

NEUROCOGNITIVE NETWORKS AND SELECTIVELY DISTRIBUTED PROCESSING

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SUMMARY

The association cortex of the human brain can be divided into unimodal and transmodal components. Unimodal (modality-specific) cortical areas are subdivided into upstream regions specialized for encoding unitary features of experience and downstream regions which are specialized for encoding composite features.

Modality-specific features lead to multimodal knowledge through the mediation of transmodal areas in the brain. These transmodal areas include cortical regions that are conventionally designated as heteromodal, paralimbic and limbic cortex.

Contrary to earlier formulations, it is no longer thought that these transmodal areas contain a convergent residue of knowledge. Instead, it appears that the role of these transmodal areas is to contain a road map for the multifocal binding and calling up of distributed information in multiple modalities. Knowledge can thus be encoded in a flexible distributed rather than rigid convergent form.

Observations on patients with focal neurological lesions indicate that transmodal areas act like neural hubs (or gateways) for accessing critical domains of knowledge rather than as dedicated centers for specific cognitive functions. In the processes related to memory, a limbic structure such as the hippocampus does not act as a bank for specific memories but as a critical node for accessing distributed information related to recently acquired experience. Damage to a sufficient volume of the limbic system interferes with the coherence of recall and storage even though the constituent fragments of the corresponding experiences may remain stored quite well in other parts of the brain.

Additional observations based on the phenomenon of hemispatial neglect lead to the conclusion that transmodal areas and unimodal areas are interconnected with each other to form large scale neural networks that can sustain complex computational architectures including those that rely on parallel distributed processing. Networks organized in this fashion can rapidly access a vast informational landscape while simultaneously considering many goals and constraints. The final compromise into which the network settles is identified as the solution to the cognitive problem.

In this neurological model of cognition, the unimodal areas of cortex provide the most veridical building blocks of experience. Transmodal nodes bind this information in a way that introduces temporal and contextual coherence. The formation of specific templates belonging to objects and memories occurs in distributed form but with considerable regional specialization. This arrangement leads to a highly flexible and powerful computational system which could be described as Selectively Distributed Processing.

Réseaux neurocognitifs et traitement à distribution sélective.

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RÉSUMÉ

On peut diviser le cortex associatif du cerveau humain en composants unimodaux et transmodaux. Les zones corticales unimodales (à modalité spécifique) se divisent en zones d'amont spécialisées en codage des éléments unitaires de l'expérience et en zones d'aval spécialisées en codage des éléments composites.

Les éléments à modalité spécifique sont responsables de la connaissance multimodale grâce à la médiation des zones transmodales du cerveau. Certaines régions corticales, que l'on appelle par convention le cortex hétéromodal, paralimbique et limbique, font partie de la zone transmodale. A l'inverse des formulations antérieures, ces zones transmodales ne contiendraient pas un résidu convergeant de connaissance. Au contraire, il semble que ces zones transmodales contiennent une carte des liens multifocaux et de rappel des informations distribuées par modalités multiples. Ainsi peut-on coder la connaissance sous une forme de distribution flexible plutôt que sous une forme rigide convergente.

Les observations chez les patients ayant des lésions neurologiques focales, indiquent que les zones transmodales agissent comme des aiguillages neuraux pour l'évaluation critique des domaines de connaissance plutôt que comme des centres de fonctions cognitives spécifiques. Dans les processus de mémoire, par exemple, l'hippocampe n'agit pas comme une banque de mémoires spécifiques, mais comme un aiguillage neural en rapport avec l'expérience récente. Les dégâts, d'un volume suffisant, au niveau du système limbique interfèrent avec la cohérence du rappel et du stockage, même si les fragments constituants des expériences correspondantes sont bien stockés dans des nœuds multiples des zones unimodales et transmodales.

