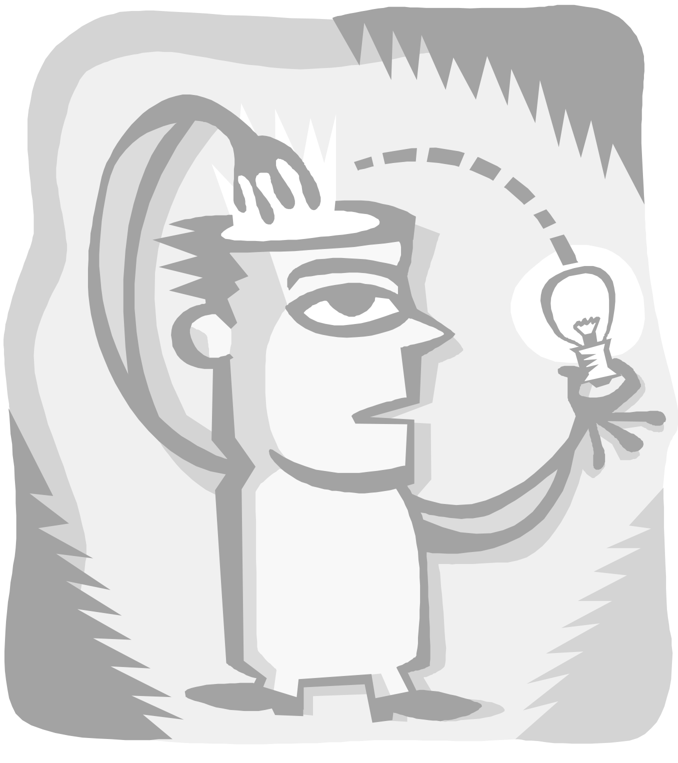
Université Victor Segalen Bordeaux 2

Maîtrise de Sciences Cognitives

A NON-LOCALISATIONIST THEORY OF COGNITION: A NETWORK THEORY



2 fundamentals features:
- semi connectivity of the brain
- transient response plasticity

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INTRODUCTION

Nowadays, a lot of researchers are trying to identify which cognitive functions are assumed by each module of our brain. Thanks to this approach, they succeed in finding statistically significant results but when they reproduce the same tests on subjects who have brain lesions, it appears some incoherencies.

Two major types of paradoxical functional facilitation effects must be distinguished. On one hand, some patients have multiple lesions in their brain but these damages bring to normal or near normal a previously subnormal or abnormal level of functioning. This is known as restorative paradoxical functional facilitation effects. On the other hand, there are situations where a subject with nervous system pathology or sensory loss performs better than normal control subjects on a particular task. This one is called enhancing paradoxical functional facilitation effects.

The main problem consists in the fact that a lot of researches have been conducted on patients who are presenting some deficits in functioning but a very few consider these that are presenting an improvement. If we are in this situation, this is partly due to the existence of two disciplines: Neurophysiology and cognitive psychology. Neurophysiology has partly evolved from study of the basic properties of neurons without much link to overt behaviour beyond simple reflexes. Conversely, cognitive psychology has developed through careful experimental investigation of overt behaviour and how the manipulations of putative cognitive processes change the measured behaviour.

First, we'll see how neurophysiologists approach paradoxical effects of multiple lesions and how they interpret damages which result in facilitation of behavioural functions. In a second time, we'll consider spatiotemporal analysis of experimental differences in order to study a method which is not influenced by the experimenter's own biases. And at last, we'll see how this new technique can be used with a network theory of cognition so that the brain can be modelled in a lot more efficient way than it is today.

1. LOCALISATIONISM

In order to investigate the effects of separate and combined perirhinal and prefrontal cortex lesions on spatial memory in the rats, D. BILKEY and P. LIU have chosen to compare effects of these lesions on several tasks that are commonly used to test this memory and to compare with the effects of concurrent lesions made to both of these structures.

Thus, they postulate that if a primary function of the prefrontal cortex involves accessing representations that may, in part, be perirhinal dependant, one would expect that combined lesions in these two structures should either have no additional effect (if one lesion disrupts the whole system), or an additive effect (if a single lesion is only partially disruptive), when compared with the deficit produced by a lesion of either structure alone. The purpose of studying this procedure doesn’t consist in learning how spatial memory in rats is working but it’s a way to describe this type of experimentation and to understand its limits.

