Adaptive control of functional connectivity: dorsal and ventral limbic divisions regulate the dorsal and ventral neocortical networks

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The connectional anatomy of the primate cortex is now well-defined by the Structural Model, in which adjacent cortical areas are interconnected in an organized network hierarchy of communication and control. The computational theory of "active inference" can be aligned with this architecture, proposing that predictions descend from higher association areas to be updated by ascending prediction errors from lower (i.e. primary) sensory and motor areas. Given the connectivity, the limbic networks at the apex of the cerebral hierarchy must then be responsible for the most general expectancies, which are propagated through the hierarchy to organize the multiple component network levels of experience and behavior. Anatomical evidence suggests that there are dual limbic divisions, reflecting archicortical (dorsal) and paleocortical (ventral) derivations, resulting in fundamentally different neural mechanisms for managing expectancies across the corticolimbic hierarchy. In the functional connectivity literature, the dorsal attention network is seen to provide top-down or endogenous control of attention, whereas the ventral attention network provides stimulus bound or exogenous attentional control. We review evidence indicating that the dorsal, archicortical division of the limbic system provides a feedforward, impulsive, endogenous mode of motive control, whereas the ventral, paleocortical limbic division provides feedback constraint linked to exogenous events.

Key words: cognition; dorsal attention system; emotion; limbic system; memory; ventral attention system; neuropsychology.

Introduction

Recent theoretical progress has realized computational models of distributed neuronal representations (Friston 2010; Bastos et al. 2012; Wright and Bourke 2020) that can be aligned with evidence on the anatomical connectivity of the human brain (Barbas 2015; García-Cabezas et al. 2019). This integration of computation and anatomical models may help explain the burgeoning evidence on the correlational patterns in hemodynamic activity of the brain (Gusnard et al. 2001; Raichle and Gusnard 2005; Menon and Uddin 2010; Thomas Yeo et al. 2011). In a previous paper (Tucker and Luu 2021), we considered the motive controls that are integral to the adaptive regulation of unconscious inference developed through predictive coding across the cerebral network hierarchy of limbic, heteromodal, unimodal, and primary sensory and motor cortices.

In the present paper, we extend this model to include the evidence that the limbic system provides adaptive control of the cerebral cortex through two limbic divisions, each with a unique regulatory bias. The dorsal limbic division, derived from archicortex (hippocampus) and including the cingulate cortex, provides a "feedforward" form of adaptive control for the dorsal division of neocortex. The ventral limbic division, including the amygdala and insula and derived from paleocortex, provides a "feedback" form of adaptive control to the ventral division of neocortex. Understanding these different forms of adaptive control may help explain how the dorsal and ventral divisions of the human cerebral cortex—including the functional connectivity networks recognized in recent fMRI research—are organized by limbic

networks that draw upon arousal and motivational controls to provide unique forms of regulation of memory and cognition within the linked network hierarchy of the cerebral hemispheres.

Principles of limbic and neocortical connectivity in the Structural Model

Unlike the networks in the fMRI functional connectivity paradigm, which are defined by empirical patterns of correlated activity, the Structural Model of primate cortex (Barbas 1986; Barbas and Rempel-Clower 1997; García-Cabezas et al. 2019) has been constructed from anatomical studies of specific patterns of synaptic interconnections in the primate brain, with important implications for understanding processing in distributed neuronal architectures. For example, the more articulated cortical columns of the neocortex are found in primary sensory areas, which are then linked to more generalized architectures in association areas, which are then linked through specific cross-laminar connections to the more elementary (primitive) architectures of limbic cortex (Barbas 1986; Barbas and Rempel-Clower 1997; García-Cabezas et al. 2019). If connections imply function in distributed neural architectures (Rumelhart and McClelland 1986; Mesulam 1990), then anchoring cognitive theory in connectional anatomy can gain important constraints from the Structural Model.

In the present paper, we emphasize that the Structural Model can be further specified to account for the unique behavioral functions and subcortical connections observed for the dorsal

(mediodorsal) primate neocortex derived from archicortical limbic foundations, contrasted to the ventral (ventrolateral) primate neocortex derived from paleocortical limbic foundations. These two limbic foundations were described as providing dual origins of the primate neocortex by Sanides (1964, 1970). In the Structural Model of the primate cortex, Helen Barbas and associates have summarized principles of the laminar architectonics and systematic cross-laminar and lateral areal connectivity that have been characterized by fiber tract tracing in monkeys and generalized to humans (Barbas 1986; Barbas and Rempel-Clower 1997; García-Cabezas et al. 2019).

Figure 1 (from García-Cabezas et al. 2019) illustrates several of the principles of the Structural Model. As shown in Fig. 1A, the embryogenesis of the vertebrate forebrain provides an important evolutionary-developmental perspective on cerebral architecture (Puelles 2001; Puelles et al. 2013). In this view of the right hemisphere of the generic mammalian embryo, the indicators of four pallial sectors (medial, dorsal, lateral, and ventral) can be parcellated by patterns of gene expression, within an overall gradient of caudomediodorsal (hem) to rostroventrolateral (antihem) organization of neuronal specification of progenitor domains.

Figure 1b shows a coronal section of the right hemisphere of a rat, with a minimal extent of the neocortical area, in contrast with the extensive neocortical development in humans (Fig. 1C).

Figure 1d and e illustrates the increasingly differentiated cytoarchitectonics, including more prominent layer 4, that is seen proceeding across areas of different "cortical types," from limbic (agranular and dysgranular) to neocortical (eulaminate I, eulaminate II) areas. The Structural Model identifies the consistent patterns in mammalian cortical anatomy in which the limbipetal projections (feedforward pathways in the current neuroscience convention) proceed from supragranular to the granular layer 4 (blue arrows) and the limbifugal projections ("feedback" pathways, but see Tucker and Luu 2021) proceed from infragranular to supragranular layers (green arrows). The interconnections between areas of a similar cortical type (orange arrows) are described as "columnar"; the projection neurons originate in all layers (except 1 and 4) and terminate in all layers (García-Cabezas et al. 2019). These are horizontal or lateral connections in that they connect the same cortical types (also shown in Fig. 6 below).

With the dorsal pallium identified as the neocortex by this convention, we refer to the "dorsal neocortex of archicortical derivation" as the medial pallium and the dorsal half (or so) of the dorsal pallium, following the cytoarchitectonic observations of Pandya and associates (Pandya and Seltzer 1982; Barbas and Pandya 1987) and as summarized in a portrayal of the human brain by Giaccio (Fig. 3 below). We refer to the "ventral neocortex of paleocortical derivation" as the ventral half of the dorsal pallium together with the lateral pallium and ventral pallium in Fig. 1A. These derivations can be seen to converge at IPLc for the temporoparietal area and areas 46d and 46v for the frontal lobe as illustrated in Fig. 3 below.

We use the term "limbic" in the classical sense of clinical neurology and neuropsychology, referring to the region of the cerebral cortex bordering the subcortical structures. This includes both the allocortex (the primitive 3-layered cortex) as well as the adjacent mesocortex, which shows increasing lamninar differentiation but not the fully articulated 6 layers of neocortex sensu stricto. Traditionally, mesocortex includes both the periallocortex and proisocortex as shown in Fig. 3. Clearly the differences in laminar architecture between allocortex and mesocortex warrant a more specific theory of their differential functions, but we are so far unaware of evidence for developing a functional distinction and thus retain the more diffuse notion of limbic cortex adopted by Tucker and Luu (2021).

García et al. (2022) have recently provided an instructive application of the Structural Model to evaluating the Dual Origins Hypothesis of the evolution of the neocortex. Sanides (1964) proposed that the dual archicortical and paleocortical limbic foundations were elaborated with increasing differentiation of laminar neocortex in mammalian evolution. Following his investigations of the frontal lobe in humans, Sanides found that earlier investigators had also pointed to the dual origins in examining the cortex of reptiles (Dart 1934) and monotremes (Abbie 1940). García et al. (2022) have updated this important line of work with modern methods for characterizing the laminar organization of the neocortex in monotremes, rodents, and monkeys. Figure 2 illustrates the application of the Structural Model in a modern analysis of cortical lamination in a monotreme (a), rodent (b), and primate (c). The laminar cortical types are illustrated for each species in (d), (e), and (f). With these extant species taken to indicate possible stages of mammalian evolution, a clear increase in differentiation of laminar complexity can be seen as specified by the Structural Model, with the agranular and dysgranular (limbic) areas as the borders of cortical differentiation, as specified by the Sanides Hypothesis of Dual Origins.

It is important to note that Figs. 1 and 2 illustrate the increasing laminar differentiation (allocortex, agranular, dysgranular, eulaminate I, and eulamninate II) in a schematic with the least differentiation at the periphery of the schematic, with increasing laminar differentiation in the concentric rings with primary sensory and motor areas at the centers. This schematic arrangement is useful to illustrate the increasing evolutionary differentiation of neocortex within the primordial 3-layered general cortex, as expressed by Sanides's notion of "growth rings" (Sanides 1970). However, the actual position of limbic cortex is at the medial core of the cerebral hemisphere, as shown in the realistic depiction of Fig. 3 and the schematic depictions in Figs. 5C and 6. The topology of adjacency of networks of laminar differentiation is identical in each depiction, consistent with the Structural Model (Barbas and Rempel-Clower 1997; García-Cabezas et al. 2019).

Principles of neural computation communicating across cortical types

An influential computational model for explaining the relations among cortical networks, with clear implications for relations across cortical types from limbic to the most eulaminate koniocortex in primates, is "predictive coding theory" (Bastos et al. 2012). Described more generally as "active inference" (Friston 2008; Friston 2010; Friston et al. 2011), the proposal is that the Bayesian logic of conditional probability defines the likelihood of new information on the basis of what is known. Applied specifically to the interaction between adjacent networks in the corticolimbic hierarchy defined by the Structural Model, the theory of predictive coding can help to explain the active process of learning and memory that integrates new information with present knowledge. In perception, predictions are formed in association cortex for the expected features of the world to be encountered by the neural representations being formed in sensory cortex (Rao and Ballard 1999). The processing of sensory data in primary sensory cortex then provides a mechanism of error-correction to adjust discrepant expectancies from the higher association area. The very nature of information—what is informative—is thereby determined by a process of "unconscious inference," in which
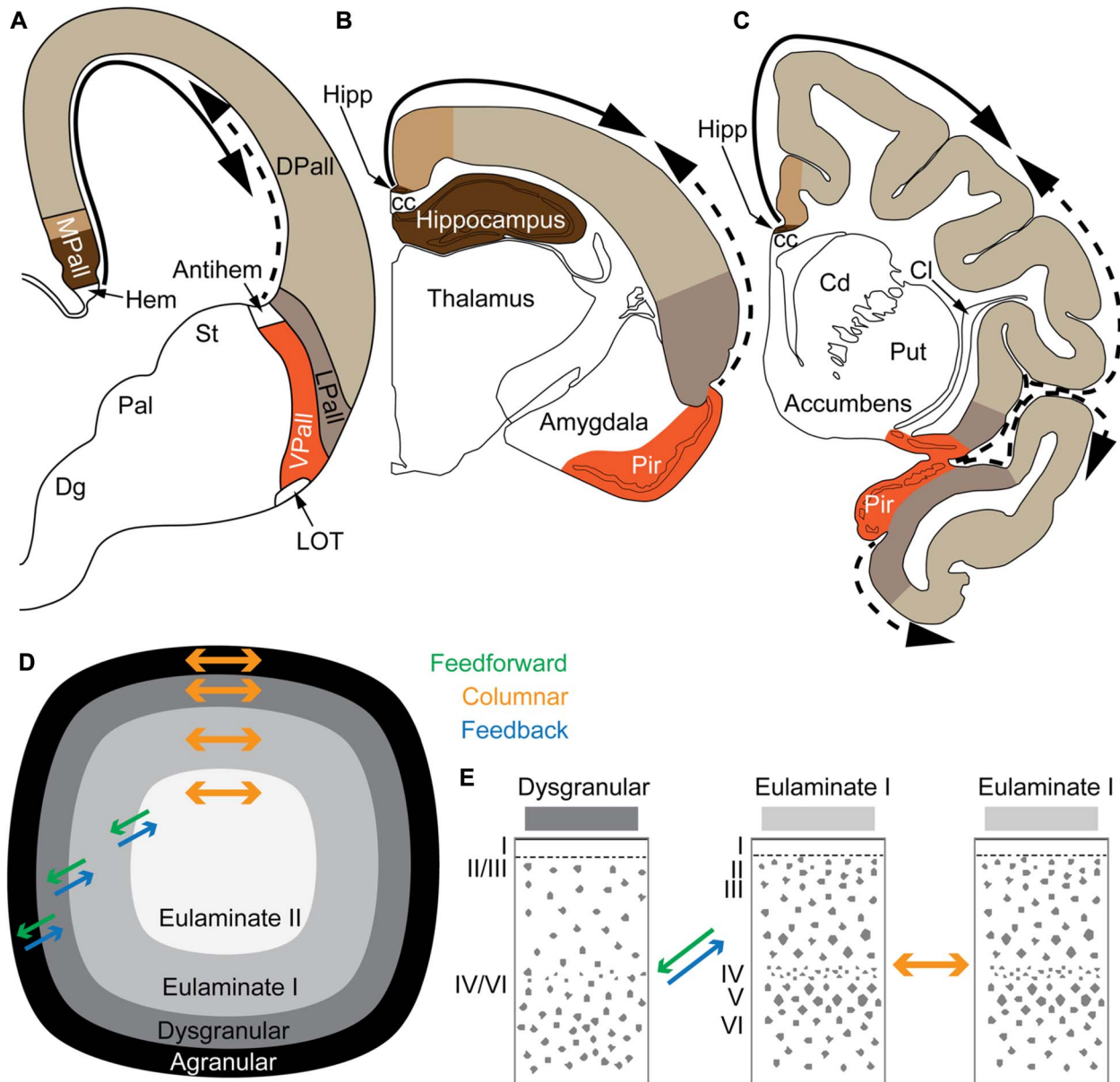
Fig. 1. Figure and caption from Garcia-Cabezas et al. (2019): two organizers for the expansion of the neocortex in development and evolution: the hem and antihem. A) Sketch of the mammalian telencephalon in development in coronal section shows the pallial (cortical) sectors [medial pallium (MPall), dorsal pallium (DPall), lateral pallium (LPall), and ventral pallium (VPall)], the hem, and the antihem according to the terminology of Subramanian et al. (2009), Montiel and Aboitiz (2015), and Puelles (2017) with the addition of the distinction of two parts on the MPall sector corresponding to allocortex (hippocampus) and periallocortex (agranular/dysgranular cingulate areas) in rats (B) and primates (C) based on architectonic analysis of these species in adults. The hem, found next to the roof plate, and the antihem, found in the corticostriatal junction, are secondary organizers that secrete morphogen proteins that form two overlapping gradients (solid and dashed arrows). B) Sketch of the rat adult brain in a coronal section; the adult derivatives of the developmental pallial sectors are colored as in (A). The solid arrow shows the trend of laminar differentiation traced to the ancestral hippocampal cortex; the dashed arrow shows the trend of laminar differentiation traced to the ancestral olfactory cortex (Pir). C) Sketch of the adult rhesus monkey brain in a coronal section; the adult derivatives of the developmental pallial sectors are tinted as in (A). The solid arrow shows the dorsal trend of laminar differentiation traced to the ancestral hippocampal cortex; the dashed arrow shows the ventral trend of laminar differentiation traced to the ancestral olfactory cortex (Pir). Note that DPall derivatives are more expansive than in the rat and extend to dorsal and ventral regions. D) Schematic of the primate cerebral cortex shows the arrangement of cortical types in rings. Laminar differentiation progresses from the outer or basal (black and dark gray) to the inner rings (lighter shades of gray). The edge of the cortex (black and dark gray) is actually thin compared with the greatly expanded eulaminate areas in the center. Cortical areas have stronger connections with other areas in the same ring and display columnar patterns of connections (orange arrows). Connections between areas in different rings (i.e. of different cortical type) are less strong than connections within the same ring and display feedback (blue arrows) and feedforward (green arrows) laminar patterns of connections. E) According to the structural model (Barbas and Rempel-Clower 1997), the laminar pattern of connections is related to the cortical type difference of the connected areas. Pathways form dysgranular to eulaminate areas are feedback (blue arrow); pathways from eulaminate to dysgranular are feedforward (green arrow); pathways between areas of comparable cortical type are columnar (orange arrow). *Cc* Corpus callosum, *cd* caudate, *cl* claustrum, *dg* subpallial diagonal domain, *DPall* dorsal pallium, *Hipp* anterior extension of the hippocampal formation, *LOT* lateral olfactory tract, *LPall* lateral pallium, *MPall* medial pallium, *Pal* pallidum, *Pir* piriform cortex in the primary olfactory cortex, *Put* putamen, *St* striatum, and *VPall* ventral pallium. Roman numerals indicate cortical layers.

