



An argument for hyperbolic geometry in neural circuits

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This review connects several lines of research to argue that hyperbolic geometry should be broadly applicable to neural circuits as well as other biological circuits. The reason for this is that networks that conform to hyperbolic geometry are maximally responsive to external and internal perturbations. These networks also allow for efficient communication under conditions where nodes are added or removed. We will argue that one of the signatures of hyperbolic geometry is the celebrated Zipf's law (also sometimes known as the Pareto distribution) that states that the probability to observe a given pattern is inversely related to its rank. Zipf's law is observed in a variety of biological systems — from protein sequences, neural networks to economics. These observations provide further evidence for the ubiquity of networks with an underlying hyperbolic metric structure. Recent studies in neuroscience specifically point to the relevance of a three-dimensional hyperbolic space for neural signaling. The three-dimensional hyperbolic space may confer additional robustness compared to other dimensions. We illustrate how the use of hyperbolic coordinates revealed a novel topographic organization within the olfactory system. The use of such coordinates may facilitate representation of relevant signals elsewhere in the brain.

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Hyperbolic geometry has been shown to describe multiple aspects of human perception, including those in vision [1–3], olfaction [4], and touch [5,6]. Hyperbolic geometry also has been recently shown to describe the statistics of natural stimuli in olfaction [4] and color [7]. The use of hyperbolic geometry is also attracting attention in machine learning research where it provides more accurate representation for diverse data sets including natural

images [9] and phylogenetic trees [10]. Hyperbolic coordinates have also been found useful to describe man-made networks, such as internet [11], where they make it possible to efficiently route signals through the network.

One reason for this ubiquity is that hyperbolic geometry provides continuous approximation to tree-like hierarchical systems and processes [8] (Figure 1). The distinguishing property of the hierarchical tree-like processes is the exponential expansion of states, which is captured by hyperbolic geometry and metric. Because of the negative curvature, the distances between points grow exponentially compared to their Euclidean values. In particular, the length and area of a circle grow exponentially with their radius in hyperbolic spaces [8]. In fact, the exponential expansion of states makes it difficult to represent hyperbolic spaces. Multiple representations exist, including the Poincaré half plane (Figure 1a) and Poincaré disk (Figure 1b). These representations use different transformations to map the hyperbolic spaces to the Euclidean space. In both cases, one observes that the geodesics connecting nodes in the networks are curved and follow approximately paths along the tree rather than straight lines between points. The ubiquity of hierarchical latent structures and hyperbolic geometry raises the possibility that hyperbolic geometry might be related to other ubiquitous properties of biological systems, namely the self-organized criticality and particularly Zipf's law [12,13], which will discuss next.

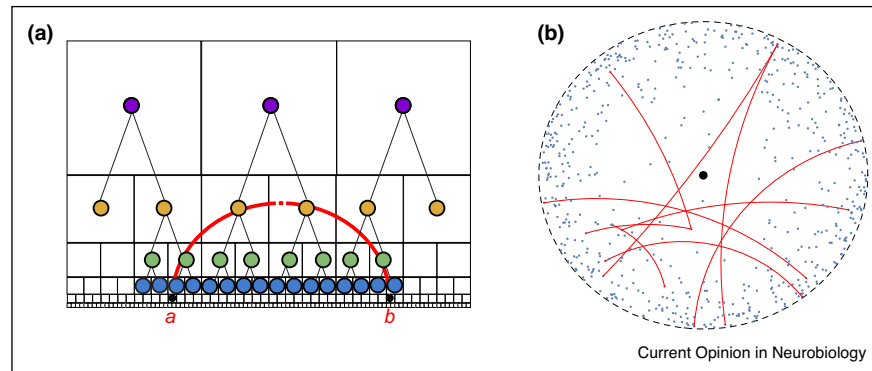
Zipf's law was originally formulated in linguistics for word frequency [12,13]. The observation is that the probability to encounter a given word σ , is inversely proportional to its rank:

$$P(\sigma) \propto \frac{1}{r(\sigma)}, \quad (1)$$

where $P(\sigma)$ and $r(\sigma)$ are the probability and the rank of the word. Generalizing words to states, this power law dependence has been observed for natural images [14], as well as across multiple scales of biological organization, including neural networks [13,15,16], amino acid sequences in the immune systems [17], flocks of birds [18–20] and other self-organized animal groups. Zipf's law also applies to multiple measures of human activity, such as the size of cities [21], firms [22] and funds [23].

