Controversies and current progress on large-scale brain network nomenclature from OHBM WHATNET: Workgroup for HArmonized Taxonomy of NETworks

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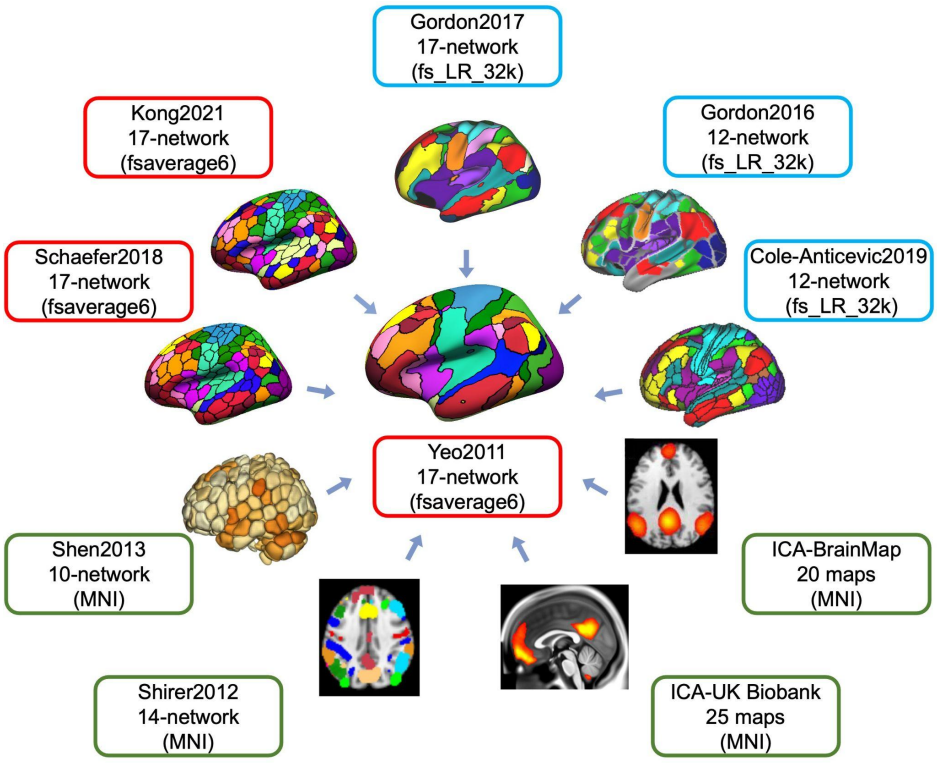
Comprehensive Summary

The idea that the brain is composed of multiple large-scale networks has steadily gained traction in cognitive neuroscience over the past decade. Still, the field has not yet reached consensus on key issues regarding terminology. The Workgroup for HArmonized Taxonomy of NETworks (WHATNET) was formed in 2020 as an Organization for Human Brain Mapping (OHBM)-endorsed best practices committee to provide concrete recommendations and reporting guidelines for the scientific community. WHATNET members spent the last two years engaging in regular discussions, conducting a survey to catalog current practices in large-scale network nomenclature, identifying barriers to progress, and brainstorming ways in which tools could be developed to help standardize reporting in future studies. Here we summarize these activities and make initial recommendations for the network neuroscience community, noting open questions and controversies that require further empirical and theoretical investigation.



Abstract

Progress in scientific disciplines is often accompanied by the standardization of terminology and nomenclature. Network neuroscience, as applied at the level of macro-scale organization of the brain, has emerged over the past decade from interdisciplinary collaborations. The field is only beginning to confront the challenges associated with developing and refining a taxonomy of its fundamental explanatory constructs. Despite initial attempts, there is currently a lack of consensus around basic questions such as "What constitutes a brain network"?, "Are there universal and reproducible brain networks that can be observed across individuals"? and "What naming and reporting conventions could be adopted to facilitate cross-laboratory communication?" The Workgroup for HArmonized Taxonomy of NETworks (WHATNET) was formed in 2020 as an Organization for Human Brain Mapping (OHBM)-endorsed committee on best practices in large-scale brain network nomenclature. The objective is to provide concrete reporting recommendations similar to those produced by the Committee on Best Practices in Data Analysis and Sharing (COBIDAS) and the magneto- and electroencephalography best practices committee. A working group was formed of cognitive and network neuroscientists, engineers, and philosophers who are actively engaged in research examining functional and structural brain networks using a range of neuroimaging modalities. The goal of WHATNET is to provide recommendations on points of consensus, identify open questions, and highlight areas of debate in the scientific community. The committee conducted a Qualtrics survey that was circulated by the OHBM executive office and advertised on Twitter to catalog current practices in large-scale brain network nomenclature. As expected, a few well-known network names (eg. default network) dominated responses to the survey. However, a number of interesting and illuminating points of disagreement emerged as well. The goal of this initiative is to move the field towards providing clear criteria and developing tools to aid in standardization of reporting network neuroscience results. Here we summarize survey results, discuss considerations, and provide initial recommendations from the workgroup. In doing so, we discuss multiple challenges to this enterprise, including: 1) network scale, resolution, and hierarchies; 2) inter-individual variability of networks; 3) consideration of network affiliations of subcortical structures; 4) consideration of multi-modal information, and 5) dynamics and non-stationarity of networks. We close with a set of minimal reporting guidelines that we urge the cognitive and network neuroscience communities to adopt while awaiting more concrete recommendations that we anticipate will be forthcoming from this group.

Keywords: brain network, cognitive neuroscience, diffusion weighted imaging, functional connectivity, network neuroscience, parcellation, resting state fMRI, structural connectivity, EEG, MEG

1. *Definitions and scope: What is a "large-scale brain network"?*

The standardization of terminology and nomenclature is an essential element of progress in any scientific endeavor. In the field of network neuroscience, the most fundamental nomenclature rests on the definition of a brain network itself. In this rapidly evolving field, there is a need to define the scale at which brain networks are being examined. Neuroimaging has focused on the macroscale relationships between brain regions in defining networks and their interactions. This scale emerges in part by virtue of data acquisition parameters, which limit resolution to levels predominantly lower than a cubic millimeter. This manuscript will focus on networks at this spatial scale, using the term "large-scale brain network" to refer to what have variably been called "resting state networks"(1), "intrinsic connectivity networks" (2), or "functional brain networks" (3) in the literature describing coherent brain signal fluctuations recorded with non-invasive neuroimaging.

One of the key issues in defining networks is that the very notion has different meanings across scientific domains and even subfields within cognitive neuroscience and neuroimaging. The term 'network' has been used to refer to patterns of co-activation, spatial patterns of coupled signals derived from multivariate analyses (e.g., independent component analysis, ICA), or a distributed pattern of brain regional activation. In network science, however, the term network is defined unambiguously. Specifically, it is used to refer to a collection of nodes and edges: nodes represent the fundamental units of a system and edges represent their pairwise interactions. This definition is compatible with some, but not all, of the definitions used in neuroimaging. Namely, it agrees with network or graphical models of the brain, wherein nodes correspond to discrete neural elements (e.g. cells, neuronal populations, brain areas), and edges correspond to structural, functional, and effective connections. However, the precise way in which networks are defined given such a model are highly variable, and can lead to varying and sometimes inconsistent definitions of specific brain networks.

The field of large-scale network neuroscience is only beginning to confront the challenges associated with developing and refining a taxonomy of relevant entities. At present, the field lacks consensus around basic questions such as "What constitutes a large-scale brain network"? "Are there reliable networks that can be observed in the brains of all individuals"? And "what reporting conventions should be adopted to facilitate cross-laboratory communication?" One can see that these questions are somewhat philosophical in nature, and are often assumed by researchers to have converged on greater consensus than the literature suggests. Take, for example, the output of a PubMed search for the term "default network", which includes over 8,000 articles. The term "default mode" of brain function was introduced into the lexicon by Raichle and colleagues in 2001, who used positron emission tomography to measure brain oxygen extraction. They reported that medial prefrontal cortex (MPFC), posterior cingulate cortex (PCC) and lateral parietal and temporal cortices consistently decreased their activity across a range of cognitive paradigms compared with rest (4,5). Greicius and colleagues used resting state (6) functional magnetic resonance imaging (fMRI) a few years later to examine

functional connectivity among these task "deactivated" brain regions, conducting the first network analysis of the default mode hypothesis (7). It was this 2003 study that first introduced the term "default mode network", which has in subsequent work often been shortened to "default network" (8). Even a cursory glance at the multitude of topographical depictions of this commonly-studied large-scale brain network reveals that, although there is a strong intuition that we "know it when we see it" in functional neuroimaging data, precise definitions of what constitutes the network in terms of critical nodes, affiliated brain regions, estimation of regional interactions, and other quantitative descriptors are often missing from published reports. To further complicate matters, the somewhat common division of the default network into subnetworks (9–11) illustrates issues surrounding network scale, resolution, and hierarchies - a topic we will return to later in the discussion. These subnetworks partially overlap in spatial extent, although the precise separation and extent of spatial overlap depends on the analytic method used. For example, spatial ICA (sICA) at high dimensionality can be used to fractionate the default network into anterior and posterior subsystems (12). In contrast, hierarchical clustering of interregional resting-state correlations dissociates medial temporal lobe and dorsal MPFC subsystems of the default network (10). Whether or not the results from fractionating a larger network should be considered subnetworks or proper networks themselves illustrates the complexity of developing standardized network definitions.

Appropriate methods for defining and characterizing brain networks in neuroimaging data have been discussed and debated for over twenty-five years (13). Recently, a draft network taxonomy rooted in anatomical terminology was proposed, delineating six canonical networks labeled "occipital", "pericentral", "dorsal frontoparietal", "lateral frontoparietal", "midcingulo-insular", and "medial frontoparietal" (14). This focus on anatomy was intended to move away from functional names that are commonly assigned to specific networks (e.g., default, executive control, salience) which may only be appropriate in certain psychological contexts and which can lack anatomical precision. The proposal acknowledged that the draft network taxonomy provided an incomplete characterization that should be refined in future iterations through a dedicated working group. Pursuant to this, the Organization for Human Brain Mapping (OHBM) Committee on Best Practices instantiated the Workgroup for HArmonized Taxonomy of NETworks (WHATNET), comprising the current authors. The current manuscript represents this work-in-progress, providing an update and further considerations for building a consensus network terminology.