Des observations supplémentaires du phénomène de négligence hémispatiale conduisent à la conclusion que les zones transmodales et unimodales ont des interconnexions formant des réseaux de grande échelle permettant des architectures de traitement complexe, y compris

celles à distribution parallèle. Les réseaux organisés de telle manière permettent l'accès rapide à un paysage informationnel tout en maintenant la considération simultanée de multiples buts et contraintes. Le compromis final que prend le réseau quand il atteint un équilibre est identifié comme la solution du problème de cognition.

Dans ce modèle de cognition, les zones unimodales du cortex fournissent les blocs de construction les plus véridiques de l'expérience. Les nœuds transmodaux fixent ces informations sous une forme ayant une cohérence temporelle et contextuelle. Les gabarits spécifiques d'objets et de mémoires prennent la forme d'une distribution ayant une spécialisation régionale considérable. Ceci donne un système d'une grande souplesse et d'un pouvoir de traitement considérable que l'on peut décrire comme un Traitement à Distribution Sélective.

The human cerebral cortex is divided into five major functional zones that can be designated as primary sensory-motor, unimodal association, heteromodal association, paralimbic and limbic. These five zones are related to each other in the form of a continuous cytoarchitectonic gradient ranging from the most specialized primary sensory-motor areas to the least differentiated allocortical limbic structures (Mesulam 1985).

Among these cortical areas, only constituents of the limbic zone have major reciprocal connections with the hypothalamus. In keeping with this connectivity, the behavioral affiliations of the limbic zone are polarized towards the internal milieu and deal with realms such as emotion, motivation, memory and homeostasis. At the other extreme of cytoarchitectonic differentiation, the primary sensory motor areas are polarized towards the extrapersonal world. These two extremes are separated by three zones of association cortex (unimodal, heteromodal and paralimbic), which bridge the gap between the internal milieu and the extrapersonal space. The unimodal and heteromodal areas deal mostly with perceptual synthesis and motor planning, whereas the paralimbic areas deal mostly with directing emotion and motivation towards the appropriate intrapsychic and extrapersonal targets.

How the architecture of information transfer among these five zones ultimately leads to the emergence of consciousness and cognition remains as one of the most challenging questions in all of the life sciences. An important milestone in this field of research occurred in 1965 with the publication of the « Disconnection Syndromes » by Norman Geschwind. Geschwind suggested that the single most important substrate for complex behavior was based on an orderly hierarchy of corticocortical connectivity. At around that time, modifications of selective silver impregnation methods made it possible to study this type of connectivity in the rhesus monkey. The initial observations based on this methodology were summarized in two classic papers, one by Jones and Powell (1970) and the other by Pandya and Kuypers (1969).

In the visual system, for example, these studies showed that monosynaptic projections extended serially from V1 (area 17) to a primary visual association zone (area 18), to a secondary visual association zone (area 19), and then to a tertiary (downstream) visual association zone in the temporal lobe. A similar hierarchical cascade of connecti-

vity was identified in the somatosensory and auditory modalities. It was also shown that the more downstream association zones in all three modalities sent overlapping projections to multimodal convergence areas in the frontal, temporal and parietal lobes. These convergence zones were thought to play pivotal roles in many aspects of complex cognition, including language acquisition, concept formation and memory storage.

The relevance of multimodal convergence to cognition initially appeared self-evident. In language acquisition, for example, a child would see a pencil and simultaneously hear the word pencil. The visual and auditory patterns would become associatively linked within a multimodal convergence area. The next time the child encountered a pencil, the visual input would rekindle the appropriate auditory association and the child would have learned to name the object.

This hierarchical associationistic model can trigger at least three types of objections. First, it is based on serial processing that is almost certainly too slow for the immensely rapid computations necessary for human cognition. Secondly, it requires an uncanny degree of accuracy if multimodal information is to be encoded in convergent rather than distributed form. Pencils come in thousands of shapes, colors and locations and this model requires each one of these visual patterns to link up with exactly the same multimodal residue in order to rekindle the appropriate auditory association that would lead to correct naming. Thirdly, there are epistemological problems with the notion that knowledge is encoded in convergent form since this can lead to considerable cross-channel contamination of the constituent information.

