Neuron Volume *80*

Supplemental Information

Scaling Brain Size, Keeping Timing:
Evolutionary Preservation of Brain Rhythms

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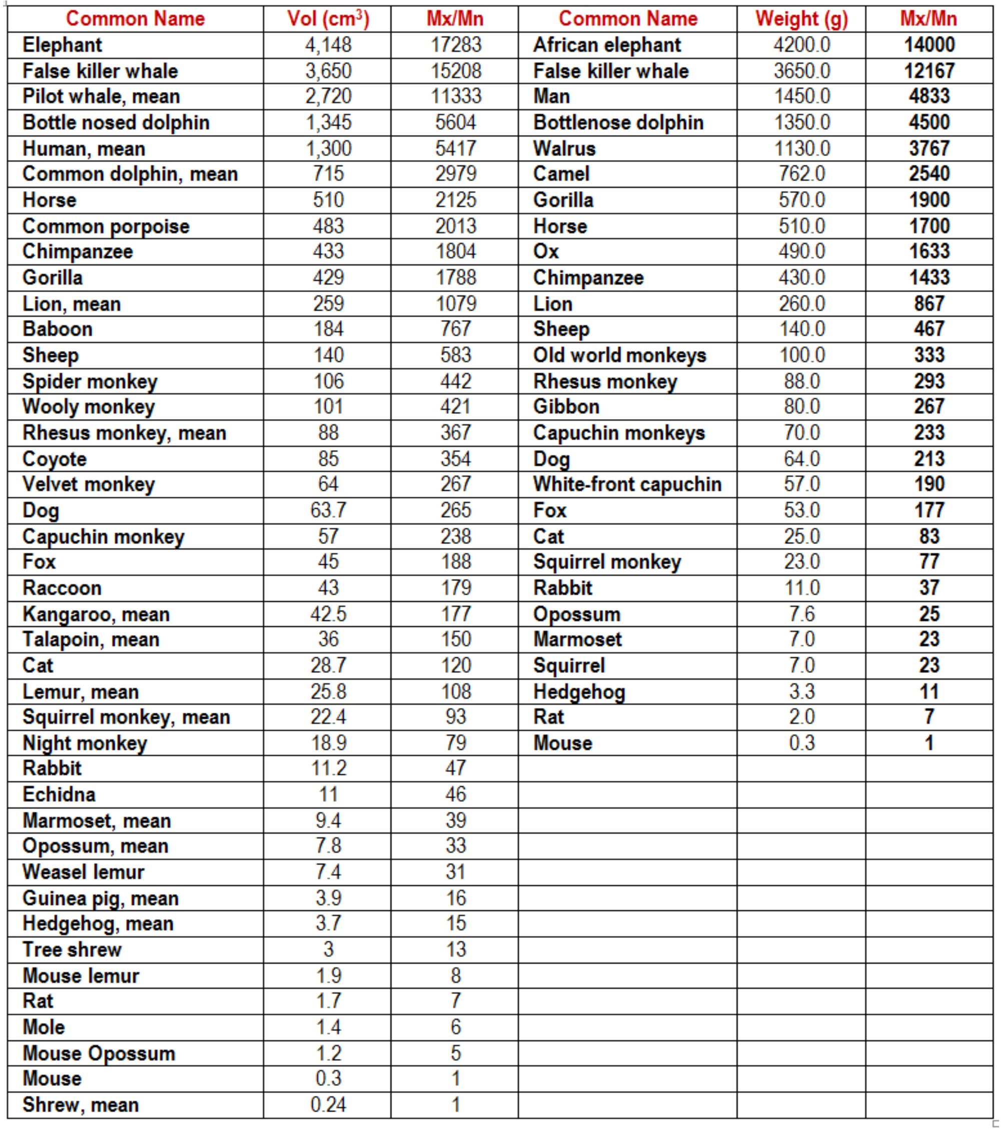
Supplementary Note 1. Table 1 was compiled based on the published works of Haug (1987) and Roth and Dicke (2005). Other important papers on brain volume, weight, neuronal density, neuronal number and body weight include Elias and Schwartz (1969) and (Roth and Dicke, 2005) and (Schüz and Sultan 2009). Further useful sources for brain weights: http://faculty.washington.edu/chudler/facts.html and http://mste.illinois.edu/malcz/DATA/BIOLOGY/Animals.html.

