



Visualizing the human connectome[☆]

Daniel S. Margulies^{*}, Joachim Böttger, Aimi Watanabe, Krzysztof J. Gorgolewski

Max Planck Research Group, Neuroanatomy & Connectivity, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

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ABSTRACT

Innovations in data visualization punctuate the landmark advances in human connectome research since its beginnings. From tensor glyphs for diffusion-weighted imaging, to advanced rendering of anatomical tracts, to more recent graph-based representations of functional connectivity data, many of the ways we have come to understand the human connectome are through the intuitive insight these visualizations enable. Nonetheless, several unresolved problems persist. For example, probabilistic tractography lacks the visual appeal of its deterministic equivalent, multimodal representations require extreme levels of data reduction, and rendering the full connectome within an anatomical space makes the contents cluttered and unreadable. In part, these challenges require compromises between several tensions that determine connectome visualization practice, such as prioritizing anatomic or connectomic information, aesthetic appeal or information content, and thoroughness or readability. To illustrate the ongoing negotiation between these priorities, we provide an overview of various visualization methods that have evolved for anatomical and functional connectivity data. We then describe interactive visualization tools currently available for use in research, and we conclude with concerns and developments in the presentation of connectivity results.

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Introduction

When investigation of the human brain was limited by what the eye could see, its structure, albeit elaborate, was within our mental grasp. But the resurgence of interest in connectivity, like that of cytoarchitectonics a century ago, has established a new dimension of information to assimilate. As our data grow in intricacy, the images we create reflect how we bestow them with significance – because implicit (and often explicit) in our visualizations of the human connectome are the categories, metaphors, and abstractions that we use to make it comprehensible.

An analogous transition in visual metaphors was underway with the emergence of mass transit systems over a century ago. Much like the complexity of the brain, the unfamiliar transport systems presented a challenge of how to effectively communicate their structure to the public. Early London Underground maps found comfort in familiarity, and wove the train paths unobtrusively into the contours of the existing cityscape (Fig. 1, top). It was only decades later that the crisp, emblematic form – subsequently mimicked the world over – came into being (Fig. 1, bottom). In emphasizing the relative

connections, rather than the underlying terrain, the resultant image offered the viewer an intuitive mapping of the *relevant* information. Maps never show us everything about a place or a space; their value is rather in the cartographer's insight to enunciate selected features over others.

Every map has a context – and when the content is overflowing with innumerable data dimensions, the task of creating *intuitive*, *informative*, and *candid* images becomes all the more challenging. The mapping of connections in the human brain has been a visual tale of increasing complexity, continuously pulled between various priorities of data presentation. Our illustrations and figures narrate the transition from describing the brain as a three-dimensional object to describing the proximity of areas in terms of the strength of connections. These two basic models of brain space, though there are more, are the basis for the territorial battles for defining space. The result in any connectome image is a content-dependent balance of *anatomical clarity* versus *connectomic complexity*.

Connectivity mapping has also been forced to struggle with evolving methodologies – analytic tools that in some cases may have overstated their actual information content. Controversies surrounding the veracity of paths derived from diffusion weighted imaging-based tractography (Dyrby et al., 2007; Hubbard and Parker, 2009; Jbabdi and Johansen-Berg, 2011) or functional connectivity derived using controversial analytic approaches (e.g., Saad et al., 2012; Smith et al., 2011) run the risk of visualizations that make the underlying data appear deceptively tangible. The aim of an image, from this perspective, is to accurately show the uncertainty in the data (Allen et al., in press) – be it statistical or methodological. Given the high

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^{*} Corresponding author at: Max Planck Research Group: Neuroanatomy & Connectivity, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany.

E-mail address: margulies@cbs.mpg.de (D.S. Margulies).



Fig. 1. Feature shift in London Underground maps. *Top*, first unified map of the London Underground from 1908 with the train lines subservient to the layout of the city. *Bottom*, lacking the recognizable geography, but maintaining the relative positions and connection points, the revolutionary 1931 design by Harry Beck.

information content of connectivity data, *prioritizing honest depictions of uncertainty, while also rendering the wealth of available data in an intuitive form*, is a formidable challenge.

A third tension of human connectome visualization is the balance of *complexity and simplicity*, otherwise stated as *thoroughness and readability*. What is the most effective and appropriate scale to chunk the data? The meaningful unit could be a parcellation of local modular regions, large-scale independent networks, or each and every unsmoothed voxel. The meaningful unit could be individual fibers, bundles, or something in between. A meaningful unit may be a hypothesis about the role of a specific region or connection, and its significance might dynamically alter from moment-to-moment or across the lifespan. The way we define it, the scale we chose, has consequences for the subsequent visual story we will need to convey. Visual simplicity may often be desired, but not necessarily at the cost of genuine information loss.

The aim of this review will be to provide a critical overview of connectivity visualization methods for the human neuroimaging community, calling attention to gaps and weaknesses, as well as innovations from other fields that may benefit our own. Pfister et al. (2012) recently reviewed connectomics for a scientific visualization audience, and provided a thorough overview of the methodologies and specific

challenges across a wide range of neuroscientific fields. While the review provides a valuable introduction to connectivity for a visualization audience, no overview yet exists aimed at the unique concerns of the human neuroimaging community, although there is growing interest in visualization-focused publications (Allen et al., *in press*; Irimia et al., 2012b; Pyka et al., 2010).¹

Reviewing the progress and current limitations, we will begin by presenting the literature related to functional and anatomical connectivity visualization, characterizing both the predominant trends and selected innovations. Research practice itself will be the focus of the following section, where we review software for the exploration of connectivity data. The final discussion on data presentation and publication considers how we currently present connectivity results and how we could in the future. We will address the impact of connectome visualization on its interpretation, online publication tools for data presentation, and domains that hold promise for innovating novel techniques.

Of glyphs and paths, matrices and graphs

The building blocks of connectome visualization are symbolic units. For anatomical connectivity these units express directional information at each voxel; for functional connectivity they may be any number of data reduction steps that result in describing a statistical relationship between regions. From these fundamental elements, various analyses produce individual connections, which together form the connectome. At each stage of data transformation, opportunities for visualization arise, each with their own emergent challenges for maintaining clarity and faithfulness to the underlying data. The following section will follow that path from data unit to connection to connectome, and finally to the added complexity of visualizing dynamics and multimodality. With each new technique, there will be options and opportunities to prioritize certain aesthetic values and information content over others, with rarely an optimal context-independent solution. The result is that the connectome emerges as a product of these choices.

Anatomical connectivity

The most visually arresting connectivity images arguably belong to the anatomical family. Composed of a variegated nest of interwoven fibers, diffusion weighted imaging-based tractography continues in many ways to stay at the forefront of computer visualization research. From the get-go, the methodological origins of anatomical connectivity were dependent on innovative visualization. To demonstrate that the anisotropy of water diffusion using diffusion-weighted MRI (DWI) reflects the orientation of white matter, the pioneering publication relied on red and blue to represent two orthogonal directions (see Fig. 4 from Douek et al., 1991). Rather than each voxel only containing a single scalar value of information (Fig. 2a), two independent values could simultaneously be represented (for an example of three dimensions, see Fig. 2b). The following two decades of research into anatomical connectivity using DWI are the further exploitation of the limited space of the voxel.

Glyphs

In order to visualize the richness of information contained in multidirectional DWI data, it is necessary to show more dimensions than possible with only the display of scalar values or the three dimensions that color easily affords. This first became apparent for diffusion tensor imaging (DTI), where diffusion is modeled as a tensor of rank

¹ Another example and resource is the Beautiful Brain project from Brainhack 2012: <http://www.brainhack.org/wiki/doku.php?id=beautifulbrain>.

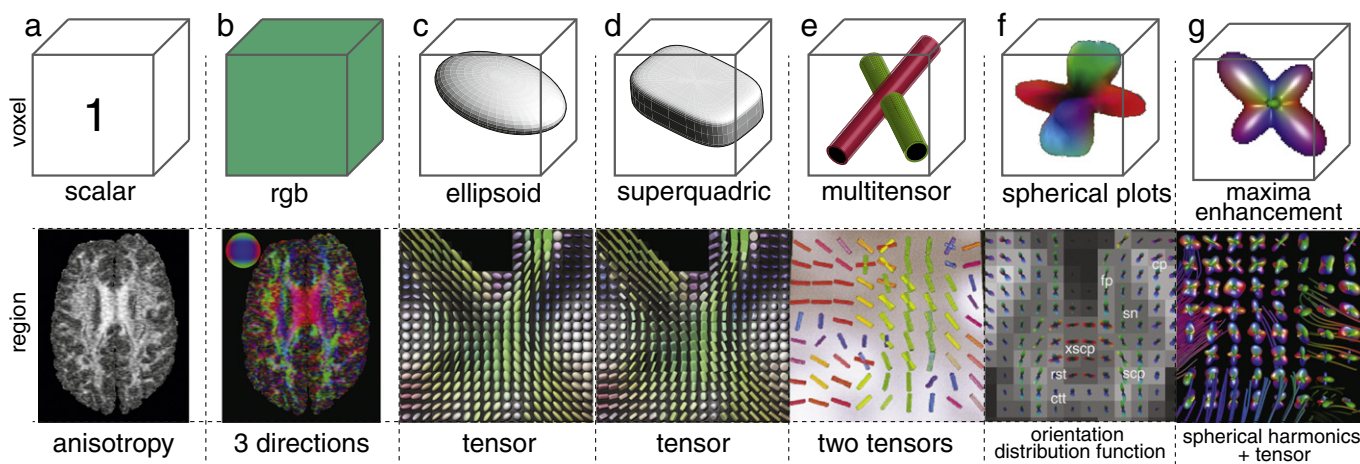


Fig. 2. Evolution of the DWI glyph. The voxelwise glyph has become increasingly complex to accommodate the directional information derived from DWI-based data. (a–d: Kindlmann (2004b), e: (Tuch et al., 2002), f: (Tuch, 2004), g: (Prčková et al., 2011)).

two (with six degrees of freedom) at each voxel. In order to display these tensors, *glyphs*, generally defined as small *localized visual representations of multivariate information*, in the shape of ellipsoids were used (Fig. 2c; and see Fig. 7 from Basser et al. (1994)). The ellipsoid was an appropriate choice for tensor representation, because it can capture directionality and magnitude of all three eigenvectors, but its disadvantage is the visual ambiguity of these three-dimensional shapes. For example, an elongated ellipsoid depicting highly anisotropic diffusion can appear indistinguishable from a sphere when projected on the viewing plane along its longest axis. Such ambiguities were the motivation for the development of more complex tensor glyphs, such as the *superquadric* (Kindlmann, 2004a), which offers unambiguous depiction of tensors by introducing sharp edges as strong orientation clues, and remains state-of-the-art for the glyph visualization of DTI data (Fig. 2d).

