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Self-portraits of the brain: cognitive science, data visualization, and communicating brain structure and function

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With several large-scale human brain projects currently underway and a range of neuroimaging techniques growing in availability to researchers, the amount and diversity of data relevant for understanding the human brain is increasing rapidly. A complete understanding of the brain must incorporate information about 3D neural location, activity, timing, and task. Data mining, high-performance computing, and visualization can serve as tools that augment human intellect; however, the resulting visualizations must take into account human abilities and limitations to be effective tools for exploration and communication. In this feature review, we discuss key challenges and opportunities that arise when leveraging the sophisticated perceptual and conceptual processing of the human brain to help researchers understand brain structure, function, and behavior.

Exploiting the perceptual processes of brains to understand brains

The human brain is one of the most complex systems that scientists have ever tried to comprehend. Each of its 86 billion neurons has an average of approximately 5000 synapses, resulting in roughly 430 trillion synapses in the cerebral cortex alone, and perhaps 1000 times as many molecular-scale switches [1]. In the face of this complexity, how can scientists hope to circumvent the Catch-22 suggested by the adage 'If the human brain were so simple that we could understand it, then we would be so simple that we couldn't' [2]? We believe that progress in understanding the brain will crucially depend on developing data-mining techniques and visualizations that make structural, functional, and behavioral neural patterns intuitively graspable. Due to the complexity of the brain and the diversity and amount of data that scientists collect from it, understanding it will likely be an effort necessitating coordination among experts from different fields of sciences: social sciences, life sciences, physical sciences, mathematics, computer science, as well as engineering. Cognitive science, because of its interdisciplinary nature, is well positioned to supply useful methods and tools for understanding the human brain because it is an interdisciplinary home to scientists interested in the power and limitations of human visual processing, the determinants of effective visual depictions, and neuroscientists with detailed knowledge of neural patterns.

One of the most promising approaches for enabling us humans to understand our own brains is to develop visualization tools that take advantage of the millions of years of evolutionary research and development that have gone into construction of the human visual systems. By harnessing data mining and visualization tools, extremely large data sets that would otherwise be impenetrably complex can be converted into carefully crafted visual representations that can be effectively processed by the brain itself. Some of the most commonly used visualization choices for neuroscience data are detailed in Box 1.

Sophisticated understandings of brain structure, function, and behavior depend on re-representing quantitative and qualitative data, but seemingly neutral choices regarding data acquisition methodology, data analysis, and visualization can have a major influence on the final interpretation of the results. As an example, consider scientific understanding of how brain regions are interconnected, a core pursuit of neuroscience [3]. White-matter tracts are the principal anatomical structure responsible for transmitting signals from one cortical region to other distant regions. Unfortunately, a simple brain dissection will not reveal the separate white-matter tracts because they are hopelessly intermeshed by visual inspection. To appreciate the organization of white matter into tracts, modern, multistage data transformation processes can produce the visualizations shown in Figure 1. Figure 1A and B contrast the anatomy of the corticospinal tract and arcuate fasciculus, estimated with two different commonly

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Box 1. Guided visualization design and frameworks

Making sense of data by designing appropriate visualizations is a complex process that involves not only human perception and cognition [88,89], but also data mining, visualization algorithms, and user interfaces. Different conceptualizations of the overall process have been developed to understand and optimize this process, and to improve human decision-making capabilities. Among others, process models focus on key sense-making leverage points [90], the match between pre-conceptualizations and expectations of visualization designers and visualization readers [91], major data transformation and visual mappings [92], or describing visualization design and interpretation to support workflow optimization and tool design. Key visualization types are listed in Table I.

Table I. Key visualization types

Name	Description	Examples[a]
Tables	Ordered arrangements of rows and columns in a grid; grid cells may contain geometric, linguistic, or pictorial symbols	Figure 4A
Charts	Depict quantitative and qualitative data without using a well-defined reference system	Examples are pie charts in which the sequence of 'pie slices' and the overall size of a 'pie' are arbitrary, or word clouds
Graphs	Plot quantitative and/or qualitative data variables to a well-defined reference system, such as coordinates on a horizontal or vertical axis	Figures 2, 3A, 3C
Maps	Display data records visually according to their physical (spatial) relations and show how data are distributed spatially	Figures 1A–F, 3B, 4C–E, 5A–C, 6A–D
Network layouts	Use nodes to represent sets of data records, and links connecting nodes to represent relations between those records	Figure 4B; see also network overlays on brain maps in Figure 4C,D

[a]Figures cited refer to those in the main text.

used tractography methods. The estimated anatomy differs substantially. Furthermore, the tracts project to strikingly different cortical regions (Figure 1C,D; [4–6]). Research groups using a variety of related methods have come to different conclusions regarding the geometrical structure of the human white-matter tracts. For example, some researchers have claimed that tracts are organized in sheaths of white-matter crossings with strict geometrical structure [7], as shown in Figure 1E, whereas other researchers have criticized the evidence supporting such strict organization [8].

Figure 1 and the corresponding debate [7,8] show one shortcoming of human perception and cognition: existing preconceptions impact future actions, including the collection, analysis, and visualization of data on the human brain. If one were to view only one of the visualizations in isolation, one might well be convinced that the visualization simply reflects the 'true' structure of white-matter tracts: the cycle of subjective perception and cognition can result in a self-fulfilling prophecy. The beauty and concreteness of visualizations can encourage investigators to take them literally, at face value [9,10]. However, all visualizations are created using many highly parameterized data cleaning, merging, analysis, and visualization algorithms (Box 2), and the interest to see certain patterns and dynamics might well lead to attempts to extract and emphasize them in the final rendering, as the juxtaposition of the different visualizations in Figure 1 highlights. That is, proper selection of analyses and visualizations are key for the design of objective visualizations, as are expert interpretations of visualizations.

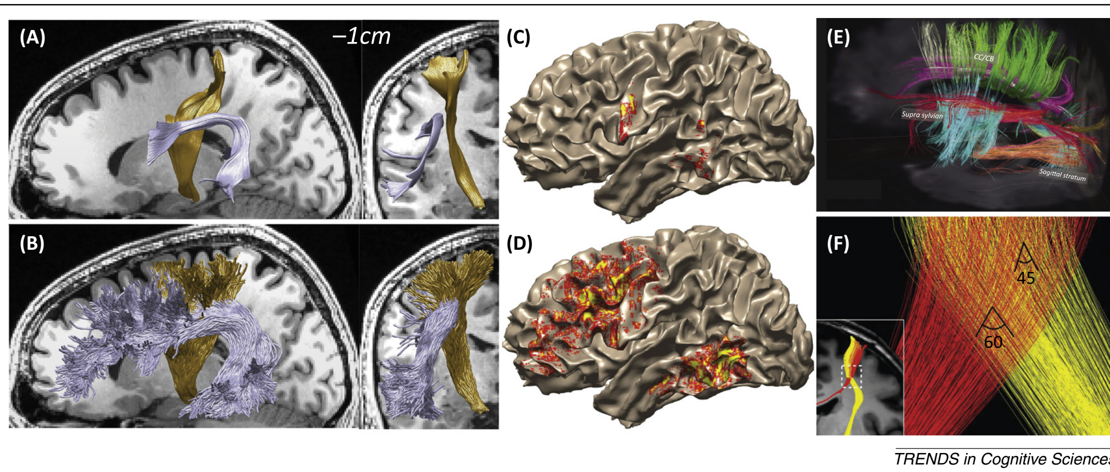

Figure 1. Anatomical visualization methods of human white matter. The panel on the left depicts trajectories of the human corticospinal tract (CST; gold) and arcuate fasciculus (AF; purple) identified using diffusion-weighted magnetic resonance imaging and deterministic **(A)** or probabilistic **(B)** tractography methods. The center panel depicts cortical projection zones of the AF estimated using deterministic **(C)** and probabilistic **(D)** tractography. The right-hand panel depicts white-matter fascicles apparently organized in sheaths with 90° crossings **(E)** [7] or crossing at different angles **(F)** [8]. Reproduced, with permission, from [4] (A–D), [7] (E), and [8] (F).