In addition to brain volume and weight, Columns 3 and 6 (Mx/Mn) show the growth of each species-brain in units of the "minimum" brain; e.g., the human brain has a volume of ca. 5400 greater than that of the mouse and is about 4800 heavier than the mouse brain.



Common Name	Vol (cm^3)	Mx/Mn	Common Name	Weight (g)	Mx/Mn
Elephant	4,148	17283	African elephant	4200.0	**14000**
False killer whale	3,650	15208	False killer whale	3650.0	**12167**
Pilot whale, mean	2,720	11333	Man	1450.0	**4833**
Bottle nosed dolphin	1,345	5604	Bottlenose dolphin	1350.0	**4500**
Human, mean	1,300	5417	Walrus	1130.0	**3767**
Common dolphin, mean	715	2979	Camel	762.0	**2540**
Horse	510	2125	Gorilla	570.0	**1900**
Common porpoise	483	2013	Horse	510.0	**1700**
Chimpanzee	433	1804	Ox	490.0	**1633**
Gorilla	429	1788	Chimpanzee	430.0	**1433**
Lion, mean	259	1079	Lion	260.0	**867**
Baboon	184	767	Sheep	140.0	**467**
Sheep	140	583	Old world monkeys	100.0	**333**
Spider monkey	106	442	Rhesus monkey	88.0	**293**
Wooly monkey	101	421	Gibbon	80.0	**267**
Rhesus monkey, mean	88	367	Capuchin monkeys	70.0	**233**
Coyote	85	354	Dog	64.0	**213**
Velvet monkey	64	267	White-front capuchin	57.0	**190**
Dog	63.7	265	Fox	53.0	**177**
Capuchin monkey	57	238	Cat	25.0	**83**
Fox	45	188	Squirrel monkey	23.0	**77**
Raccoon	43	179	Rabbit	11.0	**37**
Kangaroo, mean	42.5	177	Opossum	7.6	**25**
Talapoin, mean	36	150	Marmoset	7.0	**23**
Cat	28.7	120	Squirrel	7.0	**23**
Lemur, mean	25.8	108	Hedgehog	3.3	**11**
Squirrel monkey, mean	22.4	93	Rat	2.0	**7**
Night monkey	18.9	79	Mouse	0.3	**1**
Rabbit	11.2	47			
Echidna	11	46			
Marmoset, mean	9.4	39			
Opossum, mean	7.8	33			
Weasel lemur	7.4	31			
Guinea pig, mean	3.9	16			
Hedgehog, mean	3.7	15			
Tree shrew	3	13			
Mouse lemur	1.9	8			
Rat	1.7	7			
Mole	1.4	6			
Mouse Opossum	1.2	5			
Mouse	0.3	1			
Shrew, mean	0.24	1			

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Supplementary Note 2. Types of brain rhythms in mammals

Below, we overview some of the best-studied rhythms without the aim of being comprehensive.

Slow oscillations (slow 1 in Fig. 1; 0.7-2 Hz; Steriade et al., 1993a) are the most prominent patterns during sleep. The LFP slow waves reflect alternating phases of synchronous depolarization and spiking (‘up state’) and hyperpolarization (“down state’) of large groups of cortical neurons (Steriade et al., 1993a; Timofeev et al., 2000; Sanchez-Vives and McCormick, 2000). The down state of slow oscillations, also known as the ‘*delta wave’*, is a time frame of cortical silence and a potential rebooting and recuperating mechanism for energy conservation (Borbely, 1982; Isomura et al., 2006; Vyazovskiy and Harris, 2013, Cossart et al., 2003). Slow oscillations typically involve most of the neocortex, although isolated up and down states can also occur even within a small volume of tissue (Nir et al., 2011; Sirota and Buzsáki, 2006).

