coalitions within their troop and use these categories to predict how others will behave*" (Moffett 2019:46).

It seems clear that baboons understand abstract social categories, such as "kinship" and "dominance rank" (Seyfarth 2017). First, these social categories "*cannot be reduced to any one, or even a few, sensory att*ributes". Second, the "*recognition of a linear, transitive hierarchy persists despite frequent changes in the individuals who occupy each position. In the mind of a baboon, therefore, social categories exist independent of their members*" (all quotes from Seyfarth 2017:83).

"***can be understood***", Kandel 2000:1277.

"**The whole structure is sustained**", Clive Gamble *et al*. also recognise this process of continual re-affirmation, resulting in the "*primate pattern of working out and continually repeating who you are and what sort of society you live in through daily face-to-face interactions. It bears no resemblance to the institutional model of society with its demarcated religious, political, legal and commercial spheres*" (Gamble 2014:69).

In this respect, the continual social exchanges that bind a primate community seem to be analogous to the exchange interactions that bind electrons into atoms, and atoms into molecules (see sections 3.6, 4.1, and 9.1.1).

We've seen how a molecule is a community of atoms that are bound together by molecular electron orbitals between certain atoms (section 4.1). We can visualise a baboon social group as a kind of "social molecule", which comprises a number of "baboon-atoms", who are bound together by an interlocking ensemble of interactions that act as "social orbitals". These social orbitals can have different binding strengths that may relate to the ranking of the individual baboons involved. Whereas the electron orbitals are fixed in a molecule, in a baboon social group they are forever shifting, as individuals are born and die, and as relationships and rankings shift and change. A rank reversal within a matriline will cause only a minor change in the group's pattern of social orbitals. But a dispute that changes the ranking of entire matrilines will result in a major change in the pattern of social orbitals, and may destabilise the group.

"**We can view the baboons' social structure**", Mark Moffett sees societies as "*imagined communities*", so that our "*shared imaginings bind people with a mental force no less valid and real than the physical force that binds atoms to molecules, turning them both into concrete realities*". This does not just apply to humans, for animal societies "*are represented firmly in the minds of their members, and in that regard are also imagined*" (all quotes from (Moffett 2019:18). See also the note to section 9.1.1 – "***exchange processes at every level***".

7.6 chimpanzees – self-sufficiency and cooperation

"**This section draws on field studies**", Goodall 1986:figure 3.1.

7.6.1 a fission-fusion society

"***by reference to the most intuitive criteria***", Wilson 1975:539.

"**A chimpanzee community**", Goodall 1986:chapter 7.

"***most of the time***", Wilson 1975:542.

"**These small groups**", Dunbar 1988:10.

"***true casual groups***", Wilson 1975:542.

"***rarely sees all the members***", Goodall 1986:147.

7.6.2 solitude and self-sufficiency

"***when a male starts to leave***", Goodall 1986:159.

"**The amount of solitary time**", Goodall 1986:159 and 166 and figure 7.3.

"**In contrast, an adult female**", Goodall 1986:159 and 167 and figure 7.3.

"***she is unlikely***", Goodall 1986:159.

"**Once past the dependent stage of childhood**", Goodall 1986:231 and figure 10.3.

"**Upon finding a well-laden food tree**", Goodall, 1986:236.

"**But, while they gather at a food tree**", Savage-Rumbaugh 1994:76.

"**In general, adult chimpanzees**", Goodall 1986:372.

"**However, males are more ready**", Goodall 1986:369.

"**From the age of about three**", Goodall 1986:245.

"**Captive chimpanzees**", Goodall 1986:374, and Savage-Rumbaugh 1994:76 on sharing food, and Bullinger 2013 on feeding alone.

"**There are occasional accounts**", the details of Faben's life are pieced together from Goodall 1986:62, 64, 94, 178, 204, 418, and 518. Boyd states that Faben received no day-to day help from his conspecifics (Boyd 2012:296); Goodall does not mention this.

