AI IMPACTS

Neuron firing rates in humans

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Our best guess is that an average neuron in the human brain transmits a spike about 0.1-2 times per second.

Support

Bias from neurons with sparse activity

When researchers measure neural activity, they can fail to see neurons which rarely fire during the experiment (those with 'sparse' activity).[1] Preferentially recording more active neurons means overestimating average rates of firing. The size of the bias seems to be around a factor of ten: it appears that around 90% of neurons are 'silent', so unlikely to be detected in these kinds of experiments. This suggests that many estimates should be scaled down by around a factor of around ten.

Assorted estimates

Informal estimates

Informal websites and articles commonly report neurons as firing between <1 and 200 times per second.[2] These sources lack references and are not very consistent, so we do not put much stock in them.

Estimates of rate of firing in human neocortex

Based on the energy budget of the brain, it appears that the average cortical neuron fires around 0.16 times per second. It seems unlikely that the average cortical neuron spikes much more than once per second.

The neocortex is a large part of the brain. It accounts for around 80% of the brain's volume[3], and uses 44% of its energy[4]. It appears to hold at least a third of the brain's synapses if not many more[5]. Thus we might use rates of firing of cortical neurons as a reasonable proxy for normal rates of neuron firing in the brain. We can also do a finer calculation.

We might roughly expect energy used by the brain to scale in proportion both to the spiking rate of neurons and to volume. This is because the energy required for every neuron to experience a spike scales up in proportion to the surface area of the neurons involved[6], which we expect to be roughly proportional to volume.

So we can calculate:

energy(cortex) = volume(cortex) * spike_rate(cortex) * c

energy(brain) = volume(brain) * spike_rate(brain) * c

For *c* a constant.

Thus,

energy(cortex)/energy(brain) = volume(cortex) * spike_rate(cortex)/volume(brain) * spike_rate(brain)

From figures given above then, we can estimate:

0.44 = 0.8 * 0.16/spike_rate(brain)

spike_rate(brain) = 0.8 * 0.16 /0.44 = 0.29

Or for a high estimate:

0.44 = 0.8 * 1/spike_rate(brain)

spike_rate(brain) = 0.8 * 1 /0.44 = 1.82

So based on this rough extrapolation from neocortical firing rates, we expect average firing rates across the brain to be around 0.29 per second, and probably less than 1.82 per second. This has been a very rough calculation however, and we do not have great confidence in these numbers.

Estimates of rate of firing in non-human visual cortex

A study of macaque and cat visual cortex found rates of neural firing averaging 3-4 spikes per second for cats in different conditions, and 14-18 spikes per second for macaques. A past study found 9 spikes per second for cats.[7] It is hard to know how these estimates depend on the region being imaged and on the animal being studied, which significantly complicates extracting conclusions from these results. Furthermore, these studies appear to be subject to the bias discussed above, from only sampling visually responsive cells. Thus they probably overestimate overall neural activity by something like a factor of ten. This suggests figures in the 0.3-1.8 range, consistent with estimates from the neocortex. Note that the visual cortex is part of the neocortex, so this increases our confidence in our estimates for that, without reducing our uncertainty about the rest of the brain.

Maximum neural firing rates

The *'refractory period'* for a neuron is the time after it fires during which it either can't fire again (*'absolute refractory period'*) or needs an especially large stimulus to fire again (*'relative refractory period'*). According to physiologyweb.com, absolute refractory periods tend to be 1-2ms and relative refractory periods tend to be 3-4ms.[8] This implies than neurons are generally not capable of firing at more than 250-1000 Hz. This is suggestive, however the site does not say anything about the distribution of maximum firing rates for different types of neurons, so the mean firing rate could in principle be much higher.

Conclusions

Informal estimates place neural firing rates in the <1-200Hz range. Estimates from energy use in the neocortex suggests a firing rate of 0.16Hz in the neocortex, which suggests around 0.29Hz in the entire brain, and probably less than 1.8Hz, though we are not very confident in our estimation methodology here. We saw animal visual cortex firing rates in the 3-18Hz range, but these are probably an order of magnitude too high due to bias from recording active neurons, suggesting real figures of 0.3-1.8 Hz, which is consistent with the estimates from the neocortex previously discussed. Neuron refractory periods (recovery times) suggest

1000Hz is around as fast as a normal neuron can possibly fire. Combined with the observation that 90% of neurons rarely fire, this suggests 100Hz as a high upper bound on the average firing rate. However this does not tell us about unusual neurons, of which there might be many.

So we have two relatively weak lines of reasoning suggesting average firing rates of around 0.1Hz-2Hz. These estimates are low compared to the range of informal claims. However the informal claims appear to be unreliable, especially given that two are higher than our upper bound on neural firing rates (though these are also unreliable). 0.1-2Hz is also low compared to these upper bounds, as it should be. Thus our best guess is that neurons fire at 0.1-2Hz on average.

1. Table 1 of Shoham et al. reports on a variety of investigations of sparsity in neural behavior, most of which suggest that more than 90% of neurons are sufficiently silent that they are not easily detectable. Summarizing their own results, they say "Table 1 suggests that such proportions may vary widely among different brain regions and preparations, a notion which is consistent with hierarchical, increasingly sparse neural coding schemes. Conservative estimates may, however, be possible by considering those parameters of the neuron–electrode interface that affect the detection of unit signals… suggesting a silent fraction of at least 90%." (p. 782).