Tensors of rank two would be sufficient to describe the directionality of a voxel if the contents were all aligned. However, mapping a single tensor at each voxel is not sufficient to describe more complex configurations, such as crossing fibers, and is in fact misleading. To achieve a more complete map of the probability density function within each voxel, new methods such as high angular resolution diffusion imaging (HARDI) (Tuch et al., 2002) or diffusion spectrum imaging (DSI) (Wedeen et al., 2005) were developed to sample the three-dimensional probability distribution using scans from numerous directions (typically 60 samples on a sphere for HARDI and 500 samples on a regular lattice for DSI). As the information content of DWI approaches increased, corresponding sets of high-dimensional glyphs were also developed. Since the relevant information content is contained in the angular structure of the probability density function, a two-dimensional spherical function is reconstructed using the angle, but not the magnitude of displacement (typically based on the orientation density function). In their landmark publication, Tuch et al. (2002) pioneered two visualization approaches: (1) spherical polar plots (Fig. 2f), and (2) a decomposition of the data into two tensors, rendered as cuboids or “sticks” (Fig. 2e). Glyph visualization of HARDI and DSI data is still divided into these two general approaches.

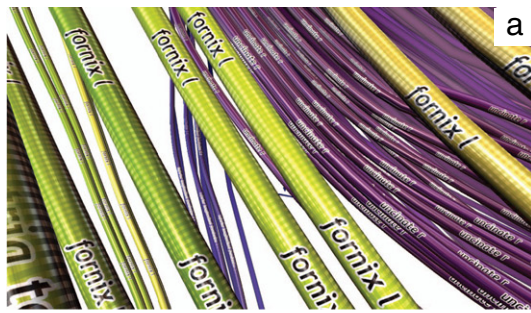
Several flavors exist for spherical polar plot glyphs (Fig. 2f) (Jansons and Alexander, 2003; Ozarslan and Mareci, 2003; Tournier et al., 2004; Tuch, 2004). While serving as a visual validation of the original data, such glyphs are vulnerable to the fact that the maxima of spherical functions do not necessarily coincide with the main fiber directions of the underlying anatomy. Visually distinguishing neighboring local maxima is especially problematic for configurations where fiber bundles with similar directions intersect in the same voxel. The inherent loss of maxima information in spherical polar plot glyphs is complementary to the

other category of glyph, which decomposes complex diffusion data into multiple tensors of rank two (Bergmann et al., 2007; Schultz and Seidel, 2008). The main directions are then derived as the largest eigenvectors of the respective tensors and displayed as crossing cylinders or cuboids (Fig. 2e). This latter approach, while not providing the richness of probabilistic information present in the spherical polar plots, emphasizes the crucial directional information for the subsequent aim of path tracing. The tradeoff in glyph selection is between emphasizing the feature of interest (maxima) or describing the directional subtleties (and uncertainties). In attempts to combine the strengths of each, augmenting spherical polar plot glyphs with arrows has been proposed (Hlawitschka and Scheuermann, 2005), as well as visually optimizing their shapes and color schemes to accentuate multiple distinct maxima (Fig. 2g) (Prčková et al., 2011; Schultz and Kindlmann, 2010). Advanced hybrid methods such as these are a notable example of cutting-edge visualization innovations in the service of providing accurate information content. The even balance of uncertainty and desired feature require not only insight into the strengths and weaknesses of each available method, but also recognition of how they could be optimally merged to achieve both intuitive and informative data illustrations. While a similar dichotomy presents itself in the field of tractography visualization, an equivalent synergy of methods remains an unresolved and an ongoing area of research.

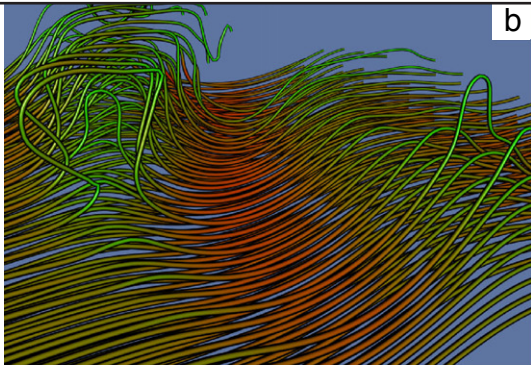
Tractography

The basic aim of tractography is to compute paths through the directional information that has been visualized using glyphs. However, where advanced glyphs were necessary to accurately reveal the complexity and uncertainty of the underlying data, traditional streamline tractography brushes any ambiguity aside by describing a concrete tract (Conturo et al., 1999; Mori et al., 1999; Wedeen, 1996). Appropriately termed *deterministic tractography*, visualizations swiftly flank any concerns about the validity of the results by offering a barrage of rendering techniques that present an intuitive semblance of the real.

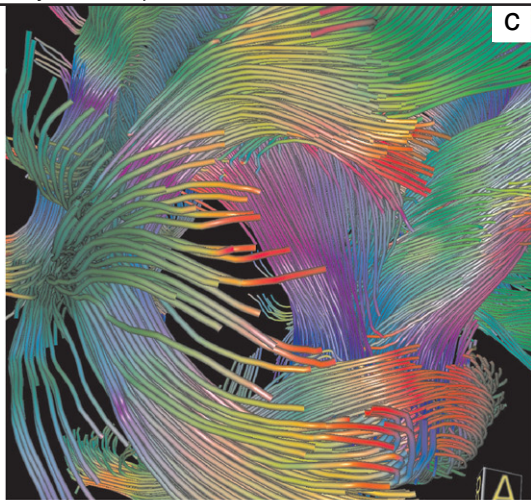
The classical, realistic rendering techniques in computer graphics (Foley et al., 1990) stem from the simulation of camera projections and light dispersion for rendering triangulated geometry, and are ill suited for the display of long, thin tube-like structures. However, the use of modern graphics hardware and the abstraction of tubes to sophisticated display stand-ins such as *tuboids* (Petrovic et al., 2007), *hair-like structures* (Peeters et al., 2006), *triangle strips* and *point sprites* (Merhof et al., 2006), *streamtubes* and *-surfaces* (Zhang et al., 2003), and *stylized line primitives* (Stoll et al., 2005) have made interactive rendering with high quality shading and shadows feasible (see examples in Fig. 3). Such approaches provide additional visualization perks



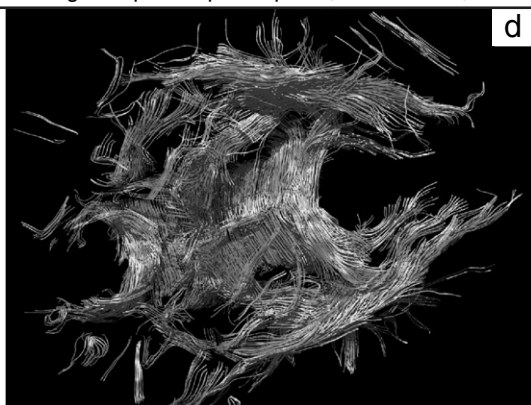
Tuboids, Petrovic et al, 2007



Stylized line primitives, Stoll et al, 2005



Triangle strips and point sprites, Merhof et al, 2006



Hair-rendering techniques, Peeters et al, 2006

such as labeling of the streamlines with textual information (Fig. 3a) (Petrovic et al., 2007), and can be computationally efficient enough to enable web browser-based implementations (Congote et al., 2012).

Although these tract-rendering techniques offer stunning images of purported fiber paths, the analytic methodology that the visualizations are based upon remains problematic. Deterministic tractography runs the risk of misrepresenting anatomical fibers, because certain structures, such as crossing and kissing fibers, splits and termination points, cannot be resolved with absolute certainty (Dyrby et al., 2007; Hubbard and Parker, 2009; Jbabdi and Johansen-Berg, 2011). Visualization in this context risks a disservice, featuring the image at a cost to information content.

Tracking uncertainty. The distrust of paths derived from deterministic, streamline fiber tracking has motivated the development of probabilistic methods. Rather than seeding each tract once, probabilistic approaches seed the same tract numerous times, and calculate the probability of the tract passing through each voxel based on the percentage of total number of path iterations. However, as the resultant tract becomes a statistical map, rather than a path, how can the tractography be made visible? When we know a tract is a tract, there are myriad visualization tools to render it with sophisticated lighting and shadows; however, when we only know a tract to be a tract with a specified degree of certainty, rendering paths becomes confounded with rendering their relative degrees of path certainty.