Box 2. Guided visualization design and frameworks

Any visualization can theoretically be analyzed and interpreted as a path along the columns of Table I. For example, given a scientific question, the question type and detailed insight need is identified, then data of different scale(s) are acquired, a visualization type is selected, and relevant geometric symbol types are chosen and visually modified (e.g., color coded) using different graphic variable types. Finally, different interaction types might be implemented to facilitate the interactive exploration of the visualization.

When visualizing the structure and function of the brain, the data that need to be represented are high dimensional and inherently complex. Many different types of visualization can be used and many different mappings of data attributes to visual attributes are possible. To ease the design of effective visualizations, different visualization frameworks (also called taxonomies or classifications) have been developed in statistics, information visualization, and graphic design [93–99]. Recent work [14] provides predefined types for the process of data visualization, including different task types, such as temporal (answering 'when' questions), spatial ('where'), topical ('what'), and trees and network layouts ('with whom'), and common insight need types (Table I, column 1).

Given well-defined general 'task types' and specific 'insight need types,' the final visualization will also depend on the type of data (see 'data scale types; Table I, column 2), the available 'visualization types (Table I, column 3), graphic symbol types (Table I, column 4), and 'graphic variable types' (Table I, column 5; Note that each type is further detailed in [14] (e.g., 'retinal: form' includes size, shape, rotation, curvature, angle and closure; 'retinal: color' subsumes value, hue, and saturation) that can be used, and the level of interaction required by the final visualization (Table I, column 6).

Table I. Visualization framework designed to ease the selection and design of data visualizations[a]

Insight need types	Data scale types	Visualization types	Graphic symbol types	Graphic variable types	Interaction types

• Categorize/cluster
• Order/rank/sort
• Distributions (also outliers, gaps)
• Comparisons
• Trends (process and time)
• Geospatial
• Compositions (also of text)
• Correlations/relationships
	• Nominal
	• Ordinal
	• Interval
	• Ratio
		• Table
		• Chart
		• Graph
		• Map
		• Network layout
			• Geometric symbols
			  • point
			  • line
			  • area
			  • surface
			  • volume
			• Linguistic symbols
			  • text
			  • numerals
			  • punctuation marks
			• Pictorial symbols
			  • images
			  • icons
			  • statistical glyphs
				• Spatial
				  • position (x, y, z)
				• Retinal
				  • form
				  • color
				  • optics
				  • motion
					• Overview
					• Zoom
					• Search and locate
					• Filter
					• Details on demand
					• History
					• Extract
					• Link and brush
					• Projection
					• Distortion

[a]Adapted from [14].

The power of visualizations for abetting scientific interpretation is also a danger. Seeing is believing, and readers will take visualizations as reflecting 'the truth' in a direct way, without reflecting on the long chain that transforms brain data into visualizations. Despite their concreteness, neuroimages are more distantly related to actual brain activity than photographs are to their subjects [9]. One way to ameliorate the human bias to overinterpret concrete depictions is to concretely show the sources of uncertainty and variability within the visualization itself (Box 3; Recommendation no. 3 in Table 1). One survey of 1451 neuroimages indicated that only 20% of 3D depictions include information about the uncertainty of the data, suggesting that considerable improvement is possible [11].

This article has several goals. For researchers of perception, we describe the case study of interpreting neuroimagery and the unique perspective it provides for accounts of high-level perception. For neuroscientists, we provide recommendations for the design of effective brain visualizations informed by cognitive science principles. For philosophers and sociologists of science, we present neuroimagery as a compelling case in which theories and data mutually inform one another, in large part because the graphic presentation that has been made visually immediate is the result of a convoluted chain of theory-infused processing.

Data sources for visualizations in neuroscience

Human brain data are high volume and, crucially, 4D: mental functions are commonly associated with brain regions localized in three spatial dimensions and neural activity or the biology of the brain tissue is tracked in a fourth dimension of time. In addition, brain data is multilevel, ranging from the molecular and genomics (micro) level to the social (macro) level when correlations of brain activity with human behavior or social networks are studied.

Figure 2 [12,13] shows the enormous temporal and spatial scale covered by data relevant for the study of the human brain together with the types of instrument and method used to acquire the data. Individual or populations of neural action potentials are measured by intracellular or extracellular electrodes; extracellular neurotransmitter levels can be acquired via micropipettes; synchronized electrical activity of entire populations of neurons are measured by electroencephalography (EEG); the degree of neural synchrony across different regions is derived from either extracellular or intracranial electrodes; the optical absorption of oxygenated hemoglobin is measured by diffuse optical imaging and near-infrared spectroscopy; the absorption of metabolically active chemicals is measured by positron emission tomography (PET); and changes in blood flow associated with neural activity are measured by functional magnetic resonance imaging (fMRI). The different types of data are represented using diverse, but increasingly standardized, visualizations.

Principles of visual interpretation of data visualization

The number, size, and complexity of data sets being produced, as well as the number of experts in and publications

Box 3. Fundamental elements for visualization: measurements, estimates, and variability

So far, we have reviewed qualitative aspects of data visualization and how interpretations are affected by perception and cognition. Here, we discuss five fundamental elements to be visualized: (i) measurements of data. This is often the mean or median measurement for one or more experimental condition; (ii) the reliability of the measurements, expressing how variable are the measurements in the data, for example how variable the data are if acquired more than once; (iii) the estimates of a model in predicting the data. Scientists often try to describe or predict the data using models; (iv) The reliability of the model prediction. Most models in neuroscience have some probabilistic component that can affect model prediction. This can come, for example, from the choice of parameters assumed when fitting the model or because of variation in initial seeds; (v) model accuracy and/or error. All models have some degree of accuracy. Model error is independent of how reliable the model estimates are; a model can be very reliable (its predictions show little variability when the mode is rerun) but not accurate (its predictions are far from the actual data). Alternatively, a model can be very accurate on average but predict very different values every time it is fit to the data.

Figure IA summarizes these five elements and their relation. Figure IB–G shows an example of the elements visualized for a case study of the human connectome and white-matter measurements *in vivo*. Most often investigators visualize (i) and (iii), (ii) and (iv) are rarely visualized, the distinction between (iv) and (v) is rarely made and model error (v) is often neglected. Visualizing uncertainty in the data (ii) and model error (v) is fundamental for giving scientists an understanding that findings and model fits should be assessed in a quantitative manner, and that point estimates for data measurements and model predictions should not be interpreted as either exact or certain despite their visual exactness.

