

Chapter 2

Understanding Cognition Through Functional Connectivity

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Abstract With every word that you read on this page, your brain orchestrates a symphony of electrical sounds – millions of neurons perform at the same time and billions of synapses coordinate their sounds. If you make yourself a break and start preparing a coffee, a new array of neural musicians will become active. While we know right now quite well how these functions that you perform are segregated in the brain – that is, which set of neurons activates to enable your reading and which to make you remember where you put the coffee jar – it still remains a challenge to understand how the brain integrates separated tasks into a coherent function. How does it happen that the letters form a word in your mind and the words form a meaningful sentence? How do you coordinate the movement of your hands when you reach for the cup with one and for the coffee pot with the other? New tools made available by complexity sciences – the modern network theory – give us a unique chance to describe and measure the integration of information in the brain that is crucial for any function it performs.

It has been a century now since we learned that the brain is a network. In the beginning of the twentieth century Santiago Ramon y Cajal ended a long standing debate on whether the neural system is composed of separate cells or a continuous mass of tissue; with histological imaging y Cajal and Azoulay (1911) proved without doubt that it was the former. These cells communicate with each other at special junction points – the synapses. While a substantial amount of research has been devoted to tracking specific connections and pathways within this web of neurons, the network nature of the brain as such has only recently been subjected to investigation with network tools. Huge advances in brain imaging on the one hand and complex systems tools on the other finally enable us to quantitatively describe – with the precision of formal sciences – the structure and complexity of brain networks. This, in turn, might provide us with an unprecedented insight into the integrative function of the brain.

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Information Integration in the Brain

The mechanisms of information integration in the brain are crucially important for our understanding of the biological basis of cognition and – more generally – the mind. Our phenomenological, subjective experience of cognitive function involves different levels of organization of processes. For example, the process of recognition starts with the combination of tiny perceptual inputs into meaningful shapes. These are then organized into bigger wholes – objects – that, in turn, may be mentally juxtaposed against stored memories about both episodic encounters with similar items as well as encoded semantic knowledge. A vital part in this process is the formation of functional units at different levels of description which, once assembled, can be operated upon without the need of analyzing their parts. That is, once a group of lines form a mental representation of a chair – a functional unit of a higher level – we do not need to operate any longer on single lines. Similarly, if the chair and all other furniture along with its placement become integrated into the mental dining room we can proceed to thinking about the family dinner without any need of disassembling the picture.

Clearly, mental processing depends to a large degree on organizing items into functional units. Even more importantly, our stream of consciousness undergoes a similar process. Single thoughts are organized into opinions, emotions, attitudes, memories, etc. which then become plans, schemas, narrations that – at the highest level – form the self. If the brain is the source of cognition, consciousness and the mind, there needs to exist neural mechanisms that provide for an analogous process of functional integration of information processing.

The anatomical structure of the brain is functionally segregated. That is, we can establish which regions – brain structures or areas – are selectively activated in the course of a specific function. In particular, the early perceptual regions are precisely mapped with regard to their function. For instance, in the primary visual cortex cortical columns are tuned to respond (by increasing the frequency of action potentials they produce) to very well defined stimuli in the visual field, e.g. gratings at specific angles (Hubel and Wiesel 1968). In areas that are further along the information processing pathway – secondary visual cortex or multimodal cortex – these preferences become more complex to combine information incoming from various other regions. Thus, the activation that spreads through the cortex from the external, perceptual input engages more and more functionally specific structures. Complex cognitive tasks activate a large set of brain regions to combine many functions to meet the demands of the task. While this segregation of function seems intricate enough to accommodate even composite cognitive processes, there still remains a question of how all this segregated information becomes integrated into coherent representation upon which we perform cognitive functions.

The most prominent – almost implicit – approach to information integration in the brain assumes that the mere act of transferring impulses from functionally specific areas to other, more complex ones, constitutes integration. That is, if a color specific region together with a shape specific region send impulses to a color

and shape specific region, and manage to activate it (increase its rate of firing action potentials), it means that color and shape information has been integrated. There are several shortcomings to this line of reasoning, though. First, there is no single area in the brain where impulses from all other regions converge. In practical terms it means that there is no single steering centre in the brain; no area where all representations are formed and acted upon. Rather, the global, widespread activation levels seem to carry this function. Second, if the number of total possible combinations of input features were to be considered it is clear that there are not enough functionally specific areas to account for it. However complex the structure of functional segregation may be, alone it is not enough to explain how the brain performs its functions. The so called binding problem provides a simple example why activation spreading through functionally specialized regions does not suffice to reproduce behaviorally observable processes.