The transition from down to up states is the most synchronous part of slow oscillations. The large sudden shift of membrane voltage in many cortical neurons is reflected extracellularly as a 50-100 msec K wave (Fig. 2a). The strong spiking synchrony of deep layer cortical neurons associated with the K wave can trigger a reverberating thalamocortical event in the form of a *sleep spindle* (12-18 Hz; cf., Steriade et al., 1993b). The K wave and the induced spindle constitute a *K complex* (Loomis et al., 1937). Despite the several orders of magnitude larger travel distances of action potentials in the thalamocortical and corticothalamic loops in larger brains, the frequency range of the sleep spindle remains the same (12-18 Hz) in all mammals investigated (Fig. 2a). In addition to the preservation of frequency, the spindle shape of the transient event and its duration (0.5-2 sec) also remain quite similar.

Alpha oscillations (Fig. 2a), another family of thalamocortical rhythms, occur in waking but relaxed brain states and involve primarily the first-order thalamic nuclei and sensory cortical areas. The best known alpha patterns (8-12 Hz) emerge after eye closure and cessation of eye movements in the occipital-posterior part of the neocortex in primates and carnivores with large cortical domains dedicated to vision (Berger, 1929; Lopes da Silva et al., 1973; 1980; Klimesch 1997; Bollimunta et al., 2008; Hughes et al., 2004). The second form of alpha oscillations, also known as the Rolandic μ rhythm (8-20 Hz) occurs in the somatosensory system during immobility but disappears upon movement initiation and even movement imagination (Fig. 2a; Gastaut et al., 1954; Pfurtscheller et al., 1996; 2000; Bouyer et al., 1983). In rodents, where face-whisker representation is particularly large, the μ rhythm occurs synchronously over the parietal-frontal areas during immobility and is the dominant form of alpha oscillations (Buzsáki et al., 1988; Wiest and Nicolelis, 2003). The third alpha pattern is the tau rhythm of the auditory system, prominent in the absence of acoustic inputs (Tiihonen et al., 1991).

Most authors agree that alpha oscillations reflect a ground state to which the respective cortical area relaxes when disengaged from its sensory input and the rhythm is replaced by ‘desynchronized’ (i.e., gamma dominant) patterns when the area is activated (Pfurtscheller et al., 1996; Haegens et al., 2011). However, there are also instances when alpha activity increases with task difficulty together with high frequency oscillations. Here source localization indicates that alpha activity serves to repress distracting signals, thereby enhancing performance (Roux et al., 2012). This slower form of alpha (with an overlap with the theta band) can be induced by cognitive tasks in the more frontal regions of the cortex (Klimesch 1997). It is possible that this ‘attention type’ of alpha may arise in the limbic part of the thalamus and associated cortical regions, similar to the ‘sensory’ alpha oscillations and is generated by different mechanisms.

Beta rhythms are oscillations in the 12-30 Hz range that are pronounced in motor cortex, basal ganglia, cerebellum, hippocampus and even in peripheral motor-units during steady muscle contractions, while a response is withheld and to a lesser extent during immobility. Their origin, mechanisms and relationship to oscillations in the same frequency band (e.g., sleep spindles and beta patterns in the olfactory areas) are not well understood. In general, voluntary movements appear to be associated with a drop in beta power, and the termination of movement is followed by a restoration of beta power (Salmelin and Hari, 1994). Beta oscillations decrease substantially also during imagination, preparation and execution of movements (Murthy and Fetz, 1996;

Salmelin and Hari, 1994). In other words, somewhat analogous to the sensory alpha oscillations, beta rhythms reflect *disengagement* of the motor system from action by stabilizing a ‘status quo’ in posture and preventing the initiation of a new movement (Brown, 2000; Engel and Fries, 2010). Support for the latter interpretation comes from recordings in patients affected with Parkinson´s disease and from animal models of this syndrome. The inability to initiate movements or to stop ongoing locomotion is attributed to the failure to block ongoing beta oscillations in striatal circuits and to replace them by high frequency oscillations in the gamma range (Kuhn et al., 2008).