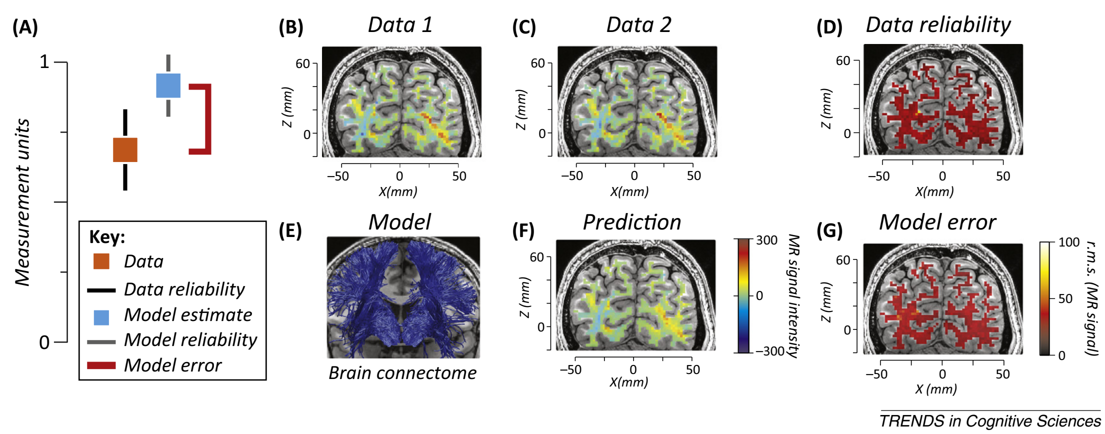

Figure I. Measurements, estimates, and variability. **(A)** Schematic of fundamental elements to visualize and their relations. **(B)** First measurement of a single diffusion direction shown on a coronal slice of a living human brain. **(C)** Second measurement. Repeated measurement of the same direction, collected during the same scanning session, using the same scanner, sequence, and subject. **(D)** Data reliability. The variability in the data when collected twice. The root mean-squared error of the data is expressed by the color map. **(E)** Brain connectome model. A set of connections from a human connectome (comprising part of the corona radiata) estimated using the first measurement (B). **(F)** Model prediction. The estimate of the model of the measurement taken in (B), obtained using a linear fascicle evaluation method [59]. **(G)** Model error. Estimate of the root mean-squared error of the model, estimated using the model prediction (F), built using the first data set (B) in predicting the second data set (C). Reproduced, with permission, from [6] (B–D,F,G).

on human brain research, are increasing exponentially [3,6]. Data mining and visualization are used to make sense of what is known and to communicate key insights [14–16]. Understanding the capabilities and limitations of human visual image interpretation is paramount in making effective brain visualizations. Hereafter, we focus on six aspects of visual interpretation that have particular relevance to how scientists construct and interpret data.

Bottom-up processes

What humans perceive partially depends on what they look for and what they know, and, in turn, what they know is shaped by their previous perceptions, as exemplified by the different visualizations and accounts in Figure 1E and 1F. Bottom-up processes take in sensory information and transform it into more abstract forms, moving information in a feed-forward manner from peripheral sensory organs to identification and interpretation activities. Top-down processing involves influences of concepts, experience, and context on perception. Both processes and their bidirectional interactions [17,18] contribute to the kind of high-level perception involved in interpreting visualizations.

Bottom-up processes, arising from the low-level visual properties of visualizations, can have a profound influence on how easy different sources of information are to cognitively process. For example, the choice of color maps in fMRI visualizations affects the salience of different brain activity levels [19]. Although it might be thought that using the full spectrum of visible light with a rainbow gradient is ideal for making color discriminations, humans perceive color hues categorically rather than in terms of a single continuous dimension [20]. Using a rainbow color map often leads humans to mistakenly believe that the data are organized into discrete levels of activity [21]. Different colors also have different saliences, which will influence how attention is naturally directed to them [22,23]. These differences can be leveraged to create intuitive visualizations of uncertainty in data, by using less-saturated colors to represent data with less certainty [24]. Data that are naturally ordered in terms of magnitude (e.g., oxygen consumption level, spikes/seconds, or electrical potential) are better depicted by continuously perceived dimensions, such as luminance or color saturation, whereas categorical data (e.g., different experimental conditions or anatomically separable brain regions) are better represented by categorically perceived dimensions, such as hue or shape [25]. Other applications of aligning graphical objects with properties of data include recommendations to: (i) use spatial proximity to reflect similarity [26]; (ii) use lines to represent connections, points to represent locations, and

Table 1. Recommendations for visualization practices and examples from neuroscience

Recommendation	Examples
1. Devote a substantial amount of research time to creating illustrative visualizations; view visualizations not as superficial depictions of scientific understandings, but as devices for generating and communicating understandings	If you only have 60 h to do your research, spend 20 h collecting data, 20 h analyzing data, and 20 h finding the best visualization and communication method for your data analysis results
2. Consider the audience for, and purpose of, a visualization	More details for experts and exploration, but fewer details for novices and communication; display intact cortical surface for spatial fidelity, but inflate or explode surface to provide global overview of entire surface
3. Show uncertainty in visualizations	Depict uncertainty in data with error bars, opacity, saturation, thickness, ranges rather than points, and distributions rather than central tendencies
4. Use strategic simplifications and idealizations	Bundle together tracts or connectivity paths (Figure 1A, main text) to avoid overcomplicated networks; align multiple brains or trials and show their overlap by brightness, opacity, or size; display complex connectivity patterns with 2D matrices; further simplify connectivity matrices with multidimensional scaling; use latent factor methods (MDS, PCA, ICA, factor analysis, hidden Markov models, Expectation Maximization) to compress high-dimensional data sets
5. Show all critical information	Use exploded brain diagrams to show entire cortical surface without occlusion; translucency; projection of brain activity onto panels; be explicit about the conventions and tools used; user-controlled rotation
6. Align graphic symbol types and graphic variable types with data scale types to be visualized and the insight needs to be satisfied	Represent continuous dimensions by saturation, size, or position on x-axis; represent categorical dimensions by shape or color hue; use time in animation to represent time since stimulus onset; represent positive EEG voltages by displacement above, not below, a horizontal midline
7. Carefully consider how best to align data from different trials, brains, stimuli, and studies	Consider aligning brains by cortical surface and anatomical anchor points rather than volumetric coordinates; use multidimensional scaling techniques to establish second-order relational similarities between stimuli
8. Create and use interactive visualization tools that support exploratory data analysis and show how complex data unfold over time	Relevant tools include mrTools, Vistasoft, Brain Voyager, Explore DTI, Camino, FreeSurfer, PyCortex, MRI Studio, AFNI, BrainBrowser, BrainVisa, EEGLab, DSI Studio, Caret, VTK, Dipy, FLS, IPython. Connectome Visualization Utility, TrackVis, LONI, Neuroimagery that can be scanned, rotated, and scaled; user-controlled overlays on top of a base map; user-controlled animations representing brain activity over time
9. Establish infrastructures that allow for sharing of data, analysis methods, visualization algorithms, and experimental methods in support of replicable results and efficient research and training	Use Flickr to share brain imaging data and visualizations, GitHub to share code, Medline to share results, open journals such as *Scientific Data* to share data and workflows

boxes to represent sets containment [16]; (iii) if consumers of a visualization need to be able to efficiently search for particular events, make sure that those events are signaled by preattentively processed features, such as discriminable colors, oriented lines, or motions, rather than conjunctions of simple features or the absence of features [27]; and (iv) use vertically higher positions, brighter colors, and larger objects to represent positive values [28,29].