The Binding Problem

If you are presented with two colorful objects – let us say a green ball and a red cube – you do not have any problems in telling which object is of what color. Since there are color and shape specific areas in the visual cortex, we may say (even though it is not entirely realistic) that in such a situation four separate groups of neurons will be highly active – those responding to shapes of sphere and cube and those responding to the colors red and green. However, the same sets of neurons would be active in the reverse situation – when a red ball and a green cube would be present. How does the brain ‘know’ which color belongs to which object so that your mind image represents the reality? How are properties, such as shape and color, integrated into a whole without any mistake? Clearly, activation of functionally specific areas is not enough and another mechanism is in action.

Recent developments in neurophysiology show that a possible integrative mechanism lies in the precise timing of neural electrical activity (Singer 1999). According to this assumption synchronous firing of action potentials by two cells or cell ensembles means that they are activated by the same object. In other words, precise correlation of activity integrates the information that is processed by specialized groups of cells. This provides a solution to the binding problem – in the situation described above correlated activity of cells coding color green and a sphere means that there is a green ball in the visual field. Similarly, synchronous firing of cells responding to red and cube encodes a red cube. If a reverse combination was present in the visual field, correlations would appear between cells for green and cube as well as for red and sphere (see Fig. 2.1 for a graphical representation).

Neural Synchrony

Correlated neural activity has been found across many topological scales and in a variety of motor, perceptual and cognitive activities both in human and animal subjects. The synchronous activity can be either evoked by the incoming stimuli

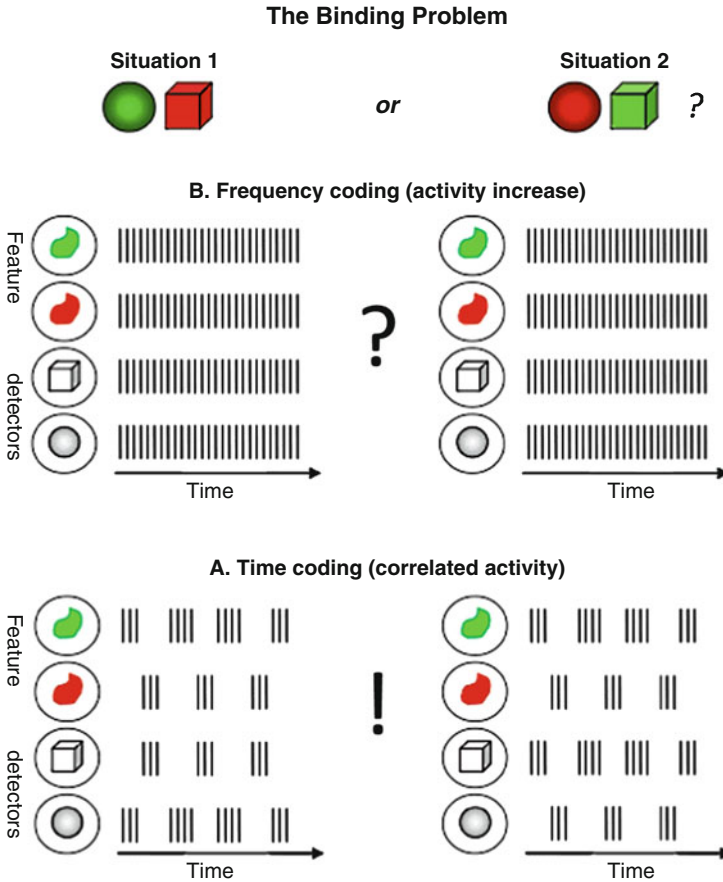


Fig. 2.1 The binding problem

(that is, time locked to the moment of presentation) or induced by it (not time locked, usually appearing after a time lag in the order of 100–300 ms). Correlation of signals within a group of cells is very often accompanied by oscillations at specific frequency ranges. It has been proposed that different frequencies of correlated activity can serve as an integrative function for different scales of processing.

It is worth noting that the time dependencies between neural signals referred to here as ‘correlated activity’ can be of various nature and therefore subject to different measurements. For example, it can be the precise timing of action potentials between cells or group of cells but also cross-coherence of aggregate electrical activity, such as local field potentials (LFP), post-synaptic potentials or electro-encephalograph signals.

