Review

Information decomposition and the informational architecture of the brain

Andrea I. Luppi, [1,2,3] Fernando E. Rosas, [4,5,6,7] Pedro A.M. Mediano, [8,9] David K. Menon, [10,11] and Emmanuel A. Stamatakis [1,2,12,@,*]

To explain how the brain orchestrates information-processing for cognition, we must understand information itself. Importantly, information is not a monolithic entity. Information decomposition techniques provide a way to split information into its constituent elements: unique, redundant, and synergistic information. We review how disentangling synergistic and redundant interactions is redefining our understanding of integrative brain function and its neural organisation. To explain how the brain navigates the trade-offs between redundancy and synergy, we review converging evidence integrating the structural, molecular, and functional underpinnings of synergy and redundancy; their roles in cognition and computation; and how they might arise over evolution and development. Overall, disentangling synergistic and redundant information provides a guiding principle for understanding the informational architecture of the brain and cognition.

Information: not a monolithic entity

The survival of humans and other animals relies on neural processes that lead to adaptive behaviours in response to the environment. Thus, a central goal of cognitive neuroscience is to articulate how the nervous system orchestrates the processing of **information** (see Glossary) to guide adaptive behaviour.

Central to this endeavour is information theory [1]: the formal quantification of information has enabled rigorous investigation of the brain in terms of information processing, typically articulated into processes of information storage, transfer, and modification, collectively also known as '**information dynamics**' [2,3] (Figure 1A). In the brain, neurons transfer information to each other (via electrical and neurochemical signalling); this information is progressively modified and combined (e.g., attention enhances some stimuli over others; incoming inputs are combined to elicit or modulate downstream action potentials); and it is stored over time (memory; synaptic plasticity). Viewing the brain primarily as an information-processing organ, and treating information as the basic currency of the nervous system, has been a cornerstone of progress in cognitive science and computational neuroscience [4–7].

Crucially, our ability to understand any information processing system, including the brain, is shaped by our understanding of information itself. A key recent breakthrough in information theory was the realisation that information is not a monolithic entity: qualitatively different types of information exist (Figure 1B). Specifically, **information decomposition** is a formal framework that makes it possible to disentangle **synergistic information**, **unique information**, and **redundant information** in empirical data (Box 1) [8–14].

As an illustrative example, consider humans' sources of visual information: the eyes (Figure 1B). Unique information is exemplified by the peripheral information that is lost when one eye is closed:

Highlights

Information is not a monolithic entity, but can be decomposed into synergistic, unique, and redundant components.

Relative predominance of synergy and redundancy in the human brain follows a unimodal–transmodal organisation and reflects underlying structure, neurobiology, and dynamics.

Brain regions navigate trade-offs between these components to combine the flexibility of synergy for higher cognition and the robustness of redundancy for key sensory and motor functions.

Redundancy appears stable across primate evolution, whereas synergy is selectively increased in humans and especially in human-accelerated regions.

Computational studies offer new insights into the causal relationship between synergy, redundancy, and cognitive capabilities.

[1]Division of Anaesthesia, University of Cambridge, Cambridge, UK
[2]Department of Clinical Neurosciences, University of Cambridge, Cambridge, UK
[3]Montreal Neurological Institute, McGill University, Montreal, QC, Canada
[4]Department of Informatics, University of Sussex, Brighton, UK
[5]Centre for Psychedelic Research, Department of Brain Sciences, Imperial College London, London, UK
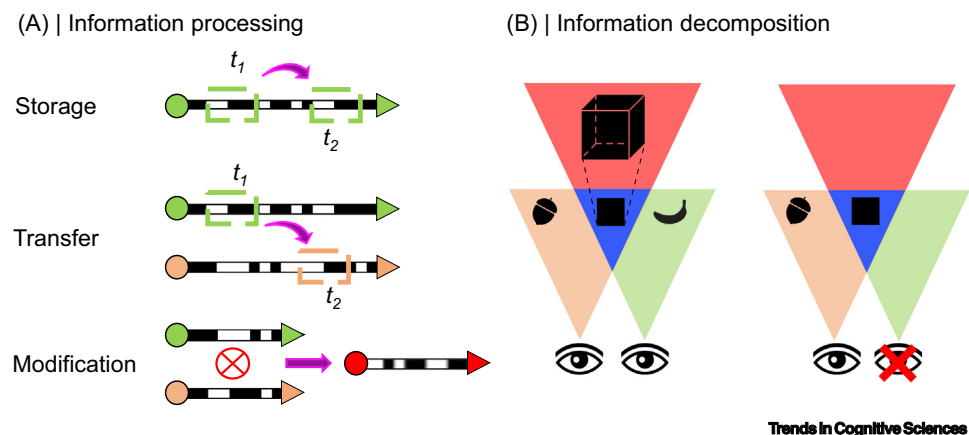[6]Centre for Complexity Science, Imperial College London, London, UK
[7]Centre for Eudaimonia and Human Flourishing, University of Oxford, Oxford, UK
[8]Department of Computing, Imperial College London, London, UK
[9]Department of Psychology, University of Cambridge, Cambridge, UK
[10]Department of Medicine, University of Cambridge, Cambridge, UK

Figure 1. Multiple perspectives on information. (A) Information processing addresses the question 'What happens to information?'. Under this view, information (represented here as binary black and white patterns) can be stored by some element of the system, such that it is present in it both at time t_1 and at a later time t_2. Information can also be transferred: it was present in one element at t_1 and is then present in another element at t_2. Finally, information can be modified: information from two elements may be combined by a third. (B) Information decomposition instead asks: 'How is information carried by multiple sources?'. Some information may be entirely carried by one source alone (here, the acorn and the banana at the periphery of each eye's field of vision, represented by the green and beige triangles), such that it will not be available anymore if that source is disrupted. This is called unique information. Other information may be carried equally by each of several sources (here: both eyes can see the square, located in the blue area of overlap). This redundant information will therefore remain fully available, so long as at least one source remains. Information may also be carried by multiple sources working together (here: three-dimensional information about depth, revealing that the square is in fact a cube). This synergistic information will be lost if any of the sources that carry it are disrupted.

