

Neural Mechanisms of Inhibitory Specification in Cognitive and Linguistic Complexity

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1. Introduction

Complexity in grammatical clause organization provides a hierarchic organization that allows efficient constructions of meaning. To understand the scarcity of neural resources that make this efficiency important, it may be useful to examine current neuropsychological models of memory organization. That human memory capacity is limited is a fact that is often experienced in daily life, yet it may not be fully apparent from introspection alone. Experimental psychology studies have documented the limits of memory, providing an important basis for understanding not only the cognitive constraints that must be addressed by linguistic constructions, but how the emergence of these linguistic constructions allowed humans novel reasoning abilities.

We theorize that the ability to organize a complex linguistic structure such as a hierarchic clause may depend upon the capacity for what may be called inhibitory specification, in which certain meanings are isolated within working memory, such that they can be sustained and grouped within hierarchic structures. Clues to the neural mechanisms of inhibitory specification can be gained from studying the sequencing and routinization of action within the motor system, and from examining the unique properties of object memory within the ventral corticolimbic pathway.

Recent findings and theoretical models in neuropsychology have suggested that memory is achieved through specific neural systems, each of which provides unique representational properties, but also unique limitations. In addition to the traditional delineation of a procedural memory system, closely linked to the capacity for automaticity and habit formation within the motor system, there are two corticolimbic circuits that support cognitive representational memory. The first is a dorsal limbic circuit centered on the hippocampus and cingulate gyrus supporting configural memory. The second is a ventral limbic circuit centered on the amygdala and anterior temporal, insular, and orbital frontal cortex supporting item or object memory. Traditional evidence on aphasia syndromes emphasizes the importance of object memory to both expression and comprehension of language. The ventral limbic pathway's unique capabilities for specifying objects, with unique features inhibitory control, may be integral to the left hemisphere's capacity for specifying denotative semantics generally, and for creating complex linguistic constructions with the aid of grammatical conventions. Nonetheless, meaningful grammatical constructions may depend on both corticolimbic memory systems, with each one contributing unique abilities in representation and control.

To outline this theoretical approach, we begin with by considering the mechanisms of memory, and their inherent limited capacity, from the experimental psychological evidence. We then review the neural mechanisms of memory and attention that must be integrated across the multiple levels of the vertebrate neuraxis. These levels include not only neocortical networks, but the limbic-thalamic-cortical circuits that are critical to memory consolidation. We argue that

a key insight is the continuity of cognitive control with motor control, such that even complex learning can be understood as a process of action regulation. Finally, we suggest that complex grammatical structures in language are one mechanism for supporting abstract thought, in which the requirements for somatic articulation of action within the motor system arbitrate with the internal, visceral motivational control of meaning in the communication process.

2 Limited Capacities of Representation and Binding

Cognitive-experimental research on memory limitations reaches back more than 50 years, to early studies marked most notably by Miller's now famous estimation of short-term memory (STM) capacity at 7 +/- 2 chunks of information (Miller, 1956). Miller also observed that recoding of information into ever larger "chunks" is instrumental in expanding the capacity of STM, emerges naturally with experience, learning and expertise, and is ubiquitous in language. At lower levels of language processing, for example, chunking is evident in the recoding of phoneme sequences into syllables, syllables into words, and words into phrases. At a higher level, sequences of coordinated phrases can be organized into hierarchic-subordinate structures that enable the more efficient expression and comprehension of increasingly complex ideas encoded into linear discourse.

By the early 70s, the construct of STM was further refined by the introduction of working memory (WM) models (Baddeley & Hitch, 1974). Like STM, WM is characterized by capacity limitations, but here, they are distributed across both on-line storage and processing functions. One important corollary of this view is that the effective capacity of WM can be increased by efficiency of storage and/or processing components. The distinction between controlled and automatic processing (Schneider & Chein, 2003; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977) is central here. Controlled processes tend to be slow and effortful, require attentional resources, and are deployed intentionally early in learning or in novel contexts. In contrast, automatic processes are fast, require minimal attentional resources, and are carried out in a ballistic fashion following extensive experience. Just as recoding and chunking can increase the amount of information maintained in WM, a shift to automatic processing can increase the pool of available cognitive resources. As experience in a language accrues, lower-level processing components such as word recognition, lexical access, or routine syntactic parsing become automatized, freeing up resources to be dedicated to higher level processes, such as integrating information across phrase boundaries and processing more complex relations among arguments.

A second implication of WM as both storage and processing functions is its relevance to goal-directed action. One typically doesn't just hold information in STM for later recall; one does something with that information. In other words, information is selectively maintained and manipulated in working memory in order to enhance adaptive behavior. From this perspective, WM is closely aligned with motivation and self-regulated action. An influential capacity view of attentional resources, the selection-for-action theory (Allport, 1985), posits that processing limits occur not at the level of perception and sensory selection, but out of the need to engage in coherent (usually sequential), behavioral responses – either as covert action, or internal thought. This can lead to selective, top-down enhancement of action-relevant sensory attributes (Hannus et al., 2005) and, conceivably, configural information, in order to bias their active maintenance in WM, and suggests that the contents of WM are not driven primarily by bottom-up sensory selection. Working memory thus may play an important role in the integration or binding of sensory information with action regulation.

