How many neurons are there?

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Abstract

We estimate that there are between $10^{23}$ and $10^{24}$ neurons on earth. Most of this is distributed roughly evenly among small land arthropods, fish, and nematodes, or possibly dominated by nematodes with the other two as significant contenders. For land arthropods, we multiplied the apparent number of animals on earth by mostly springtail-sized animals, with some small percentage being from larger insects modeled as fruit flies. For nematodes, we looked at studies that provide an average number of nematodes per square meter of soil or the ocean floor, and multiplied them by the number of neurons in *Caenorhabditis elegans*, an average-sized nematode. For fish, we used total estimates of ocean fish biomass, attributed some to species caught by humans, and used two different ways of allocating the remaining biomass. Most other classes of animal contribute $10^{22}$ neurons at most, and so are unlikely to change the final analysis. We neglected a few categories that probably aren’t significant, but could conceivably push the estimate up.
Using a similar but less precise process based on evolutionary history and biomass over time, we also estimate that there have been between $10^{32}$ and $10^{33}$ neuron-years of work over the history of life, with around an order of magnitude of uncertainty.
How many neurons are there? - Summary

In creating this estimate, in general, I looked at populations of various large and/or extremely numerous animals. I give special consideration to the ocean (which represents about 75% of the earth’s surface and 99% of the biosphere, although most of it is less densely populated than land). I find a total of about \(3 \times 10^{23} - 1 \times 10^{24}\) neurons across the world. Major categories that contribute to this are small land arthropods, nematodes, and fish, about equally.

The total estimate, with an error of an order of magnitude, seems to be fairly robust - land arthropod, nematode and fish estimates would all have to be drastically lower than predicted for the estimate to shift downwards notably. The main ways this might be wrong are if some of our estimates are far too low (e.g. at least 100 times too low), or if some of the excluded groups are extremely large, or if a systematic error is causing us to describe all three major groups as too large.

Some major missing groups are parasitic nematodes, earthworms, and small animals living on trees. I also wish I had a more accurate count for mammals or breakdown by type of mammal, more accurate data on the number of neurons in different kinds of fish, and a better guess about how many neurons small land arthropods present.

**Land arthropods**

Studies estimate about \(10^{19}\) arthropods in earth’s soils, mostly small springtails and mites. We estimated 1-5% of these were probably somewhat larger arthropods (including insects) that might be approximated as having the neuron count as a fruitfly, and the rest could be approximated as springtails. This gives us \(1 \times 10^{23} - 2 \times 10^{23}\) neurons from land arthropods.

**Nematodes**

One study at many sites compared nematode abundance in kilograms of topsoil. Another examined nematode density in the ocean floor, based on depth, finding hundreds of thousands of nematodes per square meter. Still another, older set of studies referenced “several million” nematodes in each square meter of the land and sea. *C. elegans* is a well-studied nematode that’s about 1 mm long, which is also apparently a reasonable average size for nematodes in the ocean. We multiplied these together and found \(1.17 \times 10^{23} - 7.70 \times 10^{23}\) neurons from nematodes.

**Fish**

A recent study found about \(10^{10}\) tons of fish biomass in the ocean. We use data about fish populations caught by humans to allocate some of this biomass, then try a couple ways of allocating the remainder - either all to very small fish, or all to larger fish proportional to the fish caught by humans. In each case, we find the approximate brain mass for each kind of fish, and multiply by the known density of neurons per grams in the zebrafish, and then by the population sizes. This gives us a lower and upper bound of \(4.2 \times 10^{22} - 1.4 \times 10^{23}\) neurons from fish.
Other
Also contributing, although in much smaller percentage than the above, are: krill, copepods and other pelagic zooplankton, amphibians, reptiles, wild mammals, birds, humans, and domesticated animals.
How many neurons are there? - Full report

Associated spreadsheet:
https://docs.google.com/spreadsheets/d/1MbkEkQy9OfUNfb27z0zClacMTELtdsSB1g9Ds-2WKSU/edit?usp=sharing

Intro

The neuron is the cell that provides the brain’s computing. Almost all animals have neurons, except for sponges and the flat gelatinous taxon *Trichoplax*. Animals tend to have neurons arranged into ganglia (small clusters of neurons) and brains (large complex clusters of neurons). This article tries to answer two questions:

- How many neurons are there on the earth right now?
- How many neuron-years have occurred over all of history?