One consideration that is germane to this topic is whether we consider one particular neuroimaging modality (e.g., resting state fMRI, task-based fMRI, diffusion MRI (dMRI), electroencephalography (EEG)) to be the most relevant from which to search for empirical support for a given network taxonomy proposal. After months of deliberation, the WHATNET committee decided that a truly universal taxonomy should encompass all relevant findings from multiple neuroimaging modalities, highlighting points of maximal multimodal convergence where appropriate. Still, as the vast majority of the current human connectomics literature has focused on brain networks derived from fMRI data, the findings from this imaging modality are

likely to dominate the discussion, with structural and electrophysiological neuroimaging modalities considered as complementary approaches at this time (see Section 3.D: Beyond fMRI). This balance may shift with future advances in neuroimaging technologies and their adoption in network neuroscience research. In the current work, we take the precedent set by the original Committee on Best Practices in Data Analysis and Sharing (COBIDAS) effort that focused first on fMRI reporting guidelines (15) and later expanded to include EEG and magnetoencephalography (MEG) (16). We discuss considerations for network neuroscience research primarily in the fMRI domain and present initial guidelines for reporting results. We expect that these best practices will be updated and expanded to other modalities in future iterations.

2. Summary of OHBM survey results and implications

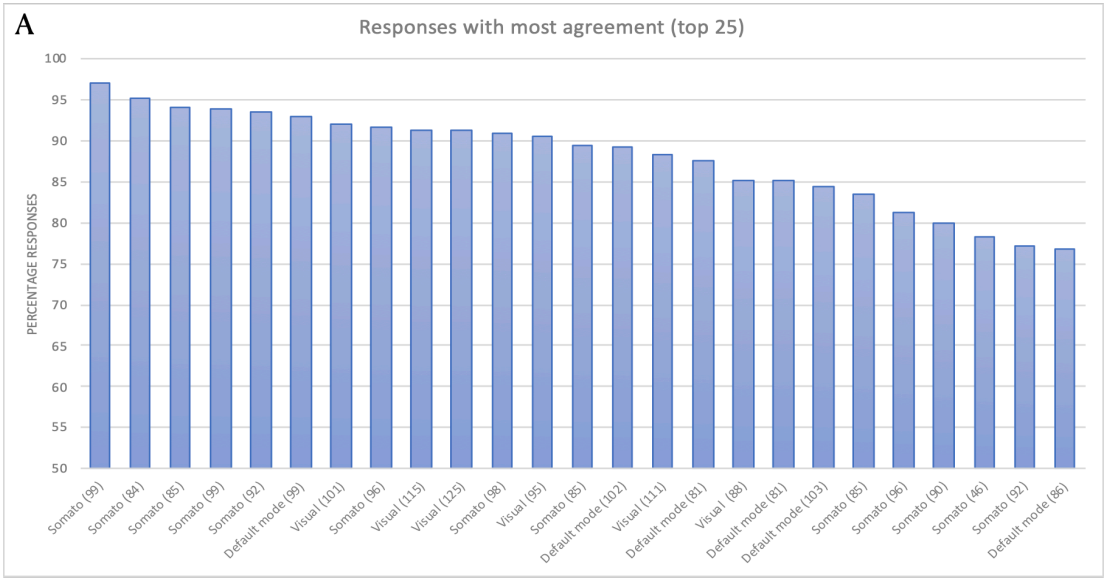
In 2021, WHATNET conducted an online survey of the OHBM community to explore current trends in large-scale brain network naming conventions. The objective of this survey was twofold: (1) to identify which terms the neuroscience community is using to characterize and describe large-scale brain networks, and (2) to determine the degree of consensus that already exists in the identification of network topographies. Members of WHATNET provided a range of images depicting large-scale brain networks derived from their own research or other sources to be used in the survey. Survey participants provided information on their academic background, including training and neuroimaging methods experience. For the survey, a randomized sequence of 93 brain network images and 7 "lure" network ensembles were presented, depicting network images in the brain volume and on the cortical surface. Participants were asked to provide open responses to the prompt: "Please name this network".

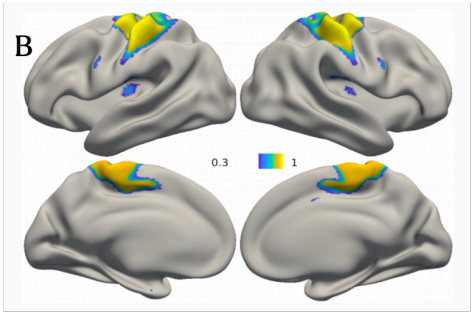
A total of 956 individuals entered in the survey. Of those, 611 responded to some of the questions, and only a total of 77 completed all of the questions. Of the 611 partial respondents, 46% were members of the OHBM, 1% were undergraduate, 29% graduate, 27% post-doctoral fellows, 36% faculty, and 7% other. The majority (65%) listed cognitive neuroscience as their area of training, followed by 33% listing psychology, 32% network neuroscience/connectomics, 16% clinical, 12% engineering, and 10% mathematics/statistics. On average, respondents reported having worked in the field of brain imaging for 9 years, although the spread of the responses varied widely, from 5% saying that they had only been working for about one year, up to 12% saying they've been working in the area for over 20 years. In terms of software used, most respondents reported using FSL (50%), followed by SPM (45%), AFNI (18%), and other (27%), with responses being non-exclusive. Most respondents reported using ICA in their analysis sometimes (35%), very often (16%) or always (2%), although a sizable group report using it only rarely (29%) or never (18%). Likewise, most respondents reported using brain parcellations in their work very often (40%) or sometimes (33%), with a small group reporting using it always (11%), relative to rarely (10%) or never (6%). Most respondents reported

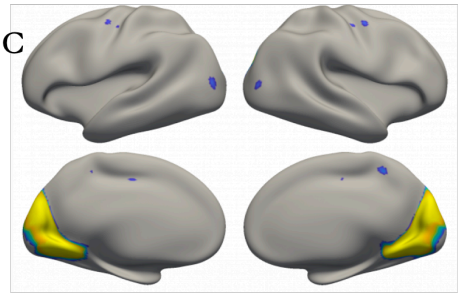
conducting research using both task fMRI and resting state functional connectivity (43%), followed by connectivity-based only (36%), and task-based only (22%).

Participants' responses were manually coded, and the language was unified (e.g., "somatic" and "somato" were considered the same response) by two independent coders. Data were initially explored in terms of percent agreement. Here, we limit our discussion to those images for which there was the most and the least amount of agreement between responses.

Three networks were identified by consensus in the upper quartile of images (**Figure 1**). The largest amount of agreement occurred for images that were identified as "somato network". Of the 25 images with the largest amount of percentage agreement across participants, 13 were identified as "somato network". The remaining 12 were evenly split between "default network" and "visual network". Of these three networks, a functional or cognitive nomenclature was provided, as opposed to a neuroanatomical network name (e.g., "occipital").







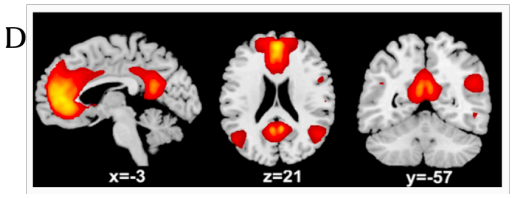


Figure 1. Survey responses with the most agreement across raters. (A) Percentage responses of the top 25 responses in terms of percentage agreement. The vertical number in parentheses next to the response term corresponds to the total number of respondents for that particular image. Sample images with the largest amount of agreement for **(B)** the "somato network" (96.97%, n = 99), **(C)** the "visual network" (92.08%, n = 101), and **(D)** the "default network" (92.93%, n = 99).

By contrast, when we look at the 25 images with lowest percent agreement in responses, the pattern of results is rather different (**Figure 2**). All of the lures were included in the images that received 50% or less response agreement. Unlike network labels with high agreement, there was a greater heterogeneity of terms used in the lower quartile of responses. Specifically, 8 of the images were labeled as "salience network", 6 as "default network", 4 as "frontoparietal network", 2 as "language network", 1 as "visual network", 1 as "limbic network", 1 as "amygdala network", 1 as "somato network", and 1 as "other". In this sub-set of responses, there was a mix of cognitive/functional terms–such as "salience" and "default"--and neuroanatomical terms–such as "frontoparietal" and "amygdala". Finally, it is worth noting that the number of responses in this lower quartile was rather low ($M_{responses}$ = 63.0, SD= 17.80), compared with the top 25 ($M_{responses}$ = 93.36, SD = 14.55). It is likely that the comparatively lower number of responses reflects participants' hesitance or uncertainty as to whether the relevant image constituted a (canonical) network or, if it did, how it should be labeled.

Cautiously, the results of this initial survey could be interpreted as revealing a preference amongst scientists to name large-scale brain networks according to their putative cognitive functions. They also suggest a certain degree of agreement regarding at least three canonical networks. These networks include two which are spatially contiguous within the somatomotor and occipital cortices. The third network, the default network, was the only spatially distributed network identified reliably. Of note, these three networks appear in the initial anatomically-based taxonomy proposal, which delineated "occipital", "pericentral", and "medial frontoparietal" networks (14).

There was much lower consensus on network labels for all other spatially distributed large-scale brain networks, including the "salience" and "frontoparietal" networks. While it is difficult to run inferential statistics on these qualitative data, there is much more that could be explored from these results. We have made the data publicly available within the Open Science Framework ((17), https://doi.org/10.17605/OSF.IO/3FZTA). Nevertheless, this initial exploration suffices to support the claim that while there is some degree of agreement among scientists regarding the labeling and identification of a few large-scale networks, there is a substantial amount of disagreement, raising concerns about the consistency with which results are interpreted as well as concerns regarding reproducibility in the field more generally. A lack of agreement about basic network definitions will complicate any attempt at replication. These problems could be alleviated by a more standardized nomenclature. In what follows, we will detail considerations for moving beyond these arbitrary naming conventions, and for developing

a universal taxonomy that can help to move the field towards greater clarity and consensus in characterizing ensembles of brain regions with reliable concision.