The Temporal Correlation Hypothesis

An integrated approach to the role of correlated neural activity in information integration is presented in the temporal correlation hypothesis, the assumptions of which were first proposed by von der Malsburg as an answer to the problem of the combinatorial nature of feature integration (von der Malsburg 1994). A more comprehensive approach, along with the name, was formulated by Singer and Gray (1995). The main proposition is that in every neural system where information processing is distributed, the solution to the binding problems lies in the temporal characteristics of the neural activity. As opposed to previous attempts at explaining information integration in the brain, where the most important feature of neural activity was the frequency of firing (frequency coding), the temporal correlation hypothesis seeks a solution in the precise timing of action potentials (time coding). The main prediction that follows from these assumptions is that each group of neurons that process information about the same object (as is in the case of perception) or the same cognitive process (more generally), will share the same temporal pattern of sending action potentials – in other words, will synchronize their activity. This process of synchronization, if it is to be realistic, needs to be enacted to within a millisecond range.

A great advantage of this model lies in the fact that it enables integration of multiple objects, or functions, at the same time. This concurrence may be possible either by differentiating temporal patterns (including, *inter alia*, different frequencies) as well as phase differences. It is also possible for one cell or cell group to partake in more than one integrated unit at the same time – for example, by synchronizing with other cell assemblies at harmonic frequencies. As such, the problem of coding multiple representations (even those that share some features) by the same group of neurons at the same time is solved.

The temporal correlation hypothesis does not stand in opposition to frequency coding, however. Rather, it proposes a complementary mechanism of integration that enhances the coding capacity of neural systems. In addition, it explains why integrated wholes may be easily acted upon at higher levels of information processing: a synchronized assembly forms a functional unit at a higher level which is easily distinguishable from other cells. In terms of neural activity this ease of distinguishing is the ability of a synchronized signal to quickly activate the next levels of information processing. Thanks to the process of temporal summation of signals, a neuron is far more likely to produce an action potential if incoming signals from other cells are synchronized. This way, synchronized cells are more visible than unsynchronized ones, even if there are more of the latter.

At each level of information processing synchronized groups form functional units that integrate more and more complex structures. Such groups may be formed within sensory areas with a single modality but also across modalities; they may also join distant processing centers in the brain. Such far reaching synchronies have been proposed as the basis of multimodal perception, sensory awareness or momentary consciousness ('scene').

The micro level assumptions of the temporal correlation hypothesis have their origins in Hebb's propositions. A synchronized neural group constitutes a cell assembly as proposed by Hebb (1949), in which activation of a single cell, through intra-group connections, activates the whole cell assembly. This in turn strengthens the connections – Hebb's synapses – according to the rule that concurrent activation fosters stronger connections. Stronger connections, again, increase the chance for simultaneous activation, closing the feedback loop. In contrast to Hebb's postulates, the temporal correlation hypothesis does not rely on the formation of stable connections. Rather, it proposes temporal strengthening of synapses (LTP – long term potentiation and LTD – long term depression) as a mechanism to facilitate the realization of synchronized functional units. This way, they are dynamical formations, appearing for a short, distinct time and disassembling shortly thereafter to enable the creation of a new configuration of functional units.

Empirical Findings on Neural Synchrony

The most influential series of studies to confirm the predictions of temporal correlation hypothesis was designed by Singer, Gray and collaborators. In their first study they showed that a grating of a specific angle elicits synchronization of a cortical area that responds (i.e. increases the frequency of firing) preferably to this angle, while other areas remain unsynchronized (Gray et al. 1989). Further, the authors stimulated neighboring areas in the visual cortex (i.e. responding preferably to areas in the visual field that are next to each other) with moving gratings. If the gratings moved in different directions in each field, the cells responded with increased frequency of firing and intra-areal synchrony. If the stimuli moved in the same direction, a weak inter areal synchrony could be observed. However, if only a single grating was used that spanned both spatial fields, cells in both areas synchronized their activity. This result proves that synchrony is indeed related to cells processing information about the same object being 'tagged' as such. Moreover, the level of synchrony is related to the extent to which stimuli form a coherent whole – if they can be viewed as a single object, synchronization is strongest, if they share some features (e.g. direction of movement), synchronization is weaker and finally, if they are totally separate, synchronization ceases.