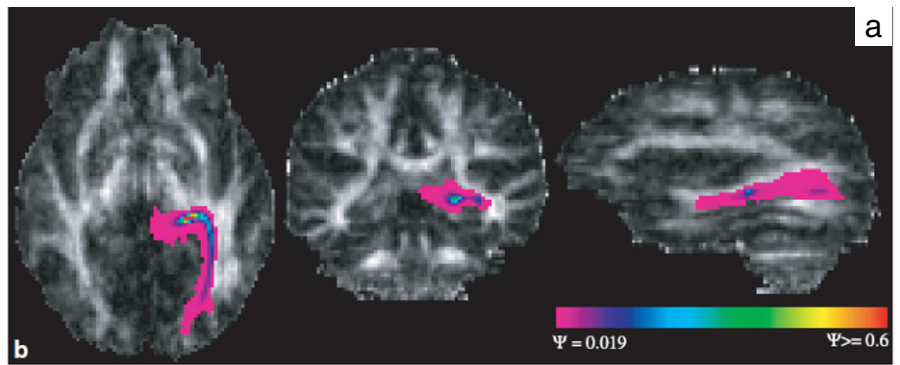
Early visualizations relied on standard MRI motifs of anatomical slices, depicting superimposed probability values using symbolic color scales (Fig. 4a) (e.g., Parker et al., 2003). The probability values have also been conveyed by varying opacity levels, with cutaway three-dimensional semi-transparent volume rendering for anatomical reference (Fig. 4b) (von Kapri et al., 2010). The problem with such rendering lies in the lack of clarity with regards to the anatomical landmarks, which are removed to enhance the probabilistic tractogram's visibility. Berres et al. (2012) have addressed this issue by using compositing techniques to minimize occlusion of salient tract information from the anatomical volume (Fig. 4c). While establishing spatial context through the cortical surface, the results still appear suboptimal in conveying three-dimensional organization. Yet another approach has been pioneered by two independent groups, who have attempted to resolve the current viewing limitations by projecting probabilistic tractography into the three dimensions of virtual reality (Chen et al., 2011; Rick et al., 2011). While such expensive three-dimensional displays may help to concurrently convey spatial structure and probabilistic information, the problem remains open for everyday visualization.

An entirely novel solution proposes to return to the original strength of tractography visualization, the concrete path, but to modify the methodology to accommodate the uncertainty of which specific path may be correct. Rather than map the probabilities onto voxels, *tract density imaging* resamples voxels at a much higher resolution than the original data, and thereby enables every possible tract to exist in super-resolution, mapping probability as density (Calamante et al., 2010, 2011).² The result is a tractogram that is distributed across a large number of independent paths (Fig. 4d), rather than transforming the results into a volume of probability values. The wealth of techniques that make deterministic tractography so appealing can then be brought to the service of visualizing results that are more accurate reflections of the inherent uncertainty in the data, yet are once again visually arresting.

While improvements in the 'realism' of renderings can be essential for the readability of the resulting images, strict adherence to pseudo-photographic rendering may not always be optimal for

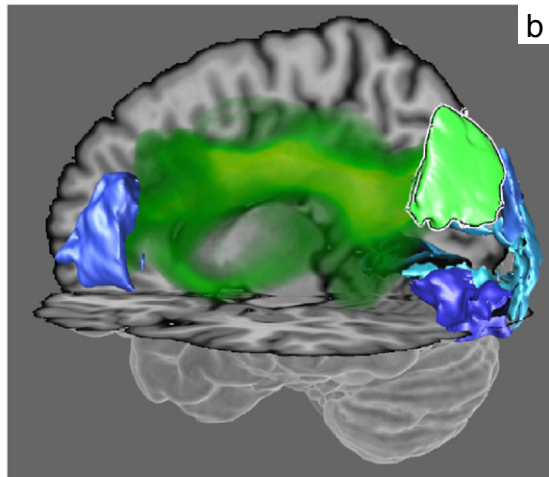
Fig. 3. Rendering fibers. Various rendering techniques have been applied to tractograms in order to improve clarity. a: Petrovic et al., 2007; b: Stoll et al., 2005; c: Merhof et al., 2006; d: Peeters et al., 2006.

² The detail contained in tract density imaging can be seen in the video created for the exhibition "Images of the Mind" at the Deutsche Hygiene Museum, Dresden, in 2012: <http://www.youtube.com/watch?v=ZpAzY5-tDWE>.

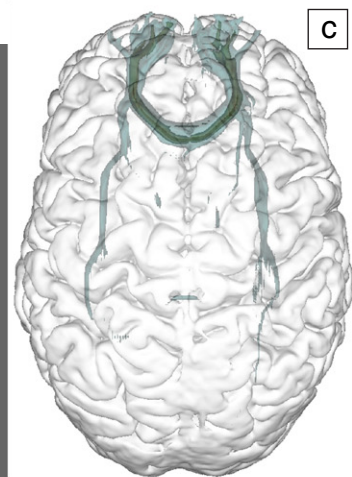


Color scale, superimposed on slices

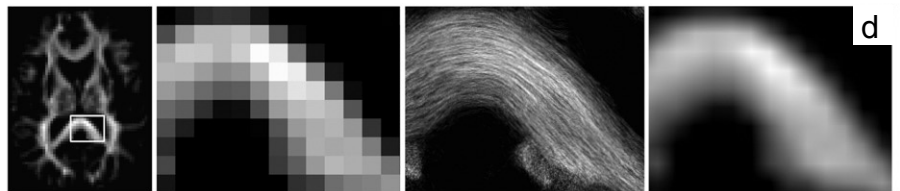
Parker et al, 2003



Volume rendering von Kapri et al, 2010

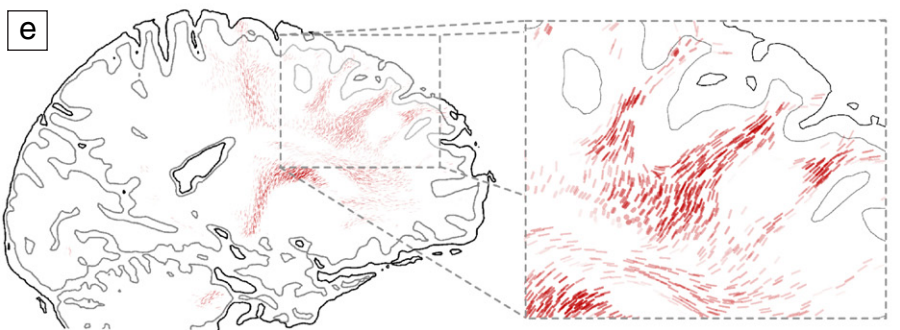


Berres et al, 2012



Superresolution

Calamante et al, 2010



Stippling

Goldau et al, 2010

Fig. 4. Probabilistic tractography. Rendering probabilistic tractography with comparable clarity and aesthetic quality as its deterministic counterpart continues to be a challenge. a: Parker et al., 2003; b: von Kapri et al., 2010; c: Berres et al., 2012; d: Calamante et al., 2010; e: Goldau et al., 2010.

intuitive representation of three-dimensional space (Penney et al., 2012). Alternative modes of data presentation have been borrowed from the history of scientific illustration. One aesthetically striking technique for probabilistic tractography uses *stippling*, which is the use of small dots to recreate the content of an image (Fig. 4e)

(Goldau et al., 2011). By presenting area-preserving line stipples on edge-traced anatomical slices, figures resembling the tract-tracing macaque monkey literature result (e.g., Schmahmann and Pandya, 2009). Different colors can then be used to simultaneously view more than one probabilistic tractography result. Although the data

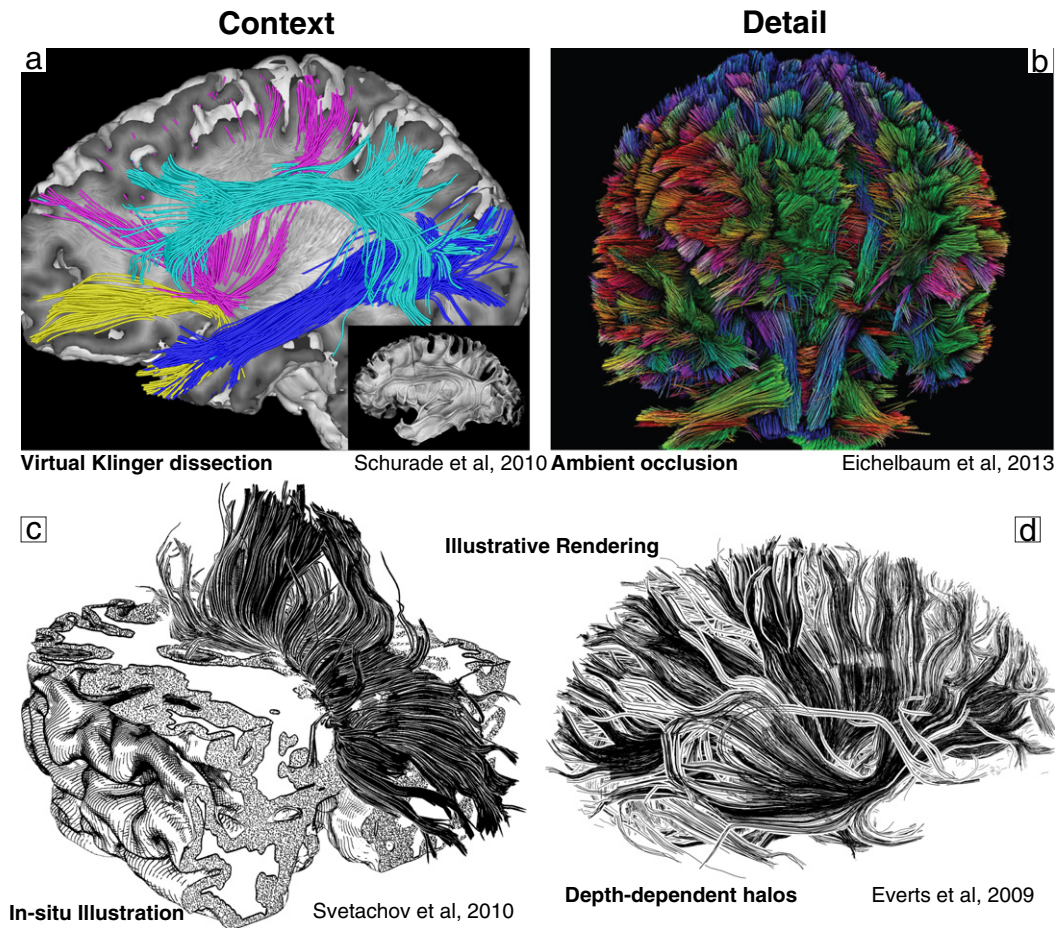


Fig. 5. Context & detail. Providing anatomical information in a tractography image requires the rendering of context and details. a: Schurade et al., 2010; b: Eichelbaum et al., 2013; c: Svetachov et al., 2010; d: Everts et al., 2009.

are presented as slices rather than volumetrically, the anatomical clarity and intuitive representation of probability offered by this technique make it a promising new direction for anatomically descriptive and information rich visualizations.