As you might imagine, these are both very large numbers, and I am not very confident in parts of the data I used to find these. I try to describe where this uncertainty is as I explain where the estimates come from.

In creating this estimate, in general, I looked at populations of various large and/or extremely numerous animals. I then attempted to find a plausible model animal with a known neuron count, and multiplied the two together. In a few cases, I use numbers that represent some kind of group of animals that are mostly but not only limited to the named group (e.g. tiny ocean floor animals that are mostly, but not all, nematodes) - in these cases, I tend to count them similarly (e.g. count them all as nematodes), and make sure that the unnamed members of that group are not counted twice.

Some major missing groups are earthworms and soil invertebrates other than insects or nematodes. These animals’ brains are quite small and they’re confined to land, and I’d expect them to contribute a significantly smaller fraction of total neurons than either insects or nematodes. I was also unable to find relevant data on them easily. I also basically ignored neurons in the rest of the body other than the brain for vertebrates, when that data was unavailable. I figured that the neurons concentrated in the brain would not affect the result by that much.

I give special consideration to the ocean (representing about 75% of the earth’s surface, and 99% of the biosphere, although most of it is less densely populated than land).

I find a total of about 1E24 - 3E24 neurons across the world. This number is broken down as follows:
Nematodes

I focused on nematodes in soil and the ocean floor. Other plausible large sources not considered are nematodes living in wild animals, in the water column, and on plants.

One source (5) refers to studies that count “several million” nematodes per square meter on each of land and sea floor. This leads to 7.4E20 nematodes across the earth. I was uncertain about this number because I couldn’t find the original study, and the source is at least two decades old, so I looked for more specifics.

Soil

One study collected nematodes at 12 sites across the world. With a lot of variation, they found an average of 9919 nematodes per kg of dry soil. (1) I guess that this represents the true world average of nematodes in dry soil. The study appeared to be looking at mixed soil from the top 10 cm of soil. While there are certainly nematodes well below the top 10 cm, I would expect that most nematodes are found close to the surface, where there are more nutrients from plants. As such, I doubled the number, assuming that the number of nematodes below 10 cm is about equal to the number above 10 cm. Using the numbers from the paper of density of studied soil, and the land area of the earth, this suggests there are 2.96E20 nematodes in the earth’s soils.

Ocean floor

A global survey of marine benthic fauna looked at 128 studies at sites across the world. The study recorded benthic fauna abundance as it correlates with depth. Using this information (2) and the amount of the Earth’s surface that occurs at various depths (3), I arrived at a number of 9.03E19 microfauna on the ocean floor. These microfauna were mostly nematodes.

Brain size

Now that we have these numbers, the question becomes how many neurons the average nematode has. The ubiquitous model organism, the nematode Caenorhabditis elegans, is 1 mm long and has exactly 302 neurons in its body. (7) The soil nematode study found that most nematodes were “less than 1 mm long”. (1) The graphs published with a study of ocean floor nematode biodiversity suggests that the mean size of nematodes is around 1.0 mm, and that few seem to be over 2 mm. (6) This suggests that C. elegans is, size-wise, a decent model for the average nematode.

This gives us 2.23 * 10^23 (using the lower nematode abundance) - 2.73 * 10^24 neurons (using the higher abundance) in all nematodes (and some other benthic ocean microfauna).
Insects and land arthropods

The Smithsonian Institute website (4) refers to several literature sources and cites a total literature estimate of 1E19 “insects” across the world. Further examination shows that these sources tend to include springtails (a primitive insect-like animal, no longer phylogenetically considered insects but included as such in the estimates made) and mites (which are arachnids) in and on soil. (I’m therefore assuming these studies gathered information on soil arthropods rather than specifically insects.) Furthermore:

“In most of the reports [of all insects collected in the top 12 inches of soil in fields in England], mites and springtails formed two-thirds or more of the total; in some, the number of springtails was nine-tenths of the total for insects.” (51)

Two other studies referred to found less than 5% of studied animals were insects other than mites and springtails, and that springtails or mites might be more numerous. (51) I figured 1-5% of the animals would include things like ants, flies, and other familiar sizeable insects, and that these might be represented on average by the fruit fly. 99% of these animals, like the mites and springtail, could be represented by the springtail. No formal count has been made of the number of neurons in a springtail, but Tomasik compares its body size to a fruit fly and concludes that if neurons scale linearly with body size between the two, a springtail has about 5800 neurons. (52) The fruit fly is said to have 1E5 (8) or 2E5 (9) neurons in its brain.