A similar result was obtained in a follow up study, in which the authors recorded the activity of cells from the left and right hemispheres that shared similar receptive fields near the centre of the visual field (Engel et al. 1991). Again, a single object moving through the field elicited inter areal synchronization of activity, this time spanning both hemispheres. A section of the corpus callosum abolished this synchrony, leading the authors to the conclusion that the zero-lag synchrony was effectuated through inter hemispheric connections rather than being stimulated by a single subcortical structure. Moreover, this result proves that synchrony is not affected by the length of connections between the areas in question, yielding similar, millisecond precision both within a single cell column as well as across hemispheres.

An important result was found in a study by Fries et al. (2002). Strabismic cats (that had undergone a section of corpus callosum at an early age) were shown distinct stimuli to each eye (binocular rivalry). In such a situation, only one stimulus can be selected for processing at a time. The inter-ocular rivalry was controlled by increasing the saliency of one stimulus over the other, e.g. by setting a specific time offset or increasing the contrast. The actual selection of one stimulus was further controlled by comparing eye movements. The stimuli used were gratings of different angles that elicit responses from a range of visual cortical areas whose multi-unit activity (MUA – action potential trains from many cells) was recorded. Whenever the rivalry resolved in favor of the stimulus preferred by specific areas, their activity was synchronous – in contrast to the areas preferring the unselected stimulus. However, the firing rate – frequency of action potentials – was independent of synchrony. That is, since both stimuli were present at all times, they elicited increased activity in all cells responding to those stimuli. What distinguished – on the level of neural activity – the stimulus chosen for awareness was the level of synchrony of the cells responding to it. In fact, the frequency rate was biased towards the unselected stimulus, leading the authors to conclude that synchrony could be translated into increased frequency at some later stages of processing. The results of this study prove that time and frequency coding are separate mechanisms of information integration that in fact complement each other, with the time coding being crucial for awareness processes.

An amassed amount of experimental data demonstrate that synchronous oscillations are present in cortical activity across a variety of perceptual and motor tasks: in visual processing in monkey (Eckhorn 1994; Fries et al. 1994), in auditory cortex of humans during the presentation of stimuli to the dominant ear (Pantev and Elbert 1994), during auditory tasks in cats (Csépe et al. 1994); in sensori-motor cortex of both human and monkey during muscle movement and reaching for objects (Murthy et al. 1994; Murthy and Fetz 1992), in human sensory cortex while discriminating the stimulated finger (Desmedt and Tomberg 1994), and in visual cortex in humans during a visual field search (Tallon-Baudry et al. 1997).

Of exceptional significance are studies which point to the crucial role of neural synchrony in cognitive tasks. Von Stein et al. (1999) have shown that independent of the modality of the presented stimulus (visual – image, auditory – word, visual – word) long range correlations of activity appear in the temporal and parietal cortices. The authors conclude that this coordinated activity is crucial for multi-modal processing of incoming information. Von Stein and Sarnthein (2000) have further proposed that long range correlations – used for more general integration – typically involve lower frequency bands, while short range synchrony within specific areas and devoted to lower level integration, such as in perception, rely on higher frequencies (specifically, the gamma band). Similarly, Wrobel et al. (2007) proposed that while perceptual processes relate to gamma band synchrony, attention requires synchrony in the beta frequency band.

Pulvermüller et al. (1994) have shown that the analysis of words elicits stronger synchronous oscillations in the left hemisphere (all subjects were right-handed) than nonsense letter combinations. Miltner et al. (1999) discovered increased

coordination of activity between visual and sensori-motor cortices in an anticipatory learning task, where a visual cue warned before an electric shock. Fell et al. (2001) have shown that successful, as compared to unsuccessful, learning involves a specific pattern of coordination of activity between structures crucial for memory formation – an initial increase of correlation that is followed by a decrease as the task nears conclusion.