Detail and context. Spatial context is crucial for reading maps of any kind.³ A major challenge for visualizing tracts on a two-dimensional plane is that the anatomical context is easily lost beneath the fibers-of-interest. Again, the history of medical illustration provides inspiration to observe realistically situated fiber bundles. Schurade et al. (2010) simulate visual perspectives achieved during the anatomical dissection of brains, focusing on selected tracts *within their anatomical context*. To achieve this effect, the surrounding anatomy is rendered using a cutting surface that is fitted to match the current fiber bundle-of-interest (Fig. 5a).

Fiber bundles can also play an assistive role in clarifying the complex spatial relationships between fibers. For the perception of these relations, the light exchange between objects in a scene can be essential. However, the classical rendering algorithms only take into account light transported from a light source directly to objects in the scene, and then to the camera. Eichelbaum et al. (2013) adapted

ideas from the simulation of global illumination in order to produce tractography renderings that show details as well as the global overall structure of a whole brain dataset, while still achieving quick rendering speeds for the interactive display of complex datasets (Fig. 5b). Everts et al. (2009) achieved similar insight through a different effect based on implementing depth-dependent halos around fibers (Fig. 5d). This approach, which leads to beautiful depictions resembling pen-and-ink illustrations, naturally emphasizes coherent bundles while deemphasizing less structured fibers. Similar illustrative techniques have also been adapted by Svetachov et al. (2010) to simulate graphical techniques such as hatching and stippling in order to make a simultaneous rendering of surrounding anatomy possible (Fig. 5c).

Illustrative rendering takes advantage of material-driven illustrative techniques to limit the complexity of anatomical connectivity presentation to intuitive, tried-and-tested composition styles. The emphasis on intuitive interaction will prove to have further benefits for data comprehension, and will be the topic of its own section.

Functional connectivity

Much like the transit maps described in the introduction, the salient features of functional connectivity are the connections between termination points, rather than the specific spatial trajectories between them. To more precisely extend the metaphor from the map to the reality of urban transit, functional connectivity represents the

³ To extend the London Underground example to a more contemporary controversy, the removal of the Thames river a few years ago caused quite an uproar: <http://www.guardian.co.uk/artanddesign/2009/sep/17/london-new-tube-map-thames>.

probability of a connection between two points. Based on the correlation between spontaneous fluctuations measured with fMRI during a resting baseline state (Biswal et al., 1995), the most basic visual representation of voxelwise functional connectivity is the two-dimensional matrix, where each point represents the functional connectivity probability value between two voxels, but no anatomical information is represented (Fig. 6). The term *connexel* has been coined to describe this connectivity point in a six-dimensional space, which is based on the combined coordinates of two three-dimensional points (Worsley et al., 1998). Notwithstanding the high dimensionality of connexel-space, the same techniques developed for visualizing three-dimensional voxel data are the most commonly used for functional connectivity – not surprising, considering that the software is often the same for both analyses. In part owing to this historical link to task-based fMRI, functional connectivity visualization has routinely prioritized anatomical clarity in visualizations over the complexity of connexels (Fig. 6). Through any number of data reduction techniques – ROI-based analyses, independent component analysis, or graph theory-based measures – the analytic trend has been to reduce the connectomic information to analytically and visually digestible chunks. When a novel framework emerges for interfacing with functional connectivity, however, this makes it all the more unique.

Graphs

Where diffusion weighted imaging-based tractography finds its visual inspiration from computer graphics and three-dimensional rendering, functional connectivity has largely turned to graph theory (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010; Sporns,

2012) – an analytic language suitably concerned with describing the connections between nodes rather than the specific spatial paths connecting them. When the visualized unit becomes the *connection* between two points rather than the points themselves, novel possibilities emerge for representing connexels in a single image. This insight shifted functional connectivity visualizations from more traditional, anatomically situated representations to figures that focused their content on the graph of *node-links* or *edges* (see *anatomical* examples from Fig. 7). Early examples provided a transition point between anatomical space and connectional space through the use of two-dimensional coordinate systems to reflect each node position from a single planar view (Achard et al., 2006; Salvador et al., 2005a, 2005b), through renderings of three-dimensional bars in a volumetric space (Worsley et al., 2005), or a unique use of curved lines across a volume-rendered brain volume (Foucher et al., 2005). In these examples, anatomical location is maintained, and the connections are articulated using lines. However, as the number of represented connections is increased, the underlying anatomical space runs the risk of becoming obfuscated by the connections. This problem was circumvented by recognizing that the path of connections in functional connectivity space is arbitrary, and that the informational content is in the link itself. Achard et al. (2006) demonstrated this shift using space to represent functional connectivity distance rather than anatomical distance (Fig. 7, *functional*). The emerging need for incorporating more functional connectivity data into visualizations renders even functional connectivity-space as over-cluttered. Tools have been introduced from the visualization community (Holten, 2006) to prioritize the clarity of connections through hierarchical edge-bundling techniques

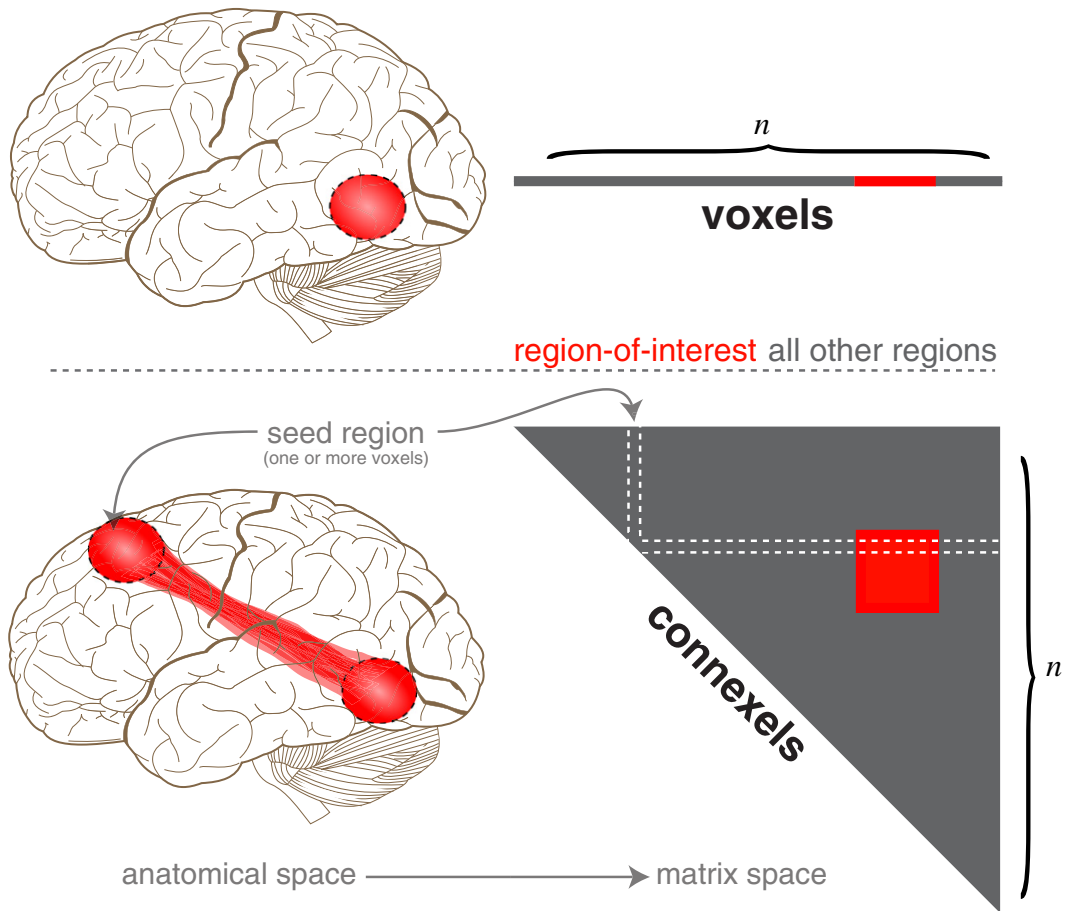


Fig. 6. Voxels and connexels.