[11]Wolfson Brain Imaging Centre, University of Cambridge, Cambridge, UK
[12]https://sites.google.com/site/ccigcambridge

*Correspondence:
eas46@cam.ac.uk (E.A. Stamatakis).
@Twitter: @ccig_cambridge
(E.A. Stamatakis).

information that cannot be obtained from the remaining eye. Redundant information is the information that you still have when closing either eye: it is carried equally by both sources. This provides **robustness**: despite losing peripheral vision, you can still see what is in front of you even after losing one eye. However, closing either eye also deprives you of stereoscopic information about depth. This information does not come from either eye alone: you need both to perceive the third dimension. This is synergistic information: the extra advantage that is derived from combining different sources. This example illustrates that in addition to knowing what information is about (e.g., a cube in front of you), and whether the sources belong to the same or different modality (e.g., vision), one also needs to consider how the sources interact to provide the information in question. Indeed, recent advances indicate that information storage, transfer, and modification can themselves be expressed in terms of information decomposition across time, with the different types of information acting as fundamental building blocks of information dynamics [3,12].

Synergistic information provides efficiency: by enabling a full exploitation of the possible combinations and interactions between elements of a system, it allows the system's joint information to exceed the sum of its individual parts' contributions, so that synergy grows faster than other information types with the number of sources [15]. However, since it depends on joint contributions from multiple sources, synergy can be disrupted by the failure of even a single element. Redundancy instead provides robustness, as the over-representation ensures that information will remain available if any one source is disrupted. However, redundancy comes at the cost of using less than the full information capacity of the system, a well-known trade-off in biology and engineering [16–19].

Acknowledging synergy, redundancy, and unique information as different types of information paves the way towards clarifying the layout of the information-processing architecture of the brain

[2,3,20]. What types of information does the brain rely on? How does it navigate the inevitable trade-offs between them? In this article, we outline how disentangling synergy and redundancy in neural recordings has led to recent advances in our understanding of brain function and dysfunction.

Integration, decomposed: resolving conceptual tensions by disentangling information

Synergy and redundancy may be seen as the two sides of a fundamental concept in neuroscience and cognitive science: integration [21–24]. Crucially, a source of much confusion is that

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Box 1. Decomposition, demystified

Here we provide an accessible introduction to the mathematical formalism of Partial Information Decomposition (PID) [14] and some of its recent extensions. PID considers scenarios with n so-called source variables $X_1, \ldots, X_n$ that hold information about a so-called target variable Y. The central quantity in PID is Shannon's mutual information $I(X_1, \ldots, X_n; Y)$, which measures the amount of information that all sources have about the target [1]. As an example, each X_i could represent the neural activity time-series of region i and Y the value of a stimulus. Mutual information may be seen as a non-linear generalisation of correlation. For the case of Gaussian variables, mutual information is a function of the ratio between the total variance of Y, and the variance of Y that remains unexplained after knowing the sources,

$$I(X_1, \ldots, X_n; Y) = \frac{1}{2} \log \, |\mathrm{Var}(Y)| \, - \, \frac{1}{2} \log \, |\mathrm{Var}(Y \,|\, X_1, \ldots, X_n)|, \qquad [\mathrm{I}]$$

making the mutual information analogous to the explained variance from multiple linear regression. Note that with only one source, the mutual information between Gaussian variables is directly related to the Pearson correlation r:

$$I(X_1; Y) = -\frac{1}{2} \log \left(1 - r^2\right). \qquad [\mathrm{II}]$$

PID solves a key mathematical problem: explaining how the total mutual information of all sources can sometimes be more or less than the sum of the information that each source individually provides about the target, known as the marginal mutual information $I(X_i; Y)$. PID decomposes the total mutual information into multiple quantities known as information atoms (Figure I). For $n = 2$ sources, the decomposition leads to the concepts of redundant, unique, and synergistic information:

$$I(X_1, X_2; Y) = \mathrm{Red}(X_1, X_2; Y) + \mathrm{Un}(X_1; Y \setminus X_2) + \mathrm{Un}(X_2; Y \setminus X_1) + \mathrm{Syn}(X_1, X_2; Y). \qquad [\mathrm{III}]$$

In practice, $\mathrm{Red}(X_1, X_2; Y)$ can be quantified as the minimum between $I(X_1; Y)$ and $I(X_2; Y)$ (noting that other operationalisations have been proposed [10,14,115–119]). Then, the information that X_1 provides uniquely, is the non-redundant portion of its mutual information with Y. Formally:

$$\mathrm{Un}(X_1; Y \setminus X_2) = I(X_1; Y) - \mathrm{Red}(X_1, X_2; Y). \qquad [\mathrm{IV}]$$

And likewise for the unique information of X_2. Finally, the information that X_1 and X_2 hold synergistically about Y is obtained as the difference between the total information that they provide, and the sum of their unique and redundant contributions:

$$\mathrm{Syn}(X_1, X_2; Y) = I(X_1, X_2; Y) \, - \, (\, \mathrm{Red}(X_1, X_2; Y) + \mathrm{Un}(X_1; Y \setminus X_2) + \mathrm{Un}(X_2; Y \setminus X_1) \,). \qquad [\mathrm{V}]$$

Alternative decompositions also exist: Partial Entropy Decomposition (PED) does not require a target [8] whereas Integrated Information Decomposition [12,13] considers multiple targets. Point-wise/"instantaneous" decompositions have also been developed for PID, PED, and Integrated Information Decomposition [13,115,117], which can provide finer-grained insights about the dynamics of these quantities at the level of each time-point.

Since the number of information atoms in PID scales super-exponentially with the number of sources [14], computing the full decomposition for more than 4-5 sources becomes impractical. This shortcoming can be circumvented (i) by focusing on specific information components instead of the full decomposition; or (ii) by employing reduced decompositions that scale linearly with the number of sources [15,120]; or (iii) by computing scalar quantities such as the synergy-redundancy index or O-information, which estimate the balance between synergy and redundancy without explicitly disentangling them [81,121,122].

Supplementary Table S1 provides a non-exhaustive list of software resources that researchers can directly use to apply information decomposition to their data.

Glossary

Biophysical whole-brain model: a computational model that simulates brain regions as neural populations of excitatory and inhibitory neurons, coupled according to the empirical structural connectivity of the brain obtained from diffusion MRI tractography (or tract-tracing, in animals).

Information: reduction in uncertainty about one variable, when one or more additional variables are known.

Information decomposition: mathematical framework to decompose the information that two (or more) sources provide about a target into synergistic, unique, and redundant contributions. Several distinct operationalisations have been proposed in the literature.