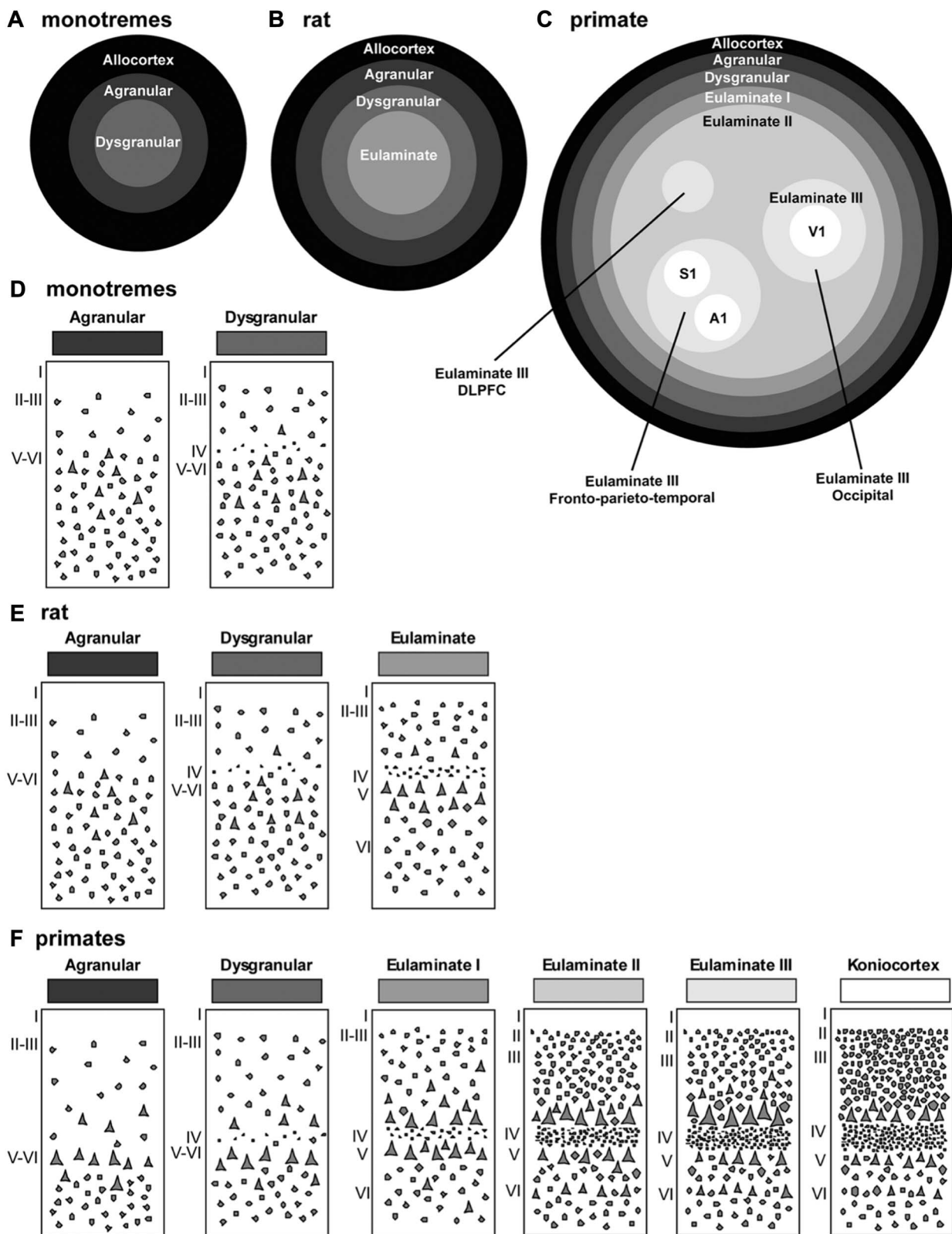**Fig. 2.** Figure and caption from Garcia-Cabezas et al. (2022): distribution of cortical types in simplified flat maps of monotremes, rats, and primates. a–c) Simplified flat maps of the cerebral cortex of monotremes (A), rats (B), and primates (C). Cortical types are colored in grayscale; allocortical areas are colored in black; agranular mesocortical areas are colored with the darkest gray; dysgranular mesocortical and eulaminate areas are colored in progressively lighter grays. Koniocortical areas are colored in white. D) Cartoons of types of neocortical areas in monotremes. E) Cartoons of types of neocortical areas in rats. F) Cartoons of types of neocortical areas in primates. Roman numerals indicate cortical layers. A1 primary auditory area, DLPFC dorsolateral prefrontal cortex, S1 primary somesthetic area, and V1 primary visual area.
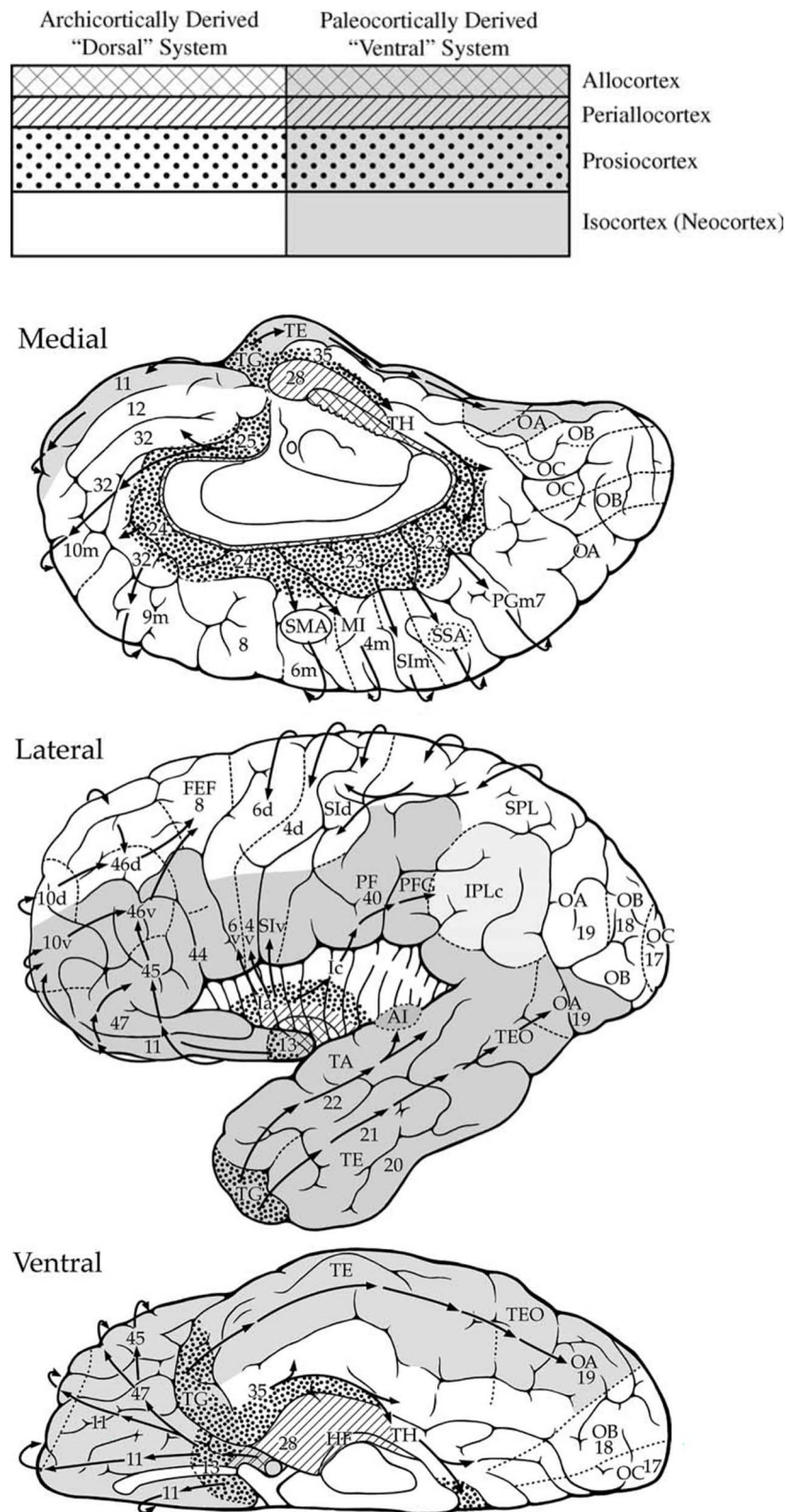
Fig. 3. From Giaccio (2006): the dual origins of the cerebral cortex. Cortical areas arising from the amygdala and adjacent olfactory cortex form the *ventral* (paleocortical) system and are shaded gray. Cortical areas derived from the hippocampal-induseal moeity form the *dorsal* (archicortical) system and are unshaded. The caudal inferior parietal lobule (IPLc), lying at the abutment of both protogradations, appears to be a transitional area (Eidelberg and Galaburda 1984) and is shaded intermediately. Arrows indicate (multiple) lines of cortical development arising by outgrowth from each of these primordial moieties. Each line constitutes a "functional unit" within the cerebral cortex and shows progressive laminar differentiation as one moves away from the central "limbic core." Each line also represents a chain of bidirectional short cortico–cortical connections linking successive architectonic stages within each line, thus providing inbound and outbound pathways for information flow to/from the limbic core. Abbreviations: AI, primary auditory cortex; FEF, frontal eye field; I, insula; IPL, inferior parietal lobule; SI, primary somatosensory cortex; SMA, supplementary motor area; SPL, superior parietal lobule; SSA, supplementary somatosensory area; a, anterior; c, caudal; d, dorsal; m, medial; v, ventral. Otherwise, numerical designations for cytoarchitectonic fields are from Brodmann (1909), letter designations after von Economo (1925).

prior experience with perceptual integration is required for the elementary interpretation of sensory data (Helmholtz 1878/1971).

Active inference

Active inference can be summarized as a formal (Bayesian) description of sentient behavior based on planning as inference (Friston et al. 2011; Botvinick and Toussaint 2012). In other words, it is a Bayesian account of active sensing that subsumes action and perception. In brief, perception (e.g. predictive coding) entails the estimation of—or inference about—the causes of sensations; namely, the latent states or events of the sensed world.

Crucially, in active inference, the sensory evidence—upon which these inferences are based—depends upon action, where both action and perception can be described as maximizing the evidence for a world model of how (observable) sensory consequences are generated by (unobservable) latent causes and context. Mathematically, this "self-evidencing" (Hohwy 2016) is the same as minimizing surprise (or, more technically, variational free energy). Stated in other words, predictive coding must resolve the discrepancy between outcome and prediction. Action is then based upon the selection of plans or policies that minimize expected surprise (a.k.a. expected disorder or free energy).

This minimization has two aspects that speaks to the two kinds of Bayesian optimality; namely, optimal Bayesian design and decision-making, respectively. Thus, expected surprise can be expressed as comprising two terms: the expected violation of preferred outcomes minus the expected information gain.

expected free energy = expected cost - expected information gain.

As a result of these dynamics of expectancy and information value, plans are more likely to be pursued if they lead to preferred outcomes while, at the same time, resolving uncertainty about latent states of affairs. This is sometimes cast in terms of "pragmatic" and "epistemic" affordances (Schwartenbeck et al. 2019). For a pragmatic affordance, active inference attempts to optimize choices that satisfy organismic values ("exploitation"). For an epistemic affordance, "active learning" takes the form of optimizing choices that increase knowledge of the world's information (exploration).

Different kinds of action

The plans (and constituent actions) prescribed by active inference can be overt or covert. Overt action may have exteroceptive consequences (e.g. motor behavior) or interoceptive consequences (e.g. autonomic reflexes) (Seth and Friston 2016). Covert action is generally cast as contextualizing perception (e.g. predictive coding) by adjusting the precisions of various (Bayesian or subpersonal) beliefs. This corresponds to endogenous or exogenous attentional selection; e.g. increasing the precision of prior beliefs or sensory precision, respectively (Shipp 2016; Palmer et al. 2019; Parr and Friston 2019).

Dorsal and ventral attentional networks and active inference

In brief, our proposal is that the dorsal attentional network is concerned with selecting motor plans and behavior whose consequences are primarily in the exteroceptive domain, for which we have relatively imprecise prior preferences. This means that the dorsal system (including the hippocampal system) selects behaviors that are epistemically motivated to resolve uncertainty via active sampling of the world. This active sampling means responding to epistemic affordances and novelty in an explorative fashion. Conversely, the ventral system (including the amygdala and associated interoceptive hierarchy) is responsible for selecting actions with outcomes over which we have precise preferences and is therefore dominated by pragmatic motivations and exploitation.

The ensuing dialectic can be viewed from a number of perspectives. First, the explore–exploit perspective suggests that the dorsal system is more concerned with exploratory behavior and the elation of resolving uncertainty, while the ventral system is concerned with exploitative behaviors that avoid aversive outcomes. Second, in terms of what versus where, the dorsal system rests upon inferences about where to sample next, while the ventral system is more concerned with "what will happen if I do this?" Thirdly, in terms of the "stability-plasticity dilemma," the dorsal system retains a flexibility in its explanatory motivation, while the ventral system affords a stability in ensuring precisely held preferences are fulfilled (e.g. homeostatic or allostatic control in the interoceptive domain) (Corcoran et al. 2020). Fourth, in terms of the exteroceptive–interoceptive distinction, it is possible that the dorsal system is more concerned with exteroceptive outcomes, whereas the ventral system holds precise prior beliefs about the interoceptive consequences of (autonomic) action; c.f., the distinction between allostasis and homeostasis, respectively.