1.1 Method

The first step of this experiment have been to create lesions to rats: Perirhinal and anterior cingulated cortex lesions were created by inserting electrodes into the brain through trephines drills at specific coordinates which was determined thanks to the literature. Then, the first experimentation was conducted; it’s consisted in a Morris water-maze task: rats have to discover a platform in a water pool. After a few days of learning, they swim freely (probe test) for two days and since the next two days, they have to reach the platform which has been shift to the centre of another quadrant of the pool (reversal training). At last, a second experiment in a radial arm maze was conducted. On the first two days, rats were placed onto the central platform and were allowed to explore the maze. For the following eight days, one reinforcer was placed at the end of each arm and the rat was allowed to choose freely between arms.

1.2 Results

This study demonstrates that rats with electrolytic lesions of the perirhinal cortex (PRC group) display a deficit in the initial stages of acquisition of the water maze task. Furthermore, they displayed a delay dependant deficit in a probe trial conducted at a short interval after a series of training trials and a significant deficit in performance in the radial arm maze. In a localisationist way, these findings are consistent with the proposal that temporal neocortex regions may be involved in spatial memory process.

Lesions of prefrontal (PFC group) cortex produced deficits in the water maze acquisition. They also displayed a deficit in a reversal procedure conducted in the water maze and in a radial maze procedure. In a localisationist way, these findings are consistent with the proposal that the prefrontal region is involved in working memory processes that require the maintenance and the manipulation of memory representations in their activated state.

Surprisingly (in a localisationist way!), the performance of rats with combined lesions was significantly better during the water maze probe than the PRC group. It appears clearly that the relationship between the prefrontal and temporal regions is not straightforward.

1.3 Discussion

In order to explain the observed paradoxical functional facilitation, we can make several hypotheses to explain these findings:

- Inhibitory mechanisms

Recent studies have shown that neural activity associated with some types of cognitive activity may involve increases in blood flow in task-related structures and parallel decreases in blood flow in neighbouring, alternative sensory modalities. Inhibitory mechanisms underlying functional facilitation may be related to reports of paradoxical increases in blood flow, in structure distal but connected to the lesion site, that have been noted in studies of patients with focal cerebral lesions. We can think that this increase is due to functional disinhibition of structures connected by inter or intra hemispheric pathways to the critical lesion site.

Models of memory that have inhibitory systems amongst their key features are now emerging. Within the range of inhibitory phenomena, there are particular effects, such as latent inhibition and negative priming, which predict better than normal performance in neurological patients with inhibitory deficits. Since cognitive functions are in interaction, the competition/interference decrease between cortical and sensory areas allows another scheme of interaction to emerge.

- Compensatory plasticity

A number of non-human studies have shown that enucleation or thalamic lesions will result in sprouting of new fibres that project in cortical areas. We can’t say whether this compensatory augmentation derives from the fact that sensory-deprived subjects take part in intensive practice in particular sensory activities, or whether it is due to more subtle mechanisms. The first possibility is the unmasking of silent synapses or pre-existent latent anatomical connections. The second is coming from the reduced competition between cortical-sensory areas. The third could be a synaptic super sensitivity. And the fourth could be new formed connections in the form of anatomical sprouting.

2. STATISTICAL APPROACH

Until recently, there were few ways to study the neurobiological correlates of human cognition. Fortunately, human functional neuroimaging has recently made some great progress which has produced a lot of new data that has added considerable information about the functional neuroanatomy of specific cognitive functions.

There are two basic types of functional neuroimaging methods: those that measure the electric or magnetic fields generated by neural activity (ERP: Event-Related Potentials and MEG: Magneto encephalography) and those that measure the hemodynamic or metabolic sequelae of neural activity (PET: Positron Emission Topography and fMRI: functional magnetic resonance imaging).

The data obtained can be acquired non-invasively from healthy normal subjects, as well as from patients with brain disorders. Thus, we can determine the way in which brain areas work together during specific cognitive tasks and we can integrate these results into a coherent picture of how specific cognitive tasks are mediated neurally; when we'll see how it's made, we'll study how it would be helpful to model the neural system.

2.1 Statistical analysis

There are many data analysis techniques for assessing functional brain imaging data. But it must be distinguished two conceptual distinctions about the application of these data analysis method

- Subtraction versus covariance

This technique is used to analyse PET and fMRI data. It includes subtraction paradigm (it rests on the hypothesis of functional specialization: different brain regions are engaged in different functions) and the covariance paradigm (it is assumed in that paradigm that the task represented by an experimental condition is mediated by a network of interacting brain regions and that different tasks correspond to different functional networks.