Information dynamics: mathematical account of how information is stored, transferred, or modified over time.
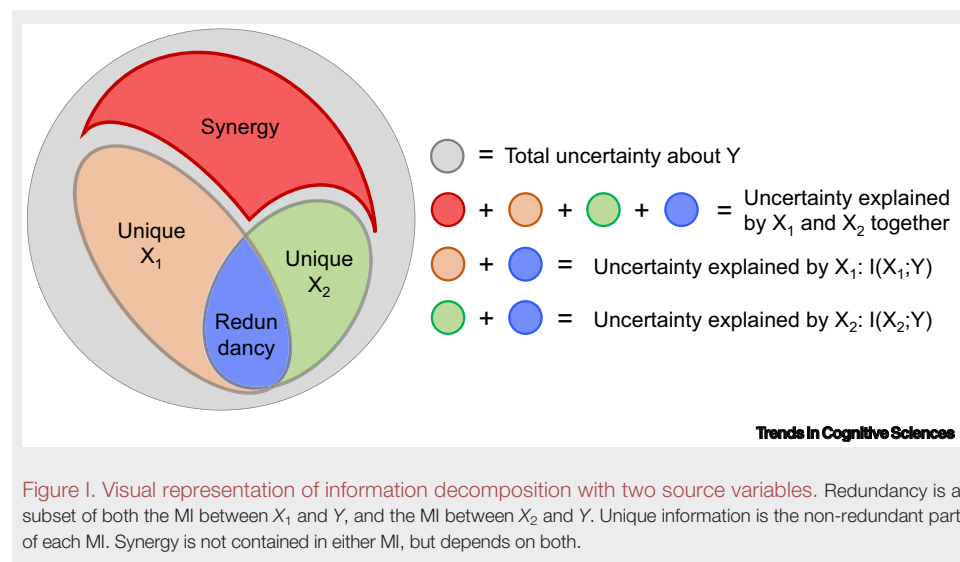
Network communication models: in network science, mathematical accounts of how signals move between nodes of a network using its connections. For example, signals may follow the shortest (most direct) path between the start and destination nodes, or they may move entirely at random until destination is reached.

Redundant information: information that is conveyed equally by more than one source, such that it could be fully obtained from any one of them. Also known in the literature as 'shared' information.

Robustness: the ability to perform a function even in the presence of interference or damage.

Synergistic information: information that can be obtained when considering multiple sources of information together and that could not be obtained when the sources are considered in isolation. Also known in the literature as 'complementary information'.

Synergy–redundancy index: an early measure of the balance between synergy and redundancy in a system. If the system's joint information exceeds the sum of the individual parts' contributions, the presence of synergy can be inferred. Conversely, if the sum of contributions is greater than the joint information, redundancy must be present. However, this measure cannot identify cases where synergy and redundancy are both present simultaneously.

Figure I. Visual representation of information decomposition with two source variables. Redundancy is a subset of both the MI between X_1 and Y, and the MI between X_2 and Y. Unique information is the non-redundant part of each MI. Synergy is not contained in either MI, but depends on both.

Unique information: information that can be fully and exclusively obtained from a specific source, regardless of interactions with other sources.

there are at least two plausible, yet almost opposite, ways to understand the term 'integration', both of which can be illuminated by information decomposition.

A first possible interpretation of integration is what we refer to as integration-as-oneness: it reflects the intuition that integrated elements are 'acting as one'. This interpretation leads to inferring high integration when observing strong correlations or synchrony between the activity of brain regions, which led many authors to propose the quantification of integration via the mutual information itself [25] or its multivariate generalisation [24,26,27]. Since it is maximised when all elements behave identically, this phenomenon can be well characterised by redundancy. This way of understanding integration finds its antithesis in differentiation: the notion that elements in the system act differently from each other (i.e., not as one). However, differentiation is itself an underspecified concept: it could refer to the elements simply being independent (providing unique information) or complementary (providing synergistic information). This distinction becomes clear when viewed through the lens of information decomposition (Figure 2).

A fundamentally different way to understand integration is what we refer to as integration-as-cooperation: the extent to which the system's information-processing capacity benefits from interactions between its elements. Integration-as-cooperation occurs when elements are complementary, such that combining them provides an advantage. Integration-as-cooperation thus maps onto synergy. This interpretation of integration is the opposite of dis-integration: when elements are not only differentiated (which still allows for interaction and cooperation) but fully disjunct and unrelated. Thus, whereas dis-integration is specific to unique information, differentiation could refer to both unique or synergistic cases. The dual nature of synergy, reflecting both integration (as cooperation) and differentiation, underpins its use, implicitly or explicitly, as a key ingredient in numerous measures of complexity for neuroscience and beyond [12,22,24,28].

To illustrate how the two meanings of integration can diverge in practice, consider epileptic seizures: all brain signals are synchronised, reflecting high redundancy and, therefore, integration-as-oneness but the absence of integration-as-cooperation. More broadly, distinguishing between different meanings of integration is essential for understanding the behaviour of any information-processing system. A system will not be able to perform cognitively useful computation just by
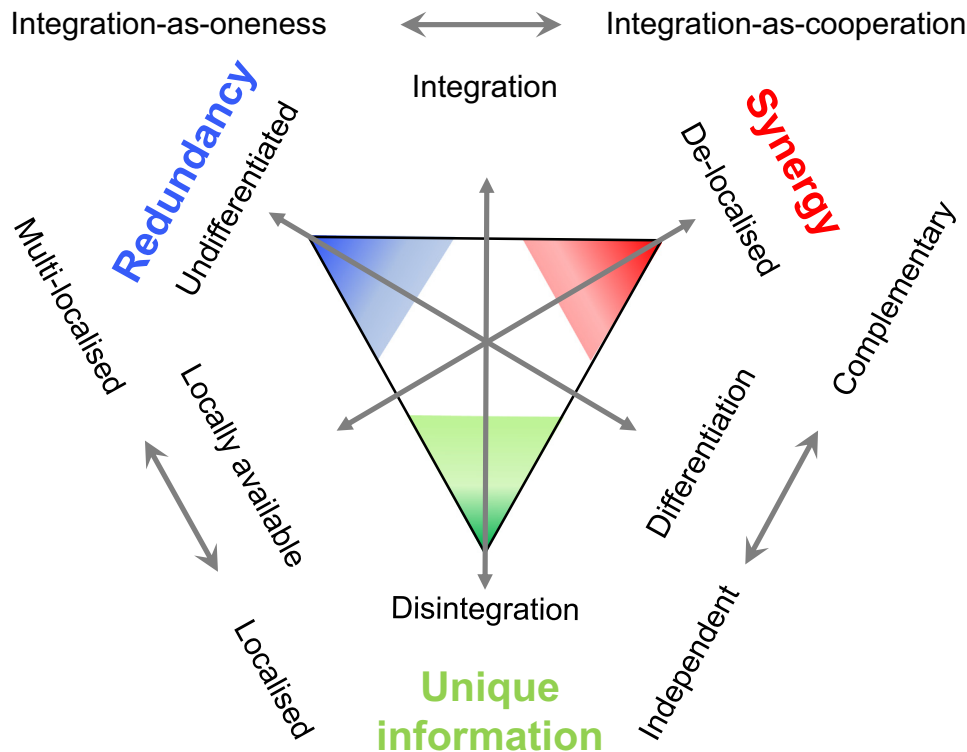
Figure 2. Information decomposition provides a unifying framework to resolve conceptual tensions in cognitive science. Each arrow across the central triangle represents an axis of dichotomy in the cognitive science and neuroscience literature. Each axis has one end corresponding to one type of information, but at the other end it conflates two distinct types of information, giving rise to apparent contradictions. As outlined in the main text, 'integration' conflates synergy (integration-as-cooperation) and redundancy (integration-as-oneness). 'Differentiation' conflates the independence of unique information and the complementarity of synergy. Additionally, the term 'local' is ambiguous between redundant and unique information: when an individual source carries unique or redundant information, all such information is available locally (i.e., from that source); it can be fully obtained from that source alone. Unlike unique information, however, redundant information is multiply-localised, because it is available from any of several individual sources. Synergistic information is instead de-localised: it cannot be obtained from any individual source. These tensions can be resolved by carefully distinguishing different information types.