Note that both the dorsal and ventral systems are responsible not only for action selection but also covert attentional selection. This requires them to have access to arousal and accompanying neuromodulatory systems that mediate attentional gain (Parr and Friston 2019); either to exteroceptive and proprioceptive sensations (dorsal system) or, primarily, interoceptive (ventral). This fits comfortably with the role of the dorsal and ventral systems in endogenous and exogenous attention, respectively (Corbetta and Shulman 2011).

The continuity from motive to memory

For a biological theoretical analysis, it is important to recognize that the Bayesian process of interpreting evidence in relation to prior knowledge must be guided not only by homeostasis but also by the organism's "allostatic" self-regulation, in which memory and cognition provide mammals the capacity not only to respond to events but to anticipate them (Schulkin and Sterling 2019). The importance of homeostatic control is well-recognized in the literature on active inference (Friston 2010; Hesp et al. 2021). The extension of adaptive control to a more anticipatory form of allostasis may provide a basis for interpreting what may be described as the dual, intertwined functions of the limbic system: motivation and memory. The network architecture of the cortex implies a multilevel process of active inference, through which evaluation of sensory data is dependent on learned expectancies (implying predictions) from sensory association cortex, and these are in turn dependent on more general expectancies formed in heteromodal cortex. Following the implications of the anatomy, the Structural Model implies that the expectancies that shape the interaction of prior knowledge with new evidence in heteromodal cortex must be supplied by the still higher level of cortex in the hierarchy of communication and control, which is limbic cortex, bringing visceral, homeostatic requirements to motivate both memory consolidation and the allostatic process of active inference (Tucker and Luu 2021).

The hypothesis of dual limbic motive controls

In the present paper, we extend this analysis of the hierarchic organization of the cerebral cortex with the "hypothesis of dual limbic motive controls." The limbic networks at the functional apex of the cortical hierarchy (although physically at the core of

the cerebral hemisphere) provide two different forms of adaptive regulation for the Bayesian process of active inference. One form emerges from the visceromotor function of the dorsal, archicortical limbic networks to regulate the dorsal division of the neocortex with a feedforward form of motive control that is suited to adaptive predictions of behavioral success. A second form of motive control is organized in the viscerosensory function of the ventral, paleocortical limbic base to regulate the ventral division of the neocortex with feedback control linked closely to environmental events, particularly threatening or aversive events. These dual control systems draw on specialized neuromodulator systems, particularly the "habituation bias" of the dorsal norepinephrine projections for the dorsal division and the "sensitization or redundancy bias" of the dopamine projections for the ventral division. These differential motive controls regulate the uniquely adapted specialization of the dorsal neocortex for spatial, contextual representations, in contrast with the specialization of the ventral neocortex for object, discrete item representations.

Overview of evidence for the hypothesis

We review and interpret the evidence that supports this hypothesis in six sections of this paper.

First, the burgeoning literature on functional connectivity networks of the human brain in the current literature points to different memory and attentional biases of the dorsal and ventral cortical networks, toward endogenous versus exogenous sources of control, respectively. We propose that these biases may be explained by the evidence on the dual limbic control systems.

Second, the rapid progress in mapping gene expression in embryogenesis has provided important evolutionary-developmental insight into the anatomy of the mammalian neocortex that defines an evolutionary frame for interpreting developmental progression. This evolutionary-developmental framework is particularly important for understanding the dorsal-ventral functional specializations in primates because, as expressed by the Dual Origins Hypothesis these specializations are explained by their venerable phyletic origins.

Third, the classical evidence on the processing in the limbic system includes separate cortico–thalamo–limbic connectivity for the dorsal (Papez) networks (the anterior nuclei of the thalamus, ANT) and ventral (Yakovlev) limbic networks (the mediodorsal nucleus, MD) that provide the anatomical basis for differential motive controls. Understanding the dual forms of limbic controls is being advanced importantly by research into the differential thalamic and frontal regulation of the limbic networks.

Fourth, a review of human electrophysiology studies supports parallels with the limbic regulation of cognition observed in animal studies. This review emphasizes the Bayesian biases, for context-updating versus discrepancy-detection, that can be seen to reflect limbic control in a wide range of electroencephalographic [particularly event-related potential (ERP)] studies of human cognition.

Fifth, the dorsal feedforward and ventral feedback limbic biases have been documented in the cybernetics (control systems) regulating elementary motor acts in both monkeys and humans.

Sixth, classical neuropsychology studies have documented how lesions to dorsal versus ventral corticolimbic networks lead to disorders of behavior and personality that may be consistent with these specific cybernetic biases observed in elementary motor control. The differentiation of impulse and constraint in motor control can thus be extended to explain the observations
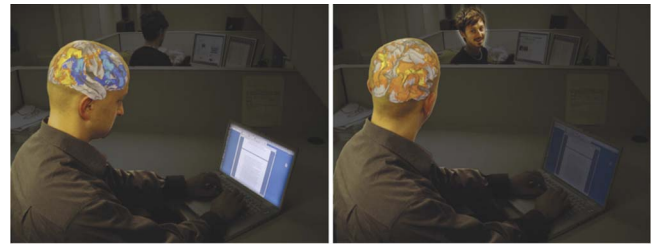

Fig. 4. From Corbetta et al. 2008: focusing attention on an object produces sustained activations in dorsal fronto-parietal regions in the intraparietal sulcus, superior parietal lobule, and frontal eye fields, as well as visual regions in occipital cortex (yellow and orange colors) but sustained deactivations in more ventral regions in supramarginal gyrus and superior temporal gyrus (TPJ) and middle and inferior prefrontal cortex (blue and green colors). (Right panel) When an unexpected but important event evokes a reorienting of attention, both the dorsal regions and the formerly deactivated ventral regions are now transiently activated.

of impulse versus constraint in dorsal versus ventral limbic contributions to self-control of the personality.

Finally, we conclude with a summary of the implications for integrating control theory (the adaptive regulation of feedforward and feedback forms of control) with the evidence that dorsal and ventral limbic divisions provide unique contributions to the regulation of experience and behavior across the multileveled networks of the cerebral cortex.

Current findings on human functional connectivity reflect the dorsal and ventral modes of motive control

The current literature on correlated patterns of human functional magnetic resonance imaging (fMRI) activity (functional connectivity) is consistent with the central role of limbic activity in human psychological function. Furthermore, there are unique roles for the dorsal and ventral divisions of the cerebral hemispheres (Corbetta and Shulman 2002; Astafiev et al. 2003; Corbetta et al. 2008; Shulman et al. 2009). In the original Corbetta and Shulman model, the dorsal attention network (DAN) regulates goal-directed endogenous attention, whereas the ventral attention network (VAN) controls stimulus-driven exogenous attentional requirements. Considerable research has supported these distinctions, including reorienting of attention by the VAN under changing environmental demands (Corbetta and Shulman 2002; Astafiev et al. 2003; Corbetta et al. 2008; Shulman et al. 2009) and organizing attention in social perspective-taking tasks (Corbetta et al. 2008). Figure 4 illustrates the engagement of the DAN but not VAN during volitional task-focus (left), and the shift to engage the VAN caused by a stimulus-generated reorienting of attention (right). Given the evidence of differential specialization of dorsal and ventral cortical regions for spatial memory versus object memory, respectively (Ungerleider and Mishkin 1982; Yonelinas 2006; Yonelinas et al. 2019), these functional connectivity findings may be consistent with the theoretical model that there are different control networks for managing the dorsal neocortex processing of spatial and configurational information (we emphasize that this is particularly important for intentional, feedforward control) in contrast with the ventral neocortex processing of specific items and objects (particularly for stimulus-driven, feedback control) (Tucker and Luu 2012).

Furthermore, differential activity in dorsal and ventral limbic circuits is observed in resting states and in tasks with specific motivational demands. The most typical resting state engages the

default mode network (DMN; Gusnard et al. 2001) with close links to classic the dorsal limbic (Papez) network including posterior cingulate cortex, anterior cingulate cortex, and medial prefrontal regions, as well as certain heteromodal integrating areas of temporal and parietal cortex. In addition, ventral limbic areas are found to be engaged in motivated perception through the salience network (SN; Seeley et al. 2007; Menon and Uddin 2010), which reflects coordinated activity in the ventral limbic division, including the insula, extended amygdala, ventral striatal, and orbital frontal areas.

Understanding the limbic regulation of neocortical function is important to a theory that integrates motivational control and memory consolidation. The evolution of human memory and cognition has been guided by the fundamental role of mammalian limbic networks in motivating cognition. Motivational control is important not only in the present moment but also in the ongoing consolidation of memory that occurs in reflective states, in the mind's unconscious background activity, and in sleep (Tucker and Luu 2012).

The limbic apex of the global architecture of functional connectivity

Recent work has taken a fresh look at the global patterns of functional connectivity in fMRI resting state data. This research has generated results that are highly consistent with the general corticolimbic architecture of the Structural Model and with the interpretation that control from limbic cortex may determine the activity of the neocortical networks of the hemisphere. We propose that the dorsal limbic division (archicortical derivation), including primary contributions to the DMN, provides a unique regulatory, motivational control for cognition in the DAN. Similarly, the ventral limbic division (paleocortical derivation), including the SN, provides a motivational source for controlling the VAN.

When we refer to the limbic apex of the hierarchy, we mean the deepest parts of a hierarchy that form the core of a centripetal organization (Fig. 5C). In this sense, top-down influences emanate from the apex or core and project toward the contact with the world (i.e. sensorium). Conversely, bottom-up sensory evidence ascends the hierarchy from the lowest level sensory periphery to the highest level limbic apex. This characterization of processing attempts to fit the laminar differentiation of the Structural Model (Figs. 1 and 2) exactly.

In a fresh approach to defining the cortical network architecture, Margulies et al. (2016) examined the dimensional structure of the full fMRI correlation matrix using a factor analytic method. The first dimension (gradient) describes the overall radial organization of the cerebral hemisphere, from the limbic area at the central apex or core, bordered by heteromodal cortex (including the DMN), which is in turn bordered by sensory or motor association areas, and finally primary sensory or motor cortices that form the outer shell of the brain (primary sensory and motor cortices) contacting the outside world (Fig. 5). This reflects the general architecture of the cortex described by the Structural Model (Barbas 1986; Barbas and Rempel-Clower 1997; García-Cabezas et al. 2019) and summarized by Mesulam (Mesulam 1998) (Fig. 5C), with the limbic networks at the core of the hemisphere providing the connectional base of the cerebral architecture (Tucker and Luu 2012). A cartoon illustrating the connectional topology of this architecture is provided in Fig. 6.

Additional work with the decomposition of fMRI time courses into statistical gradients or principal components (Gonzalez et al. 2021) has suggested that the principal gradient of the network architecture describes the overall relation among limbic, heteromodal, and primary sensory and motor cortical areas, with important implications for the adaptive control of cognition. The limbic and heteromodal areas are linked most strongly to the DMN at the base (hemispheric core) of the cerebral networks, which appear to be integral not just to nonsensorimotor or reflective cognition as in mind wandering but also to abstract concepts as well as social cognition (Gonzalez et al. 2021).

Intermediate between limbic areas and general heteromodal cortex of the DMN and SN, on the one hand, and the sensorimotor areas, on the other, is the DAN and VAN (Corbetta et al. 2008). These attention networks apparently regulate sensory and motor engagement at the shell (contact with world) with the more general and abstract cognition represented in the heteromodal, and then limbic, networks at the hemispheric core.

The findings from functional connectivity fMRI analysis are thus consistent with the interpretation, largely on anatomical grounds, that the limbic core of the hemisphere is positioned at the apex of the hemispheric architecture and thus must provide some generic adaptive predictions that organize active inference across the linked corticolimbic network hierarchy. Although the neural mechanisms of memory and cognition have long been considered separate from motivation and emotional mechanisms, we propose that this arbitrary distinction has blocked a realistic understanding of the integral motive control of memory. A functional interpretation that aligns closely with the connectional anatomy must formulate the adaptive basis of predictive concepts as organized around values: the visceral, motivational base of meaning provided by the close alignment of limbic networks with the extensive heteromodal cortical areas (Tucker and Luu 2021). Given the unique roles of dorsal and ventral heteromodal control of cognition (DAN and VAN) in the functional connectivity literature, a key question becomes how limbic expectancies are manifested adaptively in these dual attention networks for controlling memory and attention.

Understanding the unique motive controls from dorsal and ventral limbic networks

We propose that the dorsal and ventral divisions of the limbic system may provide unique biases in the motive control of cognition that differentially weigh the role of visceral, limbic influences versus neocortical mediation of sensory-motor contact with the environment. Consistent with the original Corbetta and Shulman model, the DAN appears to support top-down or predictive cognition particularly, which we propose is weighted toward limbic feedforward control of cognition based on the organisms needs and values. In contrast, the VAN supports feedback, stimulus-induced, reorienting, and error-correcting, which is weighted toward contact with the world managed in sensory and motor cortices (Corbetta and Shulman 2002). We propose that these attention control specializations are elaborations of more elementary limbic motive control biases that have evolved in the vertebrate forebrain, providing greater impulsive, projectional (and egocentric) control of approach behavior from dorsal limbic networks, as contrasted with greater constraint (and allocentric) control of avoidance behavior from ventral limbic networks (Tucker and Luu 2012).