Empirical research on the impact of memory limitations on syntactic complexity has been most extensively studied by relating individual differences in WM capacity with the comprehension of syntactically complex sentences. The reading-span task (Daneman & Carpenter, 1980) has been frequently used to assess an individual's combined WM storage and processing capacity in the language domain. King and Just (1991) demonstrated that individuals with relatively low WM capacity for language (as measured by the reading-span task) exhibited longer reading times and poorer accuracy than higher-capacity readers for complex sentences with an object-relative clause (e.g., The reporter that the senator attacked admitted the error), but they performed comparably on simpler sentences with a subject-relative clause (e.g., The reporter that attacked the senator admitted the error). Here, the more processing-intensive object-relative clause requires the reader to associate the head noun with two syntactic roles (e.g., "reporter" as subject of the main clause and object of the relative clause), whereas the subject-relative clause requires activation of only one role (that of subject) for both the main and relative clauses.

A more recent fMRI study (Prat, Keller, & Just, 2007) similarly found that low-capacity readers had slower reading times than high-capacity readers for both active-conjoined (The writer attacked the king and admitted the mistake at the meeting.) and object-relative sentences (The writer that the king attacked admitted the mistake at the meeting.). Accuracy, however, was significantly worse in low-capacity readers only for the object-relative sentences. Thus, assuming that WM capacity is the major factor in individual differences in reading capacity, slower reading times appeared able to compensate for low WM capacity when reading syntactically simple sentences, but comprehension remained impaired on syntactically complex sentences. Functional MRI results suggested that processing was both less efficient and poorly coordinated in low-capacity readers. Specifically, low-capacity readers had higher BOLD responses than high-capacity readers (particularly in frontal control, and occipital regions) suggesting they consumed more resources despite poorer performance. Functional connectivity analyses further indicated poorer synchronization among left-hemisphere language regions, including Broca's and Wernicke's areas, in low-capacity readers. The neuroimaging data may thus provide insight into mechanisms for the concept of WM, showing that low-capacity readers engaged more activity in, but less coordination among, WM-related brain areas.

In light of these and similar findings, Just and Varma (2007) proposed that working memory capacity limits may be understood in terms of resource constraints on neural activation. That is, the effective limits of working memory may reflect the capacity to recruit multiple neural regions that sustain activation of context-relevant computations or information, while at the same time coordinating communication across this dynamic network in the service of self-regulated action or thought. Although full explication of this approach is beyond the scope of this chapter, of relevance here is their 4CAPS model of sentence comprehension. Although the authors acknowledge the contribution of other brain regions, their model focuses on the respective roles of Wernicke's and Broca's areas. They propose that Wernicke's area, the "associative center," specializes in retrieving relevant, language-based associations, prior knowledge (procedural and declarative) and perceptual inputs and in configuring "designs" or templates for new language representation. Broca's area, the "structure-builder" center, then takes these loosely structured templates and their associated information (in essence the information actively maintained in WM), and builds them into recognized syntactic structures.

Finally, it may be important to keep in mind that memory capacity limits not only the number of representational elements (words, clauses) but the number of interrelations (or bindings) among those items that can be kept active in WM (Halford, Baker, McCredden, & Bain, 2005; Halford, Cowan, & Andrews, 2007). Because memory is required to maintain binding among the elements, Halford's reasoning suggests that the effective number of items active in a linguist-

tic frame may be reduced from the “magical number” seven, down to only 3.5, on average. Binding requirements may be particularly relevant when considering capacity limitations for hierarchical-embedding. The essential cognitive work to be done in comprehending such structures is to identify the relevant constituents and establish their interrelationships (i.e., who did what to whom). In this context, it is interesting to note that a recent corpus linguistic analysis across seven European languages (Karlsson, 2007) concluded that the maximum number of center-embeddings employed is three. This is in close agreement with Halford’s estimate of the number of elements and their relations that can be maintained in WM.

In summary, we propose that the relationship between working memory and syntactic processing may be associated with the need to translate a holistic relational structure--which is formulated at a global, syncretic level--into extended, linear discourse. The linear nature of linguistic expression entails that the constituent elements of this relational structure be actively maintained in working memory for integration to occur over a time delay. This may require both sustained activation of relevant processing regions and coordination of processing across those regions. Hierarchic-subordinated syntactic structures offer more efficient and elaborated articulation of such complex relations than do sequential-coordinated structures, but they increase memory demands for on-line retention and integration of multiple referents. Working memory capacity may, therefore, both enable and constrain syntactic complexity. While the ability to hold multiple referents in working memory facilitates the production and interpretation of complex sentences, inherent capacity limitations of working memory appear to place constraints on the level of complexity (e.g., number of referents, distance to resolution) that can be generated and interpreted successfully (Gibson, 1998).

3. Corticolimbic Reentrance in Consolidation

The limits on memory representation, and on the binding of information elements, may be better understood by examining the dual corticolimbic control systems that guide memory consolidation. Modern neuroanatomical studies have shown that the neocortex evolved from the limbic cortex in a nested structure (D. N. Pandya, & Seltzer, B., 1982; D. N. Pandya & Barnes, 1987; D. N. Pandya & Yeterian, 1984) in which each of four levels of neocortical differentiation emerged embedded within its predecessor. Within limbic (or paralimbic) cortex emerged the heteromodal "association" cortex, then the unimodal association cortex, and finally the modality specific sensory or motor cortex (Mesulam, 2000). One primary pattern of connectivity is between levels, with each level connecting to its adjacent, embedded or embedding, neighbor with reentrant bidirectional projections (D. N. Pandya, & Seltzer, B., 1982). The result of these several levels of interconnectivity is to create a "pathway" such that visual information, for example, is processed from primary visual areas (which receive thalamic projections) to secondary visual association cortex, to heteromodal association cortex, then to limbic cortex. In the frontal lobe, the reverse direction of network embeddedness obtains, such that actions are initially organized on a limbic base (in orbital frontal or anterior cingulate networks), and are progressively articulated through frontal heteromodal association, then premotor association, and finally primary motor cortices. For both sensation and action, the connections are reentrant in that processing is not just one-directional. For vision, for example, there are as many connections proceeding from limbic cortex out to heteromodal, to unimodal, and finally to primary visual cortex as proceed in the opposite direction.