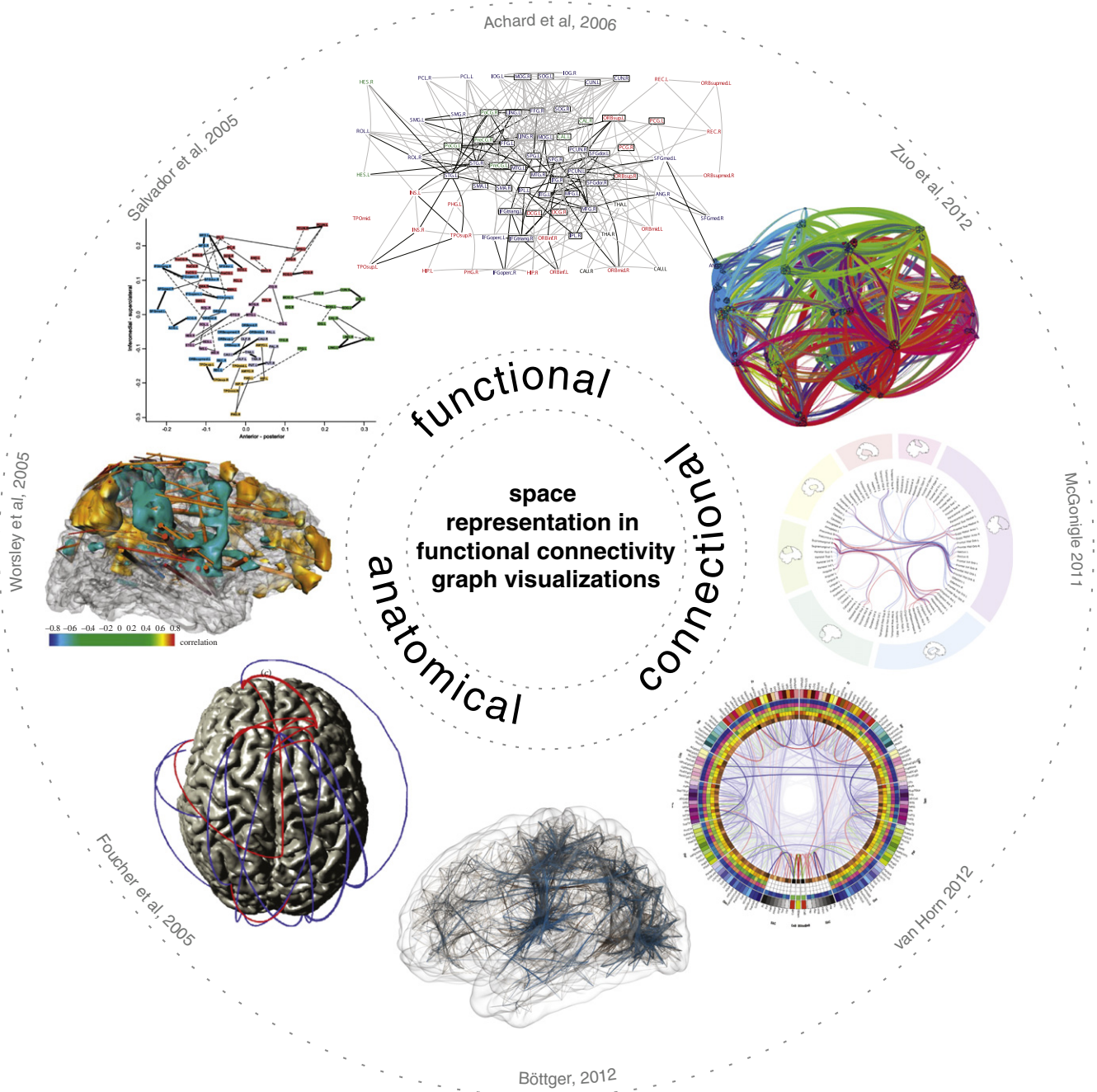


Fig. 7. Representing space in functional connectivity graphs. The connectivity images demonstrate a changing use of page-space to represent the anatomical brain space, functional connectivity distance, and connectivity edges themselves. McGonigle 2011 and van Horn 2012 are from the Brain-Art Competition (<http://www.neurobureau.org/brainart/galleries/>).

(Fig. 7, *connective*) (Irimia et al., 2012b; Schwarz and McGonigle, 2011; Zuo et al., 2012).⁴ Through the series of figures presented in Fig. 7, it becomes clear how space is transformed from being anatomically representative to dominated by functional connectivity, and most recently to a space where the connectivity itself dominates. At this stop on the circle of Fig. 7, there is nothing distinctly ‘brainy’ about this mode of spatial representation. However, as the circle closes back to anatomical space, a concern arises. The image by Böttger (Fig. 6,

bottom) applies mean-shift edge-bundling within a three-dimensional anatomical space, enabling large sets of common connections to become visible. Although this methodology is based on clustering data in six-dimensional connexel space, and does not claim that the paths presented are anatomical, it could be construed as such, and has the potential to mislead through forcing the viewer away from habits of visual interpretation.

Graph representations combat the limited dimensionality of voxel-space, but they often do so at the expense of representing the probability of connections through thresholding (Bullmore and Sporns, 2009; Habeck and Moeller, 2011; Smith, 2012). Portraying functional connectivity as a binary edge ignores uncertainty values. Much like deterministic tractography, prioritizing the question of *how* to visualize all the connections distracts from the *content* of the visualization.

⁴ In the two years the Neuro Bureau’s Brain-Art Competition (<http://www.neurobureau.org/brainart/>) has been held, the winner in the Best Representation of the Human Connectome category have both years included circular representations, suggesting that the clarity offered by this technique may be the future of connectome visualization.

Although less common, it is possible to display weighted graphs. In a recent visualization study, the user evaluation found that matrix representation was more effective at communicating weighted connectivity data than the graph form (Alper et al., 2013). The authors also offer unique forms of visually encoding the matrix information to facilitate rapid evaluation. User evaluations such as these indicate the importance of matching the visualization technique to the research question, and that the task may actually be better accomplished with a tried and tested tool. Similar to culling from the motifs of medical illustration described above, previous forms of representation may offer a more familiar aesthetic for the viewer. The study by Alper et al. (2013) is a lonely example of aiming to optimize the visualization of weighted information using a graph theoretical framework. Much like tractography's prioritization of *how* to present connections, this example emphasizes the effective display of ambiguity. For the field to achieve the aim of thoroughly visualizing functional connectivity, uncertainty cannot be sidelined as a mere problem of proper analytic thresholding.

Dynamics

We have thus far addressed the problem of visualizing the three-dimensional space of connections, taking for granted the stability of the functional connectome. An additional dimension is required when the temporal domain is brought into the image along with the spatial (Fig. 8). Early approaches to illustrating brain activity over time used color coded ROIs with representative time-series (Fig. 8a) (Fox et al., 2005) or coherence plots (Fig. 8b) (Chang and Glover, 2010). More recent depictions of the whole brain over time make use of a left-to-right montage, with brains shifting along the series to reveal dynamic changes (Fig. 8d) (Handwerker et al., 2012; Majeed et al., 2011; see Figs. 4 & 6 from Majeed et al., 2009) or correlation matrices (Fig. 8e) (Allen et al., 2012a). However, when anatomical space is not the priority of a visualization, correlations (Fig. 8c) (Hutchison et al., *in press*) offer another means of conveying the temporal complexity of signal dynamics through broad color motifs. Although there has been limited use of videos as supplementary online material, the medium offers the potential to maintain a stable anatomical position, which allows for the representation of fluctuations along the temporal dimension. AFNI has made a script⁵ available to create videos⁶ of data dynamics shown on the cortical surface.

The presentation of changes in connectivity over time is not restricted to moment-to-moment dynamic changes, but can also be a crucial need for the visualization of results from longitudinal studies. For example, Fair et al. (2009) uses colors to describe the network identities of different regions along the axis as they change from childhood to adulthood (Fig. 8f), and their Supplementary Video 1 uses a video of a graph representation of the regions to convey similar information as it changes over time. There may be substantial space for cross-pollination between the growing interest in functional connectivity dynamics and tools used to present data from longitudinal studies.

Multimodal connectivity

Anatomical and functional connectivity have fundamentally unique modes of arriving at their respective connectomes. For anatomical, it is by carving through a spatial terrain; for functional, through capturing common fluctuations in activity over time. The specific challenge of depicting two forms of connectivity information – one that requires path information to be visualized, and another that requires the probability of connectivity between termination points – poses a substantial challenge for visual integration in the same space. Although examples of combined visualizations do exist, this area has remained relatively

underdeveloped. Multimodality can be achieved by translating each data type toward a shared visual vocabulary. Though the result may appear to transcend either modality alone, something tangible is lost in this melting pot. A mosaic of side-by-side coexistence is much harder to achieve, both in life and in multimodal connectome visualization. A unique example is presented in Fig. 9a as a comparison of connectivity modalities which made use of a single axial slice of standard functional connectivity results overlaid with diffusion direction in blue line-glyphs (Koch et al., 2002). This basic multimodal example achieves a visual balance between the depiction of probabilities in functional connectivity data and the directional information of vector glyphs, without information loss from either. Tractography was later united with functional connectivity in the volume using three-dimensional (Fig. 9c) (van den Heuvel et al., 2008) or slice-based (Fig. 9b) (Greicius et al., 2009) rendering of functional connectivity clusters on a cortical surface mesh with tract-rendering. For further representation of the uncertainty implicit in group-level tractography, van den Heuvel et al. (2009) used additional colored statistical maps on adjacent slices (Fig. 9d). Although many more studies have been published comparing anatomical and functional connectivity, data are rarely combined in the same image.

Anatomical and functional connectivity can also be integrated before the visualization stage, facilitated by probabilistic tractography and functional connectivity both sharing a similar data type. Functional connectivity may be used to inform tractography segmentation into bundles (Ge et al., 2013), or anatomical connectivity may be used to weigh functional connectivity (Bowman et al., 2012). One example of a combined analysis that resulted in a unique image was by Calamante et al. (2013), who built on previous innovations with super-resolution tractography to develop *track-weighted functional connectivity*. However, by combining the data before visualization, this approach generally does not innovate ways to see both modalities in their respective contexts, thereby pulling the visualizations away from reflecting the core attributes of the actual data types.

The need for novel approaches to multimodal data presentation is all the more pressing now that acquisition of both connectivity modalities is becoming common fare in neuroimaging experiments. Through developing further visualization methods of cross-modal connectome integration that remain true to both data types, it will no doubt encourage further research in this direction.

Visualization in research practice

Research into the human connectome has become increasingly characterized by discovery science (Biswal et al., 2010). Data are acquired without the former prerequisite of a study question, and guiding hypotheses are only later articulated while sitting before the computer monitor. Effective, interactive software for data exploration is all the more central to research practice in a field where the analysis itself constitutes the experiment. Standard neuroimaging software tools such as AFNI⁷ have, since their inception, been designed to encourage and facilitate the visual proximity of researchers to their data (Cox, 2012). Others, such as FSL,⁸ have included viewers with the researcher in mind, rather than solely the published figure (Jenkinson et al., 2012). A constitutive shift has been underway in connectomic software design, however, which places exploratory analyses within a mouse click of the viewer pane once basic preprocessing steps are complete (e.g., Connectome Viewer (Gerhard et al., 2011) and Connectome Workbench (Marcus et al., 2011)). While these latter two packages offer complete interfaces for a variety of research interests, numerous other tools are available for the aspiring or weathered connectome explorer. Armed only with a thumb drive of data, the following tools offer any number of ways to trudge

⁵ http://afni.nimh.nih.gov/pub/dist/tgz/Suma_TSrestMovieDemo.tgz.