The subtraction generates activity maps and the covariance produces interactivity maps. Thus this two paradigms are complementary one another.

- Statistical assessment versus neural modelling

As opposed to statistical assessment, neural modelling explicitly chooses from the data what is hypothesized to be important prior to analysis and then tries to understand this reduced data set in a detailed and quantitative way.

- Principal component analysis (PCA)

This is a linear multivariate technique which has been most frequently used and can provide separate analysis of the spatial and the temporal relations in Event Related Potentials data (ERP). The PCA solution can be rotated to maximize the signal within individual Principal components. The goal of multivariate techniques is ultimately to describe important differences in the ERP waveform that are related to the experimental manipulation.

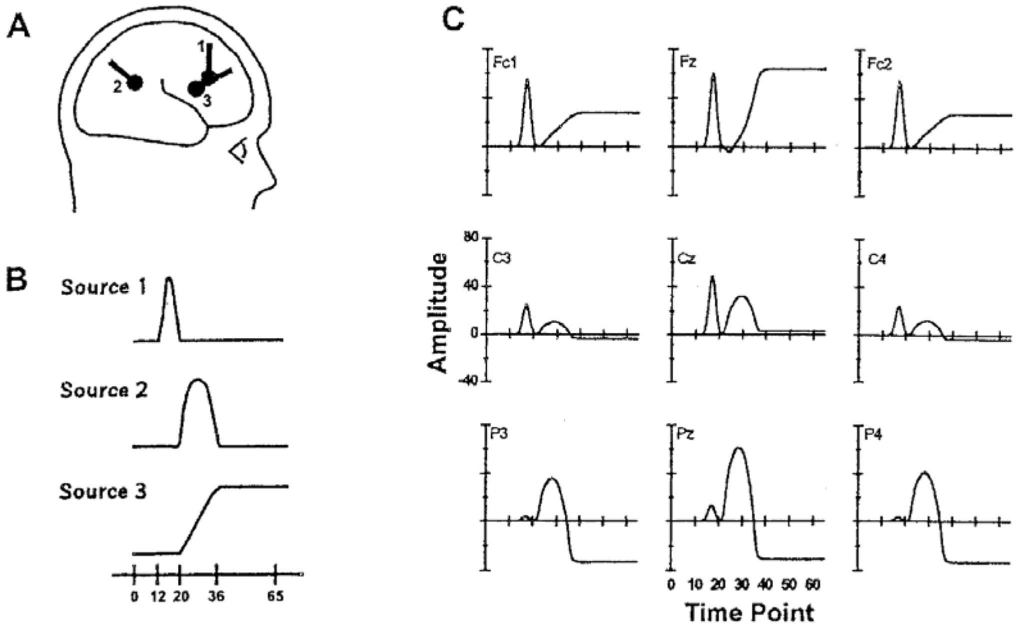


Figure 3. Simulation data. A: Location and orientation of dipoles. All three sources were placed along the midline. B: Source waveshapes corresponding to each dipole. C: Scalp topography for the baseline condition for 9 of 29 electrodes. Note that Fc1 and Fc2 show effects from Source 1 and Source 3 activity, whereas Cz shows primarily effects from Source 1 and Source 2 activity. All other electrodes express some combination of all three sources.

2.2 Structural equation modelling

- Multiple Layer Perceptron

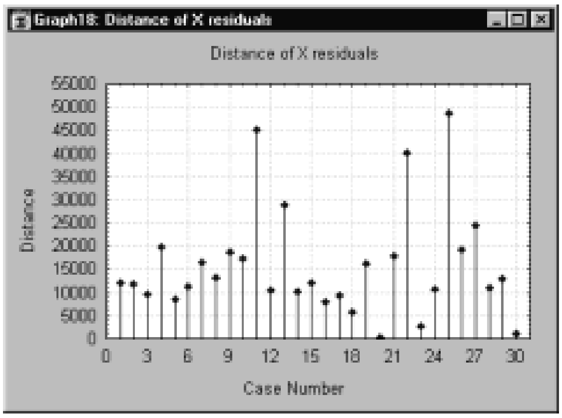
This technique was adjusted in the late fifties by Rosenblatt. The Perceptron wants to be a model of perceptive activity. It associates input configuration at response activity. It is made of three layers, one for the input cells, one for the hidden cells and one for the output cells. Each cell on a layer is connected with all cells of the neighboured layer.