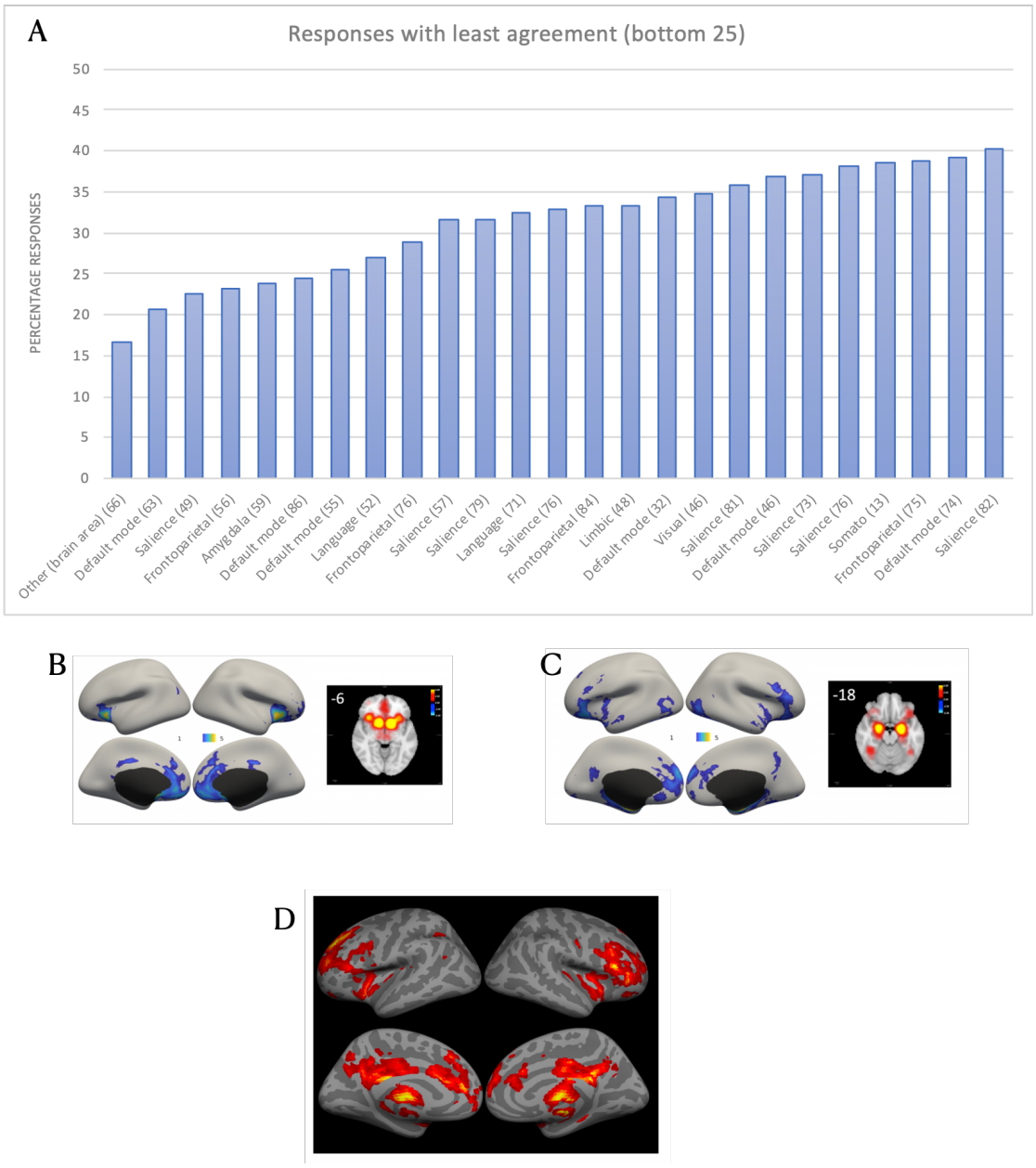


Figure 2. Survey responses with the least agreement across raters. (A) Percentage responses of the bottom 25 responses in terms of percentage agreement. The vertical number in parentheses next to the response term corresponds to the total number of respondents for that particular image. Sample images with the least amount of agreement. **(B)** Sample image 13 received a label of "other" (16.67%, n = 66). **(C)** Sample image 12 received a label of "default mode network" (20.63%, n = 63). **(D)** Sample image 88 received a label of salience network" (22.45%, n = 49).

3. *Challenges to and considerations for building a universal taxonomy of large-scale brain networks*

The results of the survey suggest that there is a potential for consensus around a taxonomy of large-scale brain networks. However, many challenges remain in building further consensus around nomenclature, particularly for spatially distributed networks interposed between the heteromodal and distributed default network on the one hand, and unimodal, spatially contiguous, somatomotor and occipital networks on the other. WHATNET identified five interrelated issues which require careful consideration in building a universal taxonomy of large-scale brain networks. First, the spatial scale and resolution of any network must be considered, as well as how networks are organized hierarchically. This entails a complete description of how a network is defined (e.g., using full correlation, partial correlation, or other approaches). Second, there is substantial variability in network topography between individuals. This variance is observable across the typical healthy young adult populations included in many studies, varies systematically in the context of lifespan development, and may become more complex to characterize in clinical populations. Third, large-scale brain networks have been reliably demarcated spatially in cortex, but these topographies are incomplete without corresponding subcortical structures that are often ignored in widely-used parcellation schemes. Fourth, the investigation of large-scale brain networks is heavily biased towards fMRI research methods. While multi-modal information provides some support for fMRI observations, a universal network taxonomy would benefit from deeper enrichment of multimodal information. Fifth, brain dynamics, non-stationarity, and contextual effects (such as task-related reconfiguration) have a profound influence on observable network ensembles. These five issues, discussed in turn, reflect ongoing research initiatives and necessarily inform the development of any network taxonomy.

3.1 Spatial scale, resolution, and hierarchies

A network is defined by its nodes and edges (18). Nodes represent the fundamental functional units of the system and edges represent the interactions between nodes (19). In brain networks, nodes can be defined across spatial scales varying over at least five orders in magnitude, from the level of individual cells (~10^{-5} mm), through populations of functionally related neurons (~10^{-4} m to 10^{-2} m), to macroscopic brain areas and distributed functional systems (10^{-2} m to 10^{-1} m) (20,21). Network edges can similarly be used to represent structural and/or functional interactions between nodes over a similar range of spatial scales. Structural edges can represent synapses, axons, bundles of axons, or white matter pathways. Functional edges can represent measures of coupled spike trains or calcium signal fluctuations between individual neurons, covarying local field potentials, or statistical dependencies of physiological recordings taken from extended cell populations (22).

The spatial and temporal resolution at which a given neural system is mapped will necessarily constrain the kinds of networks that can be observed. For instance, it is presently not

possible to measure entire nervous systems of mammals at cellular resolution, so any such networks can only be mapped within confined patches of neural tissue, precluding an opportunity to study systems with a more widespread anatomical distribution. In contrast, non-invasive methods such as MRI offer a powerful tool for assaying entire brain volumes at macroscopic spatial resolutions on the order of millimeters and the temporal resolution of fMRI on the order of seconds or sub-seconds (but see Section 3.D: Beyond fMRI). At the spatial and temporal scales currently accessible with MRI, the large-scale brain networks observed are likely to represent long-term attractors of more rapid cellular dynamics, and are shaped by underlying anatomical connectivity and prior inter-regional co-activation histories (23–25).

A particular challenge for macroscale neuroimaging is that there currently exists no gold standard for defining network nodes. This is fundamentally a question of brain parcellation. Under ideal conditions, a network node should correspond to a functional brain area, which may be defined as a contiguous patch of neural tissue that shares homogenous functional specificity, connectivity, architectonics, and topography (26,27). Since Brodmann (28) first parcellated the brain into distinct cytoarchitectonic regions, numerous investigators have attempted to identify the boundaries between functionally specialized areas and nuclei, both in cortical and non-cortical regions (29,30) often leading to conflicting parcellation schemes. Indeed, some have questioned the very existence of discrete areas (31,32) and many cellular, molecular, and functional properties of the brain appear to follow spatially continuous gradients (33,34), although statistical evidence for reproducible, discrete transitions across neocortical areal boundaries in multiple independent modalities has been observed (35). In the MRI literature, the lack of cellular or molecular probes has led different investigators to deploy various methods and heuristics for defining network nodes, including random parcellations (36), data-driven clustering based on patterns of structural or functional connectivity (37), gradient-detection algorithms (38), the use of activation foci from task functional MRI (39) or the co-localization of gradient-defined boundaries in neuroimaging measures of architecture, function, connectivity, and topography (35). These methods vary in the degree to which they capture the essential properties that define a given brain area, which ultimately determines the composition of an extended functional network. Indeed, the specific way in which nodes are defined will influence the networks that can be identified. For instance, the commonly used automated anatomical labeling (AAL; (40) and Desikan-Killiany gyral and sulcal atlases (41) treat the superior frontal gyrus as a single region, yet this gyrus contains several cytoarchitectonically and functionally distinct subregions which cannot be demarcated without a more fine-grained parcellation (42).

The method used to define network edges will also influence the composition of any networks observed with further analysis. In structural networks, edges are typically derived from dMRI tractography, a technique that produces streamlines representing axon bundles. These bundles form the backbone that supports communication between brain areas both at rest and during task performance. While the brain transitions across functional states at a sub-second rate, this structural backbone is not altered at that time scale. Thus, although some relationships are expected between structural and functional networks (e.g., a disruption in the former resulting in

a disruption in the latter), it is important to remember that these two approaches measure different features of the brain. Furthermore, various analytic choices have an impact on the edges of structural networks as measured by dMRI tractography (43–51) (see Section 3.d) and the effect of these analytic choices on the accuracy of dMRI with respect to the ground truth obtained from post mortem microscopy techniques is an area of active investigation (52,53) (for review see (54).

In functional networks, connectivity can be defined using statistical techniques (e.g., correlation or coherence) for quantifying a dependence between bivariate or multivariate time series (13). The choice of a specific coupling measure has a significant impact on network structure. The product-moment correlation coefficient is the most widely used in the functional MRI literature. However, this method is transitive, meaning that if region A correlates with B and B with C, then A must correlate with C, even if they do not share a direct anatomical connection. As such, correlation-based networks are sensitive to indirect, polysynaptic connections and tend to be strongly clustered (55). The use of partial correlations can remove these indirect effects but, when applied naively to large networks, can be too aggressive and remove important network structure (55,56). These variations in methods for node and edge definition are compounded by the myriad ways available for processing and denoising functional MRI data (57,58), which can yield divergent estimates of network connectivity.

The analysis of network organization is typically based on the idea that a network can be understood in terms of a set of separable "communities" (or "modules"). A given node belongs to one and only one community in most formulations. Whereas this assumption is a reasonable starting point, there is no inherent reason that biological networks should be organized in this precise manner (59). For example, a specific gene may participate in many metabolic pathways and thus be better understood as belonging to more than one community. Likewise, hub regions in the brain are thought to dynamically affiliate with disparate clusters of brain regions in a context-dependent fashion (60,61).