Using this, we get 1E22-1E23 neurons from large arthropods and 6E22 neurons from smaller arthropods, for a total of 6E22-2E23 neurons in soil arthropods. The greatest uncertainty here is probably in the number of neurons in a springtail, or the average small soil arthropod.

Fish

A recent estimate, the first of its kind to use acoustic sampling rather than inaccurate trawl nets, estimated that there are 1E10 tons of wild fish biomass in the world’s oceans. Most of these are mesopelagic fish. (17) Starting from this number, we can begin allocating this biomass to individual fish, and then to numbers of neurons. (Note that ‘fish’ here refers to bony fish, sharks, lampreys, etc, not a cladistic definition.)

We can start by looking at fish species caught by humans, and then allocating the remaining biomass. One project provides detailed estimates for the upper and lower tons of fish capture in several categories (ray-finned fish, sharks and rays, lobe-finned fish, etc) and average masses of the fish for each. (18) I guessed that since humans fish out a substantial fraction of the populations of ocean fish, we could multiply the resulting numbers of fish by 10, for the total numbers of fish belonging to each species fished by humans.

The numbers for each category are unwieldy to break down here - see the spreadsheet for details - but averaged as described, we get a total of about 1.03E9 tons of fish in species fished
by humans, and 1.85E13 individual fish. Finding the brain size of these fish is somewhat more complicated. Very few fish have had the number of neurons in their brain counted - the zebrafish (19) and possibly the goldfish are the only examples I am aware of. However, we do have an equation based on Haller’s Rule, which observes a relationship between body mass and brain mass within various clades. This equation is based on a few data points for fish, and can predict fish brain mass from body mass. (20) Using this, we can use the average masses for each size category, and the equation from Haller’s Rule, to find the average brain size of each category. We assume that the neuron density of the fish brain is relatively constant between species, and multiply neurons/gram in the zebrafish brain by the estimated brain mass of each fish. Finally, we multiply this by the upper and lower estimated numbers of fish in each category, and add the categories together.

This gives us an upper and lower estimate for the total number of neurons in fish species caught by humans - 2.4E21 - 6.73E21. I suspect the greatest source of uncertainty here is that neuron density in the brain is relatively constant between fish.

Of course, all of these fish species fished by humans account for about 10% of the total fish biomass. How do we allocate the remaining biomass?

We know that humans disproportionately catch large fish that are higher up trophic levels (are more top predators). This suggests that allocating the rest of the biomass (and neurons) in the same distribution as we used before gives us a lower bound on the total number. This lower bound is 3.96 * 10^21 neurons.

As an upper bound, we should consider that most of the fish biomass is from the mesopelagic zone, 200-1000 meters below the surface. We know that the mesopelagic fish genus *Cyclothones* seems to be the most numerous vertebrate on earth. (21) *Cyclothones* is a small fish. One fairly common species (22), *Cyclothones microdon*, is said to be 3.25 (23) or 4.5 (24) cm. Another species, the tan bristlemouth, is 4.3 cm long (25). Research doesn’t provide an obvious mash for these species, but one website provides an equation estimate (26) that suggests the tan bristlemouth weighs 0.324 grams. The better-studied zebrafish is around the same length and mass (27), so this seems likely to be accurate.

Given that this is a very common and very small fish, we could say that for an upper bound on the number of neurons, all of the remaining biomass is in *Cyclothones*-sized fish, and there is no other biomass. Since *Cyclothones* is around the size of a zebrafish, we can use the zebrafish neuron count of 5 * 10^6 neurons (19) and arrive at a number of 2.77E16 individual bristlemouth-sized fish, which have a total of 1.38E23 neurons.

Adding these two sets of estimates together - high and low bounds on the numbers of both species caught by humans, and species not caught by humans - we find a plausible lower bound of 4.20E22 neurons, and an upper bound of 1.45E23 neurons.