Given the ubiquity of Zipf's law and hyperbolic geometry one wonders whether they are related to each other.

Figure 1



Hyperbolic spaces approximate tree-like hierarchical networks. Poincaré half space model (a) and Poincaré disk (b) provide two different ways for representing hyperbolic spaces in the Euclidean plane. Both representations capture exponential expansion of states produced by tree-like networks near the space boundary. This boundary is planar in (a) and circular in (b). In both cases, the lines of shortest distance (red) are curved, unlike in the Euclidean space where straight lines yield the shortest paths between points. Note that these lines approximately trace the 'phylogenetic' distances between nodes. In (a) colored dots describe nodes of a network. Background squares provide discrete version of a Poincaré half-space model of a hyperbolic space. (b) Points are sampled randomly from their expected density. Node position reflects their expected degree. Hub-like nodes are assigned coordinates closer to the disk center. The number of nodes increases exponentially with radius whereas their expected degree decreases exponentially. This combination leads to power-law distribution of network degrees [8*].

In the case of Zipf's law recent theoretical work has provided an explanation for its ubiquity as reflecting networks whose states are strongly modulated by the external parameters [24*,25*]. Loosely, the requirement for the emergence of Zipf's law is that the distribution of internal states of a system should be narrow for a given value of environmental variables but that changing the values of the environmental variable should strongly modulate the mean of the distribution of internal states. Qualitatively, this arrangement should describe circuits that are strongly responsive to external perturbations. It turns out that this intuition can be formalized to mathematically show that indeed Zipf's law naturally describes circuits that provide maximal amount of information about the variables they are designed to convey [26**]. In some cases, these variables can represent signals from the natural environment. For example, a flock of birds should be able to respond well to predator threat. In other cases, the 'hidden' or 'latent' variable signal internal states of the network. For example, within the nervous system should be responsive to changes in the metabolic state of the animal. These results echo mathematical results for the 'navigability' of networks with hyperbolic geometry [11*,27–29] where all greedy-routing using information only about local connectivity and coordinates provides asymptotically shortest paths [30].

This observation prompts one to search for a mathematical connection between Zipf's law and hyperbolic geometry. It turns out that Zipf's law can be reformulated as stating that the number of states should grow exponential with energy, where energy E is defined as the logarithm of

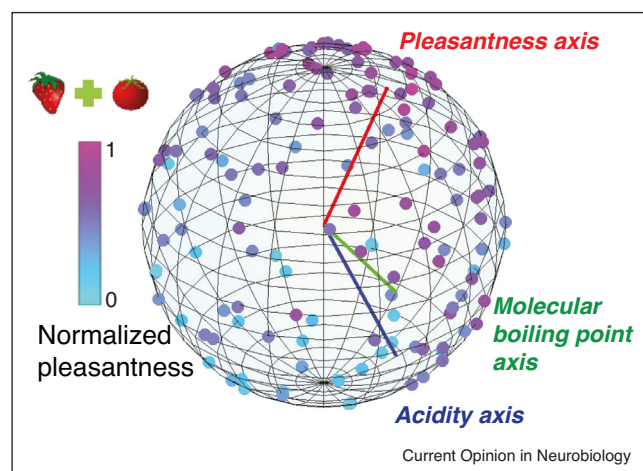
the probability, $E = -\log[P(\sigma)]$. Indeed, applying the logarithm to Eq. (1) yields that

$$E = \log[r(\sigma)]. \quad (2)$$

This indicates that the rank, which is related to the number of states N , increases exponentially with energy, $N(E) \propto e^E$. An exponential expansion in the number of nodes is one of the signatures of hyperbolic geometry [8*] and a hallmark of the tree-like networks for which they provide continuous approximation (Figure 1). Thus, this simple reasoning makes it possible to connect the observations of Zipf's law [17] and other signatures of power-law dynamics [31] with hyperbolic geometry in neural circuits [4,32] and maximally informative representations [26**,33].