In the past decade, several research groups have investigated the overlapping nature of brain communities (62–65). Among other findings, this work has revealed that select brain regions connect both within their community, and also across communities. In this way, communities have somewhat fuzzy boundaries, but it is also clear that specific nodes can play important roles in multiple communities. More broadly, this research encourages discussions that evaluate common assumptions in understanding large-scale brain networks. Are hard partitions the appropriate mathematical language, or would it be valuable to adopt a notion of "gradients of affiliation" that embraces a more continuous, albeit complex, characterization of network architecture? Indeed, even within a discrete brain region there is evidence of functional multiplicity, such that distinct yet overlapping gradients of functional organization can be identified (66). We return to these issues in the final section where we provide recommendations for dealing with these ambiguities.

For now, these issues are illustrated by considering one popular approach for functional parcellation of fMRI data, spatial ICA. sICA is a data-driven decomposition method that can be

applied to fMRI data to decompose the data into a collection of spatial signal sources, e.g., fMRI signals from brain networks and from motion effects and artifacts, that mix together to generate the measured fMRI data. There are many applications of sICA for fMRI, including data denoising, data reduction, and investigating functional connectivity. Here we discuss how sICA has typically been applied in the service of large-scale network identification.

For functional connectivity analysis, sICA is typically applied to group fMRI data created by temporally concatenating the fMRI data across subjects. Resulting group sICA spatial maps then represent a data-driven soft functional parcellation, with resulting spatial maps representing spatially independent sources of the data (neural and nuisance signals) that are common to all participants. To investigate inter-subject variability in between- or within-network connectivity, this parcellation is projected back into each participants' fMRI data to compute subject-specific spatial maps and time courses for functional connectivity analyses. In this two step procedure, the group sICA can be used to define discrete neural elements and can be tuned to different spatial scales observable with fMRI, from high-dimensional parcellations of the brain into individual or bilateral localized brain regions (~mm to few cm) to modules or sub-networks comprised of a few nodes (few cm to ~10 mm), to widely spatially distributed large scale networks (whole brain ~10 cm). The projection step, for example, using dual regression (67), extracts temporal courses for each map in the parcellation scheme from each subjects' data, which may then be used to compute subject specific spatial maps that approximate the unique configuration of the networks represented in the group sICA in each participant. The subject-specific temporal courses can be used for network modeling, for example, to assess between-network connectivity, while the spatial maps capture inter-subject variability in connectivity of individual networks that can be assessed for group differences or relationships with non-imaging variables. For network modeling using the network time courses, the same issues raised above related to edge selection apply (e.g., full correlation versus partial correlation or other (25,68)).

The spatial scale of the group sICA parcellation is determined by the group sICA model order parameter, or the number of components estimated by sICA. For group sICA of fMRI data, low model orders of ~20 result in a parcellation into large-scale networks (25,69,70), whereas higher model orders of ~30-70 parcellate the brain into sub-networks, and the highest model orders (100-300+) implement a fine parcellation into individual unilateral and bilateral brain regions as well as sub-networks that do not fractionate further (25,71). As an aside, care must be taken to balance the desired spatial scale against the particular sub-networks that may be of interest. All sICA methods implement a principal component analysis (PCA) for data reduction prior to the sICA. This step is driven by identifying orthogonal signals of interest that explain the most variance in the fMRI data, starting with the signal accounting for the most variance and progressing down to signals that account for small variance. The data are reduced by throwing away the components (ordered by most variance accounted for) that exceed the model order of the sICA. As such, it frequently happens that brain networks that do not account for enough variance to make it through the PCA reduction step are discarded and do not show up in lower model order sICA spatial maps. As the model order increases, we then see not only fractionation

of brain networks into sub-networks/regions, but also the appearance of new networks that were not observed at lower model orders (72,73). This is particularly true for subcortical and brainstem networks. For example, in Abou-Elseoud et al. (2010), the basal ganglia network does not appear until model order 40 (their Figure 2). Additionally, at the highest model orders, spatially autocorrelated noise begins to contaminate the resulting sICA decompositions (35).

To demonstrate the links between parcellation across spatial scales and model orders, we consider the open access sICA-based group level functional parcellations (71) distributed by the Human Connectome Project (74). **Figure 3** shows that in the parcellation from model order = 15 (from HCP_PTN820), two DMN sub-networks are observed in the resulting group sICA spatial maps, a dorsomedial prefrontal sub-network (or anterior DMN, aDMN) and a medial temporal lobe DMN sub-network (mtlDMN). **Figure 4** shows how these two networks persist and/or fractionate as the group sICA model order increases, from the coarsest parcellation at lowest model order to the finest parcellation at high model order. Both networks are stable as the model order increases to 25. However, at model order 50, the aDMN further fractionates into dorsal and ventral PFC DMN sub-systems (75), while the mtlDMN is represented as a single sub-network. At model order 100, the mtlDMN is split into two subsystems, while the dorsal/ventral PFC aDMN sub-systems remain stable. These systems remain stable and/or are further split at the highest model orders (200, 300; not shown). While this multiscale organization is likely to represent a real characteristic of brain organization, it also creates practical challenges with respect to node definition, parcellation and spatial scale, and how sICA can be used to investigate functional connectivity across the mesoscale.

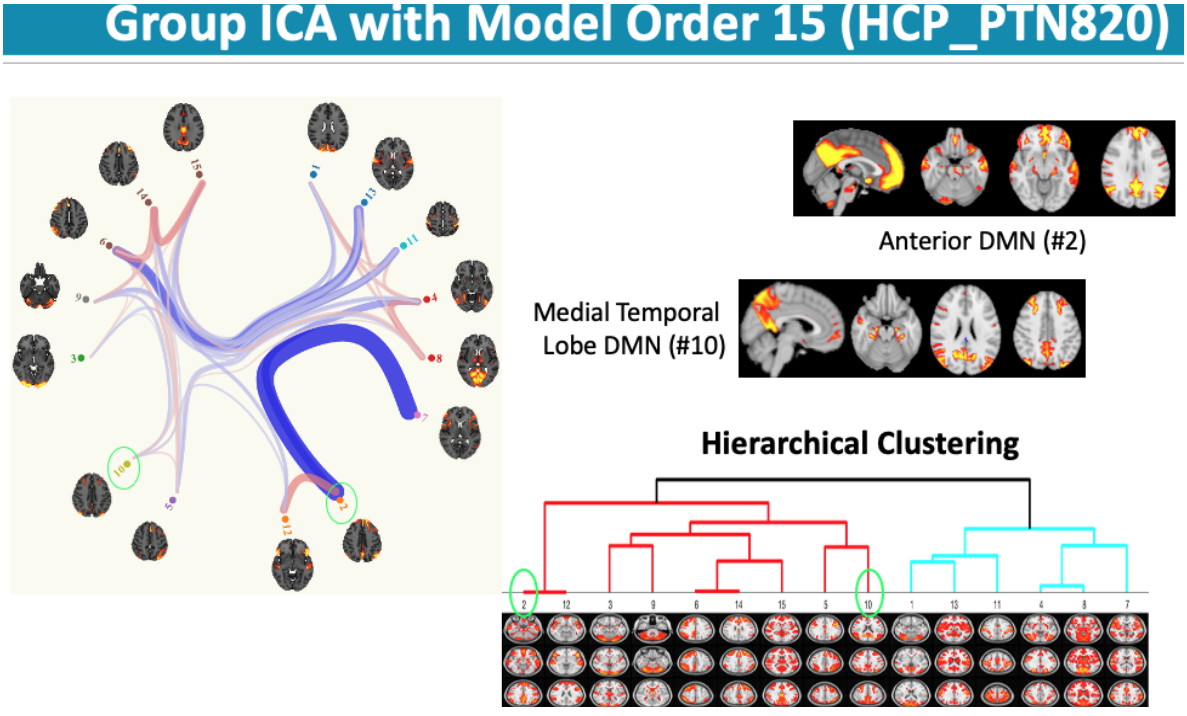


Figure 3. Default network hierarchies. Two subsystems of the DMN are identified in the group sICA with model order = 15, a dorsomedial prefrontal or anterior sub-system (aDMN) and a medial temporal lobe sub-system (mtlDMN). Hierarchical clustering shows they cluster together at the second level of the tree. Although these two systems are related, they are more strongly connected with different networks, e.g., aDMN is linked with an inferior frontal-opercular system (#12; sometimes referred to as the salience network) and mtlDMN is linked with a left frontoparietal network (#5; sometimes referred to as the central executive network).

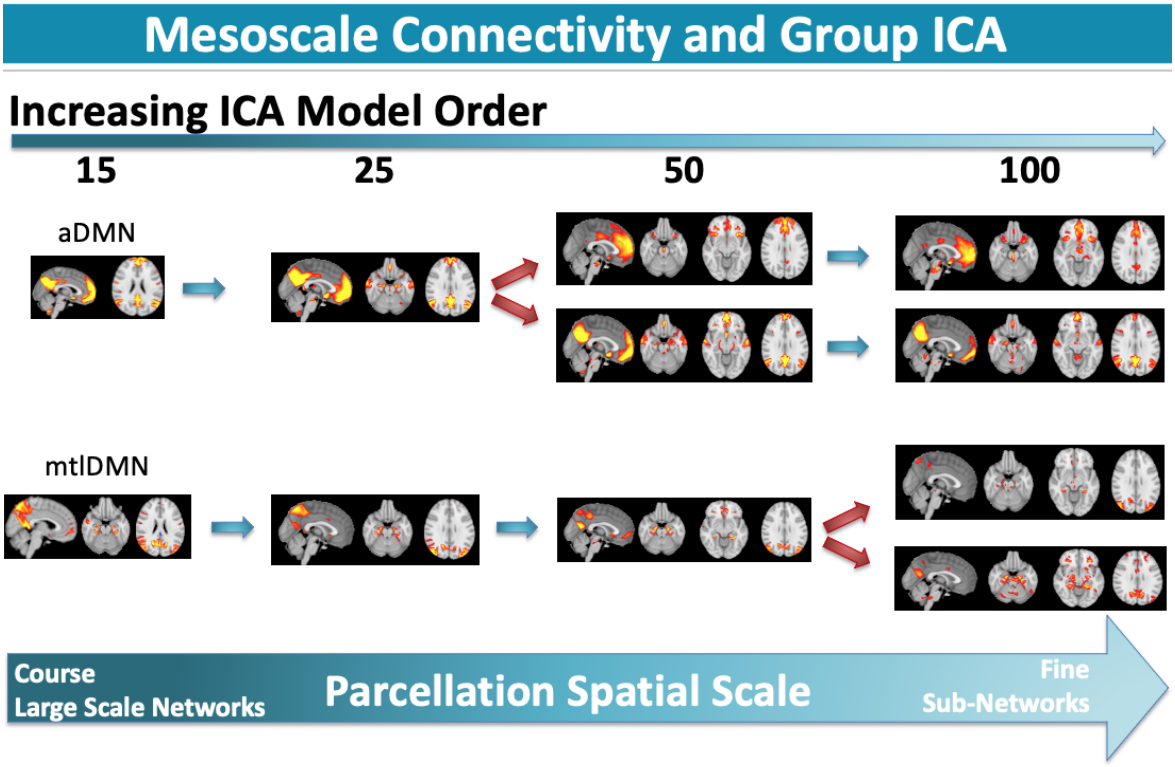


Figure 4. Default network fractionation. At model order = 15, the DMN is fractionated into two sub-networks, aDMN and mtlDMN. These two networks are stable across model order = 25, but the aDMN fractionates into two further subdivisions, a dorsal medial PFC system and a ventral medial PFC system, which are stable at model order = 100. The mtlDMN fractionates at model order = 100 into two systems that reflect a split into a precuneus mtlDMN system and a posterior cingulate mtlDMN system. These subsystems persist and/or further fractionate at even higher model orders (200-300, not shown).