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Appendix: Smaller sources of neurons

Small ocean crustaceans

Copepods (and other small pelagic organisms)

There’s a lot of room in the ocean, and hence, a lot of pelagic organisms (organisms that live in the water column, not on the ocean floor). Copepods and other similarly microscopic organisms (gastrotrichs, ostracods, larvae of larger animals) are among the most abundant animals in existence. Previously, I’ve reviewed data from sampling at different depths across the ocean that when, added together, suggest there are 1.16E18 copepods (and, in smaller number, other similarly-sized animals between 0.25 mm and 10 mm.) (34). There are also copepods under 0.25 mm - one study finds that the 200 micrometer nets used in the previous study catch only 7.08% of total mesozooplankton abundance, and that the smallest-sized plankton nets catch 99.13%. These smaller animals are "mainly early copepodite stages, nauplii and Oithona [a genus of small copepods.]" (35)

The next challenge becomes finding some representative brain sizes. This suggests there are actually 8.09E18 copepods and similarly-sized animals. A single source from personal communication finds that larval harpacticoid copepods have 400 neurons. (36) I was unable to find a similar count for an adult, or determine the size of the larva, but for a rough estimate, I found that one harpacticoid copepod is 55 micrometers long when larval, (37) and that adult copepods are 0.5 mm - 2 mm long. (38) Assuming a usual adult size of 1 mm, and that the 0.55 mm - 1 mm increase in length corresponds to an equivalent 1.82 increase in brain size, an adult ought to have 728 neurons. This gives us 2.94E20 neurons in largish copepods (and similarly sized animals).

Of course, 0.55 mm for a larva is larger than the early copepod stages that are apparently screened out of larger net sizes. Maybe 40% of that brain size is more reasonable for a very small animal. This gives us 1.27E21 neurons in very small copepods and similarly-sized animals, and 1.56E21 neurons in all the copepods (and other small pelagic animals) together.

Krill

Another famously common animal is the antarctic krill. There are an estimated 500,000,000 tons of it in the world’s oceans. (39) Based on the animal’s mass, that’s 5E14 individuals. Because krill are found in oceans worldwide, even if they’re especially common in Antarctica, I doubled that number for 1E15 krill across the world. I couldn’t find the brain size of a krill, but I have the impression that crustacean brains are comparatively smaller than insect brains. Since I had a
neuron count for the honey bee, and a bee is smaller than the 2.4-inch-long antarctic krill, I used that. There’s obviously a fair bit of uncertainty in this estimate, but it seems like krill have about 9.6E20 neurons overall.

Other wild vertebrates

Birds

One set of researchers used a variety of means to estimate the total number of birds on earth, and found fairly consistent estimates of 2E11 to 4E11 (16). In the interests of simplicity, I assumed that most of these birds would be small songbird-sized birds, with a lot of right skew. With that in mind, I used the great tit - a slightly large songbird - as a model for all birds. With 2.26E8 neurons in its brain (13), this leads to an estimate of 6.78E19 neurons in the brains of all (wild) birds.

Amphibians and reptiles

Brian Tomasik estimates that there are between 10^{11} and 10^{14} each of amphibians and reptiles. (28) His estimates seemed fairly comprehensive and cautious, so I didn’t attempt to refine them. That leaves the question of brain size. Reptile brains are related to bird brains (birds are related to crocodiles), but bird brains are famously rich in neurons (29), so a direct comparison seems like it would be too high. One source claims that the only reptile brain that has been counted is the crocodile brain, which has 25,000 neurons per milligram of brain (30), which seemed low to generalize from - it would imply that (given an 0.08-mg brain (31) ) the green lizard - a lizard up to 16 inches long - a 2-million-neuron brain, less than that of a two-inch-long fish (the zebra danio). On the other hand, one songbird (the zebra finch) has 3.63E6 neurons per milligram of brain (32), and its correspondence for the green lizard, a 2.9E8-neuron brain, would be on par with that of a rabbit, which seems too high. That said, we could assume that the true answer is an order of magnitude between the two densities, at perhaps 3E5 neurons per milligram.

For a rough estimate, we can multiply this by the brain mass of a representative reptile. Naively, I thought that a small lizard might be a reasonable choice. Podarcis hispanica, a small lizard, has a brain mass of about 37 milligrams. (33) This gives it 1.11E7 neurons, about a fifth as many as a rat, which seems believable.

Under the assumption that this is a generally representative reptile, this gives us 1.11E18 - 1.11E21 neurons.