⁶ Similar to: <http://vimeo.com/9871689>.

⁷ <http://afni.nimh.nih.gov/>.

⁸ <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>.

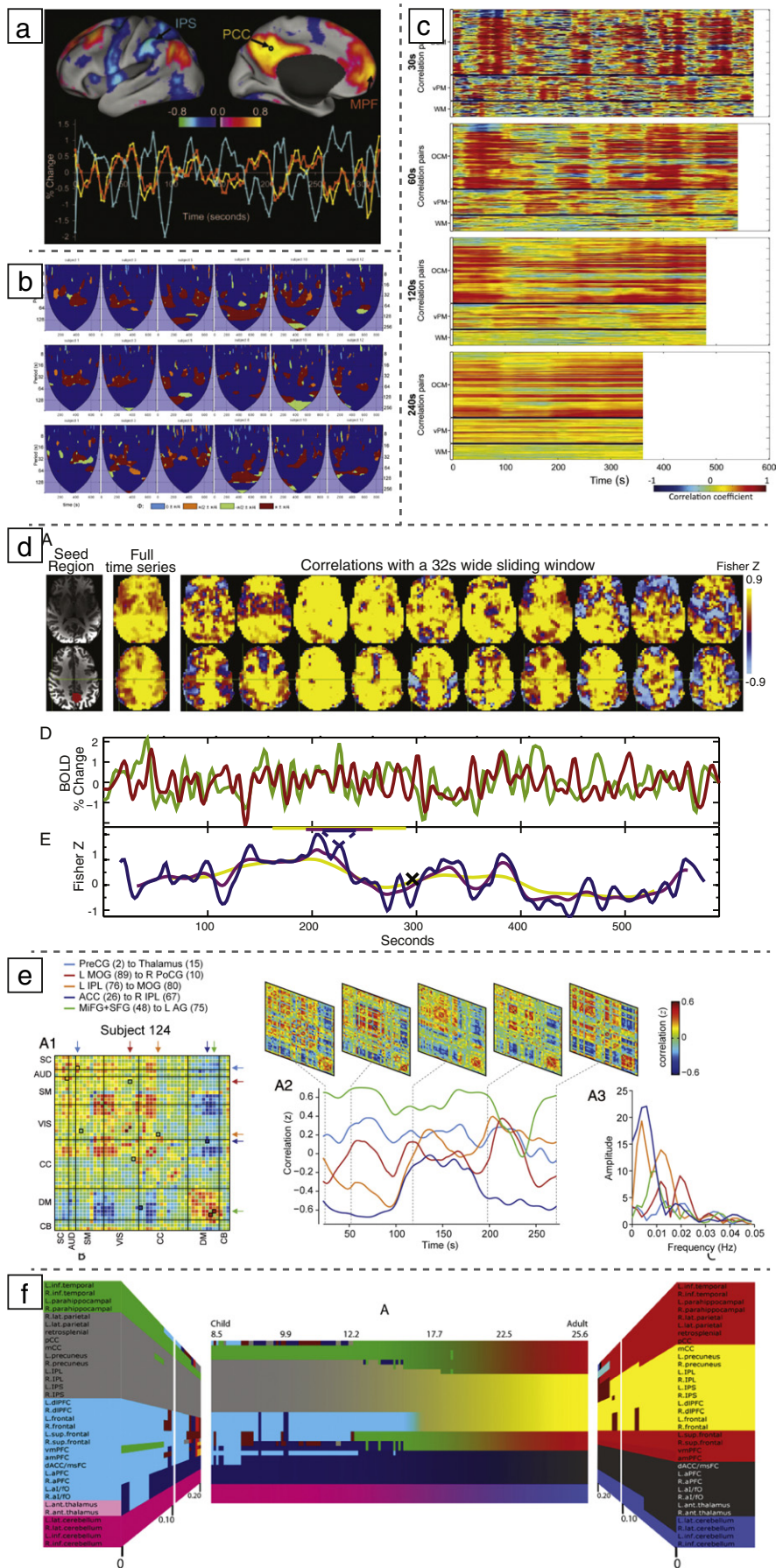


Fig. 8. Connectivity dynamics. (a) Fox et al. (2005), (b) Chang and Glover (2010), (c) Hutchison et al. (2013), (d) Handwerker et al. (2012), (e) Allen et al. (2012a), and (f) Fair et al. (2009).

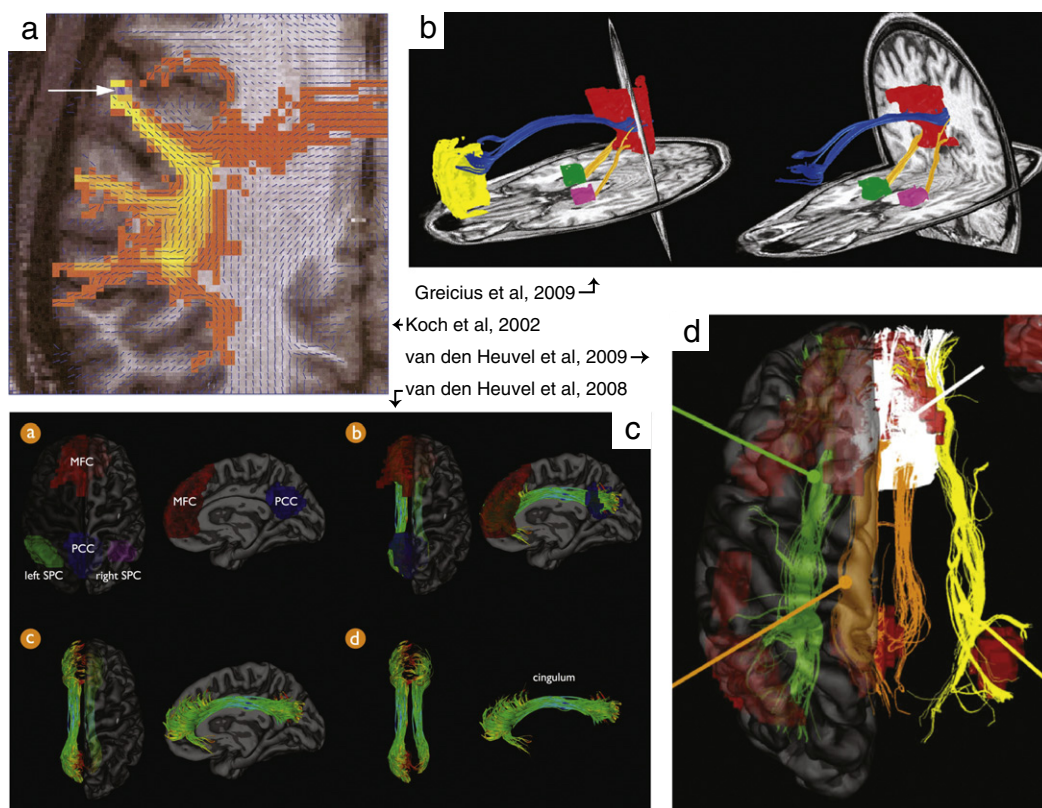


Fig. 9. Multimodal connectivity. a: Koch et al., 2002; b: Greicius et al., 2009; c: van den Heuvel et al., 2008; d: van den Heuvel et al., 2009.

through the panoply of connectivity visualization methods (see summary and respective software websites in Table 1).

Interactive software for data exploration

Anatomical connectivity

There are multiple applications designed to visualize white matter tracts in an exploratory manner. Probably the most popular is *TrackVis*, owing to its rich features and mature implementation (Wang et al., 2007). It can handle large whole brain tractography datasets by showing only every *n*th fiber. Exploration can be performed through placing ROIs of different sizes and shapes and including only the fibers they intersect. Different color coding and rendering schemes are available, resulting in some of the most striking examples of tractography (e.g., Wedeen et al., 2012). The application allows the user to plot volumetric data, which can also be used to define ROIs. All information about the input data, view angles, and ROIs can be saved in a scene file for future use.

Chen et al. (2009) developed an interface that enables for the selection of tracts not only by placing ROIs in the anatomical space, but also in abstract two-dimensional proximity-preserving embeddings of the tracts. These embeddings are calculated not from the original 3D space, but instead constructed from a similarity measure between the fibers. The embeddings have the advantage that fiber bundles are mapped to distinct parts of the view, although they might overlap in anatomical space. In a similar vein, *focus and context techniques* (Röttger et al., 2012) allow the user to explore interesting details within the context of surrounding bundles. However, instead of simply making selected tracts visible, and others invisible, single fibers are displayed in dynamic cutaways depending on the position of the mouse pointer, while surrounding bundles are depicted by their convex hulls (Fig. 5).

Taking abstraction in a different direction, Jianu et al. (2011) developed a Google-maps like interface for the exploration of whole brain fiber tracts. This application of a well-known interface for the

exploration of anatomical connectivity makes the interaction, as well as the display of additional annotations intuitive. A major point that makes the visualization work is the clustering of the fibers into distinct bundles, and simplification to a schematized skeleton. The full detail is then only displayed upon selection of the bundle in the browser. While the clustering of bundles simplifies an overview of the data, there is the danger of suggesting a subdivision of the white matter into more or less arbitrary units, which may not have an anatomical referent in reality.

Although *TrackVis* is able to calculate simple statistics along tracts, its main goal is to display the data and to allow the user to select which fibers should be visible. *OpenWalnut* takes a slightly different approach. It is as much a tool for visualizing and exploring data as it is for data processing. It has a modular design and a built-in pipelining engine with drag and drop GUI. Most existing modules deal with visualization-oriented transformations and are aimed at providing a flexible environment to design new visualization techniques. In contrast to *TrackVis*, *OpenWalnut* is open-source and has a vibrant community of developers. However, flexibility is not always compatible with ease of use. A plethora of options makes achieving simple visualization tasks in *OpenWalnut* relatively difficult. There are, however, attempts to create a similar viewer more oriented on user experience than flexibility (see *FiberNavigator2*).