In addition to these theoretical concerns, much more powerful anatomical methods, based on the axonal transport of tracer substances, started to reveal a somewhat different anatomical organization in visual pathways. The existence of monosynaptic projections from V1 (area 17) to area 18 (V2) was confirmed. From then on, however, the situation became more complex. It turned out that V1 and V2 collectively sent multiple parallel pathways to multiple « upstream » visual areas that included those designated as V3, V4, MT, V5 and VP. The subsequent flow of visual information to « downstream » association areas occurred along two divergent trunks, one directed dorsally the other ventrally. The dorsal path conveyed

visual information to parietal and frontal areas and was dubbed the « where » pathway because it dealt with spatial attributes of visual information. Damage along this pathway led to the various manifestations of Balint's syndrome and hemispatial neglect. The ventral pathway conveyed visual information to the limbic system, temporoparietal language areas and downstream visual association cortex in the temporal lobe. This was dubbed the « what » pathway because it dealt with visual object identity. Damage along this pathway led to the various manifestations of pure alexia, visual amnesia, prosopagnosia and object agnosia. Instead of a relatively simple linear and serial hierarchy, these pathways displayed a more complex organization based on multiple nodes of convergence and divergence embedded within multiple parallel lines of processing (See Felleman and Van Essen, 1991; Mishkin *et al.*, 1983 for review).

The « purpose » for these multiple nodes of divergence and convergence is probably to extract (or insulate) the elementary features of composite visual information that reach area V1 so that these elementary features can become available for multiple combinatorial rearrangements in a way that enrich the resultant re-representation of visual reality. This is like decomposing white light into its spectral constituents so that the primary colors can be mixed to produce multiple secondary and tertiary colors that are not present in the initial spectrum.

In keeping with this formulation, physiological and behavioral experiments in monkeys are showing that the more upstream (peristriate) visual association areas are specialized for encoding unitary features of visual experience whereas the more downstream areas (in the temporal and parietal lobes) are specialized for encoding composite features. For example, peristriate area V4 is specialized for the perception of color and peristriate area MT (V5) is specialized for the perception of visual motion. The more downstream visual association areas in the dorsal parietal association cortex can compute the spatial position of visual stimuli by combining retinotopic information with information about eye position. Furthermore, neuronal ensembles in downstream visual association cortex of the temporal lobe can encode the composite visual components of faces and objects (see Mesulam, 1993 for review).

It is reasonable to assume that a similar though perhaps more complex arrangement also exists in the human brain. Positron emission tomography has revealed an area of selective activation within the posterior part of the lingual and fusiform gyri (corresponding mostly to area 19) when normal subjects are shown complex colored patterns (Lueck *et al.*, 1989). This may be the location of area V4 in the human brain and damage to this part of the brain leads to contralateral hemiachromatopsia. A separate area of selective activation is detected more laterally at the confluence of area 19 with area 37 when subjects are exposed to patterns of visual movement. This region may correspond to area MT (Corbetta *et al.*, 1990; Lueck *et al.*, 1989).

The location of downstream visual association areas is also being identified in the human brain. Bilateral lesions in the more anterior aspects of the fusiform and lingual gyri, (corresponding to the confluence of areas 19 and 37), leads to prosopagnosia and visual object agnosia, suggesting that this part of the human brain may contain the downstream temporal visual association regions specialized for encoding visual templates of faces and other complex objects (Damasio 1985). Positron emission tomography has demonstrated a dorsolateral area of selective activation at the confluence of area 19 with the angular gyrus when subjects are shown written words that they do not have to process semantically, suggesting that this part of the brain may contain a downstream parieto-temporal visual association area that can encode visual word forms (Petersen *et al.*, 1988). Positron emission tomography has also helped to identify an area of selective activation dorsolaterally at the confluence of area 19 and 7 when subjects are asked to detect the spatial location of visual stimuli (Haxby *et al.*, 1991). This region may correspond to the downstream parietal visual association area specialized for computing the spatial location of visual stimuli.