having redundant copies of the same information (integration-as-oneness): computation and complex cognition demand that information should eventually be combined (integration-as-cooperation) if they are to subserve adaptive behaviour [29,30]. However, the two meanings of integration cannot be disambiguated by traditional measures of correlation alone: whereas high correlation implies redundancy, low correlation could reflect either unique information (dis-integration) or synergy, whereby differentiated elements engage in integration-as-cooperation [8,31,32]. Early studies developed the so-called **synergy–redundancy index** to quantify their balance [33–36] and further seminal work identified how correlations between neurons (carefully divided into signal correlations and noise correlations to account for their respective roles in shaping population codes [37]) provide synergy-inducing or redundancy-inducing effects [31,38–41]. However, the synergy–redundancy index can be hard to interpret when synergy and redundancy coexist (as for the eye example; Figure 1). By quantifying each information type separately, information decomposition provides the means to overcome this limitation, although at the cost of working with a more restricted view of redundancy that does not consider the redundancy contributed by noise correlations (Box 2 and Figure 2). Future work may explore how to combine the strengths of both approaches.

Information decomposition of neural dynamics

Information decomposition inherits the broad applicability of information theory. In neuroscience, it is applicable to a broad range of data formats whenever an association between multiple variables is sought: neural time-series (e.g., BOLD signals from functional MRI, electrophysiological recordings) and behaviour, but also brain maps or even networks. Complementing previous approaches to conceptualise and quantify neural information (e.g., in terms of encoding and decoding [7]), the majority of recent efforts have applied information decomposition to the analysis of neural time-series, both with and without reference to behaviour. In a cognitive task-based context, information decomposition can be applied to track how regions/neurons' activity encodes task-relevant information and how this information is then translated into behaviour [42–45]. We refer to this as 'extrinsic' information. However, information decomposition can also be applied to neural time-series from task-free contexts. Since the current spontaneous state of the brain is determined, at least partially, by its previous state(s), one can investigate the 'intrinsic' information that the past activity of two or more regions/neurons provides about their future dynamics [12,13,32,46]. Recent studies have adopted both approaches to map synergistic and redundant information in the brain.

How the brain balances synergy and redundancy

A major finding, made possible by information decomposition of intrinsic brain activity, has been the discovery that prominent synergies coexist with redundancy in the human brain [32,45–47]. Although widespread, synergistic interactions had remained undetected by previous techniques, as they could not be captured by traditional correlation-based measures of functional connectivity (FC). Such measures proved to be largely insensitive, or even anti-correlated, to the synergies between regions [46,47]. Instead, correlation-based FC primarily reflects information that is redundantly duplicated over many regions [8,46–48]. Therefore, information decomposition has deepened our understanding of what traditional measures can, and cannot, tell us about the way that brain regions interact (Box 2).

Although each brain region engages in both synergistic and redundant interactions with the rest of the brain, synergy appears to be overall more prevalent: both in resting humans' fMRI signals [46,47] and in electrophysiological recordings from task-engaging monkeys [45]. However, the predominance of either synergy or redundancy is not uniform across the brain: there exists a clear separation of cortical territory between synergy-dominated and redundancy-dominated regions, delineating a clear synergy–redundancy axis (Figure 3A). Functional MRI shows that redundancy predominates at the unimodal end of the cortical hierarchy: primary visual, somato-motor, and auditory cortices [32,46]. Synergy predominates in frontal and parietal multimodal association cortices [46,47]. Multimodal anatomical and task-activation evidence indicates that association cortex is where multiple processing streams converge [49–52]. The observation of high synergy provides information-theoretic confirmation that this convergence is translated into integration-as-cooperation.

This macroscale functional MRI evidence is supported by microscale electrophysiological recordings. Interactions between neurons are key (in terms of added information) for explaining spiking activity in prefrontal cortex, but less so in V4 and especially V1, suggestive of greater synergy in the interactions within higher-order cortices [53]. Prefrontal neurons often exhibit complex responses that change flexibly across a wide range of stimuli and tasks, supporting their involvement in complex cognition [54]. Indeed, prefrontal and other high-synergy regions are relatively decoupled from the constraints of underlying white matter, microstructure, and brain geometry, enabling flexibility [55–59]. Supporting this notion, synergy is independent from the presence of a direct physical connection between regions, whereas redundancy is coupled to the underlying

Box 2. Information decomposition provides insight about information transmission in neuroscience

Information decomposition can be used to shed light on widely used measures in neuroscience (and beyond): transfer entropy (TE) and its linear equivalent, Granger causality [123,124]. These are popular methods to infer directionality of interactions from time-series data, from single-cell recordings to EEG and fMRI [45,49,125–129]. TE can be understood in PID terms, by identifying the two sources with the past of regions (or neurons) X and Y and the target with the future of Y. Indeed, the common interpretation of TE is that it quantifies the information about Y's future that is not provided by Y's past, but only by X's past, thereby reflecting the transfer from X to Y [130]. One might think that this corresponds solely to unique information that the past of X has about the future of Y. However, in addition, TE also demonstrably includes synergistic information that the past of both X and Y hold about Y's future [130]. Therefore, it is possible (but rarely acknowledged) to have non-zero TE in the absence of any unique information from the past of X to the future of Y: a purely synergy-driven TE, without any of the unique transfer that TE is typically assumed to reflect. Information decomposition offers a straightforward avenue to disambiguate these possibilities.