Modular design and a vibrant developer community are hallmark features of another viewer, *3D Slicer* (Fedorov et al., 2012). This sophisticated tool is aimed at imaging derived surgical procedures, and places a strong emphasis on single-subject multimodal visualization. In addition to standard modes of displaying tracts, *3D Slicer* can perform online tractography — recalculating each time a seed region is moved in space.

Functional connectivity

InstaCorr, first released on the eve of 2010 as part of the AFNI software package, continues to develop novel interactive aspects. Having a long history of functional connectivity-friendly functionality, AFNI's

Table 1
Select visualization software.

Software	Functional	Anatomical		Volume	Surface	Graph	Other notable features	Website
		Deterministic	Probabilistic					
<i>Anatomical</i>								
TrackVis		x		x			Whole-brain tractography; user-defined ROIs of different sizes and shapes; different color-coding and rendering schemes; input data, view angles, and ROI can be saved	http://www.trackvis.org/
NPerspective		x					Well-known Google-maps interface; simplified to schematic skeleton; 2D-embeddings; hierarchical clustering	http://graphics.cs.brown.edu/research/sciviz/newbraininteraction/
ExploreDTI		x	x	x	x		Broad range of features for working with glyphs and tractography	http://www.exploredti.com/
OpenWalnut		x	x	x	x		Visualization, exploration, & data processing; modular pipeline engine; drag and drop GUI; open source with active community	http://www.openwalnut.org/
FiberNavigator2		x	x	x	x		User-oriented	https://code.google.com/p/fibernavigator2/
3D Slicer	x	x	x	x	x		Modular design; active community; aimed at imaging for surgical procedures; single-subject multimodal view, including tractography; interactive seed-tract visualization; Python interface	www.slicer.org
<i>Functional</i>								
InstaCorr (suma/afni)	x			x	x		Interactive data exploration; individual and group level; includes demo data	http://afni.nimh.nih.gov/afni
VidView	x				x	x	Mean-shift edge-bundling in 3D space	https://github.com/NeuroanatomyAndConnectivity/vidview
Brainbundler	x				x	x	Surface-based connectivity glyphs	https://github.com/NeuroanatomyAndConnectivity/brainbundler/
Fubraconnex	x				x	x	Novel interface, anatomical and abstract	https://code.google.com/p/fubraconnex/
VAMCA	x			x	x		Mollweide projection for cortical surface; meta-analysis; minimal distortion	http://www.nitrc.org/projects/vamca
<i>Multimodal</i>								
Connectome Viewer	x	x		x	x	x	Anatomic and functional connectivity; graph visualization; Python interface	http://cmtk.org/viewer/
Connectome Workbench	x	x		x	x	x	Investigates data acquired through Human Connectome Project; based on Caret software	http://www.humanconnectome.org/connectome/connectomeworkbench.html
BrainNet Viewer	x	x		x	x	x	Network and surface-based visuals; MATLAB interface	http://www.nitrc.org/projects/bnv/
Brain Connectivity toolbox	x	x		x	x	x	Extensive list of graph theory-based analyses; MATLAB interface	https://sites.google.com/site/bctnet/visualization
VisualConnectome	x	x			x	x	MATLAB interface	http://code.google.com/p/visualconnectome/
MNET	x	x				x	MATLAB interface	http://neuroimage.yonsei.ac.kr/mnet/
<i>Online</i>								
Slicedrop		x		x	x			http://slicedrop.com/
BrainGL		x	x	x			Structural connectivity viewers with volume and surface overlay; easy online distribution	http://braingl.de
BrainBrowser		x		x	x			https://brainbrowser.cbrain.mcgill.ca/
XTK		x		x	x		Framework for building online neuroimaging viewers	https://github.com/xtk/X
<i>Other</i>								
Connectograms	x					x	Standardized schematic of multimodal data.	http://circos.ca/tutorials/lessons/recipes/cortical_maps/

InstaCorr offers flexible interactive data exploration with results being rendered with the move of a cursor. Individual- or group-level visualization in the volume or on the cortical surface is possible, and demo data are available.⁹

Another set of novel software tools are incorporated into *BrainBundler*, and *VidView*, standing for 6D-viewer, which offer the ability to perform *mean-shift edge-bundling* in three-dimensional space (Fig. 7, Böttger) and to display *surface-based connectivity glyphs* (Fig. 10, bottom), respectively. The latter tool is designed to assist in observer-driven parcellation of cortical areas by presenting the whole-brain connectivity information directly on the surface at each node, thus making the detection of boundaries and transitions easier.

Several software packages have been released as open source in the recent years to investigate functional connectivity interactively (e.g., Eklund et al., 2011; van Dixhoorn et al., 2010, 2012). Among these relative newcomers, *Fubraconnex* is unique in its novel functionality (van Dixhoorn et al., 2010). It was built from the bottom up by visualization researchers, combining many of the innovative interface ideas one would expect from developers coming from that field. Three main panels are available in user interface: anatomical, consisting of region and network views; abstract, consisting of scatterplot of correlation value by distance, correlation matrix, and hierarchical edge-bundling views; and a filtering and selection panel.

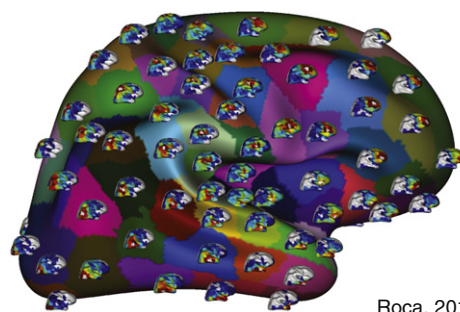
Multimodal connectivity

Although the viewers and tools previously described in this section focus on optimizing the visualization of specific imaging modality, a new generation of connectivity visualization software recognizes the challenge and necessity of integrating knowledge from various modalities. The *Connectome Viewer* (Gerhard et al., 2011), part of the *Connectome Mapper* toolkit, offers the possibility of visualizing both anatomical and functional connectivity data, and of conducting further graph theory-based analyses using a python interface. The *Connectome Workbench*, recently released as part of the Human Connectome Project, is based on the Caret software, and it offers methods for investigating data acquired through the project. Several other software packages offer means to visualize multiple modalities of connectivity data through MATLAB-based tools: *BrainNet Viewer*, *MNET*, *VisualConnectome*, and *Brain Connectivity Toolbox*. Of these, *BrainNet Viewer* is notable for its diversity with both network mapping and surface-based data presentation, whereas the *Brain Connectivity Toolbox* has an extensive list of graph theory-based analyses. These packages are generally quick to transform connectivity data to a graph, thereby facilitating integration across modalities.

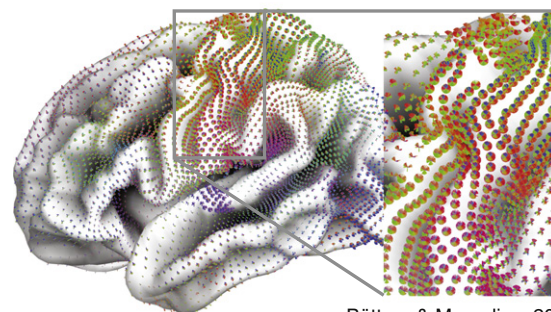
Online interactivity

Interactive or exploratory visualization has always struggled with technical issues. To explore a dataset using any of the aforementioned tools, one had to first go through the hurdles of installing appropriate software. Despite some improvements in terms of software distribution (Halchenko and Hanke, 2012), transitioning from data acquisition to exploration is not a seamless experience. However, recent advancements in web technologies give promise of a change for the better. In the past decade we witnessed a slow evolution of a new platform available across platforms – the web browser. Current web browsers go much further than traversing a sea of written text. As a result of improvements in JavaScript and WebGL it is possible to develop full-fledged applications that run in a web browser. This gives an opportunity to fuse data description in scientific publications with interactive visualization based on WebGL.¹⁰

There are several capable structural connectivity viewers (supporting overlaying volumes and surfaces) written on top of WebGL: *slicedrop*,



Roca, 2011



Böttger & Margulies, 2013

Fig. 10. Connectivity glyphs. *Top:* Rendering of functional connectivity on cortical surface glyph for each respective parcellation area Roca (2011) (also see Roca et al. (2009)). *Bottom:* The aim is a cortical surface coloring that facilitates connectivity boundary detection. At each node is a circular projection glyph of functional connectivity from that node to the rest of the cortical surface. Colors represent direction of the connections.

BrainGL, and *CBrain BrainBrowser*. Additionally there is a neuroimaging WebGL based JavaScript framework dedicated to creating interactive visualizations (XTK) (Hähn et al., 2012). Judging from the pace and direction of changes on the software landscape it is highly likely that the future of scientific data visualization will be in the web browser.

Connectograms

All the tools described above offer interfaces for exploring diverse properties of a connectivity dataset. However, none offer a uniform visual summary of a human MRI-based connectome. The charge of illustrating multiple aspects of multimodal data in a single image is a substantial research problem in its own right, and requires balancing the diverse potential applications with a standardized format that facilitates intuitive interpretation. Irimia et al. (2012b) developed the first of such standardized, schematic representations of multimodal connectome data, which they aptly call the *connectogram* (Fig. 7, van Horn). Using a circular representation of ROI-defined brain regions as the basis for the anatomical layout, spatial proximity is incorporated into the position of regions along the circle. Dimensions of data information for each region are layers along the circumference, and through the center of the circle are beveled lines that represent aspects of connectivity between respective regions using color, opacity, and thickness to present further dimensions. The connectogram has been further applied to the description of traumatic brain injury (Irimia et al., 2012a) and the famous localized lesion suffered by Phineas Gage (Van Horn et al., 2012). This line of research into methods of representing the connectogram presents the first highly articulated suggestion for a visual tool, and its necessity, in the study of the connectome.

Portraying the connectome

Scientific figures and illustrations are – to paraphrase the information visualization and design guru William Tufte (Tufte, 2006) – *where seeing turns into showing*. The capacity of these images to influence our interpretation of data and to direct the questions of

⁹ For an InstaCorr demo with data, simply run the AFNI command: @Install_InstaCorr_Demo.