A very important study by Rodriguez et al. (1999) has shown that long range correlations are present in cognitive integration of information. Subjects were presented with ‘moony’ faces – simplified, black and white images of human faces that are easily recognized when presented upright and unrecognizable when shown upside down. Such stimuli are a perfect example of a Gestalt – an indivisible figure that is always perceived as a whole. Gestalt psychology describes a set of properties of such figures, e.g. top-down influence of the whole on its parts and bottom-up mechanisms of integration of parts into a whole (Kohler 1929). Gestalt figures are, therefore, specifically appropriate for studying information integration during cognition. In the case of recognizing faces, as opposed to being unable to recognize any shape, a specific pattern of correlations was observed in the EEG signal. First, many long-range correlations appeared between the recording sites, specifically between the parieto-occipital area and the frontal and temporal regions. Then, the synchrony decreased to be finally followed by another increase, this time mostly in the parietal areas. The latter increase in coordination preceded a motor response – for which parietal activity is crucial – by which the subjects indicated whether they had recognized a face in the image. The results of this study show that integration of information into a coherent whole depends on a spatio-temporal pattern of neural synchrony. Moreover, the authors point to the fact that a period of desynchronization between distinct cognitive tasks (which was not accompanied by any decline in activity levels) might be crucial for switching from one function to another.

Of vital importance for our understanding of the role of coordinated neural activity in cognitive function are the results of a study by Tononi et al. (1998) on the coordination patterns during conscious perception. Subjects were presented with blinking gratings in a binocular rivalry condition. The stimuli for each eye had different frequencies of flickering. In such a setting, conscious perception is possible for only one stimulus at a time and naturally switches from one eye to the other every three seconds. A flickering stimulus elicits electrical neural activity of the same frequency, therefore it was possible to assess the awareness of a particular stimulus by measuring the strength of the frequency of each stimulus in the MEG (magneto-encephalograph) signals. The results show that conscious perception elicits a far more distributed activity (the activity of a given frequency spans many areas) than a non-consciously perceived image. What is more important, this distributed activity is accompanied by many long range correlations appearing between recording sites. This result shows again that information integration by synchrony is vital for conscious cognition.

One crucial study offers an experimental verification – as opposed to mere correlation – of the role of neural synchronization in perception. Stopfer et al. (1997) impaired neural ability to synchronize in bees by induction of picrotoxin,

which is known to suppress synchronization. The bees were then presented with various odors that normally elicit 30 Hz synchronized oscillations in the olfactory bulb. Bees that were treated with picrotoxin were unable to distinguish similar odors while their ability to differentiate between quite distinct odors was left unimpaired. This study proves that synchronization plays a causal role in at least some perceptual tasks.

Functional Connectivity

The temporal correlation hypothesis – that summarizes the role of synchrony in neural processing – states that synchronized activity is tantamount to integration of information processed by separate, functionally specific units. However, the process of integrating incoming information is not a sequence of synchronization events between pairs of brain loci. Rather, any cognitive action requires a vast amount of information to be integrated simultaneously. This means that at the same moment of time many areas synchronize their activity, either in pairs or in larger groups. What we observe then, as witnessed in many of the studies presented above, is an array of areas connected by correlations between their electrical signals. Such connections are termed ‘functional connections’ – as opposed to anatomical ones – and form functional connectivity.

A further distinction is between ‘functional’ and ‘effective’ connectivity (Aertsen et al. 1989). The first describes time dependencies observable in the electrical activity of given sources. The latter term is used to underscore the causal relation between two signals – if one region elicits correlated activity in the other, an effective link forms between them. In case of functional links, this is not necessarily the case – the correlation of signals between two areas may be the effect of a third region imposing its activity pattern on both. Functional connectivity is thus a wider notion that encompasses effective connectivity and, so called, spurious correlations. However, due to technical limitations it is very often impossible to establish direct causal relations between measured signals and therefore it is functional rather than effective connectivity that is subject to investigation in most studies.

To study the role of functional connectivity in information integration and more general cognitive functions, it is necessary to extract functional connections from brain imaging data. To this end a cross-coherence matrix of interdependencies between recording sites is extracted from raw signals (see also Stam and Reijneveld 2007). This can be either coherence between haemo-dynamic responses in the case of fMRI (functional magnetic resonance imaging) recording or between potentials recorded through MEG, EEG or LFP. A threshold value is then applied to each cell in the matrix such that only strong correlations between signals are further analyzed. While the threshold is chosen arbitrarily and may lead to the rejection of important correlations or the acceptance of weak ones, it is important to notice that correlations in electrical activity are ubiquitous in the brain and some filtering is needed for the data to be meaningful. Each correlation that passes the threshold is

further treated as a functional link between their respective locations that become nodes (vertices), while all correlations that fail to meet the threshold are set to zero. In effect, a set of connections (edges) is obtained that can be portrayed as a network of functional connectivity.