The purpose is to train the network until the desired output is equal to the obtained one. But this tool is limited because if the problem is not literally separable, it can’t find a solution.

➢ Partial Least Square Regression (PLS)

This mathematical process can be used after than a PCA has been completed. The PLS identifies experimental effects expressed as latency shifts at a single neural source. It identifies only the specific combinations of waveform differences that distinguish conditions. These findings indicate that PLS is a sensitive tool for detecting the spatiotemporal scalp distribution of ERP waveform differences. PLS provides a scalp wide assessment of amplitude differences and can indicate that multiple differences in waveform amplitudes are related to experimental manipulations.

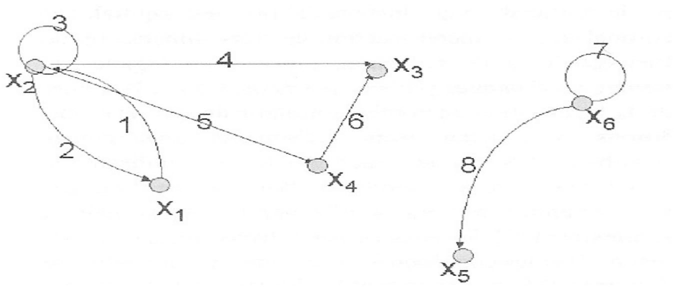
$$\mathbf{X} = \begin{matrix} A_1B_1C_1 \\ A_1B_1C_2 \\ A_1B_2C_1 \\ A_1B_2C_2 \\ A_2B_1C_1 \\ A_2B_1C_2 \\ A_2B_2C_1 \\ A_2B_2C_2 \end{matrix} \overset{\text{......main effects......}\quad\text{................2 - way interactio ns..........}}{\begin{bmatrix} 1 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 & 1 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \end{bmatrix}}$$



2.3 Large-scale neural modelling

All the approaches have features that make direct comparison of results across methods extremely difficult. This is true even within the area of functional neuroimaging because the various techniques have different spatial and temporal properties.

How can one put together data from all these methods and arrive at a coherent and consistent account of the neural basis of specific cognitive tasks? The first problem is the spatial resolution because human brain imaging is large compared with the size of neurons or cortical columns. The second one is the temporal resolution because the appropriate dimension of a process is on the order of a few seconds whereas the neuronal temporal dimension is on the order of milliseconds. The third is the location where the activity is measured: synaptic or neuronal activity. And the fourth is probably the most problematic: the connectivity because a synaptic activity is a mixture of local and afferent synaptic activity, so that we can’t determine where the activity is mostly coming from.



3. NETWORK THEORY

Modern neuroimaging tools provide an opportunity to study how the brain produces human mental functions. The first fundamental aspect that must be considered in order to examine this, is the connectivity of the brain, which occupies an intermediate position between complete redundant interconnections and independence. The second is transient response plasticity where a given neuron or collection of neurons may show rapid changes in response characteristics depending on experience.

We will see how, when we bring these two properties together, we can obtain thanks to the brain areas interactions, aggregate functions which embody the cognition processes.

3.1 Semi connectivity of the brain

- Non-complete interconnectivity

Neurons are linked to one another both locally and at a distance on the contrary to most other systems in the body which only show capabilities for cell to cell communication. Moreover, the far communication of the neural system is specialized for rapid transfer of signals, but our brain is not a Hopfield system where each cell is connected to each other.

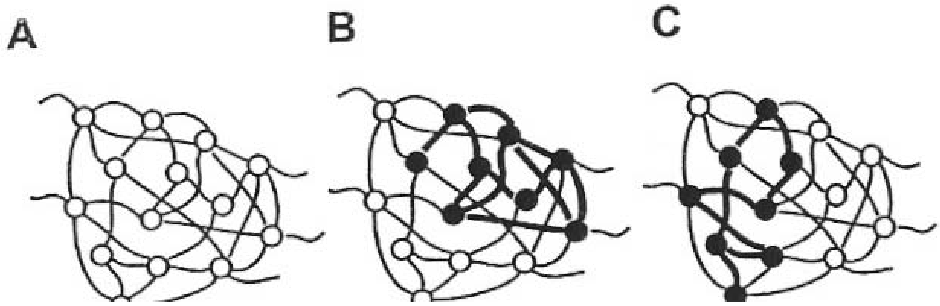
Estimates of the connections in the primate cortical visual system suggest that somewhere between 30-40% of all possible connections between cortical areas exist. This sparseness is a computation advantage for the nervous system in that it allows for a high degree of flexibility in responses at the system level.