The link between hyperbolic geometry, Zipf's law and maximally informative representations clarifies why hyperbolic geometry is simultaneously relevant for both the olfactory system [4] and word distribution [12,13**]. In the case of olfaction, plants and animals have to produce chemical signals that will be discernible by other animals. Here there are advantages for both the producer and the receiver to mutually optimize their representation. This point is illustrated in Figure 2 that shows an embedding of monomolecular odorants into a three-dimensional hyperbolic space (Poincaré ball) where distances between odors reflect how correlated they are across different fruit samples. This visualization was obtained using non-metric multi-dimensional scaling (nMDS) to embed odors produced by tomato and strawberry samples into a

Figure 2



Embedding of fruit volatile compounds from tomato and strawberry, using analysis from Ref. [4]. The points are positioned based on distances that reflect correlations in concentrations across different samples of tomatoes [45] and strawberries [46]. The color represents correlation of the odorant concentration with human rankings for pleasantness. The points fall near the surface of a three-dimensional Poincaré ball.

three dimensional hyperbolic space [4]. The dimensionality of the space and its metric were first found via a topological analysis that ruled out Euclidean and spherical geometries, suggesting instead that points distributed near a surface of a hyperbolic Poincaré ball were consistent with the measured distances. Once the space parameters were identified, the specific distribution of points was found using an nMDS with a hyperbolic metric. What is interesting about the resultant picture is that, although the distances between points within the embedding reflect correlation between odorants when produced by plants, the map shows topographical organization in terms of human pleasantness ratings. A region near the top of the sphere contain odorants that all have strong correlations with human pleasantness index for individual odors. The pleasantness index represents how correlated was the concentration of a particular monomolecular odorant with the overall pleasantness values that humans assigned to different fruit samples. Although all of the odorants are derived from plants, some are associated with much lower pleasantness ratings than others. The observed topography suggests that olfactory representations within the nervous system are orderly, even though they may appear random at the initial stages of olfactory processing [34] where random coding provides a good approximation for animal's discrimination performance [35–37]. The use of hyperbolic coordinates in Figure 2 makes it possible therefore to connect natural scenes statistics with human perception. Hyperbolic coordinates were also evident in earlier publications that analyzed human perception by itself [38–40]. Although they were not named as such, the

surfaces plotted were consistent with a hyperboloid cross-section and described as 'potato-chip' models. It seems plausible that the use of hyperbolic geometries can be helpful in identifying topography elsewhere within the nervous system.

Of separate note is the dimensionality of the hyperbolic space suggested by the analysis of both the human perceptual rankings and natural odors. Three-dimensional hyperbolic spaces are also particularly useful for visualization of phylogenetic trees [10]. Thus, one may wonder whether hyperbolic geometry specifically in three dimensions might be particularly relevant for biological circuits. This hypothesis is supported Mostow's theorem [41] that three dimensional hyperbolic spaces are uniquely determined by their topological properties, with no possibility of continuous deformations [42,43]. The three-dimensions may therefore be the lowest dimension to confer sufficient robustness of hyperbolic representations to noise.

Overall, quantifying the dimensionality of both neural signals and behavioral outputs is an active area of research [44]. Across different systems, emergent evidence suggests that both the neural activity and behavioral outputs are described by low-dimensional smooth manifolds. At the same time, at the level of behavioral outputs, there are exponentially many states organized hierarchically. Hyperbolic organization provides a way to reconcile these two observations by mapping the apparent complexity of behavioral states using hyperbolic spaces of low dimension.

Conflict of interest statement

Nothing declared.

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