Both limbic divisions share the general architectural features of limbic cortex (allocortex and mesocortex) in the Structural Model, thereby forming the adaptive base of the hierarchy of arbitration between expectancy-versus-evidence that must be achieved within each of the primary (sensory and motor) cortex, unimodal association, and heteromodal association areas. We consider here several lines of evidence suggesting that the dual limbic
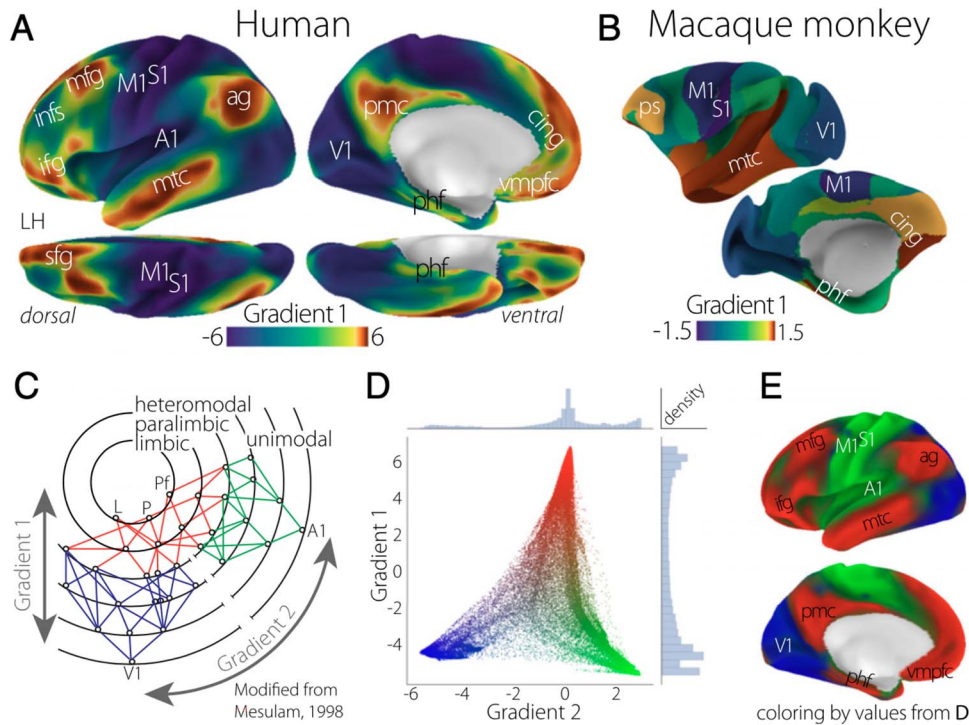
Fig. 5. From Margulies et al. 2016. The distribution of loadings on the first gradient of the nonlinear factor analysis of the functional connectivity correlation matrix for humans (A) and macaques (B). Mesulam's (1998) summary of synaptic connectivity of the primate cortex (C) is consistent with the structural model in showing the limbic cortex at the base of the cortical hierarchy. The first gradient (principal component) of fMRI correlations separates primary sensory and motor areas on one end, heteromodal areas in the middle, and limbic cortex at the other end (D), with a second gradient differentiating between visual and auditory pathways, projected to the cortical surface in e.

divisions regulate their respective spatial and object forms of memory consolidation through different—opponent and complementary—algorithms of motive control. The dorsal limbic division is proposed to operate through a habituation bias, in which control is achieved through reducing activity to constant information and thereby selecting for novelty (Tucker and Williamson 1984; Tucker and Luu 2012). This form of control facilitates global and holistic concepts within the dorsal neocortical division, consistent with skills in spatial and contextual memory, and operating with the immediate feedforward influence of the motive impulse to approach.

In contrast, the ventral limbic division operates through a neural sensitization mechanism introducing a redundancy bias to cognition, in which stability and the informatic status quo allow a focusing of attention and the articulation of specific objects that are represented in the world separately from the organism's perspective (Tucker and Williamson 1984; Tucker and Luu 2012). Intrinsic to the ventral limbic-striatal networks (including the extended amygdala, piriform cortex, and orbital frontal lobe), the redundancy bias not only stabilizes attentional focus and routinized defensive behavior under threat, but it constrains actions to be regulated continuously by feedback control from sensory monitoring of significant (particularly threatening) objects in the environment.

These differing forms of motive control appear to have fundamentally different Bayesian implications for the control of memory and cognition. The impulse or behavioral projection from dorsal limbic regions emphasizes feedforward control from prior experience, a cybernetic mode that is facilitated under conditions of success (and indeed regulated by the mood and motive control of elation). There is thus a bias favoring the limbifugal direction of processing within the dorsal limbic division, emphasizing the

valued predictions emanating across the neocortical networks from the limbic core (Tucker and Luu 2021). These are emotionally charged expectancies, providing adaptive motive control to the process of active inference.

In contrast, the constraint applied by ventral limbic regions supports feedback control and error-correction from environmental evidence (regulated by the mood and motive control of anxiety) (Tucker and Luu 2012). The bias of ventral limbic control is thus based on constraint through limbipetal processing. This is nonetheless an adaptive form of control as well, dominating neocortical processing when environmental events present threat or disconfirmation of the organism's current hedonic model of the events in the environment.

The dual evolved roots of neocortical architecture

Understanding the architecture and function of the dual limbic divisions may be aided by an evolutionary-developmental analysis that is informed by increasing insights to gene expression in vertebrate embryology (Puelles 2001, 2019; Aboitiz and Montiel 2007; Puelles and Ferran 2012). As proposed by the Dual Origins Hypothesis, mammalian neocortex appears to have evolved from the reptilian primitive general cortex (Dart 1934; Abbie 1940; Sanides 1970; Rial et al. 2010), which we now know from the gene expression evidence already included the tetrapartite organization shown in Fig. 1 (Puelles 2001). With primate and particularly human evolution, the 6-layered mammalian neocortex became critical to motor as well as sensory function (Herculano-Houzel et al. 2016), thus extending cortical control to specific sensory and motor patterns from what was a general integrative surveillance network for early vertebrates (whose specific
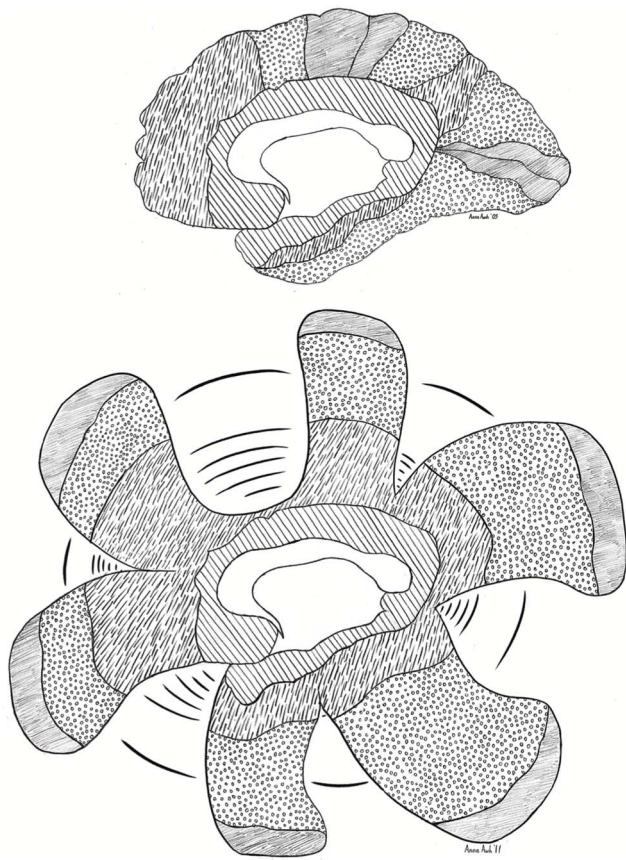
Fig. 6. From Tucker and Luu (2012). This cartoon suggests how multiple pathways (from the limbic base to the primary neocortical area) might be unfolded. Three dorsal pathways and three ventral pathways are illustrated. The lines between pathways serve to show that connections from one level or cortical type tend to target that same level or cortical type and that these lateral connections are dense for limbic areas, somewhat less dense for heteromodal areas, lesser still for unimodal areas, and virtually absent for primary areas (with the important exception of connections between motor and somatosensory areas).

sensory-motor patterns were executed largely by the basal ganglia) (Cisek 2022).

Karten proposed that the neocortex represents a mixing of cells from different patterning centers during evolution, specifically transposition of dorsal ventricular ridge (DVR) patterning mechanisms into the pallial subventricular zone (SVZ) patterning centers (Karten 1997). Although the DVR origin of neocortical evolution remains controversial, different pallial origins of neocortical evolution have been studied increasingly in recent work. Montiel and Aboitiz (2015) proposed that the upper layers of the neocortex reflect an amplification of the ventrolateral paleocortical developmental genes and the lower layers represent an amplification of the dorsal pallium. In addition, evidence shows that Cajal–Retzius (CR) cells, which guide development of pyramidal cells, derived from the ventral pallium can migrate into other pallial zones during development and may extend the patterning basis specified by their origin into these zones (Bielle et al. 2005). Bielle et al. found that when CR cells derived from the ventral pallium and septum are ablated during development, the lateral cortex is compromised (showing a reduced thickness), whereas regions of archicortical derivation, such as the cingulate cortex, develop normally.

Interestingly, a special class of CR cells (lot cells) that guide development of the lateral olfactory tract and olfactory cortex

go through a secondary migration during development toward the dorsal pallium. When this secondary migration is prevented, development of pyramidal cells in layers 2/3 are compromised (de Frutos et al. 2016). Finally, experimental evidence shows that cells of upper layers (2/3) of the neocortex express more genes that are shared with the olfactory cortex, when compared with deep layer (5/6) cells, and cells of deep layers (5/6) are more related to the archicortex, from the perspective of cytoarchitectural continuity of the deep layers of the dorsal pallium with the subiculum (Luzzati 2015).

Although the evolution of the 6-layered mammalian cortex from the 3-layered reptilian cortex remains a controversial topic, even with the increasing evidence on embryological continuity in gene expression (Puelles 2001, 2022), there is increasing recognition that the mammalian neocortex has evolved in the progression of increasing differentiation of the cortical lamina from both dorsal limbic, archicortical (hippocampal) and ventral limbic, paleocortical (olfactory cortex) origins (Aboitiz and Montiel 2007). The retention of the unique subcortical controls for these dual limbic divisions suggests that the motive regulation of the architecture of the cerebral cortex described by the Structural Model (Barbas and Rempel-Clower 1997; García et al. 2022) may take different forms in the dorsal and ventral divisions of the cerebral hemispheres.

Adaptive modes of motive control from dual limbic divisions

The differential subcortical regulation of the archicortical and paleocortical divisions is thus a key clue to understanding their differential functional roles, in emotion, motivation, and memory consolidation. A longstanding view of the dual limbic circuits has been that the dorsal division, with primary contributions from the hippocampus and cingulate cortex, is important to cognitive function, whereas the ventral division, centered on the amygdala and its connections to the anterior and orbital frontal networks, is more important to "motivation and emotion" (LeDoux 2000). In his integrative review of the dual limbic contributions to emotional and psychiatric disorders, Giaccio (2006) follows this convention in emphasizing the dorsal archicortical contributions to the "spatiotemporal organization of action," in contrast to the ventral paleocortical role in motivation generally. Although the hippocampal contributions to spatial and contextual memory are clearly foundational to cognition, we emphasize the evidence that both dorsal and ventral limbic divisions contribute to motivated cognition, in different ways. Giaccio in fact cites the finding that stimulation of the dorsal division (cingulate cortex) results in a positive mood (Damasio and Van Hoesen 1983). More recent observations of mirth and laughter following cingulate stimulation in human neurosurgical patients confirm this finding (Caruana et al. 2015; Zauli et al. 2022). These observations are consistent with the classical evidence that electrical self-stimulation is most effective for stimulation of the septal region (Olds and Milner 1954), a key basal forebrain structure of the dorsal limbic Papez circuit.

At the same time, considerable evidence suggests that this dorsal limbic division is important to habituation and to extinction of unrewarded actions (Isaacson 1982; McGuinness 1980). Our interpretation is that the habituation bias of the noradrenergic control of the dorsal division is integral to the regulation of positive affect and the associated impulsive, approach behavior. With the habituation bias, and the expansive attention to novelty that results from it (Tucker and Williamson 1984), the exploration

motive of hedonic approach is well suited to regulating spatial contextual memory.

This cybernetic mode is complementary to the opposite motivational control of the ventral division, which is sensitized to aversive and threatening events and thus suited to the redundancy bias providing sustained focus on environmental objects (Tucker and Luu 2012). Redundancy bias—in the context of predictive coding and active inference—can be read as an instance of the principle of efficient coding. This principle inherits from Bayesian inference via the minimization of representational complexity (i.e. Occam's principle)—that is sometimes expressed in terms of compression (particularly in predictive coding).

The opposing motive biases on working memory of the dorsal versus ventral divisions are then uniquely suited to regulate—differentially—the limbic consolidation of spatial, contextual, implicit memory versus object, focused, explicit memory. As we will argue in the remainder of this section, the impulsive dorsal limbic motive control emphasizes egocentric cognition emanating from limbic motives, consistent with the mood state of elation, yet with the habituation bias facilitating implicit memory. The constraint of ventral limbic motive control reflects the allocentric attention toward environmental contingencies, with the sustained focus on explicit memory consistent with the mood state of anxiety (Tucker et al. 2022). By characterizing the dual limbic modes of motive control of working memory, particularly in relation to frontal lobe regulation, it may be possible to understand how the dorsal and ventral divisions of the cerebral cortex are regulated by unique forms of active inference in human cognition. Because ongoing cognition must be supported by adaptive control of working memory, these dual modes of mammalian motive-memory may be seen to provide unique contributions to affective regulation of human conscious experience.

Visceral control of memory: the feeling of what happens

The limbic system brings visceral information—gut-level feelings—to provide motive control for ongoing cognition (Nauta 1971). As mentioned earlier, importance of insular viscerosensory signaling was integral to Nauta's (1985) emphasis on the ventral limbic network as the Yakovlev circuit (Yakovlev 1948). Lesions of ventral limbic connections to the orbital frontal lobe, such as in the Phineas Gage case, have been described as creating an interoceptive agnosia leading to a secondary psychopathy syndrome (Damasio et al. 1990). In his philosophical reflections, Damasio seems to have retained an emphasis on gut-level responses in memory as he describes the feeling of what happens (Damasio 1999).

In addition to viscerosensory monitoring from the ventral limbic network, studies of limbic control over autonomic function have observed dorsal limbic (cingulate) control of visceromotor function (Neafsey 1990). Figure 7 summarizes the findings of Neafsey and associates on limbic visceral control (Terreberry and Neafsey 1983; Neafsey et al. 1986) in a coronal section of rat brain, similar to that shown for the Structural Model characterization in Fig. 1B.

The differential visceral functions of the dual limbic networks may be a clue to their differential modes of motive control. The projectional, feedforward form of control proposed for the dorsal limbic division may be an extension of the visceromotor influence, whereby visceral urges motivate actions in a direct and feedforward fashion. From the several lines of evidence reviewed in the next sections, we will propose that the visceromotor foundations for dorsal limbic control may result in a kind of extraversion: an
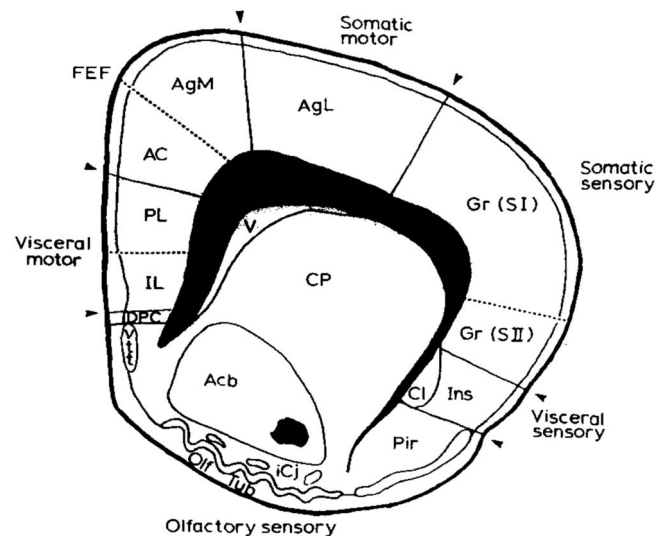

Fig. 7. Coronal section of right hemisphere of a rat brain showing visceromotor function from prelimbic and infralimbic regions of the cingulate cortex, and viscerosensory function from the insula. Acb, accumbens; AC, anterior cingulate; AgL, lateral agranular cortex; AgM, medial agranular cortex; C1, claustrum; CP, caudate-putamen; DPC, dorsal peduncular cortex; FEF, frontal eye fields; gr(SI), primary sensory granular cortex; gr(SII), secondary sensory granular cortex; ICj, islets of Calleja; IL, infralimbic cortex; ins, insular cortex; Olf tub, olfactory tubercle; Pir, pyriform cortex; PL, prelimbic cortex; V, ventricle; vtt, ventral taenia tecta. From Neafsey (1990).

impulsive projection of egocentric urges into behavior (Tucker and Luu 2012).