¹⁰ onpub.cbs.mpg.de is a cutting-edge example of such fusion.

the scientific community, as well as to consolidate and prioritize certain concepts and visual modes over others, makes visualizations worthy of careful consideration during their production (Dumit, 2004; McCabe and Castel, 2008; Roskies, 2010; Weisberg et al., 2008). After countless hours of gaining familiarity with results, the creation of descriptive figures becomes a challenge for researchers of maintaining the priority of information content and thoroughness, while simultaneously propelling the viewer through those hours of observation to smoothly arrive at our understanding of the results. The consolidation of habits and cultures of visualization help to facilitate communication within a research community, but also risk curtailing further development of novel modes of representation.

A recent debate regarding image use in functional connectivity studies lamented the pervasive uninformative figure content (Habeck and Moeller, 2011). Citing Tufte's mantra of the data-to-ink ratio (Tufte, 2001), Habeck and Moeller (2011) observe that functional connectivity figures often have an ornamental, rather than informational role in publications, and they suggest that authors attempt to explain results first entirely without images. Erhardt et al. (2011), in their response, agree that authors should use figures wisely, and take care to display as much of the uncertainty in the data as possible. Their perspective is slightly different, however, in that they argue the need for brain images in connectivity papers: the brain is spatial, and words and tables can only go so far to communicate the respective relationships efficiently to the reader. Rather than relegate images to words, we have an obligation to raise the standards of figure production (a cause they made a valuable contribution to the following year in Allen et al., in press).

What concrete visualization tools might assist in the creation of community consensus in connectivity data presentation? For the brain volume in the last decade, the novel visualization technique of the "glass brain", as distributed through SPM, offered a much needed sense of full disclosure in presenting data. Like an airport body scanner, the glass brain demonstrated that no results were concealed through subjectively chosen slices. The glass-brain was a crucial insight of data presentation, but it was not sufficient for optimally sharing every scientific result. We may have myriad techniques for visualizing connectivity, but we are still lacking semi-standardized techniques for assuring the reader that all the results are shown.

What novel tools may become valuable for connectivity visualization? One example is that dimensionality can also be offered through glyphs that present the full connectivity map at each anatomical point on the surface (Fig. 10) (for a further example of functional connectivity glyphs, see Supplementary Figs. 1 & 2 from Margulies et al. (2009)). This layout offers information both about anatomical location as well as the difference between various connectivity fingerprints, while prioritizing the parcellation gestalt. While polar plots have also served this purpose (Buckner et al., 2011; Passingham et al., 2002; Yeo et al., 2011), they lack the additional anatomical information about connectivity in exchange for gains in clarity expressing the similarities and differences between the connectivity profiles of regions. For addressing the difficulties of surface-based representation, an example of cross-pollination from cartography is the meta-analysis and visualization software VAMCA, which uses the Mollweide projection for cortical surface display. Mollweide projection prioritizes the proportionally correct depiction of area, while constraining the distortion of shape and directional relations (Kang et al., 2012).

Another field that has similar content from a visualization-perspective is meteorology. We are both committed to a concrete spatial domain, and we both have multiple modalities of dynamic data that need to be represented. We could benefit from others' insights into how to create intuitive, rather than symbolic, forms of communication in figure design – as we often use extensive figure legends with symbolic references, rather than creating features that can speak for themselves. Much as the weather map should be graspable by the average viewer, we should consider further approaches to

outsource figure interpretation to the viewer. Even such basic considerations as color use may prove beneficial for communicating the meaning of data.¹¹

The visualization habits and expectations that become widely adopted as the field matures will have a dramatic impact on the direction connectome research progresses. Will it be a graph-based technique that foregoes anatomy completely, or instead a set of proscribed images and views? Perhaps common use of online interactive modes of data presentation will help to offer flexibility to the viewer in unforeseen ways.

Publication culture

The form in which knowledge is exchanged in science is influencing the way we present data. The end product of any research is an academic paper. This form originates from the times where the most efficient way of distributing information was print. Printed journals, however, have limitations: they are expensive (which may limit the use of color in figures) and the printed page is intrinsically static and two-dimensional. Researchers have invented many ingenious methods for presenting data in printed form. However, the expansion of computing resources across all the sciences portends much larger and more sophisticated datasets to present.

The printed form, however, is slowly being phased out. Most academic journals are being distributed in an electronic form over the Internet. Hardware improvements have also made available an abundance of electronic readers. Although papers are still distributed in an electronic format that mimics their printed counterparts, novel elements, allowing the data to be presented in a much richer way, are beginning to find their ways into paper supplements. Visualization can include elements of animation, three-dimensionality, and interactivity. There have also been attempts to use recent extensions to the PDF format (widely adopted for digital distribution) which allow for the embedding of videos, audio clips, and interactive 3D models (Ziegler et al., 2011). This approach was reinforced by the *Journal of Neuroscience* decision to eliminate supplementary materials (Maunsell, 2010). Even though the prospect of having whole publication in one self-contained format is very appealing, there are some issues with using PDF as the designated format. The extended features of PDF are supported by only one proprietary reader and only partially on certain operating systems. When planning the extensions of the existing publication facilities technical aspects such as compatibility of the new format with existing software should be taken into account.

Another approach to interactive, rich and three dimensional visuals is proposed by *The X Toolkit: WebGL™ for Scientific Visualization* (Hähn et al., 2012). This framework is based on JavaScript and WebGL technologies, which enable interactive figures that can be displayed on any modern web browser across all platforms. It supports the TRK file format for displaying tracts and enables combining this data with volumes and surfaces. Interactive figures created this way can be embedded into HTML websites and included as links in publications.

Although the way in which data are presented may greatly impact its interpretation, the methods used to create figures are not usually described in a replicable manner in publications. Although not problematic when the method is well established, in the case of multi-dimensional datasets, the type of projection onto a lower dimensional plane, color and shape representation are crucial for correct interpretation and propagation in future studies. One possible solution is provided by the paradigm of Literate Programming (Knuth, 1992), where textual description of data is fused with the code used during analysis and figure creation. Solutions exist in general purpose programming languages that support both Literate Programming and the handling of

¹¹ <http://mindboggle.info/index.html>.

neuroimaging data (e.g., Sweave in R (Leisch, 2002) and IPython notebook in Python (Perez and Granger, 2007)). Common use of such tools would result in more transparency of visualization methods, and more reproducible science. While unlikely to be widely adopted owing to the additional demand on the individual researcher, increased detail in the reporting of figure methods may become increasingly important as the pace of novelty in visualizations increases. Even though better provenance tracking leads to more reproducible science it is not clear how to motivate researchers to change their habits or how such change implemented on a wide scale would influence the field. This issue, however, is by no means limited to visualizations or neuroimaging, but science in general and has been a topic of heated debates (Ince et al., 2012).

Conclusions: Caricaturing the connectome

We use visualizations to arrive at understandings of our data. The complexity inherent in comprehending the structure and inter-individual variance of the connectome requires an awareness of the implications of our available methods, as well as precision and sensitivity to analytic methods while developing new ones. A flashy graphic is insufficient to justify inclusion in a manuscript; the image should obviously first be loyal to the method and raw material it reflects, but clarity and intuitive design should also be a priority (see Table 2 for a summary of tensions in visualization). The relevance of this balance becomes apparent when reflecting on the ways in which visualization innovations, from tractography to graph representations, have steadily punctuated the landmark shifts in connectomic research. We see this trend in the transition that functional connectivity has undergone from anatomical to functional to connectional space (see Fig. 7). A counterintuitive example comes from limitations: the difficulties in visualizing probabilistic tractography as fibers actually bring it closer to the probabilistic data type of functional connectivity, thereby facilitating intermodal analyses, as well as enabling probabilistic tractography to make use of the growing set of functional connectivity tools.

Aesthetics influence user decisions as to how data gets explored. How do certain visual elements highlight or taint the results we see? As the whole connectome becomes easier to visualize, the ways in which we analyze and present it will also change. For example, if probabilistic tractography were more compelling visually, we might be more inclined to use it as the primary data source in presenting results. And if it were easier to visualize both anatomical and functional connectivity together, multimodal connectivity publications would be a step closer to becoming mainstream connectomic research practice.

We tend to be suspicious of the allure of beautiful images (e.g., see the titles of: Habeck and Moeller, 2011; Johansen-Berg and Behrens, 2006), concerned that their aesthetic qualities might manipulate us into appreciating content that is actually as superficial as the ink on the page. If we present a figure that clarifies the scientific content, but does so by creating a distortion of brain space, is that poor practice? What if the caption and methods explicitly stated that the contents of the figure were not to be taken literally? To what degree should a

visualization be allowed to stand alone? How can we ensure that images do not embellish or contradict the underlying method's claims? These are ethical concerns that are in no way unique to brain connectivity research; nonetheless, brain images seem to be held to a higher demand for authenticity than other body parts (Dumit, 2004).

In the era of connectomic research that human brain imaging finds itself, our data have, in a matter of years, increased quadratically in size (see Fig. 6). We have many challenges to address. Among them are ways of exploring, communicating, and explaining the connectome to ourselves. At the spatial resolution of current human neuroimaging, we are much closer to painting a caricature than a portrait of the human connectome. Although both artistic forms offer likenesses of their subjects, the latter, though true to form, is only skin deep, while the former is amplified by our unique perspective. With every image of the human connectome we create, we caricature. But in order to guard against the possible abuse, we need only do so without forgetting that we are so doing.

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Conflict of interest

The authors have no conflicts of interest to report.

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Table 2
Considerations for connectivity visualizations.

Concept	Questions
Key features/context	Each visualization is a transformation – what are the explicit motivations for transforming your data?
Page space	What does distance in the figure represent?
Connectivity content	Is the represented data consistent with the questions being addressed? Is there an appropriate context-specific balance between thoroughness and readability in the image?
Uncertainty	Does the image contain information about variable confidence values in the data? Is uncertainty represented, and if not, what are the justifications?

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