7.6.3 collective and cooperative chimpanzee activities

"**I now want to look at activities**", the basic idea of the universal hierarchy is that individuals, with their particular properties and capabilities, come together in communities. The point is that communities are made by individuals not doing the same thing, but doing different things, with each contributing its special property or capability. So, it's important to use the right language for this. What seems to be important is to distinguish between individuals that are all doing the same thing, and individuals that are doing complementary, and therefore different things. There are several words which mean or suggest acting together, but I'll use only two. I'll use the term "collective" for individuals all doing the same thing, and "cooperative" for individuals doing different, complementary things.

Christophe Boesch has classified different degrees of co-operation for predators hunting: *similarity* means that individuals perform similar actions; in *synchrony* they co-ordinate their actions in time; in *co-ordination* they co-ordinate their actions in time and in space; and in *collaboration* they perform different but complementary rôles to achieve the task (Boesch 1989 and 2002). In earlier chapters I've used the term "cooperation" to describe how agents act together at a particular level in the universal hierarchy, and I'll continue to use that term, and I take it to be equivalent to Boesch's "collaboration".

"**Male chimpanzees are highly competitive**", Goodall 1986:489, Mitani 2009. John Mitani also includes chimpanzees acting together in coalitions, but I've left this out because I want to look at chimpanzees acting together against an external agent, another chimpanzee group in the case of patrolling, and monkey prey in the case of hunting.

chimpanzee patrols are collective activities

"**Patrols can last two hours**", see, for example, the conflict between the Kasakela, Kahama and Kalande communities, in Goodall 1986:chapter 17.

hunting as a male-bonding sport?

This section is based on Newton-Fisher 2007 and 2014, Goodall 1986, and Gilby 2010.

"**Chimpanzees are primarily fruit-eaters**", Newton-Fisher 2014. This section is about the hunting behaviours of chimpanzees (*P. troglodytes*). Bonobos will make opportunistic kills of forest antelopes and squirrels, and they have been observed to engage in group hunting of immature monkeys, but these are not common events (Surbeck 2008, de Waal 1997:82). A recent review of chimpanzee hunting focusses on chimpanzees and bonobos are only mentioned briefly in the conclusion. Overall, bonobos eat very little meat, and it's estimated that animal foods are only about 1% of their diet (de Waal 1997:66). If bonobos encounter monkeys, they are more likely to groom them and treat them as toys and playthings than to eat them. This behaviour contrasts sharply with that of chimpanzees, who would be likely to kill and eat any monkey they encountered (de Waal 1997:65).

"**… very much favour colobus monkeys**", these are the only monkeys that have no thumbs, and their name comes from the Greek word *kolobus*, which means "mutilated" or "docked" (Carroll 2007:91).

"**Hunting frequency**", figures from Boesch 1989:555 and table 7. It's estimated that the 45 or so chimpanzees in the Gombe reserve consumed ~440 kg of meat in an average year (Newton-Fisher 2014).

"**There seems to be no simple reason**", Gilby 2010, Newton-Fisher 2014.

"**Some populations hunt only rarely**", Gilby 2010.

"**While hunts are undoubtedly physically active**", Goodall 1986:chapter 11.

"***colobus male aggression***", Goodall 1986:274.

"**There are many graphic accounts**", some instances are described in Goodall 1986:chapter 17.

"**The picture that emerges**", Newton-Fisher 2014.

A study of a large chimpanzee community concluded that hunting is primarily a male bonding activity, whereby males "*use meat as a social tool to develop and maintain alliances with other males*" (Mitani 2001:915).

"***female-centred society***", de Waal 1997:78.

"***when a capture is made***", Goodall 1986:299, and also see Boesch 1994 and 2002:41.

"**kills are fairly often discarded**", Boesch 1994, Newton-Fisher 2014.

7.6.4 the Taï chimpanzee hunters

"**The different chimpanzee populations**", see, for example Boesch's comparisons of the Taï, Gombe and Mahale chimpanzees in Boesch 1989. This section is based on Boesch, 1989, 1994, 2002 and 2005.

"**Chimpanzees are generally fearful**", Goodall 1986:274.

"**But the adult Taï chimpanzees**", Boesch 1989:557.

