
The Role of Neural Context in Large-Scale Neurocognitive Network Operations

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Brain connectivity has been a central factor in the development of theories about the mind-brain link. In its simplest form, brain connectivity analysis has revealed serial processing systems, wherein specific neural elements (neurons, neuronal assemblies, neuronal populations) cooperate to express a circumscribed function that is realized as information passes through the system in a feedforward manner. Consideration of parallel architectures provides a more complex view of system processing by revealing that each brain region may impact many other regions through direct and indirect routes, including areas from which it receives its input. Regardless of the specific architecture, the notion that cognition results from the operations of large-scale neural networks has been present in various forms throughout the history of neuroscience (Finger, 1994; Bressler 1995, 2002). For a large part of that history, it was difficult to verify this notion because most available methods only allowed investigation of small parts of the nervous system in isolation. Ideally, simultaneous measures from many parts of the brain must be analyzed to understand the operations of large-scale networks that underlie cognition. In the past few decades, advances in functional neuroimaging, including Positron Emission Tomography (PET) functional Magnetic Resonance Imaging (fMRI), and EEG/MEG-based source localization, have allowed simultaneous distributed measures of brain function to be related to cognition.

This chapter examines the role of a critical aspect of brain function, which we call *neural context*, in the selective functioning of interacting neural systems in cognition. We define neural context as the local processing environment of a given neural element that is created by modulatory influences from other neural elements. Neural context allows the response properties of one element in a network to be profoundly affected by the status of other neural elements in that network. As a result of neural context, the relevance of a given neural element for cognitive function typically depends on the status of other interacting elements (McIntosh 1999; Bressler 2003a). By this definition, the processing performed by a given brain area may be modulated by a potentially

large number of other areas with which it is connected. Since brain areas are most often bidirectionally connected, the neural context of each connected area emerges spontaneously from its interactions. Furthermore, to the extent that basic sensory and cognitive operations share similar brain constituents, they experience similar neural contextual influences.

Neural context refers only to the context that arises within the brain as a result of interactions between neural elements. In this chapter, we also distinguish a related form of context, which we refer to as *situational context*. Unlike neural context, situational context represents a host of interrelated environmental factors, including aspects of the sensory scenes and response demands of both the external and internal milieus. A red light presented to a person in isolation usually means nothing, but a red light presented to that person while driving elicits a situationally specific response. Situational context is most often what researchers have in mind when they examine “contextual effects” on the brain (Hepp-Reymond et al., 1999; Chun 2000; Herzog et al., 2002; Bar 2004; Beck & Kastner 2005).

In most normal circumstances, neural context is shaped by situational context. The environments in which animals and humans must survive have a high degree of structural complexity, an important consequence of which is a fundamental uncertainty in the organism’s perceptuo-motor interactions with those environments. Complete information is never available to allow total certainty about the state of the environment and the optimal course of action in it. The limited information that the organism has about its environmental situation usually renders ambiguous its perceptual interpretation of environmental entities and the appropriate actions to be directed toward them. The ability to utilize and manipulate information about the organism’s situational context, can dramatically reduce uncertainty, thereby enhancing the organism’s interactions with the environment and lending survival advantage to its species.

Since the complexity of the environment’s structure spans multiple structural and temporal scales, situational context must affect all types of cognitive function, including sensation, perception, emotion, memory, planning, decision making, and action generation. It is reasonable to infer therefore that neural context should also be of primary importance in the implementation of those functions by the brain. In other words, just as situational context can have effects at multiple scales and across multiple behaviors, so too is neural context expected across all spatial and temporal scales in the brain and across all behaviors.