3.2 Inter-individual variability

Functional neuroanatomy varies spatially across individuals over and above preprocessing procedures that normalize neuroimages to a standard space. This has been recognized for over 20 years by cognitive neuroscientists who engage in task-based functional localization to characterize regional brain function (e.g. (76), fusiform face area). For example, the parahippocampal "place" area can vary by up to 20mm along a rostral-caudal axis between individuals (77). Just as brain regions vary in location across individuals, so does network topography (78). A discussion of large-scale brain network taxonomy requires an understanding of variation in these systems across individuals. It also requires a clear assessment of the degree to which this variation impacts our ability to identify common networks across individuals (79)

Individual variability interacts with questions of taxonomy in at least two ways. First, networks are often first identified based on evidence that a particular set of regions are linked consistently across individuals. For example, if, in every person we examine, we find links between the posterior cingulate, medial prefrontal cortex, and angular gyrus, we increase our confidence that this is a 'network' entity and apply a label to it (e.g., "default network"). Related to this, recent work on individual variability shows that the boundaries between the default network and other networks, as well as between various sub-components within the default network, transition more sharply when networks are described within each individual than when they are combined across individuals (80–83).

Second, in the face of inter-individual variability, we need an approach for how to determine correspondence across individuals in order to implement taxonomies in practice. fMRI functional connectivity studies suggest that while some regions of the brain appear to be largely similar in their network topography across individuals, others show pronounced individual differences (78,84–86). These studies have found that association regions, especially in the lateral frontal lobe and near the temporo-parietal-occipital junction, tend to exhibit the most variable spatial topography of the cortex, with much lower variation seen in sensory and motor regions. Given this variation, how can we determine that a network is the same entity across different individuals or groups? If, for instance, we find an individual missing specific components of Network A or with a spatial topography similar but slightly displaced relative to Network A, would it be accurate to call this Network A? In what ways and to what extent can a network vary, but still represent the same underlying entity? To what extent should we expect certain networks to only be expressed in some individuals but not others?

These questions are not purely theoretical. For instance, following complete hemispherectomy - a surgical procedure wherein an entire cerebral hemisphere is removed - the lone remaining hemisphere can exhibit network properties typically observed in individuals with fully intact brain structures (87,88). Individuals with extensive cortical loss due to prenatal stroke can exhibit intact behavioral function, accompanied by networks that are entirely preserved but displaced away from the stroke (89). Even well-studied networks that appear in roughly similar brain locations in almost every person do not correspond exactly anatomically (e.g., the default network (80) or somatomotor networks (90)). A recent quantitative examination of inter-subject

variability of 14 large-scale brain networks finds that while networks exhibit a common core, consistency across individuals falls off sharply, especially in higher order networks in the frontal and parietal lobe (79). This individual variation suggests that standardized parcellation schemes that are uniformly applied to a sample without respect for functional neuroanatomic variability can mischaracterize network estimates, resulting in reductions in specificity and analytical power in inter-individual comparisons (91–94). This poses a limit on the application of anatomy-based taxonomies when network topographies vary across anatomical boundaries (14).

Implementation of a robust network taxonomy requires a way to estimate and compare networks across individuals. Below, we discuss key factors when considering the relationship between universal brain networks and inter-individual variability: (1) methods that have been used to capture individual brain networks, (2) validation of these measures and sources of potential errors, (3) what studies of individual brain networks suggest about the most common forms of individual variability, and (4) how brain networks differ across different subsets of the population (based on age or disease status).

Many approaches have been developed to estimate individual variability in brain network organization. One class of approaches applies data-driven techniques (e.g., clustering) to a large quantity of data at the individual level (80,85,90). However, this so-called 'precision functional mapping' approach requires a large quantity of data from each participant (or multi-echo fMRI data acquisition; see Lynch et al., 2020a). In addition, each participant is analyzed separately, so network correspondence between participants is not enforced, and post-hoc network assignment can be uncertain in some circumstances. A second class of approaches estimates individual-specific networks by constraining them to be spatially similar to a group-level prior (78,79,95–98). This class of approaches allows the reliable estimation of individual-specific networks with less data per individual, and also establishes network correspondence across participants. However, the use of a group-level prior might restrict the flexibility of networks to vary across participants. Approaches can vary along the full spectrum of completely data-driven to strongly prior-driven; moreover, priors can be implemented in different ways (to constrain, for instance, the size, shape, topography or location of a network), which will have different implications for the forms of variability that they can capture. Even when using a group-level prior, some approaches can accommodate large deviations across participants. Finally, a third class of approaches estimate inter-subject variability continuously at the voxel or vertex level (84,86), making no assumption about the number or form of underlying networks. However, this approach assumes voxelwise/vertexwise correspondence across participants, which is a strong assumption given pronounced individual differences across participants.

What is the evidence suggesting that the inter-individual network variability estimated from resting-state fMRI is real? First, these networks are highly replicable across sessions within the same participant (78,85,95). Second, task-evoked fMRI activations align well with the idiosyncratic network topography in individual participants (81,86,90,98,99). Third, individual-specific network topography is heritable (100). Finally, individual-specific network topography can be used to predict the behavioral traits of individual participants (78,86,101).

However, care is needed in the measurement of individual variability. In addition to reflecting variation in large-scale brain systems, variability in functional connectivity can also be induced by non-neural sources such as motion (102–106), respiration (107,108), sampling variability (85,109), and signal loss due to acquisition parameters, head shape or head position. For example, while functional networks have been described as shifting from a more local to a more distributed pattern from childhood to young adulthood, some of this variation is likely to be caused by head motion, which induces distance-dependent artifacts (102,105,110). Respiration has been associated with global BOLD signal changes, which introduces one of many sources of artifact into fMRI functional connectivity estimates (104,111,112). In addition, the fMRI BOLD signal is quite noisy and autocorrelated; a fair amount of data is needed to counteract this sampling variability and reach high reliability at an individual subject level (85,109,113,114). Finally, these factors differ across brain regions concurrent with properties of the underlying BOLD signal and MRI measurement method. Many popular fMRI sequences result in substantial signal loss and distortion near tissue boundaries and reduced signal further from the receiving coil, leading to difficulty in accurately measuring functional networks in certain brain regions, particularly impacting the ventral (especially anterior) temporal lobes and subcortex (113). Caution is warranted in interpreting variation in functional networks if these non-neural sources of variation are not adequately addressed. A growing number of papers have assessed the ability of different acquisition, preprocessing, and denoising paradigms to address these artifacts (58,104,115–120).

When such confounds are minimized, it becomes evident that several different forms of inter-individual variability are present in brain networks (**Figure 5**). The most commonly studied form of inter-individual variation is variation in the magnitude of connectivity between brain regions of a network (**Figure 5B**). Individual differences in connectivity strength are often taken as an outcome metric of interest, to be associated with external states or traits (121,122). However, when connectivity strength is used to define networks, as discussed here, large inter-individual variabilities in connectivity strength between networks can induce confusion about network membership (123,124).

A second, more recently recognized form of inter-individual variation is variation in the spatial position and extent of network nodes (**Figure 5C**) (78,80,85,86,90,95–99,101,125–131). Such variations can take the form of areal expansions, contractions, or displacements that lead to variation in the exact positions of network borders across individuals (125,126). More extreme individual spatial variations can relocate a node outside of the initialized parcel boundary, and not spatially overlap with other sample participants (98,123). Overall, spatial variation appears to contribute more to individual differences in brain networks than variations in connectivity strength (101). Still, it is not clear which form of variation may be most related to behavioral variables of interest. For example, “hyper-aligned” brains (i.e., brains that are functionally aligned to one another by re-weighting voxel signals to maximize inter-subject correspondence in functional responses from either movie activations or functional connectivity) show better prediction of cognitive variables than non hyper-aligned brains (132).

Finally, brain networks can exhibit topographical variations across individuals (Figure 5D). Single cortical areas representing network nodes can be split into multiple discontinuous regions in some individuals, while still clearly exhibiting the same properties of the unified area (35). Individual-specific brain networks also exhibit ectopic intrusions, in which a punctate region within a brain network has strong, idiosyncratic connectivity with a different network (85,86,123,125). All individuals exhibit some form of topographical variation in their brain networks (125). However, it is unclear if these violations of regional spatial contiguity reflect a differential sampling of regions on different hierarchical scales.

Each of these forms of variation is important to consider when building or applying a taxonomy of networks. In a given individual, variation in functional connectivity strength may result in a canonical network node to "fall out" of the network, or be incorporated into a different network. Spatial variation in networks may create the appearance that a network node is absent or disconnected when it is actually mis-localized by standardized parcellation schemes. Topographical variations may create apparent extra network nodes not typically present in most individuals. Any taxonomy must reflect the central tendency network characteristics of the general population, but also be flexible enough to accomodate connectional, spatial, and topographical variations found across individuals.