Reentrance is particularly important in building cognitive or linguistic models, because it emphasizes the distributed nature of representations that are recreated in the multiple instantiations across the embedded networks. Reentrance describes not only the structural connectivity,

but the processing that is implicit with this point-to-point connectivity. Information processing must proceed in some form, in some unknown recursive fashion, in both directions in each sensory or motor corticolimbic pathway (Tucker & Luu, 2006).

Although we do not know its neurophysiological nature, we do know the result of this reentrant and recursive corticolimbic processing. It is memory consolidation. Primate and rodent studies have shown that sensory data must be processed across all levels of the corticolimbic pathway to be consolidated in memory (Squire, 1986, 1998); disconnection of sensory and association cortex from the limbic base results in a profound deficit in consolidating new learning. Importantly, even though connectivity is broken across the corticolimbic pathway, prior memories may be accessed to guide behavior, depending on the intact connectivity of the residual networks. Although not as anatomically explicit as the animal evidence, the evidence on human amnesia is consistent with this general outline, such that specific agnosias are observed with lesions to association cortex in a given modality, and general amnesia is observed with lesions of limbic networks of the medial temporal lobe (Squire, 1986, 1998).

3.1 Thalamic Resonance of the Efferent Copy

An analysis of the nested corticolimbic networks thus provides an interesting theoretical basis for understanding the levels of representation in human language (Luu & Tucker, 1998; Tucker, Frishkoff, & Luu, 2008). However, it has long been apparent that any theory of cognitive and linguistic representation based on anatomical connectivity must consider the extensive network created by thalamocortical, and corticothalamic, projections (Crosson, 1999). Recently, research into the anatomy and function of thalamic connections has suggested that most if not all of thalamic afferents (input connections) reflect copies of motor control projections to subcortical circuits (Guillery & Sherman, 2002; Sherman & Guillery, 2002). As a result, thalamocortical projections would then reflect processes of action monitoring. With extensive intrathalamic connections providing modulatory control over this bidirectional traffic, cortical control over the thalamus can be understood as a key mechanism for attentional control of behavior, and of the sensory representations that guide behavior (Guillery & Sherman, 2002; Sherman & Guillery, 2002).

3.2 Limbic-diencephalic Learning Circuits

In the mechanisms underlying the language process, both corticolimbic and corticothalamic networks must be integrated in some fashion to allow executive control of working memory, such that the elements of communication (agents, acts, objects) are both maintained in the minds of the speaker and listener and bound in meaningful linguistic patterns. One insight to this integration comes from evidence that memory is achieved by two different cortico-limbic-thalamic circuits, each with a unique learning strategy. These learning strategies can be seen as different ways of optimizing the use of limited memory capacity.

Each of these circuits supports a different set of the nested corticolimbic networks. The circuit centered on the hippocampus supports the dorsal corticolimbic pathway, with its primary association cortices in the parietal regions of the posterior brain and mediodorsal regions of the frontal lobe. The circuit centered on the amygdala, pyriform cortex, and insula supports the ventral corticolimbic pathway, with its primary association cortices in the occipitotemporal regions of the posterior brain and ventrolateral regions of the frontal lobe. It is the ventral pathway that appears particularly important to inhibitory specification of meaning in language.

3.2.1 Configural Representations and Context-Updating. Papez (Papez, 1937) described a circuit engaging the hippocampus, posterior cingulate cortex, ventromedial thalamus, and mammillary bodies of the hypothalamus that readily sustained seizures and appeared to be important to the motivational control of behavior. Modern memory research has shown this circuit, supporting the dorsal corticolimbic pathway, to be critical to spatial memory in rodents, and very likely to configural representations in humans (Nadel, 1991).

In addition to being specialized for a holistic representation of the spatial or configural context, the dorsal circuit appears to be specialized to control learning in a unique way. Animal studies (Gabriel et al., 1983; Gabriel, Sparenborg, & Kubota, 1989) suggest that the dorsal circuit adapts gradually and more or less passively to changes in the environmental context, a process that can be described as context-updating (Luu, Flaisch, & Tucker, 2000; Luu & Tucker, 2003). This can be seen as a primitive form of associative learning, but one that is well suited to maintenance of a holistic internal model of the current perceptual and behavioral context.

3.2.2 Object Representations and Sustained Focus. In contrast, a second cortico-limbic-diencephalic circuit centered on the amygdala and ventrolimbic networks engages the medio-dorsal thalamus and supports the item or object memory representations of the ventral pathway (Aggleton & Brown, 1999; Mishkin, 1982). Supplying input to the orbital frontal and ventral (subgenual) anterior cingulate cortex, the ventral limbic regions provide not only consolidation of object perceptions, but organization of motor control directed by this consolidation. The specific control properties of this circuit and associated networks are suggested by animal learning studies by Gabriel and his associates. These studies found that lesions of the anterior cingulate cortex impair the animal's ability to adapt rapidly to changing circumstances (Gabriel et al., 1983; Gabriel et al., 1989). The ventral pathway seems uniquely able to detect conflict or incongruity with the current context model, and then maintain a focus of attention to organize new actions required by the discrepancy (Tucker & Luu, 2007).