1 Anatomical and Physiological Foundations of Neural Context

A fundamental factor that supports contextual processing in the brain is its large-scale connectivity structure. The anatomical connectivity of the cerebral cortex, in particular, appears to have evolved to support contextual

processing. The cortex consists of a large number of areas profusely interconnected in a complex topological structure, which places strong constraints on its functional dynamics (Sporns et al., 2000; Bressler & Tognoli 2006; Sporns & Tononi 2007). In sensory systems, local cortical networks are interconnected by feedforward, feedback, and lateral connections (Felleman & Van Essen 1991), all of which may serve to provide neural context for the processing that occurs in a given local network. Integration along convergent feedforward pathways from peripheral receptor sheets may be sufficient for some forms of sensory contextual processing, whereas other forms may require lateral and feedback connections. Contextual processing in cortical motor and association areas also critically depends on the complex patterning of interconnected local networks (Brovelli et al., 2004).

Although the local networks in different cortical areas show cytoarchitectonic variation, the cellular components and internal connectivity of cortical circuits are generally similar throughout the cortex. What distinguishes the specialized function of any local cortical network is its topological uniqueness, i.e. its particular pattern of interconnectivity with other networks. The unique set of local networks with which a given local cortical network is directly connected has been called its “connection set” (Bressler 2002, 2003a) or “connectional fingerprint” (Passingham et al., 2002). Providing direct synaptic input to the circuit elements of the local network, the networks of the connection set have privileged status in creating context for the processing in that local network. The connection set of a local network thus determines the contextual guidance that the network receives during processing, and consequently modulates the trajectory of the local processing dynamics.

A second factor in cortical contextual processing is spatial pattern formation in local cortical networks (Beggs et al., 2007). The generation and transmission of spatially patterned activity by local networks is central to interarea communication in the cortex (Freeman 2003; Andras 2005), and provides a realistic framework for contextual modulation. From this viewpoint, the processing dynamics in a local cortical network is manifested by the formation of spatially patterned activity under modulation by spatial activity patterns transmitted from the members of its connection set (Bressler 2004). Neural context is thereby implemented through the interaction of transmitted spatial activity patterns from the connection set with patterns generated by the local circuitry. Transmission uses parallel, convergent, and divergent pathways between transmitting and receiving networks (Fuster 2003).

A third aspect of cortical function necessary for contextual processing is reentrant interaction (Tononi et al., 1992). Since the anatomical interconnection of cortical areas is largely bidirectional (Felleman & Van Essen 1991), a local network in one area receives feedback from the same local networks to which it transmits in other areas, i.e. transmitted influences are reciprocated by reentrant influences from receiving networks. Reentrant interactions that a local network undergoes with its connection set modulate its spatial pattern

processing, resulting in the alteration of its generated patterns. Reentrant interactions thereby enrich the processing capability of the local circuitry.

Natural environments are rich with information about situational context. The capacity to utilize that information enhances the behavioral adaptation of animals to their surroundings. The exploitation of situational context information affords an adaptive advantage, which exerts a strong selection pressure for the evolution of neural architectures and mechanisms conducive to the efficient processing of that information. Primates appear to have evolved special behavioral prowess due to their highly developed contextual processing abilities. The behavioral capability for taking advantage of situational context information depends on the brain's faculty for processing that information. It is quite likely that the neural processing of information about situational context depends on the deployment of neural context, by which the local processing in an area of the brain is modulated by its interactions with other brain areas. To understand the use of situational context information in behavior, we consider here the implementation of neural context in the primate cerebral cortex, treating in particular some basic anatomical and physiological features that allow and promote cortical contextual processing.

It is generally agreed that the functions of local networks in circumscribed cortical areas depend on interactions among the neuronal elements of their circuitry (DeFelipe et al., 2002; Douglas & Martin 2004; Bressler & Tognoli 2006). There is also growing appreciation of the fact that cortical circuit function is expressed in real time by the dynamics of these interactions (Lopes da Silva et al., 1994; Friston & Price 2001; Siegel & Read 2001; Breakspear & Jirsa 2007). Neural context for the functional dynamics of a local cortical circuit is provided by modulations impinging on the circuit elements from other connected circuits. It may be said that the circuit dynamics undergo *contextual guidance* by such modulatory influences. In simulation studies, it has been shown that the computational capabilities of a local processor can be greatly enhanced by contextual guidance from the outputs of other processors. (Becker & Hinton 1992; Kay & Phillips 1997; Phillips et al., 1998). Contextual guidance may similarly be at work in normal cortical operations (Phillips & Singer 1997).