This fourth principle is generally followed by investigators, for example, see Figures 1C,D, 3A, and 4A, where 'more' in data is represented by brighter colors. However, it is routinely violated by traditional EEG recordings, in which positive voltage is represented as displacement below a vertical midline [30]. Another surprising violation of the general principle of visual-data alignment is the use of line thickness in Figure 4B. It is natural for readers to interpret the thickness of the lines connecting brain regions as reflecting the extent of their connectivity, when in fact the line thickness simply reflects the surface areas of the regions being connected. The authors of this illustration state clearly in the figure caption and methods that thickness does not reflect extent of connectivity, but misinterpretations are almost unavoidable because this alignment is so natural. For cases in which convention and principles of perception conflict, we generally recommend honoring the latter. Conforming to perceptually unjustified standards only further reinforces those standards. Adopting improved design practices may cause temporary confusion and require initial explication, but will promote understanding in the long run.

Top-down processes

Although we know of no empirical research directly bearing on the interpretation of brain visualizations by scientists, there is strong evidence for top-down effects on the interpretation of other similarly complex visualizations, such as graphs [16], weather maps [31,32], and air traffic control displays [33]. In these and other domains, users of a visualization prioritize their inquiry of it according to their knowledge, needs, and expectations. When scientists create visualizations, these top-down factors influence the selection of data, algorithms, parameter values, and the visual encoding and presentation of data variables. When readers interpret visualizations, top-down factors influence attention to features of the visualization, the encoding of features into internal representations, and inferences drawn from these representations [34]. One implication of the strong top-down nature of complex visualization generation and interpretation is that different scientists, equipped with different theories, will often generate different visualizations and, in turn, interpretations. That is, visualizations both reflect and motivate theorizing. In the same way that early microscopists disregarded visual evidence for the existence of mitochondria within cells

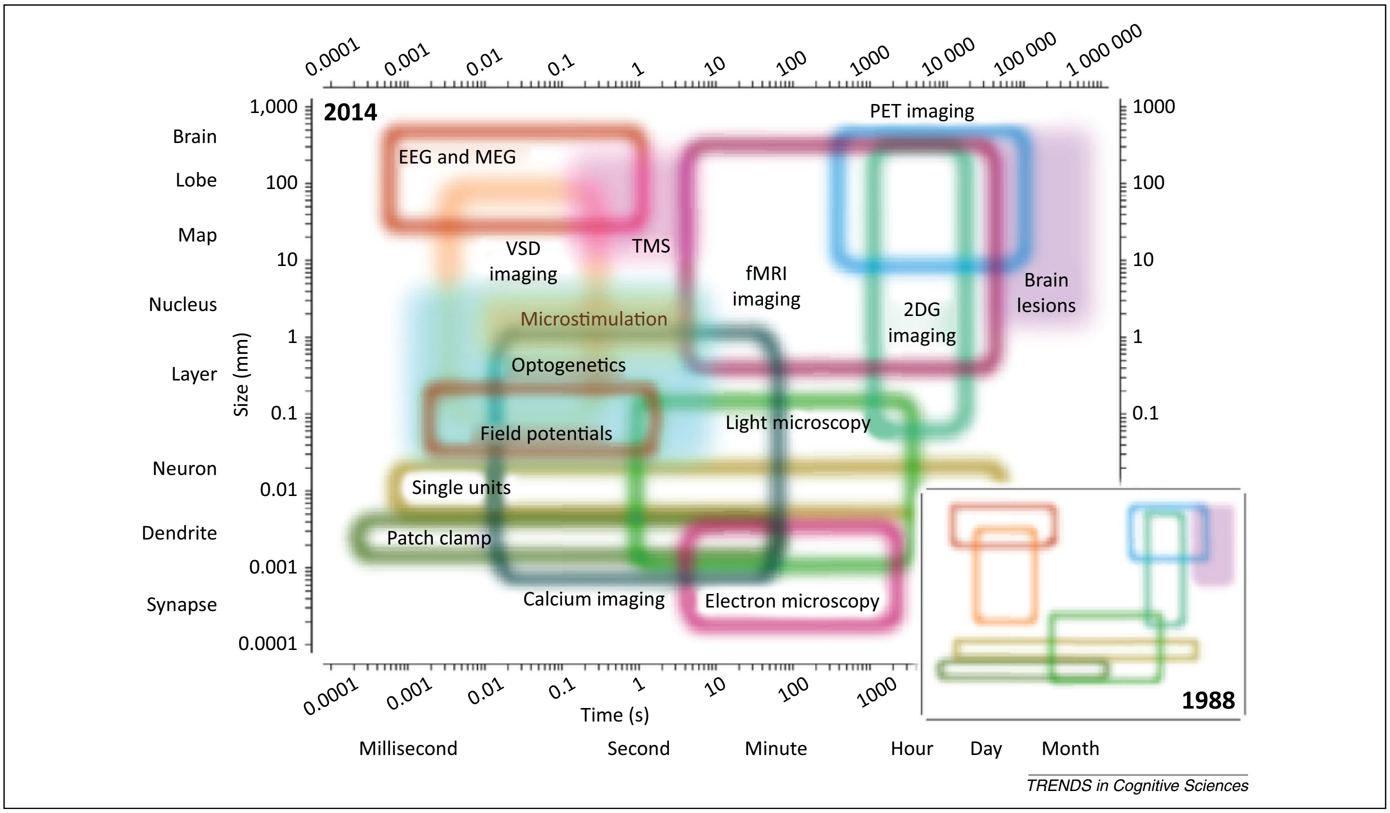

Figure 2. Spatiotemporal resolution of techniques in neuroscience. The spatiotemporal domain of neuroscience methods available for the study of the nervous system in 2014 is compared with that in 1988 [13] (inset). Colored regions represent the domain of spatial and temporal resolution for each method. Open regions represent measurement methods, and filled regions represent stimulation methods. The large gap in measurement resolution in the middle of the graph in 1988 has since been filled by the advent of *modern in vivo* neuroimaging measurements of the human brain. Reproduced, with permission, from [12].

because their presence was not predicted, so too can many neuroscientists miss a substantial white-matter tract because it is not predicted by theories [35,36].

The extent of top-down processing in visualizations becomes even greater if one takes an 'extended mind' [37] perspective on the process of perceptual interpretation so as to include the methods and analyses that a scientist uses to craft a visualization. If one considers perceptual interpretation to be a protracted, distributed, and collaborative activity that involves data collection, identification of important measurements, data filtering, data normalization, visualization construction, visual inquiry, and iterative refinement along all of these steps, then it becomes easy to understand how different laboratories can use similar tasks with similar groups of participants, focusing on similar brain regions, but still come to markedly different conclusions about whether specific functional specializations even exist or how the brain is anatomically organized. One noteworthy example of this for cognitive science is the controversy regarding whether fusiform face area (FFA) is uniquely specialized for face processing in humans. Whereas some studies show the right hemisphere FFA to be selectively active when faces are presented as stimuli [38–41], others [42–44] find the same region to be active when experts are shown objects from within their domain of expertise, such as cars being shown to car experts. Although inspection of the researchers' visualizations confirms each respective account with apparent clarity, these visualizations are the culmination of several different choices from the teams in terms of selecting experts, behavioral tasks, methods for identifying regions of interest, and imaging techniques.