It is important to realize that these nodes of visual association cortex, especially the downstream ones, act as relative specialists rather than as dedicated modules. For example, whereas of the fusiform-lingual gyri may play a critical role in forming visual templates of faces and objects, the same area may also participate in other complex visual functions such as color perception, the encoding of visual word forms and so on, but not to the same extent. Furthermore, although the formation of visual face templates may be done most effectively in the fusiform-lingual gyri, this process may also take place, though less effectively, at other nodes of visual cortex. This arrangement leads to distributed processing, but with regional specializations (Mesulam 1990). It is quite likely that other sensory modalities are organized in an analogous fashion with respect to the arrangement of upstream areas, downstream areas and parallel processing.

Modern neuroanatomy is showing that unimodal association areas (especially the upstream components) in a given modality have almost no interconnections with unimodal association areas in other modalities (Mesulam 1985). This arrangement prevents cross-channel contamination in the encoding of modality-specific information. Furthermore, physiological observations are showing that unimodal association areas can encode new information and that they have the ability to show plasticity in response to experience (Eskandar *et al.*, 1992).

If the purpose of having a brain was to keep a veridical record of ongoing sensory experience, unimodal areas would have sufficed. However, the moment that the ongoing experience stopped, a brain which had only unimodal areas would face serious challenges. First, there would be no way of knowing how information in one sensory domain was related to information in another since there are no direct connections between unimodal areas in different

modalities. The record of experience would thus be temporally and contextually incoherent across multiple realms. Furthermore, a brain consisting exclusively of primary and unimodal areas might be able to determine if sensorial qualities of two words are the same or different but could not bridge the gap between word and meaning because the sensory representation of the words could not access associations in other realms.

These limitations in brain design disappear when one considers the contributions of « transmodal » areas in the heteromodal, paralimbic and limbic zones of cortex. Contrary to earlier formulations, it is no longer thought that these transmodal areas contain a convergent and multimodal residue of knowledge. Instead, it is thought that the role of these transmodal areas is to contain an « address book » or « road map » for the multifocal binding and calling up of distributed information belonging to composite events, thoughts, concepts and memories (Damasio 1989 ; Mesulam 1990 ; Mishkin 1982).

This model has two great advantages. First, it allows knowledge to be encoded in a much more flexible distributed rather than rigid convergent form. Secondly, it protects the fidelity of modality-specific encoding (at least at some stages of processing) by preventing cross-modal contamination. This system places a great emphasis on transmodal areas for binding fragments of experience into coherent events and also for leading from partial information to associative recall, from word to meaning, from sensation to perceptual synthesis and from the sensory representation of objects and faces to their ultimate recognition. The transmodal areas also actively participate in language comprehension, memory formation and perceptual synthesis. Their unique role, however, and one that they do not share with constituents of unimodal areas, is their ability to introduce temporal and contextual coherence to distributed information. We do not exactly understand how the road maps are formed within transmodal areas but this may follow the Hebbian rule of neuronal assemblies (Hebb, 1949).

The limbic and paralimbic zones of cortex acquire a special importance in this model since it appears that the formation and reactivation of road maps belonging to recent experience necessitates the participation of transmodal nodes in the limbic system. There are at least two reasons for this. First, components of the limbic system display a high level of physiological and structural plasticity (Benowitz *et al.*, 1989 ; Bliss and Collinridge, 1993). Second, limbic structures are in a position to act as detectors of hedonic valence so as to endow distributed information belonging to motivationally relevant recent events with survival advantage (in a Darwinian sense) when it comes to storage and recall. When a sufficient portion of the cortical or subcortical components of the limbic system is destroyed, it becomes impossible to keep adequate files of how distributed information belonging to recent events is interrelated even though the constituent fragments of the event may be stored quite well in multiple nodes belonging to unimodal and other transmodal areas. This is why

patients with limbic lesions show severe retrograde and anterograde amnesia for the declarative recall of recent events even though they may show remarkable preservation of implicit memory (Schacter *et al.*, 1991). Implicit memory means that the fragments of experience have been encoded quite well (mostly in unimodal areas) but that they cannot be integrated into the overall fabric of declarative experience and consciousness. *Consolidated* memories do not display this dependency on limbic structures. In recalling the meaning of a familiar word, for example, the appropriate sensory representation of the word can access the distributed associations that lead to meaning through transmodal nodes that remain outside the limbic system, e.g. those belonging to Wernicke's area.