In our view, the neural context for processing in a local network emerges spontaneously through the reentrant interactions that the network undergoes with the members of its connection set. The modulation of spatial pattern formation that occurs in the local network as a result of those interactions constitutes contextual guidance of the local processing dynamics, constraining it to trajectories that are contextually consistent with activity in the connection set. Since reentrant interactions involve interconnected local networks distributed throughout the cerebral cortex, it is to be expected that spatial pattern formation will proceed concurrently in each local network under contextual modulation from all the networks to which it is connected. Thus, due to the massive large-scale interconnectivity of cortex, contextual effects are expected to be ubiquitous, and contextual guidance to occur concurrently in

numerous widespread local networks, each both transmitting and receiving contextual effects.

The interplay of multiple recurrent interactions across the cortex has been postulated (Bressler 2004) to lead to the emergence of a global cortical context that reflects the current situational context. This process is thought to involve the convergence of local networks to mutually consistent activity patterns that realize informational coherence and incoherence relations (Thagard & Verbeurgt 1998). Thus global neural context is proposed to achieve congruence with the situational context by convergence of spatial activity patterns in interacting networks to informationally consistent states. Currency with changes in situational context is maintained by ongoing disturbance and re-establishment of consistent states (Freeman 2006).

2 The Role of Neural Context in Cognition

Neural context at multiple scales

As a principle of brain function, neural context can be most easily demonstrated in relatively simple nervous systems, such as those of invertebrates. While these systems admittedly do not have the broad behavioral repertoire of primates, if contextual effects are indeed central to neural network operation, they should be present in simpler organisms. It has indeed been demonstrated in the *Aplysia* abdominal ganglion that the same neurons fire during performance of quite different behaviors (Wu et al., 1994). What appears to differentiate these behaviors is not the activity of a particular neuron, or group of neurons, but rather the overall activity patterns of an entire network. Such observations have been made in other invertebrate species across highly dissimilar behaviors (Popescu & Frost 2002), suggesting that the observed behavioral variation resides in the large-scale dynamics of entire networks rather than dedicated circuits (Kristan & Shaw 1997).

In the mammalian primary visual cortex (V1), neural context has been established as playing a major role in determining the receptive field properties of single neurons (Zipser et al., 1996; Gilbert 1998; Das & Gilbert 1999; Wörgötter & Eysel 2000; Gilbert et al., 2001; Stettler et al., 2002; Li et al., 2004). The receptive fields of V1 neurons were traditionally viewed as being spatially limited and tuned to simple stimulus attributes. However, it is now known that neural context influences the receptive field structure of V1 neurons. Thus, the response properties of these neurons are not determined solely by feedforward, convergent excitation from visual thalamic cells, but are also affected by lateral and feedback connections, some of which may be inhibitory. Neural contextual influences on V1 neurons reflect situational context in a variety of its forms. These include external situational factors derived from the global spatial and temporal characteristics of the visual scene. They also include internal situational factors such as the activation history of the local

cortical network in which the neuron is embedded, attentional influences, and the global state of arousal. The substantial body of evidence demonstrating these effects in V1 provides a vivid picture showing how situational context can affect neural operations through neural context.

Evidence that neural context also operates at a larger scale across cortical areas comes from studies showing that the processing of sensory input in one cortical area or region can depend on the processing status in another. Within the visual system, V1 neuron responses to illusory contours appear to depend on contextual guidance from V2 neurons that integrate spatial information over a broader spatial range (Lee 2003). Inter-sensory contextual modulation may also occur. For example, contextual modulation of responses in the visual cortex to visual stimuli can result from the concurrent processing of auditory stimuli (Bhattacharya et al. 2002).