One advantage of adopting an extended mind perspective [37,45–47] is that the normally rapid process of visual interpretation can be viewed in slow motion, revealing detailed dynamics of confirmation bias, interpretation competition, and interpretation revision. Adopting this extended understanding of the interpretive process helps explain how such impressively different interpretations about the nature of white-matter tracts, as shown in Figure 1, can emerge. Figure 1E and F lead to nearly opposite conclusions with regard to the crossing angles of white-matter tracts because, in part, they use different thresholds for determining the extent of white-matter tracts.

Another striking example, shown in Figure 5, of how the long pipeline of distributed data-processing activities can affect the interpretation of brain function, concerns the localization of the cortical region specialized for processing visually presented words [48–51]: the visual word form area (VWFA). The left side of Figure 5A shows two areas [middle temporal gyrus (MTG) and VWFA] that appear to be fairly distant in terms of distance over cortical folds, but the projection on the right side of Figure 5A shows that the two gray-matter areas happen to dwell in sulci that lie close to one another but are separated by a white-matter tract [51]. Moreover, if the resolution of the fMRI is not sufficiently high or the signals are spatially averaged, then

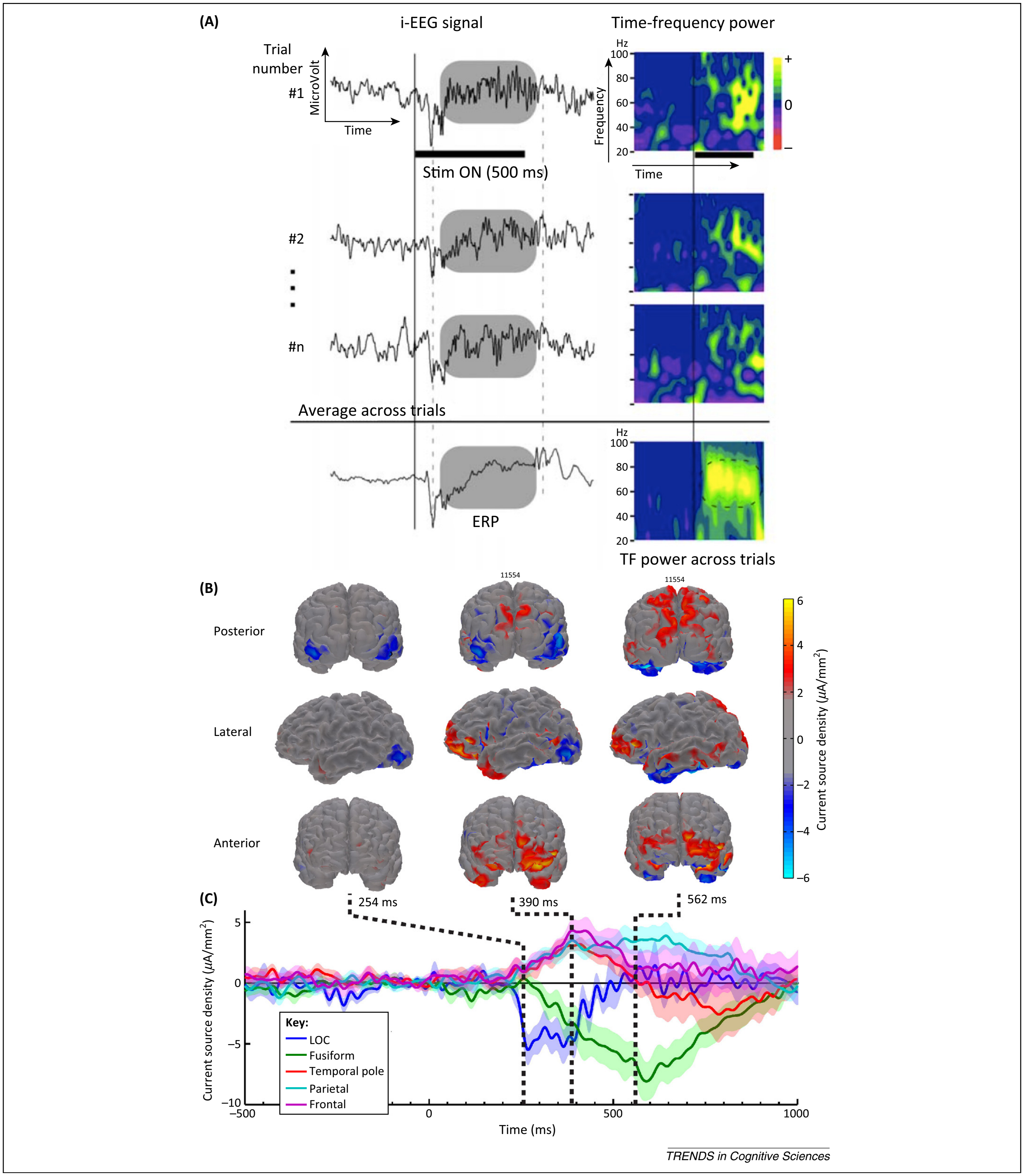

Figure 3. Visualization of signals in time and space. **(A)** Intracranial electroencephalographic recordings (i-EEG). The left column shows a time versus voltage i-EEG plot from macaque visual cortex. Signals are time locked to stimulus onset and offset (dashed vertical lines). The right column depicts a time versus frequency power plot averaged across trials. **(B)** Surface-based average of current density ($n = 12$) of target-selective extracranial electroencephalographic (e-EEG) recorded responses time locked to the stimulus. **(C)** e-EEG time versus current source-density plot. Colors indicate responses with different cortical sources (see legend). Vertical dashed lines mark peak activity in different brain areas. Reproduced, with permission, from [60] (A) and [61] (B,C).

activity from a ventral cortical location may be visualized in lateral cortex, making it possible to misinterpret activity from ventral cortex as originating from lateral cortex. Figure 5B shows a likely mislocalization of the VWFA [48–50], which stems from inadequate spatial resolution of the imaging technique, projection onto a 3D representation of the brain without depicting cortical distances, and spatial averaging based on voxels rather than following the