3.3 A Limbic Base For Consolidation

Why are these differing learning strategies manifested by different corticolimbic circuits? One answer may be functional or algorithmic, explaining the adaptive advantages of different control biases. Studies of robotic control have shown that certain cybernetic (representation and control) designs allow efficient internal guidance of action, in a feedforward fashion (Hendler, 1995). However, these designs respond poorly to unanticipated changes in the environment. Other designs incorporating feedback control are more responsive to changing action plans when events intercede, but they are poor at maintaining goal-directed actions. Because these alternate cybernetics may require fundamentally different neural mechanisms, mammalian evolution seems to have instantiated them in different learning circuitry.

Another answer is neurophysiological, and it comes from an analysis of the differing autonomic or bodily self-control functions carried out by the dorsal and ventral limbic networks. Neafsey and associates (Neafsey, Terreberry, Hurley, Ruit, & Frysztak, 1993) have shown that the cingulate cortex at the base of the dorsal corticolimbic pathway carries out visceromotor regulation of internal bodily functions and associated motivated behavior. Because visceromotor regulation emerges directly and reflexively from the hypothalamic and limbic monitoring of bodily states, this form of control may be the primitive basis for the feedforward learning strategy that appears integral to the more extended consolidation operations of the dorsal corticolimbic pathway.

In contrast, the insular cortex and associated ventral limbic networks appear specialized for viscerosensory regulation of internal functions and associated motivated behavior (Neafsey

et al., 1993). This basis in visceral control may be consistent with the feedback control mode integral to the ventral pathway's ability to detect discrepant events and to maintain focused attention to redirect adaptive actions.

3.4 The Visceral Basis of Semantic Memory

In examining the connectational architecture of limbic networks, we find them densely interconnected across modalities, compared to the isolated modules of somatic representation in sensory and motor cortices (D. N. Pandya & Seltzer, 1982). This suggests that limbic networks must provide the brain's most integrative representations, in contrast to the traditional view that these integrative representations are formed in "association" cortices such as lateral frontal, temporal, and parietal regions. Jason Brown (J. Brown, 1977; J. W. Brown, 1988) pointed to clinical studies of aphasia that appear consistent with this connectational evidence, indicating that whereas lesions of neocortex (including Broca's and Wernicke's areas of heteromodal association cortex) would produce comprehension and expression deficits, it is only with lesions of limbic cortex that patients suffer severe semantic deficits.

At the same time as providing a holistic level of representation, limbic cortex (parahippocampal and cingulate; periamygdalar, anterior temporal, and insular) is responsible for visceral, homeostatic and motivational, functions (Neafsey et al., 1993). The implication may be that memory consolidation within these temporal-limbic networks is both highly integrative and motivationally significant.

4. Motive and Complexity in Representational Actions

Although perhaps integrative, the diffusely interconnected representations of limbic networks are likely to be poorly differentiated. Cognition, and linguistic structure, formed at this level can be seen as syncretic, with multiple referential implications fused within a primitive connotative binding. To understand how more differentiated linguistic patterns including the more traditional denotative semantics, can emerge from this elemental connectational matrix, it may be helpful to consider how actions are organized to mediate between bodily needs and environmental constraints. We propose that by understanding the mechanisms of organizing memory capacity, specifically in the context of action planning, we can gain insight into the neurocognitive process that generates, and that benefits from, grammatical complexity.

4.1 Complex Constructions in the Sensorimotor Machine

One of the first to recognize the psychological significance of the evolutionary-developmental order of the brain's anatomy, Hughlings Jackson emphasized that all the brain's functional circuits are linked to sensory or motor operations, such that the brain can be seen as a "great sensorimotor machine" (Jackson, 1931). At first glance, this pithy summary appears to be too simple to help students of the brain understand the complexity of its functions, including language representation and organization. However, we suggest that Hughlings Jackson's summary can be taken as a directional pointer, emphasizing that cognition does not arise ex cathedra from the vapors, but rather emerges from the body's sensorimotor, and visceral, operations. From this perspective, basic mechanisms of action regulation suggest insight into how cognitive expressions of the mind arise from more elementary neural processes.

4.2 Chunking of Action Sequences and Attentional Capacity

Actions must be sequenced to organize coherent behavior. In his analysis of the "problem of serial order" Lashley explained that the associative chaining of traditional behaviorism could not account for even elementary challenges handled by the mammalian motor system (Lashley, 1951). As a result, a representational theory is required. To understand the hierarchic structure within embedded clauses in language, it may be useful to begin with a basic analysis of how actions are grouped within clusters or chunks, which are then able to be executed with minimal demands on attentional capacity (Keele 1981; Keele & Hawkins, 1982). A similar efficiency appears to be provided by complexity in language structure, allowing not only the speaker but the listener to automatically capture nested semantic packets, thereby freeing attentional capacity for broader interpretation of the discourse and its context.

A neuropsychological analysis of action planning shows there are dual routes to sequencing actions, one in dorsal cortex and one in ventral cortex, each emerging from a different basis in the limbic system to shape action plans of the frontal lobe, and each providing a unique form of action regulation. By analyzing the limbic circuits that give rise to these cortical systems, it is possible to frame each mode of action regulation within a more general cognitive framework describing dual modes of memory consolidation. Through extending this neuropsychological analysis, we will argue that complexity in language relies on dual modes of motor control that are fundamental to organizing cognitive and linguistic structure generally.