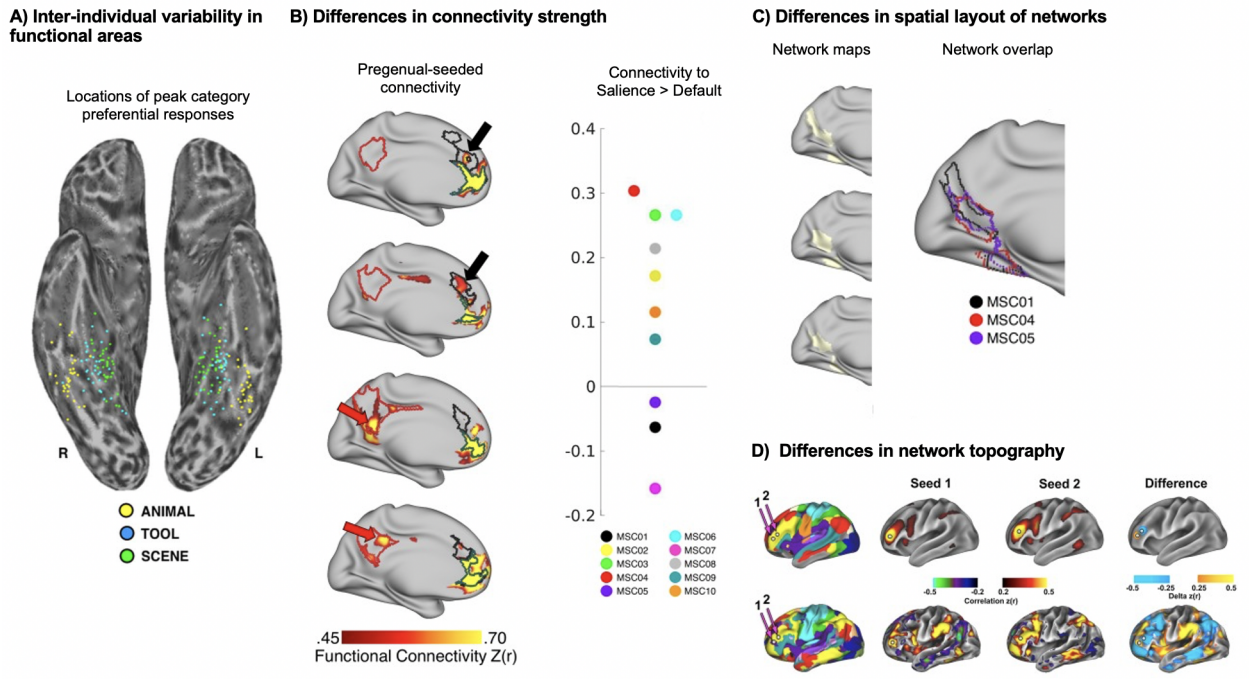


Figure 5. Forms of inter-individual variation in functional neuroanatomy and large-scale network topography. (A) Task-responsive cortical areas, which comprise large-scale networks, vary in their spatial location across individuals. (B) Similar network components are present

across individuals, but differ in magnitude of associations. (C) Large-scale networks differ between people in size and position. (D) Whole-brain connectivity, resulting from small differences in seed placement, can reveal dramatically different network topographies between people. Adapted figure panels (A) from (77), (B-D) from (123), with permission.

Inter-individual variability in large-scale network topography is seen in typical samples of young healthy adults. There is also variability across the human lifespan and in clinical populations. Developmental differences are often observed in within- and between-network connectivity. For example, developmental brain maturation entails a gradual change from more diffuse connectivity patterns in young children to more clustered systems in young adulthood (133). This pattern appears to reverse in aging, where we observe system dedifferentiation in older adults (134,135). Other examples are clinical disorders that have been described as disconnection syndromes, such as Alzheimer's disease (136) and schizophrenia (137) which both show aberrant default network functional connectivity (138,139). An important consideration in this context is whether such age- and/or disease-related connectivity differences fundamentally affect brain network organization. If they do, how should future studies consider potential differences in network organization across the lifespan or among clinical groups (140)?

The current literature shows that most canonical brain networks can be detected across different age groups and clinical populations, even if functional connectivity strength may be attenuated in certain cases (11,141,142). Moreover, the overall spatial organization of brain networks appears quite stable across individuals with or without psychiatric disorders, with group differences being relatively subtle (143). Like the observation in typical young adults (79), variability in children and older adults can be seen near the boundaries of brain networks, with the core network regions remaining relatively stable (144,145). Most studies that compare groups examine differences in functional connectivity strength using existing parcellations of pre-defined brain systems, which are commonly derived from healthy young adult samples (30). To ensure comparison of the same brain systems across groups, researchers could restrict functional connectivity evaluations to core network regions, for example as those proposed by Dworetsky and colleagues (79). However, potentially interesting information may be lost when solely focusing on signal from core system nodes, as variability across typical young individuals appears mainly due to differences in spatial topography rather than functional connectivity strength (146). Alternately, methods to individualize parcellations, discussed above, can also be applied to groups other than young adults. This approach has recently been successfully used to examine age differences in the functional architecture of the brain while respecting inter-individual variability in network topography (147,148). Future work should consider, however, whether variance should be benchmarked to normative patterns in healthy young adult brains, or be more flexibly applied to characterize systematic patterns of variance in functional network organization.

3.3 Network affiliations of subcortical structures

Human large-scale brain network identification with neuroimaging has focused on characterizing networks in the cerebral cortex (25,30,149). There are several reasons for this focus, but the most impactful is the fact that fMRI data exhibit substantial signal dropoff as distance increases from the MR coil. The result is that fMRI signals in subcortical structures tend to be noisy and have lower amplitude. As such, functional connectivity with known cortical networks is low, and network detection approaches struggle to label subcortical voxels. Specific to fMRI, the way that BOLD signal relates to neural activity varies considerably between cortical and subcortical regions. In the cerebellum, for example, (150) Purkinje cells produce weaker changes in the blood flow (151,152) than the neocortex.

This methods-driven cortical bias risks ignoring major portions of the brain's network architecture. Anatomical tracing studies demonstrate that the major subcortical structures exert critical influence over the cortex via reciprocal or looped circuits. Cortex and cerebellum communicate via the cortico-ponto-cerebellar pathway, which then feeds back to cortex via thalamus (153). Separately, cortex, striatum, and thalamus are linked in cortico-striato-thalamo-cortical loops (154). Primate (both non-human and human) research shows that these projections, while organized in a general topographic manner on the basis of cortical origin, contain complex interfaces between terminal fields from diverse cortical areas, which allows transfer of information across functional domains (155–157). This suggests that cortical networks will also serve as an organizing principle for subcortical structures (or vise versa). Indeed, specialized network identification approaches that account for low signal do find topographically organized networks in striatum (127,158–162), cerebellum (130,131,163,164), thalamus (127), hippocampus (165), amygdala (166) and basal forebrain (167,168).

In many cases, this network organization converges closely with known anatomical projections in non-human primates. For example, cortical somatomotor networks are represented with a topographically preserved organization in posterior putamen (159), in ventral lateral thalamus (127), and in both anterior and posterior cerebellar lobes (163). The occipital network has little representation in striatum or cerebellum, but is present in a posterior lateral thalamus region converging with the lateral geniculate nucleus (127).

In other cases, the subcortical representation of cortical networks that are dramatically altered and expanded in humans relative to other mammals provides novel insight into their organization. While the default network is well known to be represented in a variety of frontal, parietal, and temporal cortical regions, it also has representation in anterior hippocampus and amygdala (165,166), ventral striatum (83,159,162), the medial nuclei of the thalamus (127), basal forebrain (167,168), and at the border between cerebellar Crus I and II (163) (**Figure 6**). Recent work has begun to map subcortical connectivity of the default network using high-resolution functional imaging (169).

An accurate taxonomy of networks is incomplete without consideration and inclusion of these subcortical elements. For example, the default network has known roles in processing reward, memory, and emotion (170) These functions are incompletely understood without the

topography of the default network including subcortical counterparts such as ventral striatum, hippocampus, and amygdala. Furthermore, it is important to note that both anatomic and fMRI studies show not only segregation of subcortical projections based on cortical origin, but also substantial integration and overlap. Taking both of these aspects into account is thus crucial for better explaining function and behavior based on anatomy. A full review of subcortical affiliations with large-scale cortical networks is beyond the scope of the present work, and substantial work remains to reliably delineate these associations. In this way, any network taxonomy must continue to evolve as new discoveries regarding cortico-subcortical interactions are made.

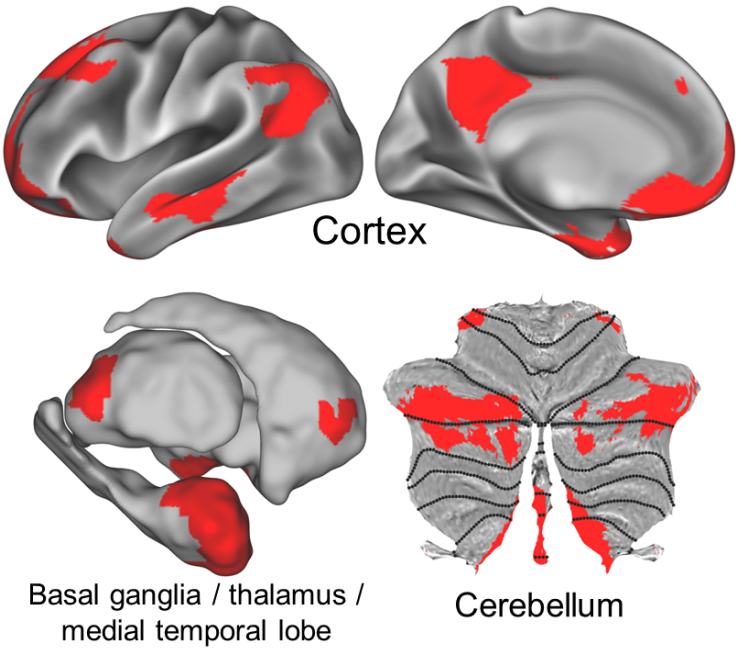


Figure 6. Cortical and subcortical elements of the default network. Anatomical locations of the default network (red) in lateral and medial cortex (top), basal ganglia, thalamus, and medial temporal lobe (bottom left), and cerebellum (bottom right).

3.4 Beyond fMRI: Multi-modal information

Large-scale neurocognitive networks were historically identified by cognitive neurology (171) and complemented by comparative neuroanatomical fiber tract tracing (172). In the last twenty years, fMRI has largely superseded this work, and resting-state functional connectivity has come to dominate investigations of large-scale brain networks. However, electrophysiological imaging modalities have been increasingly utilized in the study of functional networks. In parallel, structural networks have been probed with dMRI tractography. Several studies have compared these techniques, with the goal of investigating the concordance

between functional networks derived from fMRI and electrophysiology, or the extent to which these functional networks can be explained by the structural connections derived from dMRI. As we acknowledged at the outset of this project, future work must incorporate findings derived from multiple neuroimaging modalities to enrich our understanding of large-scale brain network taxonomies. Here we discuss points of multimodal convergence and areas where complementary evidence can be derived from modalities other than fMRI to further the goals of WHATNET.