Overall, beta oscillations appear to coordinate the timing of action potentials of neurons in widespread brain areas with large distances from each other and along with muscles. During isometric contractions, for instance, beta rhythms are coherent between motor cortex and the contralateral electromyogram and beta-band coherence can also be observed between agonist muscles, suggesting a shared cortical drive (cf. Brown, 2000). In the same vain, simple cognitive and executive functions involve cooperation of numerous cortical areas and the formation of such transient, task-dependent functional networks is usually associated with increased coherence in the beta frequency range (Roelfsema et. al., 1997; Dehaene et al., 2006). Recently, it has been proposed that bottom-up processing is coordinated mainly in the gamma – and top-down control mainly in the beta band (Buffalo et al., 2011; Bosman et al., 2012).

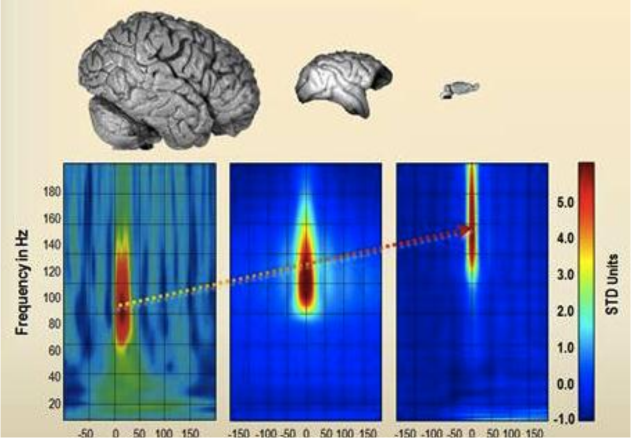
Theta oscillations represent a consortium of mechanisms, supported by various intracellular and circuit properties of the septo-hippocampal-entorhinal system (Buzsáki, 2002). They are strongly involved in various cross-frequency interaction mechanisms, in both the hippocampus and cortex. Theta rhythms, for instance, modulate the firing rate and spike timing of single hippocampal or cortical neurons (Bragin et al., 1995, Buzsaki et al., 2003, Lee et al., 2005; Liebe et al., 2012), and the gamma power of the LFP (Bragin et al., 1995; Chrobak and Buzsaki, 1998, Canolty et al., 2006). Importantly, theta-gamma cross-frequency coupling has been shown to correlate with navigation and memory performance in rats (Tort et al., 2009), as well as with memory in monkeys (Lee et al., 2005) and humans (Canolty et al., 2006, Axmacher et al., 2010, Griesmayr et al., 2010).

Rhythms in the theta frequency bands are also observed in various parts of the neocortex. In monkeys the cortical theta frequency is in the range of 3-9 Hz (Lee et al., 2005, Liebe et al., 2012), and in humans 4-12 Hz, e.g. (Raghavachari et al., 2006, Anderson et al., 2010). However, their origin and their relationship with hippocampal theta oscillations remain to be clarified. The prominent midline prefrontal ‘theta’ is often dominated by a lower frequency (4 Hz) peak, and this LFP pattern might represent a ventral tegmental area (VTA) - nucleus accumbens - prefrontal cortex “4 Hz” oscillation, independent but coupled with the hippocampal theta rhythm (Fujisawa et al., 2011; Siapas et al., 2005; Sigurdsson et al., 2010).

Gamma oscillations (30–90 Hz) are the most ubiquitous rhythm, present in all structures and brain states. The gamma generators have been studied in great detail both at the experimental and theoretical level (Jefferys et al., 1996; Kopell et al., 2000; Traub et al., 1996, 2001; Buzsáki and Wang, 2012; Buhl et al., 2003; Wang 2010). Gamma oscillations emerge from the network of reciprocally coupled pyramidal cells and parvalbumin containing inhibitory basket cells that inhibit pyramidal cells with a dense plexus of perisomatic synapses. This network of inhibitory neurons engages in synchronized gamma oscillations whenever sufficiently activated and then periodically modulates pyramidal cell excitability. The excitatory drive for the inhibitory interneurons is provided both by external input and recurrent collaterals from the pyramidal cells.