As mentioned above, it has been hypothesized (Bressler 2004) that cortical context emerges from multiple recurrent interactions among cortical areas. An important prediction from this hypothesis is that the representation of categorical information in the cortex should be reflected by patterns of activity distributed across large cortical expanses rather than by the activity in a single specific area. Category-specificity has rapidly become a major focus in human neuroimaging research, exemplified by studies demonstrating face-category-specific responses in the fusiform gyrus (Kanwisher et al., 1997). However, a drawback of many such studies is that they employ very strict univariate statistical criteria that conceal all but the largest amplitudes in the activity patterns. Nonetheless, studies that have characterized the distributed response to faces have reported that greater category-specificity is revealed by the entire activity pattern in occipital and temporal cortices than by any specific area (Ishai et al., 1999; Haxby et al., 2001). Importantly, these studies have determined that the specificity of the distributed response is not dramatically altered if the regions typically associated with the category of interest are excluded.

The effect of neural context is seen in other cognitive operations as well. Working memory function, for example, is known to be supported by mutual influences among neurons in many different brain regions, and is not uniquely localized to prefrontal cortex (PFC) as was long thought (Fuster 1997, 2003). In a study of visual working memory, similar delay-period activity was observed in dorsolateral prefrontal and inferior temporal cortices, and cooling of either area induced similar effects on the activity in the other area (Fuster et al. 1985). Furthermore, a study of spatial working memory demonstrated nearly identical delay-period activity profiles in dorsolateral PFC and posterior parietal cortex (PPC) (Chafee & Goldman-Rakic 1998), and a follow-up study showed similar effects in either area from cooling of the other (Chafee & Goldman-Rakic 2000).

On balance, these studies support the conclusion that neural context operates in working memory through mutual interactions among distributed cortical association areas (Barash 2003). Regions such as dorsolateral PFC

and PPC seem central to working memory operations, but their contribution can only be realized by the particular set of interactions in which they engage at a given point in time.

Neural context and effective connectivity

The estimation of effective (or functional) connectivity provides strong evidence for variation in the recurrent interactions between neural elements that is thought to underlie neural contextual effects. To characterize interactions within the dorsal and ventral visual cortical processing streams (Ungerleider & Mishkin 1982) McIntosh et al. (1994) applied structural equation modeling to PET data to measure the effective connections specific to object (face matching) and spatial processing (location matching). Results from the right hemisphere analysis are presented in Fig. 1 (left hemisphere interactions did not differ between tasks). As expected, effects along the ventral pathway extending into the frontal lobe were stronger in the face-matching model, while interactions along the dorsal pathway to the frontal lobe were relatively stronger in the location-matching model.

Among posterior areas, the differences in path coefficients were mainly in magnitude. Occipitotemporal interactions between area 19v and area 37 were stronger in the face-matching model while the impact of area 17/18 to 19d and the occipitoparietal influences from area 19d to area 7 were stronger in the location-matching model. The model allowed for interactions between