Functional connectivity from fMRI was spatially compared with electrocorticography (ECoG) / intracranial electroencephalography (iEEG) to establish a neuronal, rather than vascular, basis for fMRI connectivity. These concerns were addressed by the observation of spatial convergence of connectivity between fMRI and intracranial electrophysiology (173–175). Conversely, a major goal of early spatial comparisons of fMRI to *scalp* EEG/MEG was to demonstrate the capability of (source-localized) non-invasive electrophysiology to study large-scale intrinsic brain networks. In particular, large-scale brain networks akin to the "canonical" networks known from fMRI have been observed in scalp recordings (176,177) (for review see (178)). With many methodological goals largely addressed, the field can now increasingly focus on the complementary but distinct neurobiological information about brain networks provided by these different neuroimaging modalities.

Non-invasive scalp EEG/MEG is sufficiently informative to permit the study of macroscale networks, yet the necessity of mathematically ill-posed source localization and residual source leakage render these methods spatially less reliable and less resolved than fMRI. On the other hand, invasive ECoG/iEEG provides local field potentials/multiunit activity data on connectivity without providing 'whole brain' data (note however, pooling electrode pairs over a large number of patients may overcome this issue (179)). Counterbalancing these spatial weaknesses, the core strength of electrophysiological methods compared with fMRI is that they allow the study of networks at a finer temporal scale, permitting analysis of their time-varying dynamics (180).

With regards to more direct measures of neural connectivity, the spatial correspondence of whole-brain connectomes between fMRI and electrophysiological methods is significant, but seldomly higher than moderate in effect size. This observation holds true irrespective of data modalities (fMRI-to-scalpEEG, fMRI-to-ECoG, fMRI-to-MEG) and methodological and analytic choices (181). The electrophysiological and hemodynamic connectomes may therefore reflect partially non-overlapping neural populations (182). Further, there may be non-neuronal but biologically meaningful contributions to the cross-modal divergence, such as vasculature (183). The above-described studies were conducted using resting state fMRI data. Task-evoked changes relative to resting state have also been explored (184). An open question is therefore whether the spatial deviations between functional data modalities are systematic. We expect a systematic difference in precise source locations.

Several studies have investigated the structural basis for fMRI-derived intrinsic networks (see (185) for review). Early work derived structural connections either from prior tracer studies in macaques (186) or from dMRI tractography in humans (187–189), and simulated functional

time courses given these structural connections and random fluctuations in neuronal activity. The comparison of these simulated time courses to those measured empirically by resting-state fMRI showed evidence that functional connectivity may indeed arise from spontaneous activity across regions that are connected structurally. However, direct correlation between edge weights of structural and functional networks is, at best, in the low to moderate range (187,189,190). While structural connections can be used to predict functional connectivity (187,189,191,192), the reverse is not necessarily true (187) (but see (193)). This has been attributed to the fact that two regions can be coupled functionally even in the absence of a direct structural link between them, if they are linked indirectly via a third region. Several studies have shown that indirect structural connections can predict functional connectivity, although their predictive power is somewhat lower than that of direct structural connections (187,189,191). The complex relationships between structural and functional connectivity are highlighted in case studies such as split-brain patients, in whom the cerebral commissures have been disconnected (194). In the absence of direct interhemispheric structural connections, these patients can still exhibit strong functional connectivity across the hemispheres that is most likely mediated by indirect subcortical pathways (195,196).

Given the plethora of approaches to dMRI tractography, it is worth considering how algorithmic choices that affect structural connections obtained from dMRI may impact these findings. Whole-brain structural network analyses have typically utilized deterministic tractography. Validation studies that have compared dMRI tractography to anatomic tracing have shown that, when compared at the same false positive rate, probabilistic tractography methods have higher true positive rates (or, equivalently, lower false negative rates) than deterministic tractography methods (197–200). However, the default thresholds typically used in tractography tend to be conservative. That is, they correspond to low-false-positive, low-true-positive operating points (199). In that regime, any performance differences between probabilistic and deterministic methods are small. Importantly, that is a regime where all tractography methods detect the larger structural connections from each region, but miss the smaller ones. This is likely to have had an impact on any prior comparisons of structural and functional brain networks, and merits further investigation in the future.

Finally, the relationship between structural and functional networks may vary between functional states (201) and with development (202,203). While functional connectivity is of a highly dynamic nature (see Section 3.5 below), the brain is not rewired structurally at the same rate. This implies that we cannot expect full agreement between functional and structural connectomes. Thus, even after resolving all methodological issues, fMRI and dMRI will provide complementary information about brain networks. As discussed above, however, the literature does provide evidence for a link between the two, and in particular for (time-averaged) resting-state fMRI networks emerging from correlations of spontaneous activity between regions that are connected structurally. The brief overview of multimodal neuroimaging findings relevant to the goals of WHATNET provided here points to many open questions that we hope to see addressed in future iterations of guidelines for developing network taxonomies.

3.5 Dynamics, non-stationarity, and contextual effects on network organization

As discussed throughout, large-scale brain networks are typically defined using static functional connectivity. Static functional connectivity estimates are based on averaging across the entire duration of the fMRI timeseries data. However, it is important to consider that fMRI BOLD is a dynamic signal on multiple levels of temporal resolution. Contextual features of an fMRI scan, such as time of day (204), recent experience, and learning can all modulate network properties and their relationship to cognition and affect (122). Additionally, the BOLD signal is dynamic within a single scan. In this next section we discuss how correlation magnitudes fluctuate across time, resulting in time-varying dynamics in whole-brain connectome organization. While time-varying functional connectivity analyses may be susceptible to spurious findings, careful handling of motion and other artifacts, along with implementation of appropriate statistical methods, allows for important insights to be gained using a dynamic approach (205). The question we address here is whether these dynamics should be considered when defining large-scale brain networks. We address changes in network composition both in response to changing cognitive demands (e.g., when performing different cognitive tasks) and on a moment-to-moment level within a particular cognitive context (e.g., during a resting state scan).

Large-scale network organization remains largely stable between rest and task states (206–208). Data-driven weighted methods (e.g., temporal ICA) treat rest and task activation on a level playing field and find large-scale networks during both rest and task states (120). Yet differences are observed, and are thought to be meaningful and systematic (e.g., a result of differing levels of arousal or of the specific cognitive or affective context) (Bolt et al., 2017; Cohen, 2018; Gonzalez-Castillo and Bandettini, 2018; Kinnison et al., 2012; McMenamin et al., 2014; Najafi et al., 2017). Much literature focusing on network reconfiguration describes changes in overall network topology, such as the degree of modularity or across-network integration, without probing whether nodes of intrinsic networks change network affiliation across cognitive contexts (e.g., (209–212). Other work, however, reports changes in network affiliation that occur when cognitive demands change (e.g., (213–216)). Recently, it has been reported that network membership of up to 75% of nodes changes across a variety of cognitive tasks. Moreover, the specific cognitive context can be successfully predicted based on patterns of change in network affiliation (217). Thus, task context is an important feature to consider when characterizing network topography. For example, the default network consists of subnetworks (10,218–220) that are more distinguishable in terms of community membership during cognitive tasks compared with rest (219,221).

One set of brain regions whose categorization needs particular attention in terms of assignment to intrinsic networks are “flexible hubs” (60). These are nodes that connect across several intrinsic networks (e.g., connector hubs) and whose connections vary as a result of cognitive context. These regions are thought to be critical for integrating across specific task demands in complex cognitive tasks (222–224). Depending on how network affiliation is defined, these nodes increase their between-network functional connectivity (225) and even

change network membership (226) across task contexts. Given these contextual changes in network affiliation, how should these flexible hubs be defined when considering a harmonized taxonomy of brain networks? Probabilistic mapping of network membership in core intrinsic networks across cognitive contexts is one promising direction for differentiating between intrinsic network nodes that are stable across cognitive contexts and those that flexibly change their network membership such as flexible hubs; to date this strategy has largely been used to identify consistency across subjects (79).

Even *within* a particular cognitive context, the whole-brain pattern of connectivity changes, affecting moment-to-moment cognition (227). How do the relatively short-lived patterns of connectivity aggregate to generate the static connectome organization, and thus the "canonical" networks that we seek to characterize? It is known that the connections with the least amount of time-varying dynamics are those with the strongest correlations in the static connectome (228). Investigations of connectome states, defined as recurrent, quasi-discrete whole-brain connectivity patterns (derived, for example, by clustering or Hidden Markov Modelling), are in line with this observation. Specifically, static organization can be viewed as a "common denominator" that is to some degree present in most functional connectome states, while the individual states express additional state-specific spatial features (e.g., (229)). However, fMRI investigations at a finer temporal resolution further suggest that, at any given moment, a specific combination of the "canonical" intrinsic networks are co-activated, while the remaining networks are collectively inactive (or deactivated) (230). Specifically, a recent advance has introduced fMRI "edge time series" analysis, a decomposition of functional connectivity into its framewise contributions (230). Any given frame is characterized by a pattern of co-fluctuations. The authors noted that co-fluctuation patterns, when thresholded, result in binary time series that exhibit two communities -- one of nodes showing positive co-fluctuations and another of nodes showing negative co-fluctuations, creating a bipartition. This analysis suggests that the complete set of canonical networks can never be expressed at any single time point. Rather, they emerge from the temporal superposition of many dissimilar bipartitions. Additionally, other studies using the same methodology have demonstrated that not only are canonical networks largely absent at individual timepoints, most timepoints contribute relatively little to the overall organization of the static functional connectome architecture. Rather, the static connectome organization is primarily driven by short-lived but high-amplitude co-activations (231,232). Some interpret these results to suggest that the canonical networks whose strong within-network connectivity dominates the static connectome may be better thought of as recurrent *transient* phenomena, rather than a stable property of the brain (for alternative interpretations, see (233). Many of these edge-centric features can be reproduced using static, node-centric, null models (234).

In spite of the many varieties of dynamics observed, the evidence suggests that brain networks may reflect minimal "atoms" of connectivity; by and large moment-to-moment co-fluctuations respect the membership to canonical intrinsic networks. In other words, brain regions do not co-fluctuate in random sets. Rather, different recombinations of intrinsic networks

describe whole-brain spatial patterns of connectivity from moment-to-moment, while maintaining the atoms as a relatively continuous feature, thus cumulatively generating the static functional connectome organization.