Data on amphibian brains is scarce, but since abundance is similar between them, I’ll assume the ranges of neuron count are about the same. This is a total neuron count of 2.22E18 - 2.22E21 for all amphibians and reptiles. The upper count seems much higher than I would
expect, but it would take a more refined total number of amphibians or reptiles to confirm this further.

**Mammals**

Mammals are known to have well-developed brains. Unfortunately, data on total mammal abundance or biomass is quite scarce, and brain size (even brain size relative to body mass) varies by huge amounts between mammal species. This section is the most uncertain for this reason.

Tomasik reviews several sources that try to estimate overall mammal abundance, ranging from 1E11 - 1E12, a fairly narrow range. I first guessed that since the majority of mammals are probably rodents, I could multiply this by the mouse neuron count and be close, but this conflicted with a later rough estimate I made for the number of neurons in primates alone. I wondered if a somewhat larger mammal, the rabbit, would be a better model.

This gives us 4.9E19 - 4.9E20 neurons in mammal brains. I think this seems somewhat reasonable given the other results. It’s worth noting that despite the large amounts of error, this probably wouldn’t be enough to significantly shift the overall neuron number e.g. from fish or nematodes, even if it were 2 orders of magnitude smaller or larger.

**Humans and domesticated animals**

As one might imagine, the number of humans and livestock on the planet are much better understood than most wild animal species.

There were 7.3E9 humans on earth in 2015. (10) There were also 2.14E10 chickens, 1.47E9 cows, 1.01E9 goats, 9.86E8 pigs, and 3.34E12 bees. (11) Using published neuron counts for humans (15), the domestic pig (12), red junglefowl (the chicken’s wild counterpart) (13), and bee (14), we get 6.29E20 neurons in humans, 2.19E18 in pigs (and 5.53E18 for goats and cattle, using the pig brain as a model for both), 4.73E18 in chickens, and 3.20E18 in bees. This adds up to 6.39E20 neurons in humans and domesticated animals, with the great majority of that in humans ourselves.
How many neurons have there ever been? - Summary

A neuron-year is a year of a living neuron, and thus independent of its owner’s lifespan. I estimate that between 1E32 and 7E32 neuron-years have existed in earth’s history. From the above estimate, it seems like neuron counts are either dominated by insects or by nematodes.

For an upper possible bound, I used a chart to identify predicted multicellular eukaryote (plant and animal) carbon biomass over history. I estimated that if neuron count stayed proportional to this multicellular carbon biomass over history, we get a maximum of 6.84E32 neuron-years.

On the other hand, since the majority seems to be due to insects, I guessed that it might be appropriate to model neuron counts as having reached their current density during the evolution of insects 470 million years ago. This leads to 1.08E32 neuron-years.

Finally, using a similar fish-based approach since the early radiation of fish, I estimate that between 1.50E31 and 5.25E31 neuron-years have been in the history of all vertebrates.
How many neurons have there ever been? - Full report

Because of the difficulties of finding anything like an “average lifespan” for all animals (even among the ubiquitous nematodes, which might live from 3 days to 15 years (43)), and also because the object of interest here is neuron work done rather than creation of neurons, we’ll think of this section in terms of “neuron-years” rather than only new neurons. This is approximated by finding the number of neurons at any given point in time, and multiplying that by the number of years.

I find that 1E32 - 7E32 neuron-years have existed in earth’s history. I describe how I find the upper and lower bounds on this range below.

High bound

Because of extinctions, continental drift changing the amount of nutrients released into ocean water, and other evolutionary geographic events, biomass on earth - even among broad groups - has not stayed constant over time.

![Cumulative biosphere pools](image)

_Fig. 2._ Case 1. (a) Evolution of global surface temperature (solid green line). The green dashed line denotes a second possible evolutionary path triggered by a temperature perturbation in the Neoproterozoic era. The coloured area indicates the evolution of the normalized continental area according to Condie (1990). (b) Evolution of the cumulative biosphere pools for procaryotes (red), eucaryotes (green), and complex multicellular life (brown).

This figure, from (40), describes gigatons of carbon attributed to plants and animals (brown). I was skeptical at first, since it seems to suggest that single-celled eukaryotes, multi-celled
eukaryotes, and prokaryotes all have about the same amount of carbon. That said, another source corroborates that bacteria, despite outweighing plants, have a similar amount of carbon (41). Plants outweigh other multicelled eukaryotes by a significant margin, so I’m tentatively willing to accept this graph as roughly accurate. (It seems to have been created by a mix of historic data about evolution and extinction, and some atmospheric modelling based around temperature.)