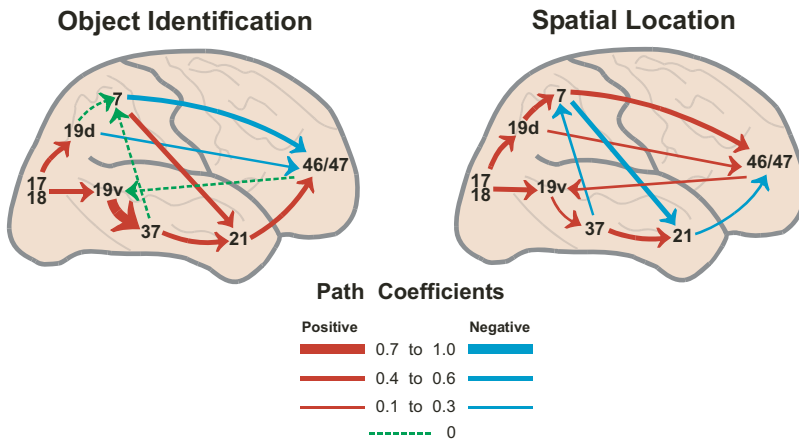


Fig. 1. Effective connectivity between cortical areas in the right hemisphere for object and spatial vision operations. The numbers on the cortical surface refer to Broadmann areas (d=dorsal, v=ventral). The arrows represent the anatomical connections between areas and the magnitude of the direct effect from one area to another is proportional to the arrow width for each path (Adapted from McIntosh et al. 1994)

the dorsal and ventral pathways with connections from area 37 to area 7 and from area 7 to area 21. In the right hemisphere, the interactions among these areas showed task-dependent differences in magnitude and sign. The temporoparietal influence of area 37 on area 7 was relatively stronger in the location-matching model. The parietotemporal influence of area 7 on area 21 showed a difference in sign between the two functional models. These results show that while the strongest positive interactions in each model may have been preferentially located within one or the other pathway, the pathways did not function independently, but exerted contextual modulatory influences on one another.

Another important result of this study is that, although the PFC did not show a difference in mean activity between tasks, processes involving PFC shifted depending on the task. The influence of the dorsal and ventral pathways on frontal cortex was similar in magnitude for the two tasks, but the origin of the positive and negative influences differed, implying that the qualitative nature of influence on the frontal lobe was different (positive influences in the location-matching model were from areas 7 and 19d, and in the face-matching model was from area 21). In terms of neural context, this result demonstrates that it is not an area's activity per se that is the key to understanding its contribution to a task, but rather its pattern of interaction with other areas in large-scale networks.

Network interactions that underlie cognitive operations are observable as differences in the effective connections between elements of the network. As illustrated above, if visual attention is directed to the features of an object, effective connections among ventral posterior cortical areas tend to be stronger, whereas visual attention directed to the spatial location of objects leads to stronger interactions among dorsal posterior areas. Another way that cognitive operations may be observed is through the modulation of effective connections that occurs when one area provides an enabling condition to foster communications between other areas. Such enabling effects may represent a primary mechanism whereby situational context is translated into neural context.

The most obvious example of neural context is top-down attentional control, whereby elements at higher processing levels can alter the processing mode of lower-level elements. In an fMRI study by Buchel and Friston (1997), subjects alternated between periods of overt attention to changes in a moving visual dot pattern and periods where they did not attend to the display. Two models were evaluated. In the first, a feedforward network from primary visual cortex (V1) to dorsal occipital cortex (V5) to PPC, visual attention was associated with elevated path coefficients as compared to inattention. The second model was an elaboration of the first, designed to assess whether the PFC had a modulatory influence on the effective connections between V5 and PPC. This second model, displayed in Fig. 2, revealed that PFC activity had a direct influence on PPC, as well as on the interaction term for the effect of V5 on PPC (PFC Mod \rightarrow PP). This modulatory effect was shown to vary

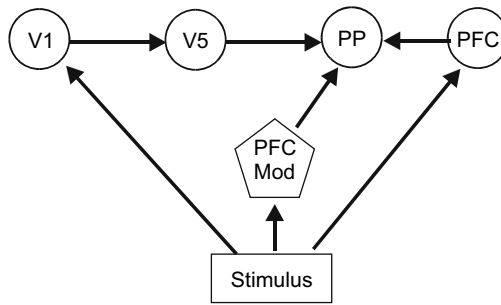


Fig. 2. Effective connectivity model for attentional modulation of visual processing of motion. Stimulus effects impact on V1 and PFC, and determine when attentional demands change via PFC Mod. The attentional effect was strongest at PFC, and through the modulatory effects, PFC also impacted the responsiveness of PP to the influence from V5. (Adapted from Buchel and Friston 1997)

in an activity-dependent manner, such that the effect from V5 to PPC was strongest when PFC activity was highest.