A classic example of the impulsive behavior from dorsal limbic control may be seen to result from removing the ventral limbic constraint over impulses. In the Kluver–Bucy Syndrome, created by complete bilateral cortical extirpation of the anterior temporal lobes (including the amygdala bilaterally), the monkeys were unafraid and unaggressive, exhibited dense object agnosia (inability to know objects), and showed various levels of hyperorality, hypersexuality, and hypermetamorphosis: "a strong tendency to attend and react to every visual stimulus" (Kluver and Bucy 1939). More recent research has shown that these striking changes in emotionality in the monkey do not require the full anterior temporal resection but can be produced by complete bilateral amygdala lesions (Aggleton and Passingham 1981).

Our interpretation of these observations is that the bilateral loss of the amygdala leads to a release of the characteristic motive control of the dorsal limbic division, which involves a projectional, impulsive expression of hedonic (oral and sexual) drives. The exaggerated orienting responses may be consistent with the attentional bias of the dorsal division, reflecting the orienting to novelty (hypermetamorphosis) that is integral to the habituation bias (Tucker and Williamson 1984) as well as the loss of focused, sustained attention normally supported by the redundancy or sensitization bias of the ventral limbic division.

The object agnosia with more extensive anterior temporal lesions of the Kluver–Bucy syndrome may emphasize the close link between ventral limbic motive control (engaging fear and aggression in vigilance for external threats) and the capacity for object memory (Pribram 1950, 1991). As a result, greater introversion in attention occurs as potentially threatening objects engage viscerosensory monitoring to provide feedback control over behavior. Thus, the opposite biases of dorsal and ventral limbic divisions in regulation of visceral motive control of behavior may be closely related to dual forms of memory consolidation,

Egocentric representations of spatial memory

The initial observations of place cells came from single-neuron recordings in the hippocampus that consistently reflected the animal's position in space (Okeefe and Nadel 1978). Other cells seem to support place cell coding with explicit—egocentric—reference to the animal's personal movements in space. In recent research on the dorsal limbic network, the evidence on coding attention in space has extended our understanding of attentional as well as memory functions of the ANT in directing dorsal limbic control through the Papez network (Aggleton et al. 2022).

Taube and associates discovered head direction cells that integrate vestibular information on the orientation of the head with movements in space (Taube 1998). The head direction cells appear to provide a self-referential frame for coding space in relation to personal movements (Taube 2007), an immediate reflection of the organism's current behavioral intentions. The fact that head direction cells are observed not only in the ANT but also in the reticular formation of the lower brainstem (Taube 1995) may provide routes for the dorsal limbic control of the lemnothalamic brainstem (particularly norepinephrine) neuromodulator projections.

The archicortex is interconnected by the Papez circuit (Papez 1937), which was the original indication of motivational control of the cortex that led to the concept of the limbic system (MacLean 1993). In addition to the cingulate cortex and hippocampus, the Papez circuit courses through the ANT and the septal nucleus as well as the mammillary bodies of the hypothalamus (Aggleton and Brown 1999).

Figure 8 illustrates the major connections of the Papez network as it might be seen in the human brain, including the multiple connections from the central coordinating center, the ANT (Aggleton et al. 2022). The alignment of the cortical extents of the Papez circuitry with the major nodes of the DMN (posterior midline, medial prefrontal) emphasizes that the default mode engages major contributions from the dorsal corticolimbic division (Corbetta et al. 2008; Gonzalez et al. 2021).

Allocentric representations of object memory

Although the organismic or egocentric reference for space as coded by head direction would be consistent with an elementary adaptive function, a more general or abstract representation of the spatial context for behavior would seem to require the integration of an allocentric reference frame as well. This may be achieved in part through integration of object representations in the ventral limbic division, in which objects are defined by their independence from personal reference.

The ventral paleocortical division of the limbic system appears to have evolved in close alignment with the olfactory system, leading to the interpretation that olfactory stimuli may be prototypes for perceptual objects. Several considerations may highlight the uniqueness of the primary olfactory cortex, piriform cortex, compared with other primary sensory areas, characterizing how information representation in this sensory cortex differs from more eulaminar sensory cortices in ways that may be explanatory for primitive object memory.

First, the piriform cortex is indeed sensory cortex, and yet, it retains the simple laminar architecture of the primitive pallium (and other allocortical areas), whereas other sensory areas, such as visual cortex, exhibit the complex columnar architecture of neocortex.

Second, the simple 3-layer allocortical structure includes cells (predominantly of the pyramidal type) in the middle layers whose apical dendrites extend into the upper layer and whose axons extend into the deeper layers. The dendrites and axons ramify widely to adjacent areas, with an organization that can be described as tangential ramification, as opposed to the columnar architecture seen in more eulaminate cortices of other primary sensory cortices (Montiel and Aboitiz 2015). The tangentially organized networks of the archicortical (hippocampal) and paleocortical (piriform) allocortex have been described as "recurrent collateral networks" that are ideal for elementary pattern completion and separation (Wilson and Sullivan 2011; Rolls 2015; Blazing and Franks 2020).

Third, olfactory information does not appear to be spatiotemporally organized, such as seen for other sensory modalities (e.g. retinotopic, tonotopic, and somatotopic). This nonspatial organization may support nonspatial, allocentric representation of odor objects, in that the representation is fully independent of spatial reference to the organism (such as is coded in relation to head direction).

Fourth, odor representation and processing, unlike processing in other sensory modalities, can be described as flat rather than hierarchic. Olfactory information is not passed through the thalamus before arriving at the olfactory cortex. The processing of olfactory cortex for identification in that modality (Blazing and Franks 2020) is essentially completed by the primary olfactory cortex. In this flat structure, identified (categorized) odor information is then passed from the olfactory cortex to other limbic structures that integrate multimodal sensory information as well as to the striatum. In contrast, cortical processing of sensory information in other areas is hierarchical, progressing from simple feature responses of the sensory specific cells in the primary sensory cortex (e.g. vision) to more complicated and abstracted representation away from the primary sensory regions and toward the limbic regions.

Fifth and finally, the olfactory cortex remains plastic throughout adulthood, unlike other primary sensory regions whose plasticity is tied to, and limited by, critical periods of development including myelination. The enduring plasticity of the olfactory cortex appears to support long-term memory formation with neurophysiological and functional features that mirror those observed in the hippocampus, such as sharp-waves and experiential replay during slow-wave sleep (Wilson and Sullivan 2011). The coordination between the piriform cortex and hippocampus has been conceptualized as constituting an "olfactory motor system" that relies on odors to create maps of external space (Jacobs 2012). Such maps can be created by a mixture of odors which can be deconstructed into elemental odorants and which have a concentration gradient. Within such maps, unique odors positioned within the map can serve as landmarks. These may be the primordial objects of mammalian experience.

Orienting to salient object identities (landmarks in space) thus allows the piriform cortex to construct fundamental allocentric knowledge of the world. In contrast to visual perception, with predictive coding extending across the neocortical hierarchy, the cognitive architecture of olfaction includes a flat connectional structure, yet close association with the hippocampus allows odor processing primitive but direct access to the goal of navigation referenced to object odors. Moreover, the highly plastic nature of the olfactory cortex and its associated memory network (the paleocortical limbic division) reflects the transitory nature of
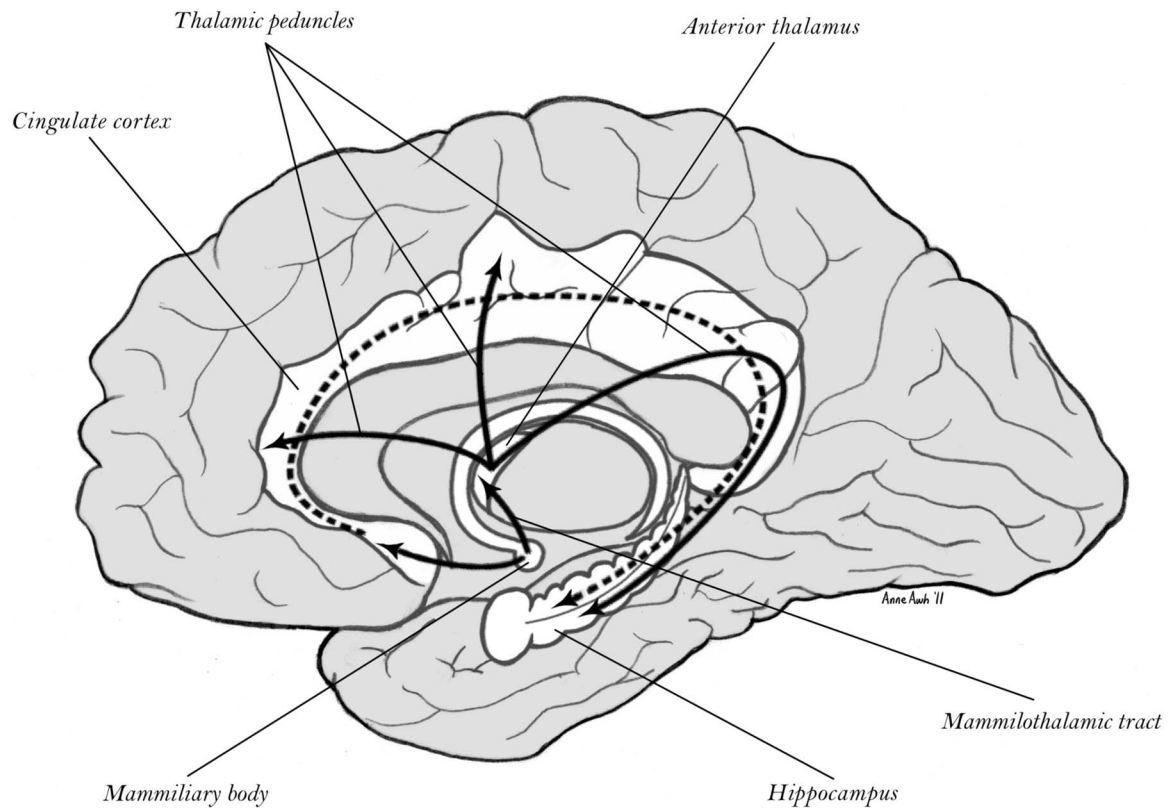
Fig. 8. Papez circuit integrating the archicortical limbic division based on the hippocampus, cingulate cortex, and ANT. From Tucker and Luu (2012).

odor maps, which in the objects of the natural environment are transitory constructions dependent on the current direction of the wind.

Adaptive control of memory: representing self in context

The dorsal and ventral limbic divisions, with their interrelations with thalamic and basal forebrain regulatory mechanisms, thus provide primitive foundations for organizing memory in relation to adaptive requirements of the organism, with representations of objects and spatial contexts providing basic foundations for organizing more complex conceptual systems. The remarkable continuity of corticolimbic architectures in widely varying mammalian species attests to the evolutionary requirement for continuous adaptation in each generation, such that more complex 6-layered neocortical architecture appears to retain its dependence on regulation by the more elementary 3-layered hippocampus. Similarly, both limbic divisions include projections to the striatum (Nauta 1982), reflecting considerable subcortical as well as cortical influence on motor output.

In memory for odors in a spatial context, hippocampal place cells appear to form functional cell assemblies with inputs from ventral limbic olfactory areas through entorhinal connections, thereby constituting the integrated elements of episodic memory (Igarashi et al. 2014). The integration of ventral limbic inputs may be important to a differential coding of external space, in a more allocentric coordinate system. "Grid cells" have been discovered in medial entorhinal cortex that appears to reflect coding of the regular dimensions of environmental space, with structured neural responses that reflect a triangular or hexagonal tessellation of physical space (Moser et al. 2015). Although external space is thus coded in an organized fashion, the code is not topographically organized in the brain, for either entorhinal grid cells or hippocampal place cells (with relations defined by connection strength rather than physical arrangement, not unlike units representing spatial patterns in an artificial neural network). The coding for the physical dimensions of external space by grid cells appears to be replicated by multiple modules of grid cells in entorhinal cortex, each module perhaps analogous to a principal component of the spatial context, such that a high dimensionality of neural representation can be achieved by combinations of these elementary grid modules (Moser et al. 2015).

Monitoring viscerosensory guidance in anxiety

In addition to the Papez circuit, the classical accounts of the limbic system also included a ventral limbic network, including the amygdala, subgenual cingulate cortex, and orbital frontal cortex, regulated by the mediodorsal nucleus of the thalamus.

From recent research, it is clear that the ventral paleocortical limbic division draws on a specific form of thalamic control from the mediodorsal nucleus (Aggleton and Mishkin 1986), which is connected to both anterior temporal areas and orbital frontal areas in a unique triangular circuit (Jones 2009). With the mediodorsal nucleus of the thalamus as the coordinating center of the network, the triangular circuit (Fig. 9) may support reverberating processing between the sensory-visceral integration of the extended amygdala (anterior temporal and insular areas) and the adaptive motor control based on orbital frontal cortex (Jones 2007).