Crucially, specific experimental questions may be better addressed by specific components of information transfer. The components of transmitted information can be considered according to the content of transmitted information, such as sensory stimuli or other features of interest [131,132]. This feature-specific analysis of information transfer provides a more nuanced understanding, because TE and related measures are agnostic to the content of the information that was exchanged: they only provide the total amount of information transmitted, which can be uncorrelated to the amount of feature-specific information conveyed between regions [131].

Interestingly, the unique transfer component within TE actually comprises two distinct phenomena: information that was exclusively in X at t, and is exclusively in Y at $t + 1$ (which corresponds to the intuitive sense of the word 'transfer'), and also information that is duplicated from X to Y from t to $t + 1$. Crucially, duplication of information means that the information is also persistently present in X, being one of the information dynamics phenomena included within the well-known measure of 'active information storage' (AIS) (Figure I) [12]. Although TE and AIS are often contrasted as distinct phenomena reflecting 'transfer' and 'storage', information decomposition reveals a richer and more complex landscape: for example, in systems that only exhibit duplication of information, TE and AIS will be literally identical, two names for the same phenomenon. Altogether, becoming aware of the underlying phenomena that these measures capture allows us to interpret them more rigorously, overcoming their limitations and obtaining greater insight from their use.
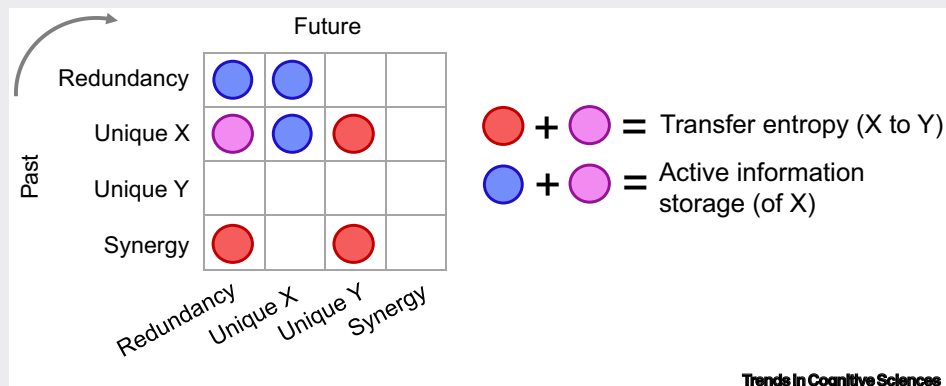

Figure I. Information decomposition of transfer entropy (TE) and active information storage (AIS) reveals their partial overlap due to information duplication. Rows indicate how the two sources carried information at t and columns indicate how they carry the information at $t + 1$. TE from X to Y (red circles) includes all information that was not present in Y at t and is present in Y at $t + 1$. This includes information that was uniquely provided by X at t and is redundantly provided by both X and Y at $t + 1$ (i.e., duplication of information; violet circle). AIS within X (blue circles) comprises information that was present in X at t and is also present in X at $t + 1$. This also includes the duplication of information from X to X and Y, which is therefore shared by TE and AIS.

structural connectivity [46]. Using the synergy–redundancy index, early studies had also shown synergy in prefrontal (but not striatal) neurons of the macaque during task performance [34] and progressive reduction in redundancy along the auditory hierarchy of the (anaesthetised) cat [60].
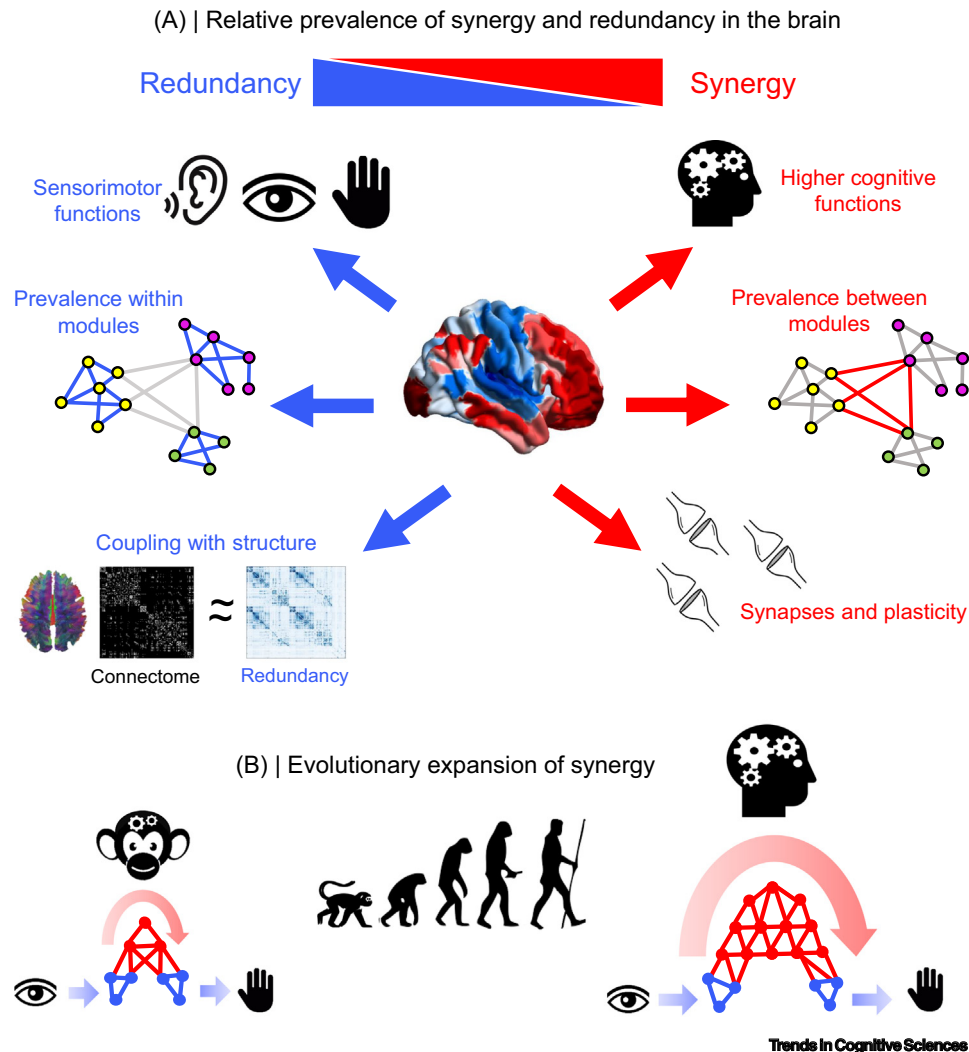
Figure 3. Synergy and redundancy in the human brain. (A) Relative prevalence of synergy and redundancy in the human brain delineates a unimodal–transmodal synergy–redundancy axis. Redundancy (blue) is associated with primary sensory and motor functions; it exhibits a highly modular network organisation, being higher within than between intrinsic connectivity networks (ICNs); it is coupled to the underlying structural connectivity. Synergy (red) is associated with complex cognition; it is greater between regions that belong to different ICNs; and it is associated with synaptic density and synapse- and dendrite-related genes and metabolic processes. (B) Schematic account of evolutionary differences in synergy between humans and other primates. Whereas redundancy is stable between macaques and humans, the overall proportion of information that is carried synergistically is significantly greater in humans. Since the high-synergy regions are also the most evolutionarily expanded, we speculate that cortical expansion may be responsible for the additional synergy observed in the human brain and, in turn, for humans' greater cognitive capacities.