"**Taï chimpanzee hunts don't last long**", all data in this paragraph is from Boesch 1989: hunt duration, table 6; hunting frequency, p. 555; success rate, table 7; group size, table 9, and though groups of more than 6 have a greater success rate, they are uncommon, and make up only about 9% of hunts; male/female ratios, table 12, which reports 254 adult hunters, of which 221 were males, 27 of whom captured a monkey, and 33 were females, of whom 7 captured a monkey, so 221/254 ≈ 87% of the hunters were male, and 33/254 ≈13% were female, and 27/221≈12% of the male hunters captured a monkey, while 7/33 ≈21% of the female hunters were captors; female kill rates, p. 560; rates of loss of female kills, p. 561; unknown theft and meat sharing, p. 563.

"**Different chimpanzee populations**", Newton-Fisher 2014.

"**For example, the tree canopy**", Boesch 1994, 2002.

"***each follows a different target prey***", Boesch 1994:663.

four rôles in a hunting party

"**The chimpanzees of the Taï community**", Boesch 1989, 2002, 2005.

"***synchronizes and spatially coordinates***", Boesch 2005:692.

"**The different hunting rôles**", Boesch 2002:33.

"**The Taï chimpanzees**", Christophe Boesch observed the Taï chimpanzees to hunt between 5 and 10 times a month, which means that a hunter with 20 years experience will have taken part in between 1,200 and 2,400 hunts (Boesch 1989:555).

"**It is the older males**", Boesch 2002:figure 2.

sharing out the kill

"***scream at the top of their lungs***", Boesch 2002:41.

"**The different hunting group rôles**", Boesch 2005:692.

"**Three activities**", Boesch 2002:39.

"***Individual effort is not directly rewarded***", Boesch 2002:41.

"**These rules are socially enforced**", this is different from the behaviour of the Gombe and Mahale chimpanzees, where dominant individuals regularly steal prey from its captor (Boesch 2002:41).

the Taï chimpanzees are cooperative hunters

“***Taï chimpanzees***”, Boesch 1989:571.

“**He likens the Taï chimpanzee hunting group**”, Boesch 2005).

“**The sophisticated hunting practices**“, some researchers have taken a different view. Michael Tomasello (2005c:676) has said it is possible that the chimpanzees are doing something less co-operative, and that “*the initiating chimpanzee is attempting to capture the monkey for itself since the captor gets most meat (or else he knows from experience that once he initiates the chase, a group kill will often ensue and he will get at least some meat), and then the others go to places where they expect to maximise their chances of capturing the fleeing monkey, which also increases the group's chances as an unintentional by-product. … The coordination is therefore an emergent property generated by individual decision making not aimed at that coordination*”.

Tomasello has also written, “*Although* [the hunt] *is a complex social activity, as it develops over time each individual simply assesses the state of the chase at each moment and decides what is best for it to do. There is nothing that would be called collaboration in the narrow sense of joint intentions and attention based on coordinated plans*” (Tomasello 2006:521).

Ian Gilby has said that the apparent collaboration of the Taï chimpanzees is “*a simple by-product mutualism whereby individuals take advantage of the actions of others in an effort to maximise their own chances of success*” (Gilby 2010:229).

However, these three proposals are insufficient to explain Boesch's detailed observations: (1) in half of the observed hunts, the group went into “hunting mode” before any prey was seen or heard (Boesch 1989:554); (2) the decision to go hunting was not down to one individual, but was a group decision, and it was observed that “*the chimpanzees become totally silent, remain very close together, move one behind the other, and stop regularly to look up into the trees, alert to the sound of monkeys*” (Boesch 1989:554); (3) the driver is the team member with the least chance of catching the prey, ~1% (Boesch 2005); (4) the drivers were the youngest and least experienced of the hunting group, and unlikely to have the social status to initiate a hunt; (5) chimpanzees developed their group hunting skills over maybe 20 years, and the oldest and most experienced members of hunting teams would take the rôle of ambusher, even though there would be a small chance (~11%) of capturing the prey (Boesch 2002:35 and 2005); (6) captors don't keep most of the kill; of 19 observed kills, in 10 cases the captor voluntarily shared it with another, in 5 cases he had to share it with other higher-ranking individuals, and in 4 cases the captor lost all the kill, although he later received some meat through sharing (Boesch 1989:561); (7) the Taï hunting teams have joint intentions and coordinated plans, in that there are distinct team rôles, with the oldest and most experienced chimpanzee usually taking the most cognitively demanding rôle of ambusher.