The specific role of the amygdala projections to the MD thalamus in regulating the posterior orbital frontal cortex (pOFC, Fig. 9) has been elucidated by new insights into how these projections support the triangular circuit (Timbie and Barbas 2015). The direct
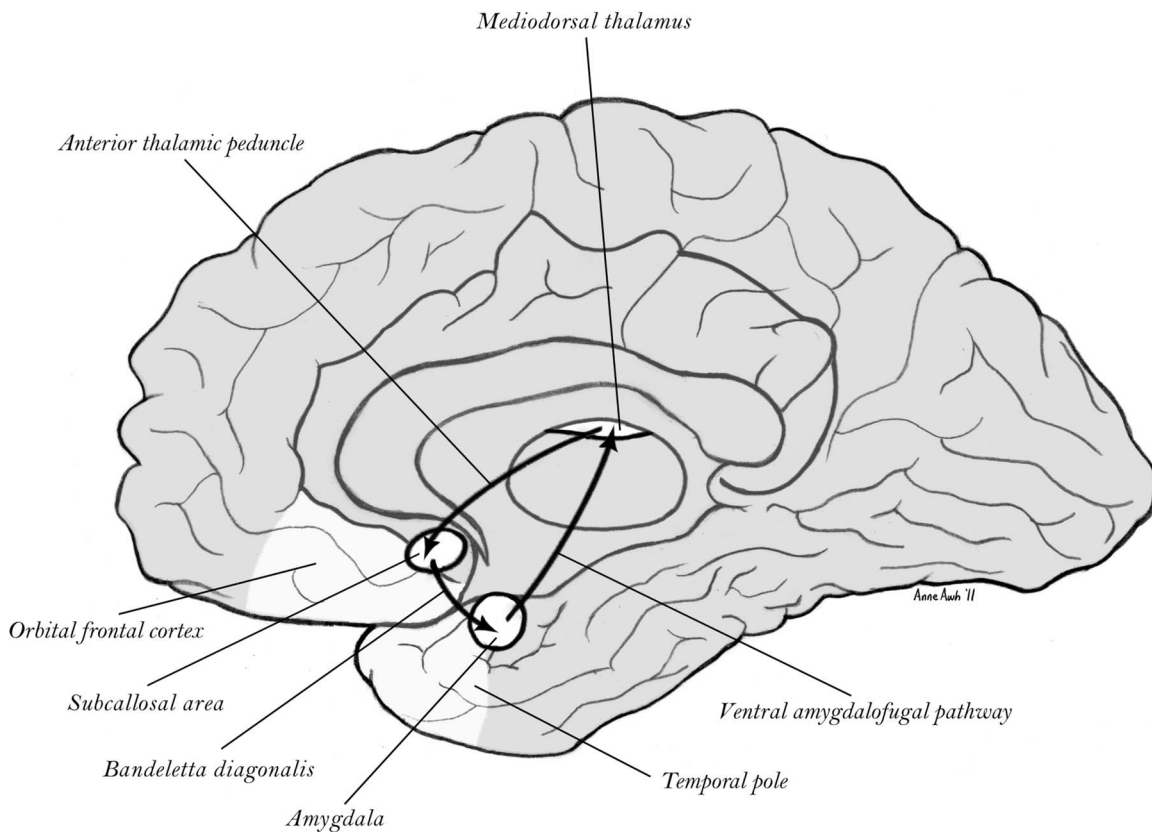
Fig. 9. Triangular circuit integrating the paleocortical limbic division with tripartite interconnections between the mediodorsal thalamus, anterior temporal lobe and amygdala, and the posterior orbital frontal lobe. From Tucker and Luu (2012).

projections from amygdala to the caudal orbital frontal cortex target inhibitory neurons across multiple cortical layers. For the indirect projections (through the MD thalamus), a question is whether the same MD neurons that receive amygdalar projections are those that target the posterior orbital frontal cortex (pOFC). Timbie and Barbas (2015) used double- and triple-labeling methods to confirm that the same MD neurons regulated by the amygdala are those that project to the pOFC. Furthermore, the nature of the amygdala regulation of both MD thalamus and pOFC was characterized by differentiating the unique synaptic vesicular transporter of the glutamatergic (VGLUT) projections. The amygdalar projections to the MD thalamus were from larger neurons and expressed the VGLUT1 transporter, which is typical of the efficient driver projections to the thalamus. The direct amygdalar projections to the pOFC were from smaller neurons that expressed the VGLUT2 transporter typical of matrix or modulatory projections (Timbie and Barbas 2015). The importance of the MD connectivity to regulating pOFC contributions to behavior has been emphasized by selective disruption of the VGLUT2 projections in rodents, which results in increased risk-taking and impaired avoidance, suggesting a disruption of normal self-regulation by anxiety (Wallén-Mackenzie et al. 2009).

The specific role of MD regulation of the visceral and emotional components of anxiety was demonstrated by Rotge et al. (2012) in research examining possible deep brain stimulation sites for treating anxiety and obsessive–compulsive disorder. Enhancing MD function in monkeys through microinjections of a GABA$_A$ antagonist led to signs of increased anxiety, including behavioral activity, emotional vocalizations, and autonomic dysregulation. Because the MD thalamus receives collothalamic projections from the midbrain (Erickson et al. 2004), which in

turn regulates dopamine modulation of both mesolimbic and frontal networks, the MD thalamus may be a critical node of the dopaminergic, collothalamic midbrain regulation of both anxiety and its visceral manifestations of the fight-flight response (Luu and Tucker, submitted).

More recently, Timbie et al. (2020) examined the nature of the terminals of amygdalar projections to the MD thalamus and found that these are similar to the complex terminals that motor areas project to signal self-initiated movements, apparently reflecting a form of corollary discharge. The implication may be that the triangular circuit through the MD thalamus allows a reentrant monitoring of both visceral and affectively significant sensory signals by the amygdala to regulate the orbital frontal lobe's contribution to action (Timbie et al. 2020). It seems clear that the phenomenology of activity within this circuit would be the experience of anxiety.

The amygdala is a remarkable structure with both pallial and subpalial components, with interconnections not only with limbic but striatal structures (Nauta 1982). Recent evidence in humans suggests that the ventral limbic-MD-frontal network may be important to the beta rhythms that regulate striatal-thalamo-cortical loops to establish the status quo or stability in current cognitive as well as motor processing (Engel and Fries 2010; Ketz et al. 2015). Altogether, the limbic, MD thalamic, and frontal components of the triangular circuit may be coordinated with amygdalar control over the striatum to provide a key mechanism for the "redundancy bias" (Pribram and McGuinness 1975; Tucker and Williamson 1984) that allows the stabilization of object memory through thalamic mediation of ventral corticolimbic and striatal network dynamics (Tucker and Luu 2012).

When coupled with the monitoring of the affective corollary discharge (Timbie et al. 2020), the combined ventral limbic and striatal circuits may thus provide a visceral constraint on working memory that is integral to the role of anxiety in regulating behavior, including the exaggerated regulation of redundant actions in chronic and severe anxiety, such as in obsessions (ideational ruminations) and compulsions (steretoped, ritualized actions) (Shapiro 1981; Tucker and Williamson 1984). Yet, as Sanides (1964) points out, there are also pathologies of insufficient anxiety, such as caused by orbital frontal lesions, leading to personality disinhibition and psychopathy, reflecting the loss of what Sanides described as "ethical and conscience reactions."

Anxiety is thus an essential personality control, mediated by the ventral limbic division, for tuning the adaptive focus of cognition, and for maintaining an essential affective quality of critical conscious appraisal, allocentric awareness, and appropriate behavior in the social context.

Visceromotor foundations for human initiative

We propose that there is a similar complexity of fronto-thalamo-limbic monitoring of visceral function for the dorsal limbic Papez circuit (Fig. 8). This elaboration of the visceromotor function within the dorsal limbic circuit requires the regulation of arousal by the ANT, which appears under control not from the collothalamic midbrain projections but from the lemnothalamic projections from brainstem reticular activating system (Luu and Tucker, submitted; Poremba et al. 1994). This dorsal limbic circuit, with both its mediodorsal frontal lobe regulation and its reticular brainstem arousal support, appears to be integral to the elaboration of the visceromotor function in memory and cognition. The visceromotor function not only expresses hedonic impulses (oral, sexual) in elementary motivation; it also may support human intentionality in more complex functioning (Tucker and Luu 2012).

In his initial development of the theory of dual dorsal and ventral origins of the cerebral cortex, Sanides drew on his studies of the human frontal lobe (Sanides 1964). He emphasized that the frontal lobe's higher level control of cognition and behavior is dependent on the more elementary regulation of arousal by the reticular activating system. In differentiating the dorsal and ventral divisions of the human frontal cortex, and their dependence on the unique influences of dorsal and ventral limbic protogradations (the increasing laminar articulation, now characterized by the Structural Model), Sanides drew on Kleist's distinctions between the "disorders of personality inhibition" with orbital frontal lesions, versus the impairment of drive or initiative observed with cingulate and mediodorsal frontal lesions (Sanides 1964). These distinctions are highly congruent with the more general mammalian limbic functions of constraint and avoidance provided by ventral limbic control, versus impulse and hedonic urges provided by dorsal limbic control (Tucker and Luu 2012). Yet Kleist's classic distinctions point to more complex elaborations of these elementary limbic motive controls in the human frontal lobe, as captured in his prescient observations on focal dorsal and ventral frontal lesions from gunshot wounds in World War I.

Just as the characterization of specific neural mechanisms in the triangular circuit (Timbie and Barbas 2015; Timbie et al. 2020) has led to theoretical insight into the potential ways that the amygdala may support limbic monitoring of affective states, the understanding of higher frontal executive networks may be advanced by characterization of the specific circuitry through which the frontal lobe regulates primate limbic-thalamic

circuitry, for both the dorsal Papez circuit through the ANT and the ventral triangular circuit through the MD thalamus. Zikopoulos and Barbas (2006) have traced the projections from multiple frontal sites in the macaque to the thalamic reticular nucleus (TRN), which provides inhibitory control over the thalamocortical projections. Several of the frontal sites, including those on the orbital surface (BA 13), lateral surface (BA 46), and medial surface (BA 9), were found to project to central and posterior regions of the TRN that appear to regulate sensory thalamocortical projections, thus providing routes through which frontal regulation may be applied to inhibitory (and disinhibitory) gating of sensory attention in the thalamus (Zikopoulos and Barbas 2006). In contrast, the most focal projections to the rostral pole of the TRN were from the rostral pole of the frontal cortex (BA 10) as well as the anterior cingulate cortex (BA 32), suggesting that these regions apply more generic frontal regulatory control over thalamocortical relations, rather than specific sensory attentional modulation.

As an integral component of the Papez circuit, the anterior cingulate cortex (BA 32) appears important to regulating the impulsive, feedforward control of limbic visceromotor control. In the rodent, the dorsal limbic control is associated with the head direction cells (Taube 1998), suggesting an elementary egocentric basis for intentionality. When the dorsal limbic circuit with its septal foundations in the forebrain is disinhibited, through lesions of the amygdala, the effect is hyperorality and hypersexuality (Kluver and Bucy 1939; Aggleton and Passingham 1981). The focal projections from BA10 to the anterior TRN in the monkey may be relevant to frontal executive control over thalamocortical function in these domains of visceromotor intentionality. We can infer that this form of executive control must be particularly important in humans, given the remarkable expansion of BA10 in recent human evolution (Semendeferi et al. 2001).

A uniquely human disorder of frontothalamic control is absence epilepsy, in which the person briefly loses conscious control intentional actions but (unlike with limbic seizures) does not fall down, and does not become amnestic for recent events (Niedermeyer et al. 1985). Several sources of evidence including recording of local field potentials suggest that absence seizures engage the cortico-TRN-thalamocortical circuitry (Lopes da Silva et al. 2003). High-density electroencephalographic (EEG) localization during human absence seizures has shown that the "generalized spike–wave" discharges of these seizures, although they are bilateral, are not diffusely generalized, but rather involve focal spikes localized to the frontal pole (BA 10) (Tucker and Luu 2007).

The implication of these several observations may be that the human development of conscious intentionality may be supported by the large frontal pole as well as the anterior cingulate cortex and the dorsal limbic Papez circuit (Tucker and Holmes 2010). This elaboration of dorsal limbic function in humans may extend the visceromotor impetus to action to support the regulation not only of crude impulses, but the behavioral initiative in personality captured by Kleist's characterization of the human dorsal frontal lobe (Sanides 1964).

In contrast, the orbital frontal regulation of socially appropriate behavior in Kleist's model may depend on the greater connectivity with ventral limbic control (and awareness) of the viscerosensory functions of anxiety, mediated by the amygdala, MD thalamus, and the triangular circuit. Although human capacities in executive control and conscious awareness are clearly supported by the uniquely evolved anatomy of the human frontal pole, the essential circuitry for supporting these capacities is shared by

other primates and is being increasingly clarified by anatomical insights into structural connectivity (Zikopoulos and Barbas 2006; Timbie et al. 2020; García et al. 2022).

The excitement of active inference

Thus, the foundations of homeostatic control of active inference can be studied in the essential circuitry of constraint and anxiety in the viscerosensory domain, balancing the impulse of urges emergent in the visceromotor domain. As mentioned in the introduction, the process of active inference must be grounded in the adaptive control of homeostasis, maintaining organismic complexity in the face of entropy (Friston 2010). Through characterizing the neural mechanisms of motive control of memory representations, it may be possible to understand the extension from basic homeostasis to active allostasis, through integral forms of excitement and inhibition that regulate the adaptive control of memory and concept formation within the multileveled neuraxis.

We propose that the differential forms of motive control from the dual limbic divisions have direct implications for the Bayesian process of active inference. The dorsal limbic mode of control, contributing to allostasis and control of memory through the visceromotor function, may be important to generating hedonic, pleasurable expectancies to influence processing in the neocortical hierarchy (heteromodal, unimodal, primary) to guide predictive coding in a feedforward fashion. In contrast, the ventral limbic mode of control, with its sensitization and redundancy bias providing a tonic and sustained control over allostatic adjustments, may be important to directing the constraints of sensory and motor feedback that are involved in error-correction of ongoing expectancies.

The integration of computational architectures for feedforward versus feedback control is a classic challenge of self-guided systems, including brains (Hendler 1995). In artificial intelligence architectures, a common solution has been to separate the computational apparatus for feedforward control into actor systems that work well to implement actions in space, versus critic systems that are architected to evaluate these actions in relation to system goals (O'Doherty et al. 2004; Tasdighi et al. 2023). Vertebrate neural evolution may have arrived at a similar efficiency. The delineation of motive control between impulse and constraint may have allowed vertebrate neural evolution to differentiate forms of limbic control into the actor (dorsal) and critic (ventral) roles.

In the next section, we review evidence that the dual modes of human limbic control of active inference may be measurable as differential forms of limbic excitability in human cognitive processes generally, as evidenced by EEG studies.

Dynamics of context-updating and error-correction in distributed learning systems

Interpreting how cognitive representations (concepts) are organized and regulated in cortical networks is being informed increasingly by computational models of distributed representations, of which active inference is particularly important to illustrating the cybernetic as well as representational processes of cognition. The recognition that existing knowledge (Bayesian priors) may constrain the process of new learning became apparent in the early connectionist models of learning (Rosenblatt 1958). Training the simple distributed network to encode new information inherently disrupted the connection weights that encode prior knowledge. This was then criticized as an inherent

failure of the distributed representational model (Minsky and Papert 1969). The problem became known as "the stability-plasticity dilemma": whether to maintain the stability of existing memory or disrupt it through plasticity required for new learning (Grossberg 1980).

Once it was realized that distributed representation of information is essential to biological cognition, it became clear that regulating the plasticity of the memory system as a function of the adaptive significance of new information is a key challenge for brains as well as computational architectures that emulate them (Carpenter and Grossberg 1993; Raizada and Grossberg 2003). Although the stability-plasticity dilemma was only rarely seen as a phenomenological reality for human cognition (Tucker and Desmond Jr. 1998), the negotiation between stability and plasticity can be seen as a way to interpret a large literature in human cognitive electrophysiology, where brain responses seem to track the person's spontaneous maintenance of a cognitive model of the environment. The context-updating evidence in electrophysiological studies suggests that cortical representations are updated regularly but gradually (a feedforward mode). In contrast, distributed cortical representations are changed most rapidly when attention is focused by anxiety because information is discrepant with existing expectancy (a feedback mode).