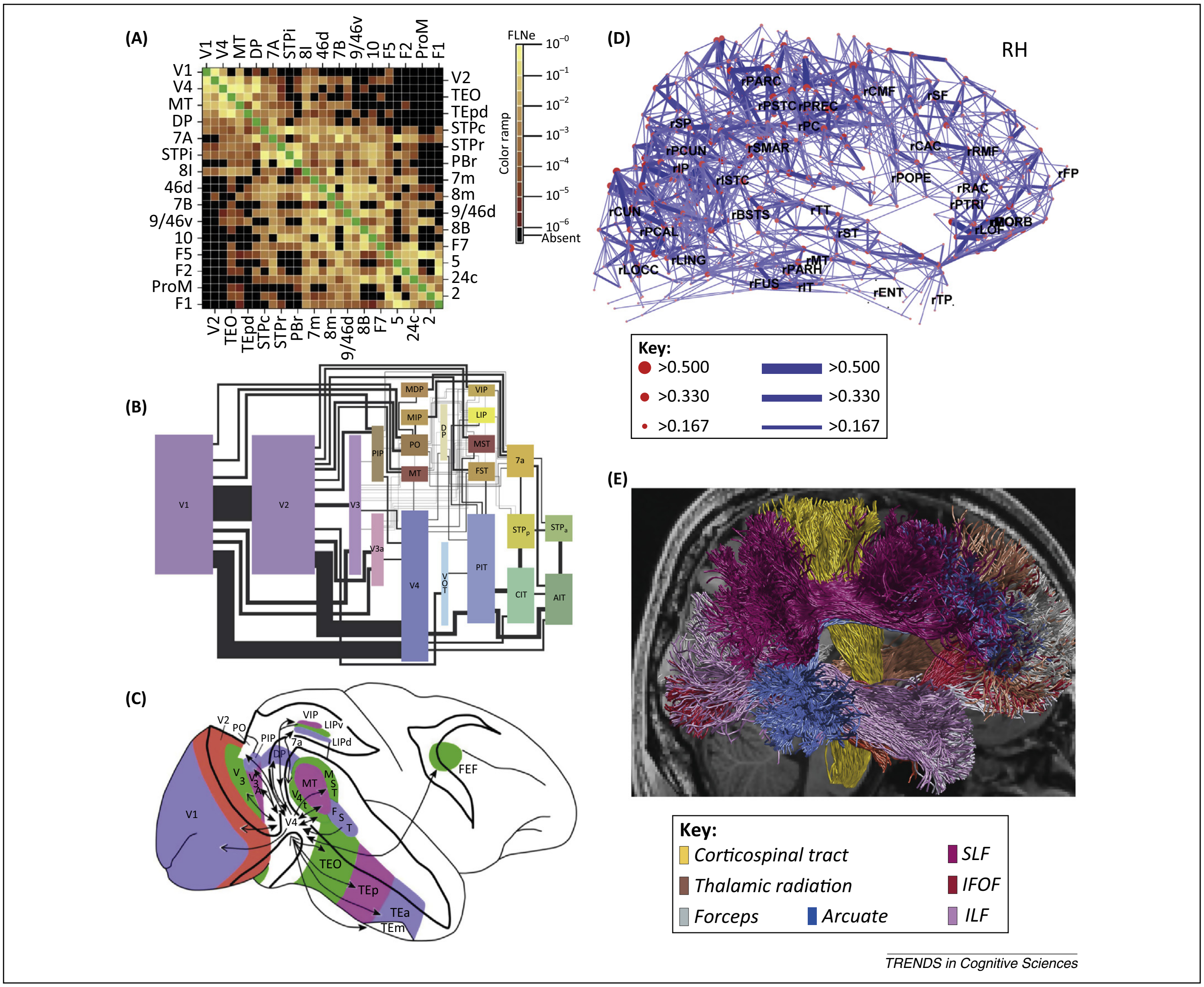

Figure 4. Visualization of connectivity data. **(A)** Tabular (asymmetric matrix) representation. Rows represent 29 tracer source areas, whereas columns represent 29 injected target areas. Color shows the strength of projection, whereby black indicates an absent connection and green indicates intrinsic projections (see color bar). **(B)** Coarse topological network layout. Schematic representation of 24 richly interconnected visual cortical areas in the macaque brain. **(C)** Neural projections to one brain region, mapped onto brain. Schematic representation of the connections of brain area V4 in the macaque brain. **(D)** Human connectome. Dorsal view of the connectivity backbone, node (red), and edges (blue). **(E)** Human white-matter tract anatomy. Seven of the major human white-matter fascicles are shown. Reproduced, with permission, from [100] (A), [63] (B), [64] (C), [65] (D), and [4] (E).

cortical folds of the gray matter (Recommendation no. 7 in Table 1). Figure 5C shows a contemporary understanding of the location of the VWFA [51–53], which looks to be in a different location than the dominant activity shown in Figure 5B. Perceptual interpretation is always a constructive process, but the extent of this construction becomes dramatic when one considers the entire chain of processes involved in visualizing brain activity that is invisible without recording, analysis, and rendering technologies.

Exploration versus communication

Visualizations can be used to explore data in search of patterns or to communicate key results. Although exploratory visualizations are interactive and customizable, communicative visualizations are typically polished and static.

When trying to explore data, scientists typically interrogate the results of a study using several different analysis methods, filtering choices, measures, and algorithms for uncovering patterns. In this mode, scientists are interacting closely with their computers, measurement devices, visualization software, and algorithms to view the data from different vantage points and at different levels of detail, continuously adjusting their visualizations. Interactive visualization tools (Recommendation no. 8 in Table 1) have a crucial role in this early exploratory process.

Once a scientist converges on an interpretation based on this exploration, he/she will then wish to communicate it to the scientific community. For communication, optimization of the visualization for the settled interpretation is often the goal. Confusing exploratory and communicative goals have led to some counterintuitive results. For example, many studies have shown that viewers of animated visualizations demonstrate a poor understanding of the

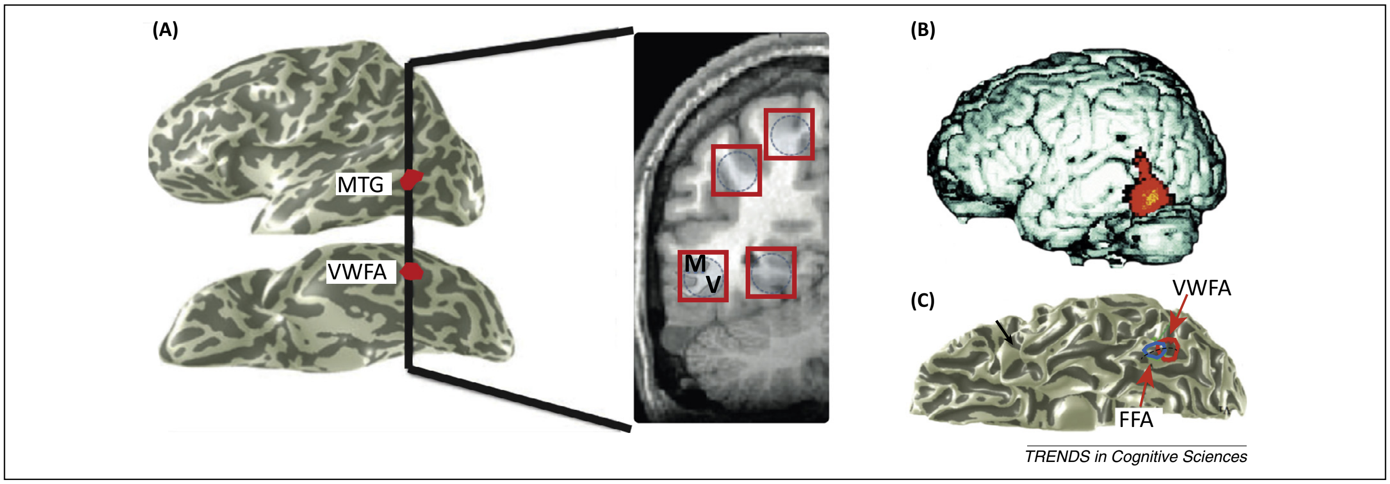

Figure 5. Visualization can change brain interpretation. **(A)** Idealized example of misleading visualization of brain activity in ventral cortex activity (V, VWFA) in lateral cortex (M, MTG) due to low spatial resolution of data (e.g., both M and V fall within a single blue square). **(B)** Depiction of brain activation during a reading task [48–50]. In former times, data were acquired at low spatial resolution and large smoothing kernels were applied, risking mislocalization of brain function. **(C)** Location of frequent brain activity during reading tasks (VWFA) visualized correctly on the ventral surface of brain in ventral cortex [51]. The VWFA is shown in relation to the location of the face responsive cortical area (FFA [101]). Modern methods show higher fidelity in functional measurement and visualization. Reproduced, with permission, from [50] (B); modified, with permission, from [102] (A) and [51] (C). Abbreviations: FFA, fusiform face area; MTG, middle temporal gyrus; VWFA, visual word form area.

depicted system, compared with the comprehension of viewers shown static visualizations [54]. Animated visualizations are often too fast and complicated for unacquainted viewers. Even when interactive controls are added to animations, understandings can be poor [55]. However, these reviewed studies are typically probing the communicative, not exploratory, value of a visualization.