- Non-complete independence

Local cell networks are highly interconnected, but neither this mean that adjacent cells can't only have one common and unique connection, nor this mean that modules work independently and are just sharing some data after they've completed their treatment.

3.2 Transient response plasticity

- Overlapping



The plasticity considered here is more short-lived that the reorganization which could be observed after prolonged training. Transient plasticity is considered to be a property of higher-order brain regions only, which thus specializes them for cognition. However, physiological investigation has shown transient plasticity in the earliest parts of the nervous system.

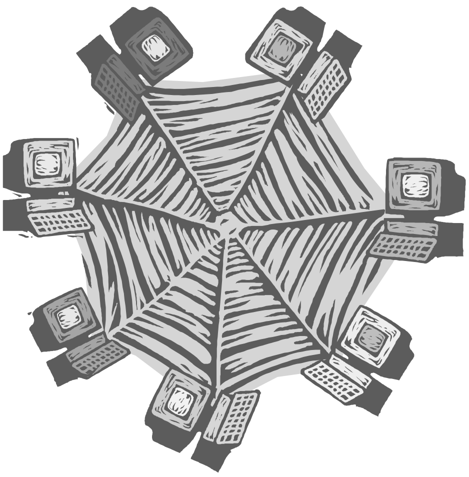
Neurophysiological studies show that the brain is specially designed to modify its responses depending on prior experience at all levels of organization.

- Aggregate properties of neural populations

Single neurons may show distinct patterns of activity that separately may not seem to represent anything cohesive. If we move the examination to the level of small neurons groups, responses reflecting fundamental properties such as learning, memory and attention emerge albeit with a limited number of functions.

Indeed a small group of neurons creates what is called microfunction. This is known in logical as "and" "or" "exclusive or"… This is the smallest element that could spatially limit cognitive functions but, since the great connectivity of neurons, I presume that we can find a majority of these microfunctions in the most of our modules.

Cognitive function may be determined by how the properties of different regions are combined, or aggregated, through interregional interactions rather than by the involvement of any specific region. However, the anatomy of our brain puts some limits in the possible interactions may have.



3.3 Network Connectivity

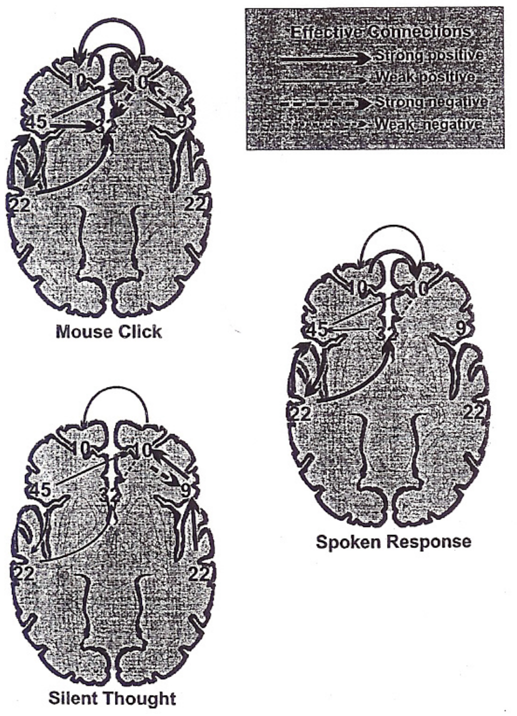
This is the exploration of functional end effective connectivity. It is not important to focus on activity differences but on the relation of activity between areas. Because the goal is to quantify and understand neural interactions, the methods of analysis must focus on the relations between neural elements.