Bayesian electrophysiology of context-updating

As cognitive neuroscience researchers examined the electrical fields of the human cortex during studies of learning and memory, the neural responses generating ERPs were initially interpreted in relation to apparent requirements for stimulus processing and response preparation, reflecting the traditional experimental psychology model of discrete mental faculties mediating stimulus–response relations (Callaway 1973). Yet an irritating discrepancy for the research paradigm appeared when the ERP evidence reflected more complex properties of information representation than just input and output processing (Donchin and Heffley 1979). A robust ERP, the P300 or "late positive complex," seemed to reflect not just stimulus processing, or motor preparation, but the brain's maintenance of a model of the environment. The key finding was that a person could complete a successful response to a task before the P300 develops. The implication was that the brain mechanisms are not simply performing the task, but rather organizing the information of the cognitive context more generally.

This process was described in terms that had been developed in the computational theory of adaptive resonance (Grossberg 1980; Carpenter and Grossberg 1993) as "context-updating" (Squires et al. 1977; Donchin and Coles 1991). Careful analysis of the timing of P300 and similar positive potentials showed that they continue to develop after cognitive decisions have been made, and sometimes even after responses have been generated.

The idea of context-updating in fact implies that the core task of cognition is not just completing the experimental task and pushing the button, but rather updating the context (neuronal) model to be current with the developing evidence. This process of context-updating inherently requires a Bayesian arbitration of the stability-plasticity dilemma. The implication is that the brain maintains a model of self-in-context, not unlike Sokolov's "neuronal model" that determines orienting responses to significant changes in the environment (Sokolov 1960). As a result, cognition (even in psychology experiments) is inherently Bayesian, continually guided by a model of the world which must be kept current through an ongoing process of context-updating to maintain relevance with new environmental evidence.

Electrophysiology of unexpected error

When information is presented that is incompatible with the person's expectations, the feedforward adjustment of context-updating is insufficient, and a different ERP response is observed, typically a cortical-surface-negative potential. The N400, for example, is observed while reading an unexpected word, such as "He spread the warm toast with *socks*" (Curran et al. 1993). Another surface-negative potential, the "error-related negativity" or ERN, is then recorded as a response is made on a task that the person realizes is an error (Gehring et al. 1993). Similar surface negativities are observed in response to new memory demands, as if responding to the unpredicted events (Curran 2000). Network responses to discrepant information analogous to surface-negative potentials have in fact emerged in computational modeling with adaptive resonance theory (Grossberg 2021).

Although there are various interpretations of these and related ERP findings in the literature, this evidence emphasizes that perception and cognitive evaluation are not de novo operations but are determined by the person's current expectancy for events. In this Bayesian process, expectancies are built from prior experience, such that confirmation of expectancy is efficient, and there is a strong engagement of neural processing only when expectancies are violated.

In examining the neural sources generating the ERP with high-density EEG, Luu, Tucker, and associates observed that cortical-surface-negative responses in detecting errors, and in monitoring feedback, were typically localized to cingulate cortex (Bush et al. 2000; Dehaene et al. 1994; Luu, Collins, et al. 2000; Luu and Pederson 2004; Luu and Tucker 2003). The conventional ERP analysis involves averaging of multiple trial events. However, when the underlying EEG oscillations of each event were examined it became clear that the error-related and feedback-related negativities were not isolated transient fields but resulted from phase-alignment of the midline (limbic) theta rhythm in response to the discrepant stimulus (Luu, Flaisch, et al. 2000; Luu and Pederson 2004).

If we integrate these electrophysiological findings with the insights to learning in distributed networks and the neocortical anatomy of the Structural Model, we find that widespread areas of heteromodal association cortex appear to be coordinated by limbic areas in ways that support the gradual integration of new events into the neuronal context model, thereby achieving context-updating. When significant discrepancies with the context model are detected, there is a more focused processing (including considerable ventral limbic input to the anterior cingulate) for the rapid memory changes required to respond to prediction errors and other unexpected events (Luu and Tucker 2003; Luu et al. 2011).

In our theoretical interpretation of these findings, we have considered the roles that limbic networks play in the adaptive regulation of cognition. The linked networks of the pathways in the cerebral hemisphere are not isolated modules, but rather a hierarchy of core-to-shell (visceral limbic to somatic sensory-motor) networks of the Structural Model whose electrophysiological excitability is managed by the limbic core, determining the phasic update of the P300 or the sustained surface negativities of discrepancy responses (Tucker and Luu 2012). The implication of the consistent limbic contribution to ERPs is that human cognition is regulated by limbic dynamics in each instance.

As evidenced by these electrical signs of cortical excitement, the ongoing cognitive process is inherently Bayesian, in that the person maintains a valued cognitive representation of self

in the world—described as the "hedonic context model"—such that accurately processing events in the world therefore requires context-updating. When events are unpredicted by the context model, attention must be directed to the prediction errors, with unique ventral limbic activity recruited by neocortical processes to engage motivated attention for emergent updating of the context model to adjust and maintain accurate predictions of self-in-world to guide adaptive behavior.

Elation and anxiety regulating feedforward and feedback expectancies

Predictive coding in this model is thus not restricted to adjacent neocortical regions, such as local predictions from association cortex interacting with sense data in primary sensory cortex (Bastos et al. 2012), although these interactions indeed define the relations of adjacent networks in the Structural Model. Rather, the cognitive process of implicit expectancy reflects large-scale, organismic limbic, and neocortical networks, continually developing the memory for the ongoing context model while managing the effort to correct its errors. Our working hypothesis is that the hedonic context model has an inherently positive valence, mediated by norepinephrine control of elation (Stein 1980; Tucker and Williamson 1984), consistent with the subjective intentionality suggested by head direction cells within the dorsal limbic division.

Similarly, the detection of errors appears to shift from this egocentric perspective toward an allocentric one, with feedback expectancy tuned by the level of anxiety, as ventral limbic and amygdalar networks are engaged in response to the external threat posed by discrepant events in the world (Tucker and Luu 2012).

The specific roles of dorsal and ventral limbic divisions were not initially apparent in the ERP studies but may be inferred from several findings. Whereas context-updating appears to engage particular activity in mid-cingulate and posterior cingulate areas (Luu et al. 2009; Luu and Tucker 2003), error-monitoring engages anterior cingulate regions specifically (Bush et al. 2000; Dehaene et al. 1994; Luu, Collins, et al. 2000). The anterior cingulate cortex receives strong input from ventral limbic regions through the subgenual cingulate area (Price et al. 1996; Price 1999), and this ventral limbic engagement may be particularly important to error-monitoring and effortful attention under the adaptive threat posed by prediction error.

Dorsal and ventral attention networks regulating limbic expectancies

Hemodynamic neuroimaging methods have confirmed the key roles of posterior versus anterior cingulate cortices in regulating attention to expected versus unexpected events (Posner et al. 1988; Chein and Schneider 2005). Furthermore, animal studies of the neurophysiology of learning have provided results that may be consistent with this interpretation of differing dorsal and ventral limbic roles in organizing the hedonic context model and in managing discrepancies.

Michael Gabriel and associates recorded neural activity in cingulate cortex as rabbits engaged in various learning tasks (Gabriel et al. 1980; Gabriel 1990; Gabriel et al. 1996). They observed neural responses in posterior cingulate cortex that changed only gradually with learning, consistent with the phasic arousal of context-updating. However, responses in anterior cingulate cortex were sustained in response to changes in learning contingencies, consistent with the tonic activation supported by ventral limbic sensitivity to discrepancy.

We interpret these anterior cingulate cortex responses to reflect a focused form of working memory regulated by ventral limbic networks (with direct projections to the ventral, subgenual anterior cingulate). This form of working memory supports the rapid error correction required when the hedonic context model is violated. These electrophysiological findings in animals and humans may thus provide the limbic basis for the hemodynamic correlation evidence of dorsal cortical networks of the DAN in top-down feedforward control, contrasted with the ventral cortical networks of the VAN in stimulus-dependent feedback control (Astafiev et al. 2003; Corbetta et al. 2008).

Exaggerated examples of human motive control of learning and memory are revealed by the effects of strong motive control by anxiety. Given the importance of the amygdala and ventral limbic areas to anxiety (Derryberry and Tucker 1990; Tucker and Derryberry 1992), a key finding in the EEG and ERP literature is that persons high in anxiety and negative affect show exaggerated responses in anterior cingulate cortex in response to making errors (Luu 1997; Luu, Collins, et al. 2000). Because the error-related negativity in the ERP average can be shown to arise from phase-alignment of limbic theta in the anterior cingulate cortex (Luu, Flaisch, et al. 2000; Luu and Tucker 2001; Luu et al. 2004), a related finding now widely replicated is the enhanced midline frontal negativity in anxious persons (Cavanagh and Shackman 2015). The relevance to dynamic limbic theta regulation of hierarchic networks in the neocortex (Grossberg 2021) may be important.

Studies with fMRI, when examined through meta-analysis (Etkin and Wager 2007), have shown a consistent pattern of amygdala activation in anxiety disorders including PTSD, social anxiety, and specific phobia. An exaggeration of ventral limbic regulation in anxiety disorders, reflected in enhanced anterior cingulate engagement in error-monitoring (Luu, Flaisch, et al. 2000; Luu and Tucker 2001; Luu et al. 2004), may help to explain the enhanced attention to errors and threat that are typically observed in anxiety disorders (APA 2013).

Limbic motive control of action

The role of limbic biases in regulating cognition through primitive cybernetics of habituation versus redundancy may be understood most clearly through a control theory analysis (Wiener 1961) of the frontolimbic networks regulating simple actions. Neuropsychological studies of problems in behavior caused by brain lesions have demonstrated deficits that were initially difficult to interpret but that may be more clearly understood by recognizing that the dorsal and ventral divisions of the hemisphere provide unique modes of sensory-motor control. The distinction of ventral-object versus dorsal-spatial visual processing appears to be extended to motor control, as exemplified in ideomotor apraxia versus optic ataxia.

Lesions to the inferior parietal lobe produce motor deficits that are manifested dissociations between motor acts and visual information, particularly in relation to cueing on objects to guide action. In "ideomotor apraxia," caused by the lesions to the inferior parietal lobe, patients can verbally describe the function of the object and how it is used, but they are unable to demonstrate (e.g. pantomime) the action associated with the object (De Renzi et al. 1980), apparently because of a disconnect between the ventral object memory and the dorsal, archicortical capacity for the generative, predictive mode of action control.

In contrast, lesions to the superior (dorsal) aspect of the parietal lobe produce motor deficits, known as "optic ataxia," that involve difficulty in reaching toward targets, particularly those that are presented the periphery of visual view. As argued by Pisella et al. (2009), optic ataxia represents a deficit transforming visual information, within an egocentric reference frame relative to the eyes, into reaching movements.

Thus, in the parietal lobe, we can see dual cybernetic modes of action regulation. A more ventral control process is centered on objects constraining motor acts. A more dorsal control, related to ballistically reaching out to targets in the periphery, is based on egocentric, spatial information.

This distinction in organizing actions by the ventral and dorsal parietal modes of cognition is continued in the premotor motor regions of the frontal lobe, as seen in the functions of the arcuate premotor area of the ventral frontal lobe contrasted with the cingulate and supplementary motor area of the dorsal division. Similar to the close relation between action and visual information seen in the inferior aspects of the parietal lobe, functional studies show that neurons in the arcuate premotor area are responsive both to visual inputs (presentation of an object) as well as haptic object contact, as when the object is grasped (Murata et al. 1997). In contrast, cells of the cingulate premotor areas do not respond to the sensory stimulus, but rather to holistic aspects of the motor action (such to instructions, cues, etc.), implying a more global, internal representation of the action plan (Hoshi et al. 2005). Our interpretation is that these classical clinical observations can be interpreted to reflect opponent biases of feedforward versus feedback forms of motor control as implemented by dorsal versus ventral divisions of the cerebral hemisphere, respectively.

Projectional feedforward and constrained feedback cybernetics in human action

Similar control biases of dorsal and ventral limbic divisions have been clarified in the analysis of the effects of brain lesions on the human control of movements in the rehabilitation setting (Goldberg 1985). Importantly, this analysis of dual strategies of action control aligns well with the evidence from invasive recordings in dorsal and ventral frontal cortex in monkeys (Shima et al. 1991; Tanji et al. 2002). In regulating action, the archicortical and paleocortical limbic foundations of the frontal lobe appear to exert opponent and generally balanced influences that are consistent with the parietal cybernetics. The archicortical limbic influence creates the egocentric, subjective feedforward control generating actions in mediodorsal frontal networks, whereas the paleocortical influence is anchored in the allocentric, objective, feedback constraints from ventrolateral frontal areas that become necessary as the action makes contact with the environment.

As with the differential limbic contributions to learning and memory, this analysis of action regulation has been theoretically anchored in the unique anatomical characteristics of the dorsal and ventral divisions of the frontal lobe. The unique feature of the mammalian neocortex, which is not found in the more generic reptilian (3-layered) pallium, is the thalamic sensory input to granular layer 4. As a result, the minimal granular layer 4 in the dorsal frontal neocortex of primates, including humans, presents theoretically significant evidence for functional analysis (Shipp 2005, 2016). The implication is that the dorsal (dorsomedial) frontal lobe must proceed with minimal sensory guidance from granular layer 4 input, thus operating in a more purely feedforward, projectional, limbifugal fashion. In contrast, the ventral (ventrolateral) frontal lobe has access to sensory guidance through its well-developed layer 4, allowing greater control of action through external sensory feedback (Goldberg 1985). This sensory feedback is then communicated across the frontal

neocortical hierarchy through limbipetal error-propagation (Tucker and Luu 2021).

Goldberg's study of the qualitative features of human motor control was based in his recognition of these dual architectonic characteristics of dorsal and ventral frontolimbic cortices. The dorsal frontal input to motor cortex, through the supplementary motor area, appears to operate in a ballistic (impulsive) fashion, launching actions toward goals with feedforward expectancy (and little need for sensory feedback). This appears to be particularly important in the early stages of an action, such as reaching for a glass of water, when the directed motive urge and the bodily balance (supported by axial postural control) are all that is needed to launch the action toward the goal. With primary control from the dorsal limbic circuits, the feedforward projection of the impulse can be seen as the adaptive basis for what has been observed as top-down control in the DAN (Corbetta et al. 2008).

The ventral frontal input then becomes more important when constraint and guidance from sensory feedback is required. For example, haptic or visual feedback may be needed to adjust the action process. The process was initially launched under dorsal control as a ballistic urge (prediction) to achieve the goal. But as the hand approaches the glass, sensory feedback guidance from the ventral network is required for precise close of a precision grip on the glass.

Recognizing these differing cybernetic biases may be important for framing the process of active inference in organismic terms. In proposing that the limbic foundation of the cortex provides a form of expectant, predictive motive control, Tucker and Luu (2021) considered a generic model of limbic-neocortical architecture in which the limbifugal direction of processing across the cortex provides feedforward control through generative predictions sent to the adjacent cortical area. Processing in the limbipetal direction then provides feedback control in the form of sensory and proprioceptive evidence on external constraints that impinge on these predictions.