Idealization

Medical books feature hand drawings instead of photographs to highlight important structures and features. These so-called 'strategic idealizations' depart from a working assumption of 'the more realistic the better' by subtly caricaturing, highlighting, and coarsening important features. Needless to say, these transformations can also mislead and so should be applied in a nuanced way that does not obfuscate. Systematic departures from realism are valuable because they promote high-level interpretation, deemphasize irrelevant and potentially misleading details, and enable viewers to see overall trends that might otherwise be masked [56,57].

Interestingly, several studies have revealed that both novices and experts have a tendency to wrongly believe that their performance will be better with realistic compared with idealized visualizations, when the reverse is true [58]. For example, many participants viewing weather maps intuited that task-irrelevant variables and realism would improve their interpretive performance, when they were in fact hindered by their inclusion [59]. This metacognitive failure may arise because humans do not sufficiently appreciate the difficult perceptual, attentional, and cognitive processes required to give a coherent interpretation to a raw visualization.

Figure 3A [60] shows a powerful example of idealization. The left side of Figure 3A shows raw EEG traces. These can be averaged as shown in the bottom of the panel (see also Figure 3C [61]). However, this summary waveform hides crucial structure. An often more revealing representation is to submit individual waveforms to a Fourier transformation that expresses each wave in terms of its power at different frequency bands (right side of Figure 3A).

Another example is the idealized connectivity shown in Figure 4A [62] compared with the more literal connectivity patterns shown in Figure 4B [63] and C [64]. In both cases, there is significant interpretive gain, particularly for seeing global patterns in data, derived from the shift to a less literal, more derived representation. In Figure 4A, connectivity is no longer represented by intuitive lines, but this may be more than compensated for by the viewer's gained ability to see the sequential and hierarchical organization of visual areas; for example, that V1, V4, MT, and DP form a tightly interconnected group of areas is revealed by the noisy, bright square in the upper-left corner of the matrix. Figure 4C shows a different choice for simplification. It visualizes only projections to and from one specific area:V4. It would be difficult to simultaneously preserve the basic geometry of the brain, as done in Figure 4C, and simultaneously show every major connection between areas, as done in Figure 4A and B. An undecipherable spaghetti of connections is likely to result, given that Figure 4B already risks interpretation difficulties because of its dense connection pattern. Figure 4D shows another point along the continuum of idealization representing the human connectome [65]. The figure depicts all strong connections between cortical areas and risks impenetrability because of its sheer density of connections. It is nonetheless an idealization of the highly complex nature of the pathways that connective tracts take, representing these paths as simple straight lines. The complexity of the anatomical pattern formed by some of the tracts comprising the connectome can be appreciated in Figure 4E [4], which is itself a simplification of the actual neurobiology. The various diagrams in Figure 4 show the value of idealization for revealing global patterns of brain connectivity, and the necessity of choosing visualizations wisely based on 'insight need types' (Box 2); Figure 4E can answer questions about the specific anatomy tracts connecting different brain areas, although even this idealization can be too detailed to support claims about the global organization of the brain into hierarchical modules, a role better played by Figure 4A.

A first specific recommendation that derives from considering idealization is to apply a systematic caricaturization process. A caricature of an object $O(x)$ can be defined as an exaggeration $O'(x)$ that emphasizes its distinctive aspects compared with other confusable entities. Although caricaturization might be interpreted as misleading, even basic processes, such as dyes and stains, can be interpreted as caricaturization. The Golgi stain of silver nitrate that revealed the branching patterns of neurons exaggerates the differences between the neurons and their environment, but should not be interpreted as deceitful. Likewise for the modern technique of optogenetics, which uses light to control and record from neurons that have been genetically sensitized to light [66]. In both techniques, it is important that exaggerated differentiation is performed in a systematic way to avoid arbitrary bias and distortion. A second recommendation is to use smoothing and averaging within spatial or temporal windows to produce coarse-scale representations. With the caveats reported in relation to Figure 5, this may sound like a counterintuitive suggestion. How can throwing away high spatial frequency details improve one's ability to decipher patterns? The empirically supported [67] answer to this question is that if there are broad patterns that result from low spatial frequencies, then they will be masked by prominent higher spatial frequencies.

Coordinating interpretation needs with visualization affordances

No visualization is perfect for all uses (e.g., insight needs and/or user groups) because there are unavoidable tradeoffs that will make a visualization more apt for some purposes but thereby less apt for others [68]. For example, visualizations that allow viewers to see the decomposition of the brain into quasi-modules are not typically compatible with visualizations that reveal the anatomy of the tracts that connect these modules together. Figure 1A and B show the anatomy of the tracts connecting modules, whereas Figure 1C and D show the anatomy of cortical modules being connected.

Detailed visualizations that are appropriate for focused identification tasks are inappropriate for providing an overview of major regions [58]. Bar and box-plot graphs emphasize main effects in an experiment, whereas line graphs emphasize interactions between variables [14,69,70]. Tasks and insight needs that require the integration of several pieces of information benefit from visualizations composed with integral (psychologically 'fused together') dimensions, such as saturation and brightness for colors, or features in close spatial proximity [71]. By contrast, tasks that require focused attention to specific values benefit from visualizations with easily separable dimensions, such as brightness and size, or elements that are spatially separated (see, for example, the physically separated representations of space and time in Figure 3B).

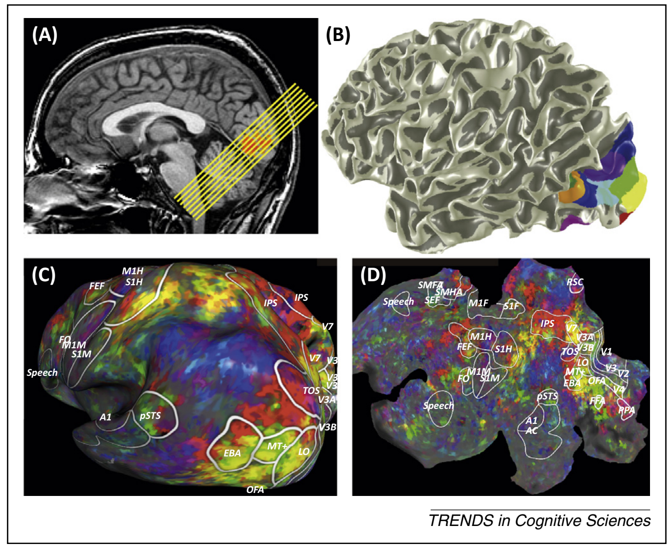

Figure 6. Visualization of the brain surface. **(A)** Sagittal view of a structural magnetic resonance image (MRI) of the brain with an overlay of the acquisition volume for a functional MRI scan (yellow) [100]. Image created using mrTools [103]. **(B)** Digital representation of the surface boundary between gray and white matter in the left hemisphere, demonstrating cortical folding of a human participant; sulci (dark gray), gyri (light gray). Colored areas show early visual areas. Image created using Vistasoft. **(C)** Computationally inflated brain surface of an individual human left hemisphere. **(D)** Flattened brain surface of the same hemisphere as in (C). (C,D) were generated using the online tool Pycortex, colors represent data from [104]. Reproduced, with permission, from [105] (B).