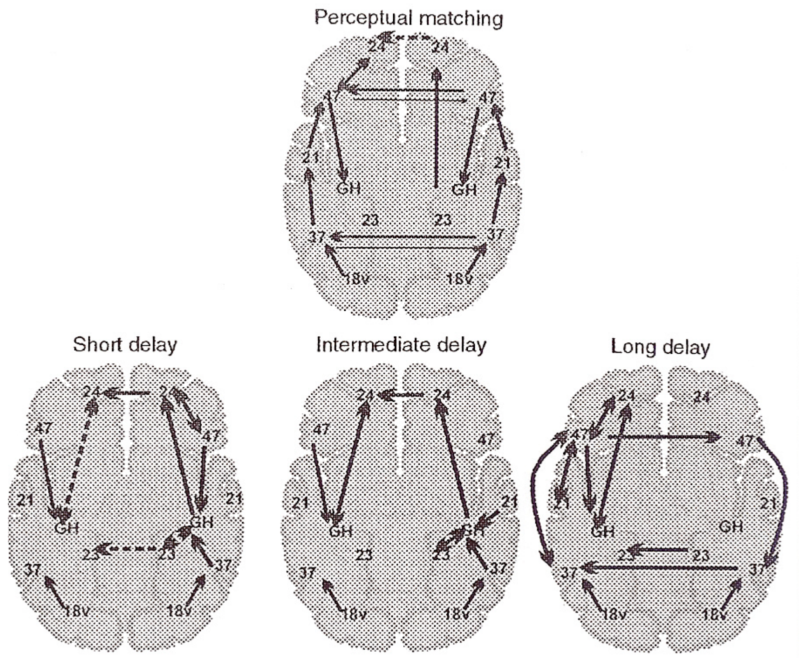
To explore some of the network interactions within an anatomical reference, structural equation models must be constructed for a subset of regions.

- Functional connectivity

This is a statement that two regions show some non zero correlation of activity, but does not specify how this correlation comes about. The same area may show very similar patterns of activity between conditions, but different network interactions.

By example, when a subject learn the association between a tone and a visual stimulus, since the activation of visual areas would occur without overt visual stimulation, we could make the hypothesis that this activation would be mediated through effects from higher order cortical areas, likely posterior association or prefrontal cortices. Thus, the analysis of the functional connectivity identifies four areas that could have influenced the activity of these visual areas.





- Effective connectivity

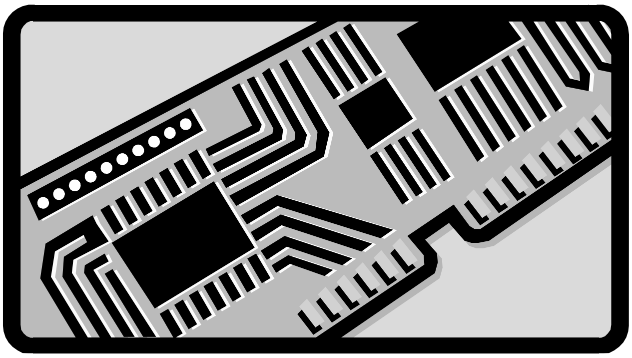
This is a statement about the direct effect one region has on another, accounting for mutual or intervening influences.

If we use again the previous example, a statistic analysis show us that two areas exert a dominant influence on the visual area as the association was learned. This two both changed their effect on visual cortex from suppressive to facilitory as the association was learned. This outcome emphasizes the need to explicitly quantify effective connections.

CONCLUSION

We've seen that localisationnists can't explain a lot of results in their experiments. Of course, these little problems are taken for testing artifacts because they can't envisage that this theory may not be accurate. It is right to say that localisationnism is clearing up most of cognition's problem but it seems that our brains don't operate like this.

Thus, functional brain imaging has become central to understanding how neurological behaviour is linked to cognitive functions because subjects can perform specific cognitive tasks while a huge mass of data is acquired from many brain regions simultaneously. With models obtained from functional brain imaging data, cognitive neuroscientists will be in a position to relate them on the one hand to detailed neuronal-based models, and on the other, to cognitive models.



If we find that similar brain regions can serve different cognitive functions, this would imply linkages between the cognitive functions. While it is convenient to consider attention, memory, language, and perception to be the domain of independent neural systems, the physiology of the brain would suggest strong, if not complete, overlap of these operations.

In conclusion, we can say that it seems that the rudimentary functions of a neural population interacting with one another, combine themselves and the obtained aggregate is the cognitive processes. Cognitive operations are not localized in an area or network of regions, but are the consequence of dynamic network interactions that depend on the processing demands for a particular operation. The same collection of areas may be engaged across a variety of cognitive operations because of the semi-connectedness of reg transient ion and transient plasticity.

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