Specific parts of transmodal areas act like neural gateways for accessing relevant domains rather than as centers dedicated to the execution of specific cognitive functions (Mesulam 1990). Paradoxically, these transmodal areas also provide « neural bottlenecks » in the sense that they constitute the regions of maximum vulnerability for lesion-induced deficits in the pertinent cognitive domain. In the process of memory, for example, the hippocampus does not act as a bank for specific memories but as a neural hub (or gateway) for accessing relevant sets of distributed information. When limbic structures such as the hippocampus are damaged, the patient does not lose the representation of specific memories. Instead, it is the coherence of recall and storage which is impaired. A further example is provided by the role of posterior parietal cortex (area 7) in forming a spatially-addressed representation of the extrapersonal world. This does not occur because area 7 contains a convergent pellet of multisensory information but because it acts as a critical node for accessing distributed, spatially-addressed information in multiple sensory realms. When area 7 is destroyed, the constituent sensory information is still available but it cannot be integrated interactively into a coherent spatial representation of the extrapersonal world, leading to complex deficits such as unilateral neglect.

A third example comes from considering the neurology of language. Lesions in Wernicke's area lead to comprehension deficits not because this area acts as a word bank but because it provides a critical node (or funnel) for two-way interactions between sensory word representations and the distributed associations that lead to meaning. Damage to Wernicke's area does not necessarily lead to a loss of individual word representations. Instead, thoughts cannot be transformed into the appropriate words and words cannot lead to meaning.

This computational model places a great emphasis on transmodal areas of the cerebral cortex. Recent observations, especially those based on the neurology of hemispatial neglect, are indicating that these transmodal areas are interconnected with each other and with downstream nodes of unimodal association areas in a way that can sustain complex computational architectures including parallel

distributed processing (see Mesulam 1981 ; 1990 ; Morecraft *et al.*, 1993 for review).

Clinical observations had initially suggested the existence of a one-to-one relationship between unilateral neglect and lesions in the posterior parietal cortex of the right hemisphere. Subsequent reports, however, indicated that unilateral neglect could also occur after lesions of frontal and cingulate cortex. Physiological and anatomical experiments showed that each one of these three cortical areas had a special contribution to make to directed attention. It appeared that the parietal component was closely related to the sensorial aspects of directed attention, the frontal component to the exploratory motor aspects and the cingulate component to the motivational aspects. Neuroanatomical experiments in monkeys showed that these three areas were interconnected by reciprocal monosynaptic projections.

On the basis of this information, the suggestion was made that the process of directed attention to the extrapersonal space was organized at the level of a large scale distributed network containing three cortical components. One component was centered around the posterior parietal cortex (area 7 in the monkey) and acted as a critical node for accessing a spatially-addressed multimodal representation of the extrapersonal space. The second component was centered around the frontal eye fields (area 8 in the monkey) and acted as a node for accessing motor maps involved in the distribution of exploratory motor acts with the head, eyes and limbs. A third component was centered around the cingulate gyrus (areas 23-24 in the monkey) and acted as a node for accessing motivational maps involved in expectancy. The proper execution of directed spatial attention requires the integrity and harmonious interaction of these three components. Damage to any one of these components or to their interconnections could give rise to neglect. The multiplicity of neglect-causing lesions did not reflect a chaotic anatomical organization but, instead, showed that the anatomical mapping was at the level of a distributed network rather than at the level of a dedicated center in posterior parietal cortex.