Functional connectivity networks have been subjected to analysis using graph theoretical measures. Most of the research in this area focuses on determining stable properties of global functional networks of the brain in a resting state (that is, without engaging subjects in cognitive tasks). Just as has been found for anatomical connections (He et al. 2007; Sporns and Zwi 2004; Watts and Strogatz 1998), functional networks display small world properties but usually no scale-free nature (Salvador et al. 2005a; Salvador et al. 2005b; Yu et al. 2008). Interestingly, functional connectivity networks also display hierarchical modular organization (modules within modules), fairly similar across subjects (Meunier et al. 2009b), that is believed to be typical for complex systems and that enables them to be adaptive (Simon 1962). Such organization reflects the notion of functional units forming at different levels of description that enable smooth cognitive function.

A promising line of research has been devoted to differentiating the properties of functional networks in normal and pathological function of the brain – epilepsy (Ponten et al. 2007), Alzheimer's disease (Stam et al. 2007) and brain tumors (Bartolomei et al. 2006). In all these cases the pathology is related to a network structure closer to a random configuration of connection, while healthy subjects display small world properties in their functional connectivity networks. In contrast, healthy aging is associated with a functional network structure deviating from random connection configuration, preserving small world properties (Meunier et al. 2009a). However, older subjects have functional networks with fewer long-range, inter-modular connections and more short-range, intra-modular connections than younger subjects.

A few studies have investigated the relation of functional network measures and motor and cognitive tasks. Micheloyannis et al. (2006) compared structural properties of functional networks of groups of subjects differing in the number of years of formal education. The group that had only a few years of education had a more small-world like structure of their functional connectivity during a working memory task than the subjects with university degrees. The authors conclude that the more small-world network structure, being more functional, serves to increase the efficiency of processing that is specifically crucial for subjects with fewer years of education.

Bassett, Meyer-Lindenberg et al. (2006) have shown that whole brain functional connectivity networks in both resting state and motor task demonstrate fractal small-world properties, i.e. the small world structure is conserved across many frequency and topological scales. Moreover, the motor task increases the number of long-range connections between frontal and parietal cortices while still preserving the small world properties.

Finally, in a study of MEG derived functional networks, Valencia et al. (2008) have shown that a variety of network measures dynamically changes in a visual stimulus paradigm, evolving to meet the demands of the task. Namely, for the

15–25 Hz functional connectivity networks there is a peak in the clustering index, mean degree and efficiency at around 250 ms after the presentation of the stimulus. While there are changes in the network structure, the global small world properties are preserved. The authors conclude that such dynamic reconfiguration of the functional network serves efficient local and global functional integration.

Summary and Discussion

Cognitive function requires both segregation and integration of information, which imposes very demanding constraints on the system that produces it – the brain. Moreover, this segregation and integration of information needs to be structured in a hierarchical manner, with parts at one level being integrated into wholes that form units at the next level, while preserving their distinct, segregated features. Such hierarchical modular systems are believed to display complex properties and enable adaptation to a changing environment.

While the subjective experience of cognition is characterized by fluency and ease, it has so far proven very difficult to explain its neural basis. Our knowledge of the way information is segregated in the brain is by now sufficient – especially at the early stages of processing; however, we still lack definite understanding of how it is integrated into small and bigger functional units. The functional connectivity approach is a promising line of research that has the potential to explain how information may be locally and globally integrated while remaining segregated throughout the brain. By deriving its assumptions from the neural synchrony theories, it offers a comprehensive description of information processing during cognitive function.

First, it proposes a molecular mechanism for micro-integration – intermittent changes of synaptic strengths enable easy formation of synchronized cell ensembles. These produce a salient signal that can be distinguished – again, thanks to molecular mechanisms – from unsynchronized activity. Further, empirical data on synchronous oscillations recorded from larger regions points to their vital role in a variety of motor and cognitive functions, specifically in conscious processing. Finally, functional connectivity networks extracted from correlated signals permit a formal analysis of functionally integrated units to be made at various levels of description. The empirical results of such studies show how the global network properties relate to cognitive function as well as being able to distinguish between normal and pathological brain processing.

In summary, the concept of functional connectivity fulfills the requirements for explaining the neural correlates of cognition. While it is still a novel approach, it has a potential to finally provide us with a breakthrough in our understanding of the biological basis of the mind.

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