4.3 The Visceral Basis of the Motive-Memory

Somewhere between the visceral representations of needs and motives and the somatic representations of sensory inputs and motor outputs are processes that give rise to what psychologists would consider higher-level cognition, including such constructs as executive control and working memory. How can we understand these processes within an action-regulation framework? Yakovlev (Yakovlev, 1948) provided a key insight when he proposed that the evolution of language can be seen as another extension of the more general evolution of motility. In primitive brains, such as that of salamanders, movement and homeostatic control are closely linked within brainstem structures, such as the tectum and tegmentum (Herrick, 1948). Actions are characterized by core, axial movements, reflecting the holistic (and undifferentiated) nature of actions and motivation. They emerge directly from internal motive processes to engage the external environmental process. For Yakovlev, the general organization of motility is a process of "exteriorization," as the internal urge is manifest in actions contacting the world. Yakovlev viewed language within this general framework of motility, thereby providing a theoretical model for understanding communication as bounded both by biological needs and the constraints of action regulation.

This organization of actions and motivation within the primitive brains of amphibians stands in contrast of course to that mammalian brains, wherein motor control spans a more complicated hierarchy that includes the neocortex. Yet, with increasing complexity in brain organization, the translation of motivational influence to action remains central to adaptive behavior. A particularly illuminating example is the seemingly inappropriate behaviors of monkeys with lesions to the amygdala, producing the Kluver-Bucy syndrome. These monkeys approach all objects without fear and react to them as if they are novel, and they also demonstrate inappropriate behaviors to peers. Pribram (Pribram, 1991) noted that this syndrome reflects the lack of visceral familiarity that usually imbues sensory experiences; without intact visceral-sensory associations, actions become not only amnesic but dysregulated. Pribram refers to the contribution of diencephalic and limbic structures as a protocritic function--holistic, undifferentiated, and motivationally relevant--that gives meaning to actions. Pribram's theory suggests how the vis-

cerosensory functions of the insula, amygdala, and associated ventral limbic networks (Neafsy, et al., 1993) may be integrated within the motive basis of action regulation.

Complementing the viscerosensory function of the ventral limbic trend is the visceromotor control integral to the dorsal limbic circuit (Neafsy et al., 1993). The unique symptoms of lesions to the dorsal limbic core of the hemisphere have long been known (Barris & Schuman, 1953). Bilateral anterior cingulate lesions result in akinetic mutism, a condition in which the patient exhibits little to no spontaneous action, and yet is able to react with coherent action and cognition when prompted. We can infer from this deficit that the dorsal limbic base of the frontal lobe is normally involved in the spontaneous, motivated direction of actions to the world.

4.4 Projectional and Feedback Modes of Action Regulation

From these dual foundations in motivated operations of memory consolidation, actions must emerge. Modern functional and anatomical analyses have suggested that these viscerosensory and visceromotor divisions of the mammalian cortex evolved from the primitive telencephalon of birds and reptiles, each division applying different control properties in the organization of action.

In addition to supporting configural cognition and memory for the spatial context of behavior (Mishkin, 1982; Aggelton & Brown, 1999), the dorsal pathway supports a projectional, feed-forward mode of action, in which behavior is launched toward a goal (Goldberg, 1985) (Passingham, 1987; Shima & Tanji, 1998). Animal studies show that cells within the SMA are preferentially active (and fire several seconds before the actual movement) when actions are initiated from memory, as opposed to when they are guided by sensory input (Mushiake, et al., 1990). In humans, patients with SMA lesions can reproduce sequences of actions when they are visually cued but can not produce the same actions from memory (Halsband et al., 1993). These observations are consistent with the notion of projectional, ballistic control in the dorsal pathway for motivating and regulating action.

The ventral corticolimbic pathway evolved from the perirhinal cortex of the temporal lobe, closely connected with the insula, amygdala, and orbital frontal region (Pandya, et al., 1982). In addition to supporting representation of objects or individual items in memory (Mishkin, 1982; Aggelton & Brown, 1999), the ventral pathway supports action regulation with strong feedback control, in which sensory guidance operates to restrict the action plan to achieve the desired target (Goldberg, 1987; Passingham, 1987; Shima & Tanji, 1998). Recordings of cells from the arcuate premotor area, the ventrolateral frontal homolog of the mediodorsal SMA (Barbas & Pandya, 1986) show cells that are preferentially activated when actions are guided by visual cues (Tanji, 1987).

An important theoretical challenge is to link the cybernetic qualities (projectional vs feedback control) to the cognitive representational qualities (configural versus object control). We argue that expectancies provide the links. Expectancies can be seen as consequences of the integration of the unique cybernetics of action regulation with the essential resources of memory representation to guide the cognitive process. Both dorsal and ventral corticolimbic pathways must contribute to the formation of expectancies (Tucker & Luu, 2007). The dorsal region of the anterior cingulate cortex is particularly important to the general dorsal corticolimbic network involved in the representation of context-generated expectancies. The representation of a contextual map appears to have evolved to include the representation of reward expectancies as an integral component of the memory operation. That is, within an appropriate context, goal-directed actions can be internally generated independently of external input. This ballistic direction of action is supported by the expectancy for hedonic outcomes (Tucker & Luu, 2007). Functional neuroimaging studies show that the anterior cingulate cortex is particularly active when

subjects must generate hypotheses (i.e., expectancies) about appropriate actions. In this light, akinetic mutism can be interpreted as reflecting an expectancy deficit, in that with no hedonic projection, there is no action. In everyday situations, the mediodorsal limbic-motor system appears to generate hypothesis that guide the launching and learning of appropriate actions, including communications with others.

We theorize that the cybernetics of action regulation in the dorsal and ventral pathways maintains continuity with the unique motivational base of action in each pathway. The feedforward projectional control of action in the dorsal pathway is not only guided by the cognitive representation of configural relations (with the hippocampal support of spatial memory as the iconic exemplar); it also entails an inherent motivational bias toward hedonic expectancy that is consistent with launching goal-direction actions. This integrated operation of the brain thus supports a motive-memory, not a neutral or disembodied cognitive function. As a result, it may be that in human cognition the representation of the current behavioral context within the dorsal pathway entails a positive hedonic tone to thoughts and actions.