   Experimenters recording from a rat cortex find "Both electrical and optical recordings consistently revealed that individual neurons as well as populations of neurons display sparse spontaneous activity. Single neurons displayed low AP rates of <0.1 Hz, in agreement with previous *in vivo* studies." (Kerr et al 2005) ↩

2. 'But generally, the range for a "typical" neuron is probably from <1 Hz (1 spike per second) to ~200 Hz (200 spikes per second).' -'Astra Bryant, Ask a neuroscientist! – what is the synaptic firing rate of the human brain?'

   "A typical neuron fires 5 – 50 times every second." – *www.human-memory.net*

"The brain can't handle neurons firing all the time. Neurons fire around 10x per second and already the brain is consuming 20% of the body's energy at 2% of the body's weight." – Paul King, computational neuroscientist, on Quora

"Modern computer chips handle data at the mind-blowing rate of some 10^13 bits per second. Neurons, by comparison, fire at a rate of around 100 times per second or so. And yet the brain outperforms the best computers in numerous tasks." – MIT Technology Review ↵

3. Dunbar references anatomical measurements from 1981 and writes "With a neocortical volume of 1006.5 cc and a total brain volume of 1251.8 cc (Stephan et al. 1981), the neocortex ratio for humans is CR = 4.1." (p. 682). ↵
4. "Using the best estimate, in the normal awake state, cortex accounts for 44% of whole brain energy consumption in 200 ms, the brain's normal energy consumption supports a strong (solid horizontal line, intercept on ordinate)." – Lennie 2003 ↵
5. "The average total number of synapses in the neocortex of five young male brains was 164 x 10(12) (CV = 0.17)." Tang et al, 2001

   "Number of synapses in cortex = 0.15 quadrillion (Pakkenberg et al., 1997; 2003)" – Eric Chudler

   "The human brain has a huge number of synapses. Each of the 10^{11} (one hundred billion) neurons has on average 7,000 synaptic connections to other neurons. It has been estimated that the brain of a three-year-old child has about 10^{15} synapses (1 quadrillion). This number declines with age, stabilizing by adulthood. Estimates vary for an adult, ranging from 10^{14} to 5 x 10^{14} synapses (100 to 500 trillion)." Wikipedia accessed April 13 '15, citing Drachman, D (2005). "Do we have brain to spare?". *Neurology* **64** (12): 2004–5. We have not accessed most of the Drachman paper, but it does at least say "Within the liter and a half of human brain, stereologic studies estimate that there are approximately 20 billion neocortical neurons, with an average of 7,000 synaptic connections each". It seems improbable that the average number of synapses per neuron in the brain is the same as that in the neocortex, weakly suggesting the Wikipedia contributor made an error.

   These figures suggest that the neocortex accounts for between a third and most of synapses. ↵

6. “The cost of propagating an action potential in an unmyelinated axon is proportional to its surface area.” – Lennie, 2003 ↩
7. “spikes were recorded while a given video sequence representative of natural scenes was played. Data were collected from three cats, and two macaques. The cats were anaesthetized and the macaques were awake and free viewing. Only visually responsive cells were used… For V1 of the anaesthetized cats, the firing rates for the video-stimulated neurons were low (mean = 3.96Hz, s.d. = 3.61Hz). This was lower than has been previously reported (Legendy & Salcman 1985) for the unanaesthetized cat (mean = 8.9 Hz, s.d. = 7.0 Hz), but was significantly higher than when the cells were stimulated with high contrast white noise (mean = 2.45Hz, s.d. = 2.18 Hz). It is proposed that the low average rates were partly due to the effect of the anaesthetic (which could be tested by systematically varying its level). For the macaque IT cells, generally in the upper bank of the superior temporal sulcus at sites similar to those in (Rolls & Tovee 1995), the average rate was higher for both video stimulation (mean = 18 Hz, s.d. =10.3 Hz), and blank screen viewing (mean = 14 Hz, s.d. = 8.3 Hz.)” Baddeley et al 1997 (p. 1776) ↩
8. Therefore, it takes about 3-4 ms for all Na^+ channels to come out of inactivation in order to be ready for activation (opening) again. The period from the initiation of the action potential to immediately after the peak is referred to as the **absolute refractory period (ARP)** (see Figs. 1 and 2). This is the time during which another stimulus given to the neuron (no matter how strong) will not lead to a second action potential. Thus, because Na^+ channels are inactivated during this time, additional depolarizing stimuli do not lead to new action potentials. The absolute refractory period takes about 1-2 ms…

   …During the absolute refractory period, a second stimulus (no matter how strong) will not excite the neuron. During the relative refractory period, a stronger than normal stimulus is needed to elicit neuronal excitation.

   After the absolute refractory period, Na^+channels begin to recover from inactivation and if strong enough stimuli are given to the neuron, it may respond again by generating action potentials. However, during this time, the stimuli given must be stronger than was originally needed when the neuron was at rest. This situation will continue until all Na^+ channels have come out of inactivation. The period during which a stronger than normal stimulus is needed in order to elicit an action potential is referred to as the **relative refractory period (RRP)**. ↵

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