In a second study, Buchel et al. (1999) provided a convincing demonstration that changes in effective connectivity are directly related to learning. Training subjects to associate visually-presented objects with their location in space forced a learning-dependent change in the effective connections between dorsal and ventral visual processing streams. Furthermore, a remarkable correlation was found between the rate of learning and the change in the influence of the dorsal-stream PPC on the ventral-stream inferior temporal cortex.

A salient demonstration of neural context comes from a recent paper examining functional connectivity of the medial temporal lobe (MTL) in relation to learning and awareness (McIntosh et al., 2003). In a sensory learning paradigm, subjects were classified as AWARE or UNAWARE based on whether they noted that one of two tones predicted a visual event. Only AWARE subjects acquired and reversed a differential response to the tones, but both groups showed learned facilitation. The observation that MTL activity was related to learned facilitation in both groups at first appeared inconsistent with an earlier hypothesis that the MTL is critical for learning with awareness, but not when learning proceeds without awareness (Clark & Squire 1998). However, it was discovered that the functional connectivity patterns of the MTL were completely different for the two subject groups. In the AWARE group, dominant MTL effective connectivity was observed with prefrontal, occipital and temporal cortices, whereas in UNAWARE subjects, functional connectivity was more spatially restricted to inferior temporal cortex, thalamus and basal ganglia. We conclude that the MTL was involved in learning in both groups, but its functional role differed between the two groups because the neural context for its processing was different.

Another perspective on working memory emphasizes its close relation to sustained attention (McElree 2001; Fuster 2003; Deco & Rolls 2005; Bressler & Tognoli 2006). Both working memory and sustained attention involve activity in overlapping regions of PPC, PFC, and anterior cingulate cortex (ACC). In an fMRI study of the relationship between attention and working memory, Lenartowicz and McIntosh (2005) used two variants of a two-back working memory task: a standard version with strong attentional demands, and a cued version that more strongly promoted memory retrieval. Activation of ACC was found in both tasks, though it was more sustained in the standard condition. However, the regions functionally connected to the ACC, and the relation of the connectivity patterns to memory performance, differed completely between tasks. In the standard task, the observed pattern was related to a speed-accuracy tradeoff, with strong functional connection of ACC to PFC and PPC. In the cued task, the connectivity pattern was related only to better accuracy, and involved functional connections with middle and inferior PFC, and inferior temporal cortex. By virtue of these different patterns of functional connectivity, the contribution of ACC to attention- and memory-driven performance was similarly changed. In other words, although the activity of ACC was similar in both tasks, each task invoked a different neural context within which the ACC interacted, resulting in two very different behavioral profiles. The difference in neural context, and not in the activity of ACC per se, reflected the difference in the functional role that this region fulfilled.

In another study of ACC functional connectivity (Stephan et al., 2003), the question was examined of whether hemispheric functional asymmetry was determined by a word stimulus (short words, with one letter colored red) itself or by the task, i.e. the situational context. In one instance, subjects judged whether the word contained the letter "A", ignoring the red letter, and in another instance, they made a visuospatial judgment indicating whether the red letter was right or left of center. A direct comparison of the activity (measured with fMRI) revealed strong hemispheric differences. The letter task produced higher activity in the left hemisphere, while the visuospatial task produced higher activity in the right hemisphere. The ACC was similarly active in both tasks relative to baseline, but showed distinctly different patterns of effective connectivity between tasks. Specifically, during the letter task, the ACC was coupled to the left PFC; during the visuospatial task, the ACC was linked with the right PPC. These data are a compelling example of how situational context (in this case, task demands) can modulate the neural context within which a cortical area (i.e., the ACC) operates.