In the ventrolateral system, the amygdala is involved in forming object (i.e., cue)-outcome associations, grounded in feedback control by viscerosensory constraints represented in insular cortex. This function supports the role of the adjacent orbitofrontal cortex in representations of object expectancies (reward or punishment, Schoenbaum & Roesch, 2005) that guide actions. Likely, the representation of object-based expectancies provides required support for the ventrolateral prefrontal cortex involvement in rapid acquisition of arbitrary and abstract cues with actions (Bussey, Wise, & Murray, 2001). That is, with the ability to form reward and punishment expectancies for arbitrary cues, these cues can now motivate actions in a manner consistent with feedback control.

5. Aphasic Disorders of Action Plans

Aphasia syndromes provide important clues to the subcomponents of language, including the capacities required for hierarchic organization of grammatical structures. We propose that the mechanisms of language, as revealed by the aphasias, are fully interdependent with the mechanisms of action regulation (Tucker et al., 2008). The specificity of grammatical deficits with lesions to Broca's area implies that this ventral corticolimbic network, at the base of the ventrolateral frontal motor system, is critical to complexity of clause structure. Several features of the ventral pathway, including the inhibitory control of semantic objects and the capacity for automatized action sequences, are critical to language generally and complex clause structure specifically. Even more generally, the cybernetics of the ventral trend may suggest new insight into the left hemisphere specialization for language, which we view as fundamentally a specialization of the entire hemisphere for the processing strategies of the ventral pathway (Liotti & Tucker, 1994; Tucker et al., 2008).

At the same time as we emphasize the primacy of the ventral pathway for object memory and feedback control of actions, it should be apparent that the hierarchic organization of language structure, and its interpretation, require general cognitive skills requiring multiple brain networks. We suggest that an analysis of the unique memory mechanisms of both dorsal and ventral corticolimbic pathways, integrating both anterior motor and posterior sensory controls, is necessary for a full account of the process of organizing complex linguistic patterns.

5.1 Broca's Area: Motor Planning in the Ventral Pathway

Lesions to a fairly restricted region of the brain, a few square centimeters in the caudal extent of the left inferior frontal lobe, result in deficits in language fluency. Because there are striking limitations in grammatical organization of speech, in contrast to relatively intact semantic reference, it is within Broca's area that we must find critical capacities for organizing grammatical complexity. To understand these capacities, we argue that it is necessary to appreciate the interdependence of this region of premotor (or perhaps pre-premotor) cortex with the memory capacities the left temporal lobe. These memory capacities extend the unique inhibitory cybernetics of the ventral trend to create the powerful modular structures of language.

5.1.1 Inhibitory Structure and the Feedback Control of Action. Within distributed neural networks such as make up the human brain, representational processes tend to engage the entire network, unless there are mechanisms for separating them. Concepts are therefore intrinsically holistic and syncretic, so that the separation of conceptual elements into chunks or packets--such as occurs with the clauses of speech--requires an active organizational mechanism. We suggest this mechanism is inhibition. To separate semantic units into interpretable bindings, the neural mechanisms of syntactic structure provide inhibitory control that is exerted by one representational unit (e.g., clause) on its associative neighbors.

In typical language production, an important result of inhibitory specification of concepts may be the differentiation of the serial order of word production, aided by the routinized conventions of grammar, and carried out in the premotor networks at the ventral base of the left frontal lobe. When grammar is expert, its conventions allow complex organizations in which inhibitory control separates the meanings of subordinate clauses from superordinate ones, allowing scarce attention and working memory to be allocated to the superordinate level. Within this process, the culturally-trained automatization of meaning units within familiar clause structures provides sufficient memory capacity to hold the full structure of the utterance for an adequate interpretation.

Lessons for the neural mechanisms producing this inhibitory specification of language may be provided by the mechanisms of action sequencing. Particularly important is the feedback form of action regulation within the ventral corticolimbic pathway. In contrast to the projectional control of the dorsomedial motor pathway, the feedback control of the ventrolateral motor pathway integrates perceptual checkpoints that are compared with the ongoing action sequence to allow sequential updates of the motor plan (Goldberg, 1985). This specification of the motor sequence requires inhibitory control that not only restricts the extent of each component of movement, but separates each component in relation to the sensory targets. To the extent that language production evolved from more generic communicative actions such as gestures (Givon, 1998), and to the extent that this evolutionary process required linguistic actions that are highly routinized, differentiated, and repeatable, it should not be surprising to find that it is specifically the ventral motor pathway and its capacity for inhibitory specification that has become the critical path for assembling intended meaning into linguistic structure.

5.1.2 Automatization of Action and Object Structure. With the specification of discrete actions within well-organized sequences, the ventral limbic-motor pathway is particularly suited to the development of routinized action patterns. Whereas the dorsal motor networks appear to embed actions within the episodic context that is elaborated within the configural representations of the posterior dorsal corticolimbic networks, the ventral motor networks appear to articulate more modular actions that are suited to serve as habitual patterns that can be disembedded from the immediate episodic context (Luu & Tucker, 2003; Tucker & Luu, 2007).