The progression from redundancy-dominated unimodal cortices to synergy-dominated multi-modal regions dovetails with evidence of a relationship between synergy and complex cognition. A NeuroSynth meta-analysis [61] of over 15 000 neuroimaging studies indicated that high-redundancy regions activate in response to modality-specific tasks, whereas high-synergy cortices load onto terms pertaining to higher-order cognitive functions [46]. To combine relevant information flexibly, complex cognition relies at least partly on synapses and their experience-dependent plasticity [62]. *In vivo* PET imaging [63] and data-driven transcriptomic analysis [64]

provided convergent evidence that high-synergy regions exhibit high synaptic density and are enriched for genes pertaining to synapse and dendrite development [46]. Thus, synapses may provide a neurobiological link between flexibility, complex cognition, and synergy.

Synergy and redundancy also vary in nuanced ways with different timescales of neural dynamics. For microscopic dynamics, evidence from neuronal cultures shows that synergy is more prevalent at shorter timescales while redundancy is more prevalent at longer timescales [65], and calcium imaging in mice indicates that this long-timescale redundancy is beneficial for behaviour [66]. In macroscopic dynamics, models of fMRI signals show synergy dominating at longer timescales [22]. This latter finding is supported by human fMRI studies showing that the high-synergy default mode and fronto-parietal regions also have longer intrinsic timescales [46] and exhibit the most complex activity, correlating with measures of fluid intelligence [67], and supporting the association of synergy with both complexity and higher-order cognition. Overall, it is likely that the mechanisms generating synergy and redundancy are different across timescales: providing a unified mechanistic account of this relationship across scales is a promising avenue for future work.

Finally, the association between synergy and higher cognitive capacity also appears across species. The proportion of total intrinsic information accounted for by redundancy is not different between humans and macaques; however, humans surpass macaques in terms of their brains' capacity for synergy [46]. High-synergy regions exhibit the greatest degree of evolutionary expansion between humans and chimpanzees and are enriched for human-accelerated genes pertaining to brain development, synapses and dendrites [46,68]. One of the microscale differences between humans and other primates is the greater dendritic branching of human pyramidal neurons, including in prefrontal cortex [69,70]. This is noteworthy because of the recent discovery that the dendrites of human pyramidal neurons can separate linearly non-separable inputs [71]: an example of purely synergistic computation [72], which has not been shown in non-human neurons. This evidence may provide a microscale explanation for the greater synergy observed in humans at the macroscale.

Role in neural computation and behaviour

Although the results reviewed earlier align well with theoretical expectations about the roles of synergy and redundancy, they are mostly based on the resting brain. Thus, we next turn to empirical evidence directly linking synergy and redundancy with computational capacity and behaviour.

Elaborating on the role of redundancy, recent studies have proposed that the benefits of redundancy in some cases outweigh its information-limiting downside, by facilitating the behavioural readout of the sensory signal [66]. In mice, correct perceptual discriminations are associated with greater functional correlations in calcium imaging signals and greater information redundancy [43]. By explicitly considering stimulus-related information about specific features of interest and relating it to behaviour, recent work showed that synergy and redundancy between mouse auditory neurons increase during correct (versus incorrect) trials. The increase in redundancy was especially pronounced, with the proportion of redundant information discriminating between correct and incorrect trials [73]. Greater redundancy means that less stimulus-related information can be encoded, but this information-limiting phenomenon is compensated by increased consistency of the transmitted sensory information, facilitating its conversion into correct behavioural choices [43]. This may be an example where the profligacy of redundancy is, computationally, more beneficial to the organism than the parsimony of synergy. This phenomenon may also explain why the relative prevalence of global redundancy in macaque electrophysiological signals is enhanced upon task-relevant movement execution [45].

Pertaining to synergy, the ability to decode stimulus information from a population of V1 neurons increases with the number of high-synergy neurons (as opposed to high-redundancy ones) in the population [74] (since each region can engage both in synergistic and redundant interactions, being redundancy-dominated does not preclude the presence of synergy). In humans, a recent study considered neural and behavioural information, with participants discriminating two texture stimuli using visual or haptic cues, or both together, during electroencephalogram (EEG) recording [42]. Individuals with greater synergy between the two unimodal EEG signals performed better in terms of multisensory decision-making accuracy [42]. Considering human behaviour in a complex environment, analysis of 1.75 million hands of online poker revealed that winning players are better at exploiting the synergistic information between their own cards and their opponents' behaviour, further reinforcing the computational advantage granted by synergy, across multiple scales [75].

Complementing these multi-species, multimodal behavioural and neural results, intriguing recent evidence comes from computational modelling using artificial neural networks (ANNs). Larger ANNs represent information by spreading synergy across larger groups of neurons [76]. As they learn, ANNs first become redundancy-dominated and then individual neurons become specialised, increasing their unique information [76,77]. This finding offers intriguing hypotheses for neurodevelopmental studies. Tapping directly into the effect of cognitive domains, recent work showed that synergy increases in ANNs as they learn multiple tasks when doing so requires the ANN to flexibly combine additional sources of information [78]. Performance on tasks requiring multimodal integration-as-complementarity critically depends on synergy: performance deteriorates most upon removal of the most synergistic neurons, compared with low-synergy ones. The same study showed that redundancy is related to robustness: if neurons are randomly turned off during learning, the redundancy in the ANN increases [78]. After training is complete, ANN performance will be substantially more robust to perturbations induced by artificial lesions [78]. Supporting both theoretical predictions and empirical observations, these results suggest that high-synergy neurons play a greater role in the total computational capacity of the system, but they also represent points of vulnerability, which redundancy can offset. Overall, these studies confirmed that synergy and redundancy are directly related to cognition and behaviour, as predicted by their mathematical properties.