A more detailed investigation of interconnections between the two major components of this network, the frontal eye fields and posterior parietal cortex, showed that these two areas were interconnected not only with each other but also with an additional set of identical cortical areas. This anatomical organization, summarized in *figure 1*, may well represent a general principle of network interconnectivity. A and B in *figure 1* stand for the epicenters of a large scale distributed network. In the case of memory function, A and B would represent the amygdala and hippocampus. In the case of language function, A and B would correspond to Wernicke's and Broca's area. In the case of directed attention, A and B would correspond to the frontal eye fields and posterior parietal cortex. The neuroanatomical experiments in the attentional network of the rhesus monkey suggest that if A is connected to the additional cortical association areas 1, 2 and 3, then B is also connected to 1,

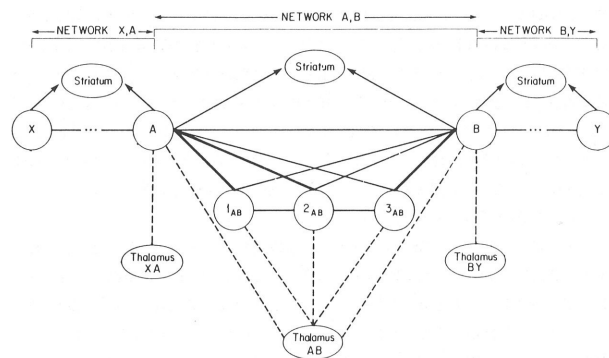


FIG. 1. — A schematic representation of large scale neural networks. From Mesulam, 1990.

Une représentation schématique des réseaux neuraux de grande échelle. De Mesulam, 1990.

2 and 3. The resultant architecture of connectivity is compatible with parallel distributed processing.

In resolving a cognitive problem, a set of cortical areas arranged in this fashion can execute an extremely rapid survey of a vast informational landscape until the entire system settles into a best-fit with respect to the multiple goals and constraints engendered by the problem. This computational architecture is quite compatible with cognitive tasks such as deciding which words best express a thought or how to reconstruct a specific complex memory. There are no single « correct » answers but an entire family of possibilities, each leading to a different solution within the relevant matrix of goals and constraints.

Anatomical experiments have also shown that members of an interconnected pair of cortical areas (e.g. A and B) are likely to send interdigitating projects to the striatum (Yeterian and Van Hoesen, 1978). The striatum receives cortical input but does not project back to cortex. We therefore made the suggestion that the striatum could act as an « efference synchronizer » for such a set of cortical areas (Mesulam, 1990). There is also evidence to show that if a thalamic subnucleus projects to both members of an interconnected pair such as A and B, it is also likely to project to areas 1, 2 and 3. Cortical areas have extensive corticocortical connections so that each member of association cortex is likely to belong to multiple intersecting networks. Thalamic subnuclei, however, have almost no interconnections among each other and may thus play an important role in setting coactivation boundaries for individual networks (Mesulam, 1990). The thalamic, cortical and striatal components shown in *figure 1* represent the major constituents of large scale neurocognitive networks.

The organization shown in *figure 1* has several practical implications. First, it implies that even a discrete lesion in transmodal cortex may lead to multiple cognitive deficits since each transmodal area belongs to more than one distributed network. Secondly, this organization implies that the same complex cognitive deficits can be disrupted

after lesions in many different parts of the brain, cortical as well as subcortical, as long as these parts belong to the same distributed network. Thirdly, this arrangement also indicates that functional imaging studies are likely to reveal multiple areas of activation even when the subject is engaged in a single task and when all the appropriate « subtraction » controls have been obtained.

These considerations show that the hierarchical transfer of information and the predominantly convergent encoding of knowledge is unlikely to offer a suitable substrate for cognitive processes. The alternative Selectively Distributed Processing model that I am proposing is one in which the most veridical building blocks of experience are embedded within unimodal association cortex. Transmodal areas of the cerebral cortex fulfill their function by coordinating or binding this distributed modality-specific information into coherent multidimensional knowledge. Transmodal areas and the downstream components of unimodal areas appear to be interconnected in a way that allows complex and flexible computational architectures, including parallel processing. These cortical components, together with corresponding regions of the thalamus and striatum, make up large-scale distributed networks which provide the immediate anatomical substrates of individual cognitive domains.

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