The most parsimonious explanation is that the coordination of the hunting Taï chimpanzees is indeed an “*emergent property generated by individual decision making*” (Tomasello 2005a:676), but these individual decisions are all directed towards cooperation and a collectively beneficial outcome. The different rôles in the hunt have different cognitive demands. The cognitive demands of the driver, chaser and blocker rôles are fairly low, and perhaps are covered by Tomasello's (2006) comment, but chimpanzees in these rôles are still not just acting to maximise their own chances of success. The ambusher has the most cognitively demanding rôle, because he has to predict which way the monkey will go, and how its actions may change in response to the actions of the blockers.

“**Colobus monkeys**”, Boesch 2002:30 and 42.

“**The blockers**”, Boesch 2002:42.

“**To coordinate their efforts**”, while the team members have to comprehend each other's different *spatial* perspectives, they all have the same shared *cognitive* perspective on the joint task of catching the prey. We'll see in the next chapter that chimpanzees are not capable of comprehending another individual's differing or conflicting perspective on a situation. I'll return to this in chapter 8, when I look at the hunting and scavenging activities of our human ancestors. The features of a chimpanzee hunt seem to be: a shared cognitive perspective, understanding different spatial perspectives (that is, knowing whether another individual can see what you can see), convergent attention on the prey, and team members being able to see each other, at least most of the time.

“**I think that here**”, Andrew Whiten has come to the same conclusion: “*the most sophisticated primate hunting, done by the chimpanzees of the Tai forest, seems already to depend on skilled reading of the intentions and attention of those others engaged in the hunt*” (Whiten 2000:190).

The hunting practice of the Taï chimpanzees is equivalent to a task involving shared plans and goals, which is one of the 8 behaviours that depend on theory of mind, according to Simon Baron-Cohen (Baron-Cohen 2000:262). An example of such a joint task is two chimpanzees using a log to climb a high wall. The first animal holds the log steady while the second climbs up it to the top of the wall, then the second holds the log steady while the first climbs up it. The goal “*is not achievable without the help of the other animal, and both animals cannot help each other without realizing what both are aiming at. With this joint plan in mind, each can recognize why the other is taking the different role that they are (e.g. the holder of the log versus the climber of the log)*” (Baron-Cohen 2000:264).

Mark Moffett considers that “*the most specialized outings in the animal kingdom may be when a party of chimpanzees hunts for primate meat, or when gray wolves or spotted hyenas gear up for the chase*” (Moffett 2019:113).

It appears that chimpanzees in the Ngogo community, in the Kibale National Park, in Uganda, are also capable of some cooperative behaviours in hunting colobus monkeys, though not as advanced as the Taï chimpanzees (Mitani 1999:446).

7.7 the limits to primate cognition

“**In the first example**”, de Waal 2007:169.

“**High-ranking males**”, de Waal 2007:163.

“**The second example**”, de Waal 2006:222 and 2007:34.

“***Yeroen walks past***”, de Waal 2007:34.

“**Yeroen wanted Nikkie**”, Frans de Waal suggests that Yeroen's pretence of being injured was to make Nikkie feel guilty for hurting his coalition partner and show him some sympathy (de Waal 2007:36, 2006:222). Whether the deception succeeded, and it changed Nikkie's behaviour towards Yeroen doesn't matter; it was clearly important enough to Yeroen that he maintained the pretence for nearly a week. The lack of language is not an issue, because a chimpanzee could simply have taken Nikkie to see Yeroen walking normally, as Dandy did with Yeroen in the first example. I'll come back to this example of deception in section 8.1.4.

a cognitive boundary

“**Here we have our cognitive boundary**”, there have been careful comparative studies of the cognitive development of chimpanzees and humans, and Michael Tomasello has played a large part, see for example, Tomasello 2005a, 2005b, 2012, 2013, and 2018. This is not the place to go into this, and I discuss this in section 8.1.4. What I wanted here was some examples of natural chimpanzee behaviour, that would reveal the cognitive boundary between them and humans, and I think that the interactions between Dandy, Yeroen and Nikkie do this.

7.8 review of Level 7

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