Synergy and redundancy across alterations of brain function

The definition of synergy suggests that removing any one of the involved parts may impair synergistic processes, a theoretical observation that has found computational support [78]. Though preliminary, these findings may contribute to explaining why experimental work consistently shows that transmodal association cortices, which are the most synergistic, are often implicated in a variety of mental disorders [68]. Additionally, the regional synergy–redundancy balance is one of the best predictors of cortical functional susceptibility to acute pharmacological perturbations by anaesthetics, psychedelics, and cognitive enhancers [79].

The vulnerability of synergy is further supported by recent evidence combining pathological and pharmacological perturbations of consciousness. A set of high-synergy transmodal regions consistently reduce their synergistic interactions when consciousness is lost, whether due to anaesthesia in healthy volunteers, or brain injury in patients with disorders of consciousness (DOC), and then exhibit restored synergy when consciousness is recovered after anaesthesia [80]. These results about the susceptibility of synergy to anaesthesia were complemented by electrocorticographic recordings in macaques [81]. The authors' spectrally resolved measure of synergy–redundancy balance showed a broadband shift away from synergy and towards redundancy induced by anaesthesia, driven by delta and gamma bands.

The balance of synergy and redundancy also shifts across the healthy lifespan. Older individuals (60–80 years old) exhibit a higher predominance of redundant over synergistic interactions in the brain than younger individuals [82]. An increase in redundancy may fit with the hypothesis of reduced differentiation between neural systems in aging [83,84]. However, future investigations will need to show whether a loss of unique or synergistic information is also observed.

What are the key factors that regulate the balance between different types of information in the brain? On one hand, neuromodulatory influences may suffice to control the relative prevalence of synergy, as evidenced by studies about susceptibility to anaesthesia [80,81], which incurs no anatomical changes to brain structure. High-synergy regions exhibit diverse profiles of receptor expression, making them receptive to varied neuromodulatory influences [46,85]. On the other hand, there is convergent evidence for a role of the structural connectome in supporting different kinds of information. The empirical loss of synergistic dynamics in DOC patients was successfully replicated in a **biophysical whole-brain model** based on the patients' connectomes [86]. An analogous model also showed that the empirical age-related increase of redundancy reported by Gatica and colleagues [82] could be replicated *in silico* based on ageing participants' own structural connectomes [87]. A different computational model, also based on individual structural connectomes of different age, showed that while some regions increase their synergy until around age 30, others instead exhibit a continuous decrease with age [88]. Although based on different models, and different ways of quantifying synergy, these studies converge to indicate that the effects of both healthy ageing and disease on the structural connectome may have repercussions on its ability to support different kinds of information. Thus, both network structure and neuromodulation appear capable of influencing the brain's information properties.

The informational architecture of the brain

Altogether, the results reviewed earlier reveal how the brain's informational architecture exploits the strengths of different types of information. On one hand, a redundant architecture anchored on the brain's structural backbone ensures that information is robustly available within the brain's input and output modules. Reliable sensorimotor channels are essential for survival, warranting the additional robustness provided by redundancy. This need for stability may explain various redundancy-related features of sensorimotor cortices: why they exhibit relatively low plasticity in the adult brain [89]; why they are constrained by the underlying anatomical connectivity [46,55,57,58]; and why they exhibit the least variability over time, across individuals, and even across species [32,46].

On the other hand, synergy provides the brain with the computational capacity to support flexibility, being less coupled to the underlying structure and more variable over time [32,46]. High-synergy regions are metabolically and genetically poised to support synaptic development and plasticity, being engaged across a variety of complex tasks that require cooperation between distinct cognitive modules [46]. This flexibility, and the computational capability and efficiency it provides, may be part of the reason why synergy is overall more prevalent in humans than other primates and especially in association cortices [46], which have undergone the greatest evolutionary expansion [68,90,91]. However, parsimony comes at a price: synergy appears particularly susceptible to injury and pharmacological perturbations [80]. The human brain's reliance on synergy for flexibility may also underpin its vulnerability to neurodevelopmental and psychiatric disorders, generating testable hypotheses that warrant further exploration (see Outstanding questions).

These observations suggest a tentative evolutionary account of how this informational architecture came to be. Evolution may have first pursued redundancy to provide reliability in sensory

and motor systems (i.e., inputs and outputs). Subsequently, once additional robustness was no longer needed, synergy emerged between these redundancy-dominated modules (Figure 3B) if environmental conditions converged to make additional processing capacity both advantageous and energetically sustainable [89]. Hence, we posit that a solid redundancy scaffold would provide a foundation for evolution to build finer information-processing systems that can flexibly combine and process multiple sources of information. A progressively more synergistic neural architecture may then contribute to explaining how the higher cognitive capacity of our species arose *vis-a-vis* other primates.

Alternative approaches to synergy and redundancy in neuroscience

Being implementation-agnostic, the information-theoretic approach is applicable across imaging modalities, across species, and even in artificial systems. However, the price of this generality is that it does not address how the information-carrying signals physically move between regions across the brain's network of anatomical connections: it only considers the end-result of this process. This question is explicitly addressed by **network communication models**, an area of vigorous research in network neuroscience [4,92–98]. Although different patterns of information can take place over the same network [99,100], communication strategy and information dynamics are intertwined [95,101]. Indeed, 'colliding' signals arriving at the same time can interact constructively or destructively, potentially giving rise to synergistic effects [95,101]. Conversely, if communication between regions A and B occurred by broadcasting duplicates of the same signal across all possible paths connecting the two regions, we should observe widespread information redundancy. Another point of contact with network science is the use of topological data analysis techniques to examine high-order interactions (dependencies that involve more than two elements) from a network perspective, rather than in terms of information [102–104]. Since both redundancy and synergy constitute high-order interactions [8,105], the convergence of these approaches represents an exciting area of active development.

Finally, although here we reviewed the fast-growing literature examining synergy and redundancy in terms of information, alternative operationalisations exist. The notion of Shapley values provides a game-theoretic view on synergy, quantifying the value (e.g., contribution to task performance) of a coalition of 'players' (e.g., brain regions) beyond the sum of individual players' contributions [106–109]. Recent work explicitly derived an information decomposition from Shapley values, suggesting a way to unify game-theoretic and information-theoretic approaches [110]. Redundancy can be defined in graph-theoretic terms, based on the multiplicity of parallel paths linking regions A and B [111–114]. This view of redundancy reflects the potential for signal duplication, rather than the actual occurrence of signal duplication as reflected by information-theoretic redundancy, providing a complementary perspective. Overall, our understanding of synergy and redundancy in the brain will be greatly enriched by progressive unification of the information-theoretic view reviewed here, with game-theoretic and graph-theoretic perspectives.