In this way, the automatization of action in the anterior ventral networks is similar to the formation of perceptual objects in the posterior ventral networks, and it may rely on a similar

mechanism of inhibitory specification. Objects are groupings of perceptual features that are sufficiently bound to be separated from the contextual frame. Routinized action packages are similar object representations of motor elements. It may be from the unique cybernetics of action objects the ventral pathway that the patterns of grammar evolved in Broca's and nearby networks. The patterns of grammar are automatized conventions of speech shared by a culture, allowing the members ready access to both the specific conventions and the more complex language structures that can be built on the foundation of these conventions.

5.1.3 Grammatical Complexity in the Motor Pathway. The position of grammatical complexity within the limbic-cortical pathway can be approached through developmental evidence. Grammar generally, and complex grammatical structure more particularly, are readily acquired by young children. But they are more difficult to acquire by second language learners after puberty, in contrast to basic lexical representations (agent, action, and object words). This differential learning capacity leads to pidgin constructions. This evidence can be interpreted to suggest that grammatical forms become rigid with the maturation of the neocortex of the motor pathways, which is relatively complete by the end of childhood.

Even more fixed within motor neocortex are the prosodic and articulatory routines that allow native speech. Whereas grammar of a second language can be learned after puberty, speaking without an accent cannot. A similar fixity appears to hold for the sensory networks of language comprehension, such that even if they learn the vocabulary of a new language rapidly, adults have great difficulty in "hearing" the unique sounds of a foreign language.

The rationale for this reasoning about differential maturation in limbic versus neocortical networks comes from studies of maturation in the primate and human brain. It has long been apparent that a major sign of maturation, the increasing myelination of cortical fibers, occurs first in sensory and motor areas (Yakovlev & Lecours, 1967). More recently, studies of cortical anatomy have suggested that limbic cortical areas retain an immature biochemical composition well into adulthood (Barbas, 2000). The implication is that plasticity is developmentally asymmetric between visceral-limbic and somatic-neocortical networks, such that by human adolescence there is rigidity in the somatic (neocortical) domain at the same time as there remains childlike plasticity in the visceral (limbic) domain.

This neurodevelopmental perspective places grammatical complexity in an interesting position in the epistemology of human cognition. In contrast to lexical semantics, which remain plastic and dynamic into adulthood, grammar generally--and complexity specifically--become a mold for the mind, acquired automatically through experience with the culture of origin and quickly becoming resistant to later experience.

5.1.4 Left Hemisphere Specialization for the Ventral Trend. The realization of the inhibitory representational cybernetics of the ventral pathway raises interesting questions for understanding a more well-known aspect of language localization in the brain, its left-lateralization. There is an integral role of object representations within the left hemisphere's analytic cognitive capacities. This contrasts with the right hemisphere specialization for the spatial, configural concepts organized in the dorsal pathway. In light of the new understanding of dual corticolimbic representational systems, brain lateralization must be approached in a new light (Liotti & Tucker, 1994; Tucker, 2007). Not only do the right and left hemispheres' perceptual skills align differently with the dorsal and ventral trends, respectively, but their motor capacities appear to do so as well. The ideomotor apraxias that are more common after left hemisphere lesions reflect not only a generic motor dominance of the right hand, but a precision of control that is commensurate with primary engagement of the inhibitory specification of action sequences in the ventrolateral premotor networks, elaborated particularly within the left hemisphere.

Although there are of course both dorsal and ventral corticolimbic pathways within each cerebral hemisphere, there appears to be an asymmetry in the "dominance" of the archicortical (dorsal) and paleocortical (ventral) pathways within the right and left hemispheres, respectively. There may be a new way of looking at hemispheric specialization here, reflecting differential elaboration for one or the other of the corticolimbic pathways of perceptual integration, memory consolidation, and action regulation. For language, it is interesting to consider that many of the unique features that have been attributed to left hemisphere specialization may in fact represent more fundamental mechanisms of the object representations and sequence differentiation of the ventral corticolimbic pathway.

5.1.5 Restricted Spreading Activation and Object Memory. In neural network models, and in neural networks, inhibitory control is critical to providing complex structures (Buzsaki, 2006). With only excitatory influences, interactions in the network are restricted to a kind of spreading activation, suitable for epileptic seizures but not for hierarchically organized neurocognitive processes.

Spreading activation has become a useful model for understanding the cognitive mechanisms of semantic memory (Meyer, Osman, Irwin, & Yantis, 1988; Schvaneveldt & Meyer, 1976). Studies of reaction time have suggested that meaning spreads quickly and automatically from one word to related words. In making a word/nonword decision, subjects are faster to name words that have been "primed" by previous words that are semantically related (Meyer et al., 1988; Schvaneveldt & Meyer, 1976). Under an operative mechanism of spreading activation, there would be multiple meanings activated during the comprehension of a sentence, such that precision of meaning requires suppression of unintended associations.

The left hemisphere may have special mechanisms for inhibitory specification of meaning, and we would argue that these mechanisms draw on the cybernetics of the ventral object memory pathway. Researchers have used right or left visual field (left or right hemisphere) presentation of prime and target words to examine whether spreading activation operates differently in the two hemispheres. Consistent with other evidence that the right hemisphere is important to comprehension of the gist or global meaning of language, some evidence has suggested that spreading activation appears to broadly and indiscriminantly in the right hemisphere (Chiarello, 1985, 1988, 2000). In contrast, the spread of meaning is more restricted in the left hemisphere (M. Beeman, 1993; M. J. Beeman, Bowden, & Gernsbacher, 2000), consistent with greater inhibitory control of related meanings that are inappropriate to the immediate linguistic context.