Figure 6 shows several different representations of brain regions varying in their structure and function. Each panel has a different portfolio of preserved and lost information, and which is best adopted depends on one's needs. Figure 6A (volumetric, brain slice) perfectly preserves the spatial relations between cortical areas but at the cost of showing only one 2D slice. Figure 6B (surface of the boundary between white- and gray-matter, uninflated) shows more of the cortical surface and preserves information about the cortical folds with shading, but much of the brain is still hidden, either because a region is occluded by more foregrounded brain regions or because the region falls deep within a sulcus. Figure 6C (inflated surface) sacrifices information about cortical folds by 'inflating' the brain (eliminating the difference between sulci and gyri), but consequently gains the capacity to show activity information associated with regions deep within sulci. Figure 6D (flattened cortex) goes still further in sacrificing the natural geometric structure of the brain by strategically cutting the surface at several points, but gains the capacity to show the entire brain surface. Which of these visualizations should be chosen depends on how important it is to preserve aspects of the geometry of the brain versus show increasingly large percentages of the entire brain.

When designing visualizations of the human brain, researchers should first specify the task(s) for which the visualization will be used (see Box 2 for common task types and insight needs). Common tasks in neuroscience are: identifying functional specializations for compact brain regions; understanding functional dependencies or structural connections across brain regions (see 'correlations/relations' in Table I in Box 2, column 1); tracing prominent brain subnetworks (also 'correlations/relations'); identifying common or distinct structures across individual brains ('categorize/cluster' and 'comparisons'); and determining the time course of neural activity from the onset of a stimulus ('trends'). Given that a scientist's interests and tasks may shift from moment to moment, one effective strategy is to overlay different data on the same brain reference system (see Figure 6 for options) that highlight different patterns. If this is done, it is important for overlays to be coded in a consistent manner to help users map across the different representations [72].

Novices and experts

Although some visualizations are designed for exclusive use by experts, many are used by expert and novice users alike. Designing apt visualizations for both kinds of users is difficult because of the expertise reversal effect, according to which adding additional scaffolding information to a visualization often helps novices but hurts experts [73]. For example, expert dermatologists performed better medical diagnoses when given only photographs than when given photographs and verbal descriptions, whereas the reverse trend was true for nonexperts [74]. The generally greater reliance on visualizations for experts compared with novices belies the claim that perceptual processing is superficial and conflicts with sophisticated understandings. Experts often acquire their deep understandings by training, not trumping, their perceptual processes [75]. This expertise reversal effect is also worth keeping in mind for authors as they prepare communicative visualizations. Readers who are not as familiar with a visualization type will typically need more descriptive scaffolding to effectively understand images.

At least two recommendations stem from an awareness of powerful individual differences related to expertise. The first is to match the complexity of a visualization to its intended audience. Figure 1A is more appropriate for a novice wishing to understand the basic connectivity patterns of the two tracts, whereas Figure 1B is more suitable for an expert wishing to understand the full possible extent and coverage of the tracts. Second, as graphical depictions become more processed, derived, and idealized, their optimal audience shifts rightwards along the novice-to-expert continuum. Students first learning about EEG will benefit from seeing the raw traces on the left side of Figure 3A, but experts will tend to spend more time perusing the transformed and compressed representation of the right side of the figure. Figure 4C is useful for its concrete grounding for novices, but as expertise increases, representations such as Figure 4B and then Figure 4A will become increasingly beneficial. The strategy of progressively idealizing originally concrete representations has been shown to be a cognitively effective way of creating grounded yet flexible understandings [76,77].

Concluding remarks

Theoretical insight is often irreducibly just that: in sight. Neuroimages have a strong psychological impact because of their concreteness and intuitive appeal. For a lay audience, studies have shown that neuroscience research is judged to be more scientifically credible [78] and more understandable [79] when it is accompanied by brain images rather than by bar graphs or more abstract topographical maps. Although other studies fail to replicate a general effect of neuroimagery on scientific persuasiveness [80,81], there appear to be at least some limited contexts [82] in which neuroimagery does add gravitas to scientific arguments. In light of results showing that imagery depicting the 3D geometric structure of a brain (e.g., Figure 6B) is more scientifically convincing than a flattened topographic map (e.g., Figure 6D) for lay audiences [83], one conjecture is that lay audiences are naively interpreting the 3D, object-like depictions as directly capturing and displaying brain activity [8,9]. Researchers should be sensitive to this likely misconstrual of neuroimagery, articulating rather than concealing the long pipeline needed to create images that seem to directly reflect brain activity. There may even be cases in which concrete, 3D neuroimagery should be avoided so that viewers engage in a more critical, reflective process of analyzing and assessing the images [84].

Another possible case of disproportionate influence of neuroimagery is that amateur and professional designers' visualizations of the same data can lead to different reader responses. Viewers might trust the latter readily but not the former. Similarly, low-quality data rendered by a professional designer may disguise data quality or other issues: viewers will likely assume that the well-designed visualization reflects accurate results. Accordingly, devoting a substantial amount of time and effort in training scientists to prepare professional scientific visualizations has the power to amplify the impact of research.

Nine theoretically grounded yet practically useful recommendations for novice and expert makers and users of visualizations are listed in Table 1. They may guide the design of effective visualizations and the development of *de facto* standards in support of data, code, and workflow sharing, replication, and further development.

This review may leave the impression that humans are slaves to their own eyes, and that the constraints of their perceptual and cognitive systems limit how they interpret scientific visualizations. In fact, human perceptual and cognitive constraints should guide graphic design decisions when visualizing brain data. However, there are two important ways in which humans are not strictly limited by their perceptual and cognitive constraints. The first is that humans are capable of impressive feats of perceptual learning [85]. Quite a bit is known about some of the neurological underpinnings of these changes [86] and, as humans, we can systematically adapt our perceptual systems so as to provide more useful representations for downstream cognitive processes [75,87]. The second way in which humans can rise above their perceptual and cognitive constraints is by creating new measurement devices, experimental protocols, interactive technologies, and visualization algorithms to make otherwise invisible brain processes visible. Thus far, too much of neuroscience has grown as a cottage industry in which each laboratory creates its own idiosyncratic tools. For neuroscience to progress with rapidity in the future, greater effort must be made to build visualization tools and infrastructures that facilitate replication, reuse, and extension [6]. Armed with sophisticated systems designed for widespread use, the neuroscience community would be poised for a revolution in theoretical insights. As scientists, our conjectures are governed by what we perceive, but what we present to ourselves is limited only by our imagination.

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