Recordings in patients with epicortical (ECoG) and depth electrodes revealed task dependent increases in the power of LFP activity in a frequency range above the classical gamma frequency band (epsilon; >90 Hz) (Lachaux et al., 2000; Mukamel et al., 2005). This power increase is often broad-band and does not produce a distinct peak in the 1/f spectrogram. Although this broad-band activity is often labeled as ‘high gamma’ and discussed together with gamma oscillations, its oscillatory nature has yet to be demonstrated. It most likely reflects increased spiking and spike afterpotentials without an oscillatory component (Whittingstall and Logothetis, 2009; Belluscio et al., 2012; Ray and Maunsell, 2011).

Ripples. The most precisely synchronized cortical rhythm is the fast ‘*ripple’ oscillation* of the hippocampus (130-160 Hz: Buzsáki et al., 1992; O’Keefe and Nadel, 1978) and neocortex (300-500 Hz: Kandel and Buzsáki, 1997; Buzsáki and Lopes da Silva, 2012). The physiological importance of hippocampal ripples is that in the short time window of the ripple event (50-100 ms) spikes of neurons active in the preceding learning and exploration experience are replayed in a compressed manner (Wilson and McNaughton, 1994; Carr et al., 2011). Selective abolishment of ripples prevents consolidation of previously learned information (Girardeau et al., 2007). Given its local generation, it is perhaps not surprising that the frequency of these fast rhythms remains constant over the course of mammalian evolution (Fig. 2a). On the other hand, the synchronous hippocampal output can exert a powerful influence on both widespread cortical and subcortical structures in both rats and monkeys (Siapas et al., 2005; Logothetis et al., 2013) and appropriate timing of these widespread regions demand structural support.



Wavelet illustration of dominant spectral power of hippocampal ripples in the human (100 Hz), monkey (120 Hz) and rat (140 Hz) brains. Data from the human brain is after Axmacher et al. (2008); monkey ripple from Logothetis et al. (2012).

Ultraslow rhythms (<0.1 Hz; slow 2-4 in Fig. 1B) involve coherent fluctuations of resting state activity across large areas of the neocortex and subcortical sites that can even be detected in the slow fMRI signals. Such slow and coordinated oscillations (0.1-0.02 Hz) of cortical network excitability have been discovered in humans (revealing the so called “default network”, (Raichle et al., 2001), confirmed in a variety of species, (monkeys: Leopold et al., 2003, cats: Popa et al., 2009; rats: Sirota et al., 2003) and now routinely used to identify functional networks.

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Supplementary Note 3. References related to Figure 2 and the discussion of brain rhythms above are listed below. This selected list contains only in vivo experiments and typically drug free states. Numerous informative experiments have been carried out on the various oscillations in vitro as well, which are not listed here. The references are broken down into oscillatory patterns and species.

Alpha/mu/tau oscillations

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Theta

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Swine

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Human

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Beta

Human

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Slow oscillations (~1 Hz)

Human

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Mouse

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Ultra slow oscillations (<0.1 Hz)

Human

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Supplementary Note 4. A systematic comparison of evoked responses across various species should be a subject for another review. There is consensus that the magnitude, shape, brain structure localization, pharmacological sensitivity, synaptic-circuit mechanisms and behavioral correlations are preserved across the various mammalian species. The latency of the various components of evoked signals in rats and mice (N1, P2, N2 and P3) are 30-50% shorter than in humans. Note, however, that the signal has to travel much longer distances in the human brain. In humans these components roughly correspond to N100 msec, P200, N250 msec and P350 msec, whereas in rats and mice they correspond approximately to 50, 100, 170 and 250-350 msec (Begleiter et al., 1967).

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See extended references in:
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