We speculate that these left and right hemispheric differences in spreading activation could reflect the more fundamental memory control biases of the ventral and dorsal corticolimbic pathways, respectively. With its specialization for the object memory and feedback control of the ventral limbic pathway, the left hemisphere gains a tight control over semantic structure, consistent with the inhibitory specification of actions that the ventral pathway appears to provide to motor control generally. With its specialization for the configural representation and feedforward mode of motor control of the dorsal corticolimbic pathway, the right hemisphere gains a less constrained and more holistic structure of linguistic meaning that is suited to global comprehension of discourse and the implicit semantics of humor and allegory (M. J. Beeman et al., 2000).

5.2 Wernicke's Area: Online Self-Monitoring

Lesions of the posterior left hemisphere (Wernicke's area) that lead to deficits of language comprehension do not simply impair comprehension. These lesions result in well-known expression deficits (jargon aphasia) in which grammatical form is correct, but semantic content is

disordered (Goodglass, 1993). The presence of intact grammar with Wernicke's aphasia is consistent with the argument that grammatical complexity is primarily a property of the motor preparatory networks of the frontal lobe. However, the interdependence of multiple networks in linguistic self-regulation is well-illustrated by the deficits of Wernicke's aphasia. The routinized cultural packets of verb and noun clauses have little meaning when they form automatically within inferior frontal networks and yet are unconstrained by semantic self-monitoring in the posterior receptive networks.

The critical language networks of the frontal lobe are situated primarily within the ventral pathway. Similarly, those of the posterior temporal parietal (Wernicke's) area must have considerable input from the ventral object memory pathway. However, it is in interesting question of how much dorsal pathway input is integrated within Wernicke's area (Galaburda & Pandya, 1983). Just as the parietal networks (dorsal pathway) are essential to motor control, apparently through providing dynamic monitoring of on going actions (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), there may be considerable integration of configural representations from the dorsal pathway as the posterior left hemisphere guides ongoing linguistic comprehension and expression.

5.3 Transcortical Motor Aphasia: Inertia of Language Action

A definite role for dorsal pathway control in language is shown by transcortical motor aphasia in which lesions of the mediodorsal regions of the frontal lobe lead to a paucity of spontaneous speech, even in the presence of intact articulatory capacity (Freedman, Alexander, & Naeser, 1984). This form of aphasia appears similar to akinetic mutism, with the motive deficit more specific to language processes. When questioned regarding their lack of spontaneous speech, transcortical motor aphasia patients often report that nothing comes to mind. This syndrome may thus reflect an impairment in the dorsal pathway's normal contribution to the language process, which is a motivated, goal-oriented impulse to communicate. Lacking this normal feedforward extension of the visceromotor function, language is then directed only by the ventral pathway's feedback control, such that speech is absent unless feedback direction is immediately present in the form of interpersonal confrontation.

5.3.1 Alien Speech. Another clinical syndrome observed with lesions of the mediodorsal frontal lobe is the alien hand sign. The patient reports observing the actions of a hand, but not experiencing it as his/her own (Goldberg, Mayer, & Toglia, 1981). The implication of this disorder is that the motivational control of actions in dorsal pathway is associated with an experience of the actions as integral to the self. Certainly we would expect that the consolidation of memory, arbitrating as it does between the somatic networks of sensory and motor neocortices and the visceral networks of the limbic cortices, would result in representations with both environmental veracity and personal motive significance. However, the clinical literature shows no counterpart to the loss of felt personal significance of actions with lesions to the ventral limbic-motor pathway. Instead, patients with lesions to orbital and ventrolateral frontal cortex often show behavioral disinhibition, puerile impulsivity, and indifference to social norms, in the pseudopsychopathic syndrome (Blumer & Benson, 1975).

If language can be carried out more or less independently within the ventral pathway, but the experience of personal agency requires the participation of the dorsal pathway, it is interesting to consider the thought disorder of schizophrenia, in which internal speech is apparently divorced from the sense of personal agency, and is instead experienced as an alien intrusion into the mind (Bick & Kinsbourne, 1987).

6. Dialectical Cybernetics of Linguistic Complexity

We have theorized that there are unique neural mechanisms necessary for grammatical complexity, emergent from the capacity for inhibitory specification of objects from their embedding contexts that is achieved by the ventral limbic networks of the left hemisphere. These mechanisms appear to build upon similar capacities for inhibitory specification of discrete and serial actions within the ventrolateral regions of the frontal lobe. These are control processes, and yet they have critical implications for representation, allowing relational clauses to be bound as units, to be organized hierarchically within expressive or receptive sequences.

At the same time, however, as the cybernetics of object memories are applying inhibitory specification to differentiate and maintain clausal structure, any hierarchic organization of the semantic context must draw on multiple brain systems. Although the patient with right hemisphere damage may appear to have intact language, more careful testing shows important limitations in understanding the implicit, connotative, and contextual referents in extended discourse (Borod, 2000).

The left hemisphere's ventral frontal language networks are thus highly specialized and critical for language, but they normally operate in a balanced, perhaps dialectical, fashion, with opposing control biases at one level leading to stability at a higher level. The left frontal organization of efficient grammatical constructions is continuously monitored by posterior networks to provide constraints of meaningfulness against which the construction proceeds effectively. Verbal objects are differentiated from the embedding semantic context within the left hemisphere's ventral networks, and yet that context can be maintained on-line together with its configural implications, perhaps most clearly within the dorsal networks of the right hemisphere. More fundamentally, the motive to communicate grounds the linguistic process in an adaptive context. The representation of self and other that frames that motive may be preferentially formed within the dorsal corticolimbic pathway. In this way, the neural mechanisms of syntactic complexity can be seen as affording an efficiency of memory usage that expands conscious access to the multiple streams of information processing that contribute to social communication.

7. References

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