Disruption of contextual processing in cognitive disorders

We propose that the interplay between situational and neural context lies at the heart of normal brain operation. It follows that brain dysfunction should result from disruption of this interplay. In neurodegenerative diseases, neural

contextual effects may change as a result of primary damage, and also as the brain attempts to compensate for the degenerative process. In this regard, Grady et al. (2001) observed that patient with mild Alzheimer's Disease (AD), showed a distinctly different pattern of functional connectivity supporting working memory for faces, despite having similar behavioral profiles as age-matched controls. More direct evidence for new patterns of interactivity supporting cognition was provided by Grady et al. (2003), where increased functional connectivity in ventral prefrontal cortex was directly related to preserved memory performance in episodic memory of AD patients (Fig. 3).

In mental disorders, it is likely that the exact mapping between situational context and neural context is altered, such that changes in situational context are not properly reflected in neural context changes. In seeking to understand the neural basis of schizophrenia, some authors (Cohen et al. 1999)

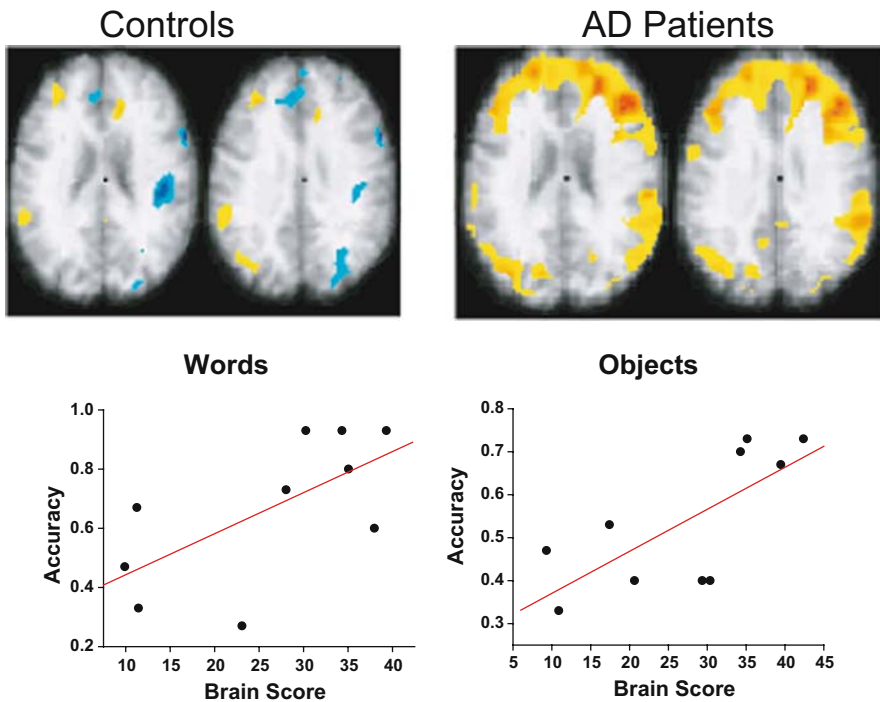


Fig. 3. Pattern of ventral prefrontal cortex (VPFC) functional connectivity in patients with mild Alzheimer's Disease (AD patients) and age-matched controls in an episodic memory task. Areas in yellow indicate strong positive functional connection (correlation) with VPFC, while blue indicates a negative correlation. Areas are plotted on an axial structural MRI (left is left). Scatterplots on the bottom indicate the relation to the functional connectivity pattern (brain scores) with memory accuracy in the AD patients, indicating the stronger the functional connection, the better the memory performance (Adapted from Grady et al. 2003)

have focused on the impaired utilization of situational context, whereas others (Bressler 2003b; Phillips & Silverstein 2003; Must et al., 2004; Dakin et al., 2005) have emphasized the impairment of neural contextual operations. Yet, these two aspects of contextual processing are likely to be related, as described above. The relation between situational and neural context may hold the key for both the understanding and treatment of mental disorders. Semnowicz et al. (2004), using estimation of effective connectivity, demonstrated distinctly different interaction patterns of limbic, cingulate and prefrontal regions across three groups of patients with major depression. Importantly, the groups were defined based on the form of therapy that was most effective in treating their depression. Patients responding to cognitive-behavioral therapy were distinguished from patients responding best to pharmacotherapy by the pattern of limbic-cortical and cortico-cortical effective connections.