This model can now be extended to account for the differing control biases applied by the dual limbic divisions of the neocortex that help to organize both frontal generation and temporoparietal monitoring and control of actions. Whereas the limbic-neocortical hierarchy operates through limbifugal expectancy and limbipetal error-correction in each of its major sensory and motor pathways, the dual limbic divisions each impose their unique biases on this linked hierarchy of cortical networks, with the dorsal division engaging the hierarchy in a projectional, impulsive, and feedforward fashion, and the ventral division biased more toward constrained guidance by sensory feedback. The result is dual forms of control, not only for memory representation (contexts versus specific objects) but also for memory process (expectant prediction versus constraint satisfaction).

In an analysis of motor control in terms of active inference, Friston and associates have emphasized that the difficult computational problem of specifying motor commands with optimal control theory can be addressed parsimoniously with the Bayesian principles of active inference, as cortical predictions are continually refined by sensory, proprioceptive, and kinesthetic outcomes in iterative fashion (Friston 2011; Adams et al. 2013). Predictions are a kind of feedforward control, whereas error-corrections through limpibetal communication reflect feedback (sensory-guided) control. The control theory difference is between a ballistic missile versus a guided one. Recognizing the complementary dorsal and ventral limbic control biases, linked through specialized cortical cytoarchitectonics, we can consider how the specialization for feedforward versus feedback control in the

limbic divisions may bring unique forms of motive control, and unique affective qualities, to behavior and cognition generally.

The apparent grounding of the archicortical division in the egocentric reference frame for modeling self-in-world may be well-suited to the generation of action impulses under conditions of expected success, as needs and urges are manifested directly in the impetus for action. The scope is holistic, which means closer-to-limbic in the more diffuse minimal columnar and laterally diverging network architecture. Here, the unique motive control for the dorsal division may be aligned with feedforward control, with elation and positive affect of the dorsal limbic network supporting the impetus in the head direction, with the inherent intention of egocentric expectation for success (Tucker and Luu 2012).

In contrast, the tight feedback control of sensory guidance from the ventral division may be suited to error-correction with respect to allocentric events, such as under conditions of expected threat, with the necessary motive bias provided by extended amygdalar regulation. In a primitive sense, this ventral limbic regulation engages anxiety and avoidance. Furthermore, if the threat is close, the mood turns to anger (Adamec 1990). In human cognition, both anxiety and hostility may be subtle but necessary forms of affective control of memory to provide the tonic activation and thus extension of focus in time to support critical, analytic control of differentiated concepts with precision and constraint (Tucker and Luu 2012).

Changes in personality with brain lesions

We have seen that Sanides's influential analysis of dual origins of cortical differentiation from limbic origins drew upon Kleist's clinical neurological analysis of dorsal and ventral frontal lesions (Sanides 1964). In general terms, a balance between limbic motive influence and neocortical regulation of this influence is implied by the classical neuropsychological evidence on the effect of neocortical lesions on motivation and emotion (Gainotti 1972; Lezak 1983; Heilman and Watson 1989). There is often a release of limbic motive control as a result of neocortical lesions. In the intact brain, this would imply that cognitive representations, anchored in the large human heteromodal association areas, may be essential to the normal regulation of emotion at its limbic base (Tucker and Luu 2021). More specific changes in motive control and emotional regulation, with unique effects of dorsal versus ventral fronto-temporal lesions, may suggest that the control biases in motor studies reviewed in the previous section are also involved in more general personality regulation. These biases are conveyed in a kind of implicit Bayes model, through the viscero-motor charge (urge) of prediction in the archicortical division, and in the bias toward sensitization of viscerosensory charge (angst) to error feedback in the paleocortical division.

In a now classical review of the literature on personality changes with brain lesions, Blumer and Benson (1975) confirmed Kleist's basic observations. They observed that bilateral mediodorsal frontal lesions may lead to a "pseudodepression" syndrome, in which the person shows lack of initiative and apparent emotional depression subsequent to the lesion. This observation of neurological mechanisms of depression may be consistent with Kleist's observation of a loss of drive or initiative with dorsal frontal lesions and with the theoretical proposal that the intact dorsal limbic division supports a positive hedonic expectancy and impulsive engagement of behavior, supported by the mood/arousal control of elation (Tucker and Luu 2012).

The evidence of septal control of approach motivation, at the basal forebrain of the Papez network (Cox and Heath 1975;

Heath 1976; Olds and Milner 1954; Phan et al. 2002), may help explain the positive affect integral to the dorsal limbic division. The examples of released dorsal limbic action, including hyperorality, hypersexuality, and hyperactive attention to change (hypermetamorphosis) in the amydalar lesioned monkeys (Kluver and Bucy 1939), can serve as examples of release of the primitive impulses at the root of the dorsal limbic intentionality. It seems therefore likely that the generation of valued predictions though this intentionality will generally show an inherent positive bias. Furthermore, the habituation bias of elated arousal forms an integral novelty detector, energetically exploring possible approach avenues (Tucker and Williamson 1984).

With orbital and ventrolateral frontal lesions, on the other hand, the patient may recover to manifest the pseudopsychopathic syndrome (Blumer and Benson 1975). This syndrome reflects damage to the normal constraint provided by the ventral limbic division, which is motivated by the mood/arousal control of anxiety (Tucker and Luu 2012). The patient with pseudopsychopathic syndrome then suffers from inadequate anxiety and thus inadequate constraint (Damasio and Van Hoesen 1983; Sanides 1964), not unlike the personality disorder of psychopathy without brain lesions. Consistent with these effects, as well as the amygdalar lesions in monkeys, is the normally adaptive role of the amygdala and its ventral frontolimbic networks that becomes exaggerated during negative affect and anxiety in neuroimaging studies (Etkin and Wager 2007).

The cybernetics of self-regulation in personality thus seem to be balanced between dorsal and ventral corticolimbic networks in the same way as the regulation of simple actions. The important point is that there is complete continuity in the human motive-memory, between the limbic motive control and the neocortical actualization of action and cognition. As anxiety focuses analysis, or as elation expands conceptual scope, conceptual structure emerges directly from motive control.

Thus, as we recognize the differing modes of motive control emergent from the dual limbic divisions of archicortical and paleocortical derivation, there may be an opportunity to revisit classical theoretical models of personality and psychopathology in relation to more explicit neural mechanisms (Giaccio 2006). Personality can be seen as inherently Bayesian in that it develops as a cumulative process, with specific forms of motive control allowing the person to proceed efficiently under positive affect with behavior that is consistent with the hedonic context model, until discrepant events require a change. Change is then mediated by anxiety, vigilance for errors, and by constraint of personal impulses, until conditions allow re-establishing the hedonic context model that allows the feedforward and impulsive flow of self-in-world (Tucker and Luu 2012).

Conclusion

In the present paper, we have proposed that the limbic regulation of the neocortical network hierarchy involves unique motive biases emergent from homeostatic needs and that these biases then provide unique contributions to the cognitive process of active inference that differ for the dorsal and ventral cortical divisions. These biases in motive control appear to be integral to the major functional connectivity networks in the fMRI correlation studies, leading to the feedforward or top-down control of the DAN and the feedback or bottom-up control of the VAN. The process of organizing concepts through active inference and constraints from perception and action thus takes different forms, with an egocentric, impulsive, feedforward control for the dorsal cortex

and an allocentric, constrained, feedback control for the ventral cortex.

The Bayesian arbitration of expectancy with evidence that organizes active inference is thus inherently biased, toward certainty and confirmation in the dorsal division and toward uncertainty and disconfirmation in the ventral division. The simplest evidence for these cybernetic biases comes from the dorsal and ventral contribution to action regulation, as seen in the human rehabilitation setting as well as in the experimental study of motor control in monkeys. But the parallels with the evidence on personality changes from dorsal and ventral frontolimbic lesions suggest that the same control mechanisms are operative and must be balanced in adaptive human psychological function generally.

Self-regulating cognition through primitive motive controls on uncertainty

The differing forms of motive control from dorsal and ventral limbic networks apply unique biases on uncertainty in information processing. The habituation bias of the dorsal limbic division supports the orienting response to perceptual events, and it supports the rapid and direct translation of urges to actions in the motor system. Both of these effects can be described as primitive neural controls with high certainty. If the orienting response of the dorsal division is not followed by threat detection (and ventral limbic focusing), then processing rapidly habituates with the incorporation of the perceptual events within the holistic neuronal (hedonic context) model (Sokolov 1960, 1963). This is a cybernetic mode for maintaining stability of concepts that are held with certainty, thereby supporting confident action.

This unique feedforward, impulsive motive control of the dorsal limbic division may be seen in exaggerated form in the release of oral and sexual impulses following bilateral lesions of the ventral limbic network, centered on the amygdala, which normally provides constraint over those impulses (Kluver and Bucy 1939; Aggleton and Passingham 1981). In human psychological functioning, self-regulation through elation may lead to similar impulsivity when exaggerated in mania. Yet, at more optimal levels, the positive affect of elation leads to enhanced self-confidence and certainty of decision and action. Attention then shifts to the subjective (top-down DAN) perspective, where not only approach motives but confidence in personal agency converge to guide the decision process.

In contrast, as anxiety develops in ventral limbic networks, a different form of limbic excitement arises that has clear roots in the mesencephalic dopamine system, with integral striatal engagement, and with greater regulation of cognitive and memory function by the amygdala and the ventral limbic division (Tucker and Luu 2012). The evidence of ventral limbic engagement with anxiety can be seen in multiple cognitive and behavioral signs. Neurophysiologically, the engagement of midline frontal theta in anxiety disorders (Cavanagh and Shackman 2015) tracks the amygdalar regulation of the anterior cingulate cortex, not unlike that seen in the influence of anxiety on error monitoring (Luu, Collins, et al. 2000). This is a system-wide regulation of uncertainty, not at the level of discrete sensory or motor predictions, but at the ventral limbic and VAN levels of organismic self-regulation.

As a result of the ventral limbic influence of anxiety, cognitive structure takes a specific form in the neocortical hierarchy. The engagement of object memory is reflected in the exaggerated attention to detail and analytic cognitive structure characteristic of anxiety disorders (Shapiro 1965). The aversive vigilance, tight constraint on actions, and exaggerated error-monitoring are

characteristic symptoms in anxiety disorders (APA 2013). An integral effect of anxiety is inhibition of impulses, yet the dopaminergic influence seems to provide a redundancy or sensitization bias that does not simply suppress activity but maintains stability of the status quo of working memory in both action and attention (Tucker and Williamson 1984; Derryberry and Tucker 1990; Engel and Fries 2010).

Along with greater vigilance, the uncertainty of anxiety is a primitive and fundamental cybernetic effect. The focus of attention within the VAN brings vigilance not just to actual threats but to the diffuse uncertainty that is experienced palpably by the anxious person. The pathologies of anxiety, including obsessive–compulsive disorder and paranoia, could be described as disorders of unresolved Bayesian uncertainty in the relation of self to world. In the optimal level, anxiety supports vigilance for errors, critical thinking, and rational analysis. Whether optimal or pathological, anxiety shifts attention to an objective, allocentric perspective, where the locus of control in cognition is focused on external objects and events in the world.

In the neurophysiology implied by the connectivity of the Structural Model of the primate cortex, the dynamic interaction between limbic motive charge and neocortical cognitive processing is clearly bidirectional. In the limbifugal direction of influence, the strong mood states of anxiety and elation immediately determine the cognitive process, often unconsciously. Thus, the bipolar manic person finds herself with extreme certainty, confidence, and grandiose expectations, with little or no ability to remember the dejection and catastrophic pessimism when she was depressed just a week ago. Similarly, the anxious person's painful uncertainty may include a fleeting awareness that his actions are irrational, but he cannot stop himself from focusing on threats, and checking the locks on the doors again, as the anxiety is recruited.

Balancing these limbic cybernetics, the limbipetal direction of influence can be seen when thoughts provide rational interpretations to moderate the actions of motive controls. In this way, the complex conceptual representations centered in heteromodal cortex may provide structured, countervailing control over the more dynamic and excitable limbifugal influences from the limbic base of the cerebral hemisphere. The greater differentiation of cortical columns in eulaminate neocortical areas may be relevant to the greater differentiation of cognition in association areas versus more primitive components of cognition in the excitable allocortex and mesocortex at the limbic base. In line with the architecture, the moderating influence of rational interpretation over emotional arousal is not only recognized in the conventions of our popular culture. It has been extensively demonstrated by the literature on the effectiveness of cognitive therapy in managing disordered emotions (Beck 1991; Tucker and Luu 2007).

Cognition organized across the neocortical hierarchy can also engage and recruit the limbic charge, as when a small rush of elation accompanies remembering the approach a desired event, or when a brief surge of anxiety follows the imagining of a threatening experience. These are the furtherances and hindrances that William James observed to color the affective quality of his own cognition and to provide evaluative monitoring of his stream of consciousness (James 1890). The recruitment of emotion through ideational access is not unlike the recruitment of activation in classic neurophysiology through thalamocortical circuits (Morrison and Dempsey 1943) or the experimental kindling of limbic discharges (Adamec 1990). The dynamic process of cognitive self-regulation involves interactive exchange between the conceptual structure of neocortical representation, on the one hand, and the arousing neural excitement of limbic control, on the other (Tucker and Holmes 2010; Tucker and Luu 2021). This exchange appears to be organized by the dual limbic networks through primitive and opponent forms of motive control. One emerges from hedonic excitement of approach and is biased toward confirmation of valued intentions. The other is primed by the anxious anticipation of threat to detect errors and exert the necessary self-constraint.

An important implication from this line of reasoning is that the meaning of information becomes defined by its motivational and emotional significance. What is informative to a developing Bayesian system depends on the present state of uncertainty. The nature of integrating information within the brain's architecture then takes different forms as a result of the integral motive queries of the dual divisions of the limbic system. The feedforward bias of the dorsal division is well-aligned with personal intentionality (the human equivalent of the head direction), confirming expectancies for success. We can describe the psychological mode of this cognitive bias as extraverted: the perspective is inherently egocentric and impulsive, and the relevant information is that which is closely aligned with the implicit expectancies of current adaptive intentions.

On the other hand, the salience of negative feedback from environmental contingencies is heightened for the constraint mode of self-regulation, tuned by anxiety within the amygdala and ventral limbic division, selecting for a different form of meaningful information for self-regulation and cognitive integration: that which is likely to disconfirm current hedonic expectancies. The objects parsed by the inhibitory dynamics of the ventral corticolimbic division are inherently critical and allocentric, reflecting the features of the environment that are separate from the current behavioral expectancy. Here, what we might call introverted cognition is regulated less by intention from internal motives and more by attention to the implication of external constraints.

Tracing the adaptive motive control of cognition to these specific limbic control biases on the process of active inference may allow theoretical insight into the way that the motive control of cognition is not an ancillary influence, separate from the cognitive apparatus, but an integral mechanism regulating the generation and constraint of cognition across the multileveled network architecture of the cerebral cortex.

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