3.6 Interim conclusion

In this section, we reviewed five significant issues which directly impact the formulation of a universal taxonomy of large-scale brain networks. These issues included the spatial scale and hierarchical organization of networks, inter-individual variability, the consideration of subcortical structures, multimodal evidence, and brain dynamics. It is important to emphasize that each of these areas represent ongoing programs of research from multiple labs, including members of WHATNET. Given the plurality of ongoing discoveries necessary to arrive at consensus, and the multitude of plausible solutions given the existing evidence, a universal taxonomy could not be agreed upon at the time of writing this report. In light of these issues, we do not provide concrete recommendations for network nomenclature. However, there was broad agreement on reporting guidelines and avenues for future research to conduct in order to more efficiently integrate current and future findings together towards a broader consensus of large-scale network topography.

4. Towards minimal reporting guidelines for network results

The original COBIDAS report included recommendations and a checklist for sharing statistical maps and for reporting functional connectivity results (15). Specifically, the guidelines suggested that for ICA results, researchers should report the total number of components analyzed, and the rationale for their selection. For graph analyses, the recommendation was to state the null hypothesis of the test and how the statistic distribution under the null was computed. We concur that these are important pieces of information to include in results sections of manuscripts. As we have discussed throughout, coming up with a complete checklist of reporting guidelines similar to that in the original COBIDAS report that is specific for network neuroscience results is no simple task. Here we summarize some points of consensus amongst WHATNET members regarding best practices for reporting results from studies in which large-scale brain networks are investigated (**Box 1**).

There is a growing use of network-based approaches to identify large-scale brain networks from task fMRI data in cognitive neuroscience. Researchers often compute functional connectivity from task fMRI data to reveal how large-scale brain networks respond to experimental manipulation (235). Still, one point for researchers conducting task-based fMRI to keep in mind is that the results of a univariate general linear model (GLM) contrast between two cognitive conditions does not necessarily equate to a network, however tempting it may be to use network nomenclature to describe activation results when they spatially resemble other large-scale brain networks that have been described in the literature. One suggestion from this group is to avoid giving descriptive cognitive names to networks, particularly when describing

idiosyncratic cognitive domains (e.g. reward network, pain network). In this way, we can avoid proliferation of network naming terminologies and more readily compare results across studies. For example, large-scale brain networks occupying the territory of the lateral frontoparietal area have been variably referred to as the central executive or executive control network (2), the multiple-demand system (236), the extrinsic mode network (237), the domain general system (238), the frontoparietal control network (239,240), and the cognitive control network (241). Our own survey showed that these networks were among the least agreed-upon among independent raters. We suggest that naming networks by a single purported cognitive function is antithetical to the goal of understanding the broad role large-scale brain networks play in cognition, and hinders the development of a universal taxonomy.

The suggestion instead would be to evaluate any new findings, whether in the task fMRI or resting state fMRI domain, against one or more commonly-used parcellation schemes. This recommendation extends to large-scale connectivity in electrophysiological data (cf. Section 3.4), in spite of the fact that the currently common parcellation schemes are derived from fMRI. Given a previously published parcellation and a set of functional maps, one can determine the extent to which a novel functional map overlaps with a predefined atlas (242) (**Figure 7**). In doing so, we suggest that one clearly state which reference atlas is being utilized, and whether the demographic characteristics of the individuals used to make that atlas match the characteristics of the group from which the novel data were obtained. Acknowledgement of potential sources of variability should be openly discussed. Probabilistic atlases such as (79) can in some cases be referenced to note what types of individual differences might be expected, and discuss how this might affect the network designations in any new report. For example, one might exercise more caution in applying the "frontoparietal network" label than the "visual network" label given the greater potential variability in the former than in the latter.

Complimentary anatomical labels may be specified alongside functional atlas-based labels in some cases to provide additional information (14). That way, if a new study reports findings relevant to a scholar interested in following research on a given large-scale brain network, the results will be more readily discoverable. Researchers should clearly report which atlas or parcellation scheme was used, and follow the original COBIDAS guideline regarding which space the findings are reported in, as well as the guidelines for sharing raw data and maps.

An additional guideline from this workgroup relates to the discussion in Section 3.5 on brain dynamics. When defining or describing networks in a particular study, one should consider that large-scale brain networks undergo functionally relevant spatial variations across time and cognitive contexts, and consequently may not fully match standard network parcellations derived from static resting state fMRI data.

5. Unresolved issues and future directions

We have aimed to cover a range of literature relevant to the problem of building a universal taxonomy of large-scale brain networks. However, we readily acknowledge that this

manuscript should be considered a living document, subject to continuous revision to incorporate new data and theoretical frameworks as they become available. Note that here, we provide recommendations for the types of information that we suggest network neuroscience papers should report going forward. Unlike the 2019 taxonomy proposal (14), however, we do not provide recommendations for specific names and labels to give to large-scale brain networks in future studies. For the reasons outlined throughout, we now believe that a strictly anatomical labeling scheme may in some cases fail to capture aspects of individual variability and brain dynamics that are as yet open questions for the field. Still, we contend that a strictly functional scheme would likewise be insufficient, given the plurality of functions subserved by nearly every large-scale brain network that has been identified to date.

As alluded to earlier, the field is only beginning to tackle the issue of how best to categorize large-scale brain networks in developmental, aging, and clinical populations. This is particularly problematic given that network fractionation appears to be observable both in early development (144) and in aging/late life (145). This issue has been addressed in the developmental neuroimaging literature using study-specific templates for normalization (243). One can imagine an analogous scenario in which study-specific parcellations might be appropriate for a specific research question, such as studying a developmental cohort (244).

With regards to network variability as observed in clinical populations, several open questions remain. For example, if we see that a portion of a network is missing consistently in a clinical group, does this tell us something about the "core" components of that network? It is not always clear whether differences observed in clinical populations index loss of function, decreased efficiency, or compensatory reorganization processes associated with recovery.

We have not yet attempted to consider relevant cross-species comparisons in the current work. There is increasing evidence, for example, that an analogue of the human default network can be identified in non-human primates (245) and rodents (246). Understanding these cross-species convergences may help further delineate large-scale network properties in the human brain by permitting investigation of the degree to which network topologies are evolutionarily conserved (247).

A subset of the WHATNET group is currently working on a tool that will allow users to quantify the spatial overlap between their findings and one (or more) of 16 commonly used parcellation schemes (242). This tool will provide a means for mapping between any given set of new results and one or several widely used brain atlases for reporting purposes. We suggest that this type of atlas-referenced reporting should become the norm for future investigations.

Finally, we suggest that the field of cognitive neuroscience might make rapid progress towards the goals of WHATNET by adopting the practice of adversarial collaboration, whereby investigators committed to different theoretical views collaborate to test opposing predictions. Our survey of the neuroimaging community revealed the least amount of agreement among raters when they were naming networks involving frontoparietal and midcingulo-insular cortical areas. One suggestion would be for researchers who have coined particular network names such as "salience" (2), "cingulo-opercular" (239) and "ventral attention" (248) to collaborate to design

a set of experiments that would engage the putative cognitive functions associated with each of these large-scale brain networks. Collaborative efforts of this type may help resolve ambiguities and inconsistencies going forward. Adversarial collaborations are currently under way in the field of consciousness research, which has for years been fragmented due to multiple theoretical perspectives (249). We envision that well-planned, preregistered cognitive neuroscience investigations that more closely map large-scale brain networks to cognitive processes might help reduce the proliferation of network names going forward.

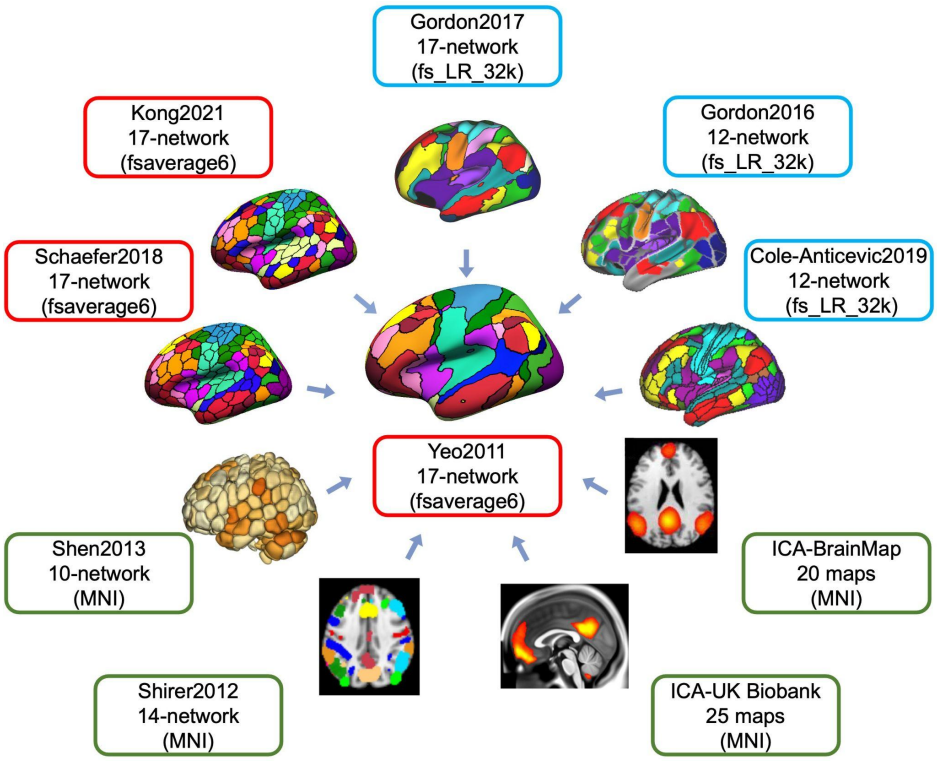


Figure 7. Ten representative group-level functional brain network atlases. In this example, Yeo's 17-network atlas serves as the reference atlas, and all other atlases are projected to the same space to compute overlap with the reference network (from(242)).

Box 1. Recommendations for reporting network results

1) Task fMRI contrasts derived from univariate GLM analysis do not necessarily comprise a network
2) Avoid labeling patterns of brain activity or connectivity with only an idiosyncratic cognitive term
3) To determine network affiliations of novel findings, use and reference one or more existing parcellation schemes
4) Report sample variation from the population used to generate the reference parcellation scheme
5) Consider supplementing atlas labels with additional anatomical network labels (such as those proposed in (14)) for ease of integration across studies
6) Follow COBIDAS reporting guidelines (15) for connectivity analysis

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