For a high bound, we might guess that the number of neurons has stayed proportional to total multicellular biomass since animal life took off. We could use the cambrian explosion, when several animal clades evolved in a very short span of time around 540 million years ago. (Of course, animals existed at least fifteen million years before the cambrian explosion, but since we think fish and insects were large parts of this number and evolved much later, it seems safe to start from 540 million years ago even for a generous estimate.

Keeping this proportional to multicellular biomass as described above Using the number of gigatons approximated over each 100-million-year chunk, drawn from the graph, we can work backwards and observe a varying number of neurons each year in each time period. Added together, this gives us 6.84E32 neuron-years in history.

Low bound

On the other hand, since counts appear to be either slightly or largely insect-dominated, perhaps neuron count only really took off reached substantial levels after the evolution of insects. Insects seem to have evolved 470 million years ago (49), although they did not radiate quickly - the authors note that “the diversification of insects is undoubtedly related to the evolution of flight,” 324 million years ago.

One important question when considering the impacts of this on a total neuron count through history is replacement - surely before insects evolved, there were other organisms filling their niche? I think that’s actually less likely - insects colonized land at around the same time as plants. This suggests that they were filling niches that previously didn’t exist. However, certainly some other organisms existed beforehand, and certainly insects took some time to radiate after their evolution.

As a rough estimate, and in hopes that these balance out, I multiply the full lower-bound neuron estimate of today - 2.29E23 - by the years since insects have evolved, 470 million years. This suggests 1.085E32 as a possible lower likely bound for the number of neurons that have ever existed.

How many neurons have there ever been in vertebrates?
Vertebrate neuron counts appear to be dominated by fish - they seem to have at least two orders of magnitude more neurons than any other vertebrate. As above, we'll look at fish abundance over time as a baseline for this.

Unfortunately, again, there's basically no data on fish abundance over, say, 50,000 years ago, and certainly not the millions we'd be interested in for a really comprehensive look. The very first fish were about 500 million years ago. But they were quite simple and probably had very small brains, and may well have taken a long time to reach their current abundance. I decided instead to use a diversity of predators as a metric - only once there were a large number and variety of fish, could a wide range of predators have been evolutionarily successful. The oldest predatory fish evolved around 423 million years ago (44), but as far as I can tell, fish predators didn't really expand and diversify until the Devonian “Golden Age of Sharks”, 360 MYA. (45) I'm going to use this as the main indicator of fish abundance, and start our fish count from there. (Possibly fish still weren't as numerous until after the Devonian anyway, just more diverse - I'm hoping this levels out or is close enough for an approximation.)

I was concerned that human fishing has drastically altered fish abundance in the ocean, and it certainly has for large fish (e.g., 46, 47). But most individual fish are those small mesopelagic fish, which aren't commercially used and are too deep to be fished by humans. In fact, human fishing of predators may have increased abundance of small prey. (48) Given these uncertainties, I'm going to assume that human interaction hasn't changed the total neuron count of fish notably.

By adding this up, we get $1.59 \times 10^{31} - 5.15 \times 10^{31}$ neuron-years since modern levels of fish abundance.

We should throw in the land vertebrates as well. Based on the numbers we found earlier, there are $8.16 \times 10^{20} - 3.48 \times 10^{21}$ non-fish vertebrate neuron-years right now. The first land vertebrates crawled out of the sea in 375 MYA (46), so since they had a lot of land to crawl over, we could imagine they reached their current level of abundance at 300-350 MYA.

It's possible, but not certain, that a large number of these land vertebrate neurons are human neurons. About $1.07 \times 10^{11}$ humans have ever existed, so we'll add these up (with an imagined average lifespan of 30 years) and then add humans afterwards. That will add $2.34 \times 10^{22}$ neurons from all the humans that have existed.

As it turns out, this doesn't really change our results - land vertebrates are a small percentage compared to fish. Even with the highest and lowest numbers, we still get a range of $1.50 \times 10^{31} - 5.25 \times 10^{31}$ neuron-years that have ever existed within all vertebrates.
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