Concluding remarks

Disentangling different types of information is crucial for understanding the brain as an information-processing organ. The theoretical and empirical evidence synthesised here reveals how the brain balances the relative strengths and weaknesses of various types of information, bringing together distinct lines of research while also opening rich avenues for future work. Information decomposition overcomes fundamental limitations of current approaches to characterise the interactions between brain regions, resolving enduring conceptual confusions in neuroscience and cognitive science by disentangling phenomena that traditional approaches are either blind to, or collapse together.

Outstanding questions

It is often the case that ontogeny recapitulates phylogeny, including in terms of cortical expansion. Does the emergence of synergy across development mirror its evolutionary increase?

How does synaptic pruning over healthy development and disease influence synergy and redundancy?

How plastic are synergy and redundancy to the effects of learning in the brain?

Can we use the regional distribution and overall prevalence of different information types as an endophenotype of neurodevelopmental, neurodegenerative, and psychiatric conditions?

Can we devise intervention protocols to tune different types of information?

Can we use *in vivo* or simulated lesions to experimentally validate theoretical predictions about the role of different information types (e.g., greater deficits when lesioning high-synergy regions)?

Are different types of information conveyed via different network communication protocols over the structural connectome?

Since synergy and redundancy are susceptible to neuromodulatory influences, what is the role of brainstem neuromodulatory nuclei and other subcortical structures in shaping healthy and pathological information architecture?

How does the organisation of a region determine its synergistic or redundant character? Is it a single mechanism, or multiple ones, such as dendritic morphology, recurrent connections, diversity of receptor expression?

Most studies have focused on distinguishing synergy from redundancy: what is the role of unique information in the brain?

How do environmental demands shape the needs for different types of information, over evolutionary timescales?

Box 3. Information as a bridge between biological and artificial cognition

Information theory is widely applicable across organisms, as well as beyond biology. The discoveries outlined in this review highlight the role of synergy in supporting human cognition and raise the intriguing prospect of harnessing the informational architecture of the human brain as a blueprint to develop more human-like artificial intelligence (AI) systems.

To what extent do existing ANNs rely on synergistic information for their impressive capabilities? It is tempting to suspect a connection between synergy and computational capability, since a major driver of recent AI progress has been the size of the model and synergy grants the ability to encode information in a way that scales super-linearly with the size of the system [72]. This intuition is reinforced by the observation that larger models tend to exhibit increasing synergy and synergy grows when ANNs learn to flexibly perform multiple tasks [78], a hallmark of the kind of human-like intelligence that recent AI models have begun to display. However, over-reliance on synergy could be a source of concern if synergy is inherently fragile. Thus, there may be a pressing need to discern these different types of information in the artificial systems that we develop. Doing so also holds the potential to open the 'black box' of many current AI models [106,133], by providing information decomposition as a *lingua franca* to understand different architectures and their properties (Figure I) [134,135].

Artificial models also provide a powerful tool to test key questions about the computational role and development of different types of information, beyond what is currently possible with *in vivo* experimentation. Whereas we have evidence that synergy grows under complex task demands, the reverse could also be evaluated: does explicitly favouring synergy (e.g., through evolutionary algorithms that select for it among a population of ANNs) result in ANNs that also have greater computational power? Focusing on extreme cases (e.g., a synergy-only system) will bring to light their intrinsic strengths and weaknesses, in a way that would simply not be possible with biological systems. Computational models of brain dynamics [136–139] provide an excellent avenue to investigate the neurobiological mechanisms supporting different types of information. For instance, the local or global connectivity of these models can be perturbed, or they can be enriched with multimodal annotations such as the regional distributions of excitation–inhibition ratio, receptors, and cell types [138,139]. Doing so may also pave the way towards understanding how to restore a healthy balance of information.

Trends in Cognitive Sciences

Figure I. Using information types as a Rosetta Stone to relate the structure and function of biological and artificial systems. In the biological brain, information dynamics can shed light on the relationship between the structural and functional organisation of the brain and cognitive and behavioural variables (for both humans and other species). In artificial systems, information dynamics can likewise illuminate the relationship between the system's architecture and its computational properties and performance. Because information dynamics are substrate-independent, they can be compared across humans, non-human biological systems, and artificial cognitive systems, providing a common language. Figure adapted in part from [49], originally published under CC-BY license, and with permission from Margulies *et al.* [140].

How wide are the differences in synergy and redundancy across different species?

How can we use the informational architecture of the human brain to guide the development of artificial intelligence?
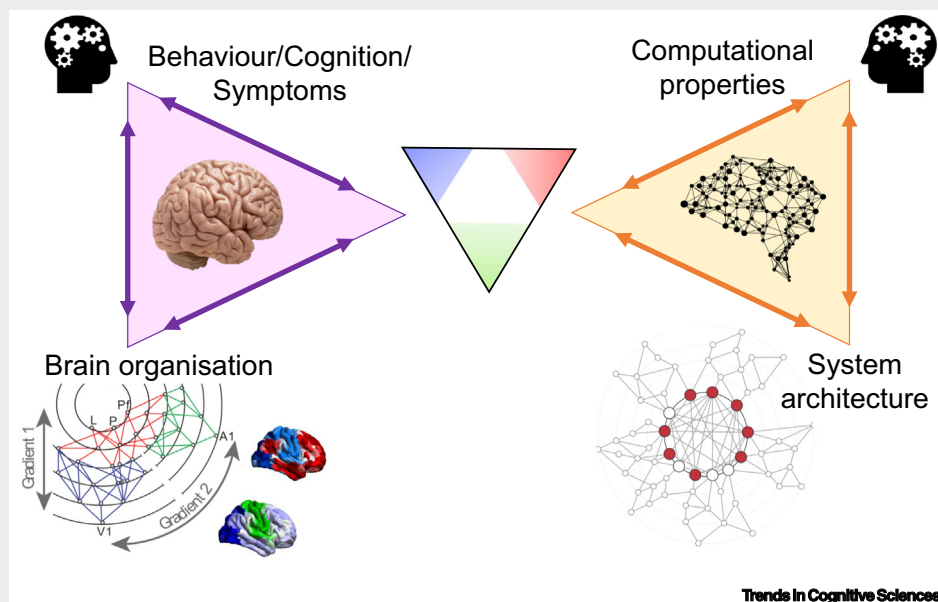
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