3 Concluding Remarks on the Generality of Neural Context

Although the notion of neural context may appear to be at odds with the idea of specialization of function in the brain, this is not the case. In our view, a brain area is only able to contribute to cognitive operations through the interactions that it undergoes with the other areas to which it is connected. From this perspective, a brain area plays a specialized role in any cognitive function by virtue of its unique position within the overall connective framework of the brain. However, for the same brain area to be involved in a number of different functions does not necessarily imply that it exercises the same functional role in each. To the contrary, a large body of neuroimaging results indicates that different cognitive functions are associated with different neural contexts, and individual areas may contribute in a differentially specialized manner within each neural context. For example, since frontal cortical areas typically interact with parietal cortical areas in performing central executive functions (Collette & Van der Linden 2002), frontal or parietal areas may be considered as playing a specialized role in each function based on their contribution within the unique neural context associated with that function.

Clearly, we view neural context as a general effect that modulates the processing which occurs in any part of the brain. The neural context for processing in any area is firstly dependent on its connectivity with other brain areas, and secondly on the processes occurring in those other areas. Nonetheless, within the overall connective architecture of the brain, some areas may occupy privileged positions for translating situational context into neural context.

As one example, the dorsolateral PFC may play a special role in establishing the neural context of working memory. Located at the apex of the frontal

executive hierarchy (Fuster 2003), this area is ideally situated to integrate information about situational context, such as the input modality and the type of response required in a given task situation. Our picture is that the PFC contributes to working memory by shaping the neural context of distributed sensory and motor networks through the modulatory influences that it exerts on them. Furthermore, its own neural context is shaped by the modulatory influences that it receives back from them. In this process, the PFC interacts with different other areas to instantiate different aspects of situational context, as when it interacts with the basal ganglia to maintain cross-temporal context (Dominey and Boussaoud 1997). By virtue of its different interactions, its own neural context is expected to depend on the situational context.

The hippocampus (along with surrounding medial temporal areas) also appears to occupy a privileged position with regard to the learning of situational contexts (Chun & Phelps 1999; Bucci et al., 2000; Smith & Mizumori 2006). In some theories of memory consolidation (e.g., Squire et al., 2004), the hippocampus acts gradually to strengthen the synaptic connections among neocortical areas representing the long-term memory content; after a sufficient degree of neocortical reorganization this memory content can be accessed independently of the hippocampus. From our perspective, this neocortical memory content is constrained by the global neocortical context that exists at the time that the consolidative processes are in effect. In this way, neural context may impact the integration of new memory into existing representations, and affect the ultimate accessibility of long-term memory to retrieval.

In this chapter, we have only touched on some of the main aspects of neural context with respect to the operation of large-scale neurocognitive networks. A number of additional facets of neural context are highly important in their bearing on neurocognitive function. The concept of contextual congruence, for example, may be a relevant aspect of that function. Laurienti et al. (2003) have demonstrated that the ACC and adjacent medial PFC are sensitive to the contextual congruence of multisensory input. Whether the congruence of this type of context, which is situational in nature, has a correspondence in some property of neural context, such as spatial coherence (Bressler 2004), remains to be tested.

This chapter has been concerned with the relation between neural context and one form of non-neural context, namely situational context. It is clear, however, that contextual effects can encompass a long list of other influences such as the personal and evolutionary history of the organism. We predict that the concept of neural context will take on increasing significance for brain research in coming years as researchers come to grips with the functional consequences of large-scale brain connectivity, and that it will come to be seen as a common form of implementation for a number of different types of non-neural context.

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