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Pre-frontal executive committee for perception, working memory, attention, long-term memory, motor control, and thinking: A tutorial review

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Abstract

As an explicit organizing metaphor, memory aid, and conceptual framework, the prefrontal cortex may be viewed as a five-member ‘Executive Committee,’ as the prefrontal-control extensions of five sub-and-posterior-cortical systems: (1) the ‘Perceiver’ (dominant-right-hemisphere ventral-lateral prefrontal cortex—*VL/PERC-PFC*) is the frontal extension of the ventral perceptual stream (the *VL/PERC system*) which represents the world and self in object coordinates; (2) the ‘Verbalizer’ (dominant-left-hemisphere ventral-lateral prefrontal cortex system—*VL/VERB-PFC*) is the frontal extension of the language stream (the *VL/VERB system*) which represents the world and self in language coordinates; (3) the ‘Motivator’ (ventral/medial-orbital pre-frontal cortex—*VMO-PFC*) is the frontal cortical extension of a subcortical extended-amygdala stream (the *VMO system*) which represents the world and self in motivational/emotional coordinates; (4) the ‘Attender’ (dorsal-medial/anterior cingulate—*DM/AC-PFC*) is the frontal cortical extension of a subcortical extended-hippocampal stream (the *DM/AC system*) which represents the world and self in spatiotemporal coordinates and directs attention to internal and external events; and (5) the ‘Coordinator’ (the dorsolateral prefrontal cortex—*DL-PFC*) is the frontal extension of the dorsal perceptual stream (the *DL system*) which represents the world and self in body- and eye-coordinates and controls willed action and working memory. This tutorial review examines the interacting roles of these five

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systems in perception, working memory, attention, long-term memory, motor control, and thinking.

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1. The pre-frontal ‘executive committee’

1.1. Pre-frontal lobe in the temporal organization of behavior and language

Fuster (1995, 1997, 1999) maintains that prefrontal cortex (with lateral, orbital, and medial/cingulate surfaces) creates temporal organization of behavior and language through its control of four cognitive ‘executive’ operations. *Motor working memory* prepares and directs motor attention to potential responses; *perceptual working memory* holds sensory information on line to shape such responses; *attention and motivation* determine the streams of perception to hold on line and the responses to make; and *inhibitory control* suppresses rejected streams of perception and responses. Fuster presents single-cell and pathological evidence to assign both motor working memory and perceptual working memory to the dorsolateral prefrontal surface; attention and motivation to the medial/cingulate surface; and inhibitory control to the orbital surface (see Fig. 1).

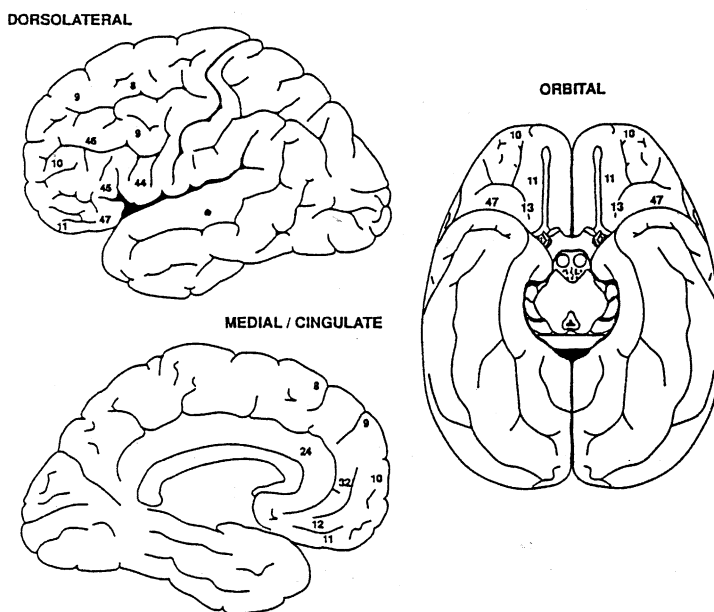


Fig. 1. Fuster diagram. Three schematic views of the human brain with frontal cytoarchitectonic areas indicated according to Brodmann's map. From J. Fuster (1999), Guilford Press.

1.2. The use of the ‘executive committee’ metaphor for the pre-frontal lobe

This tutorial review examines vast amounts of evidence from Fuster, Passingham, Goldman-Rakic, and many others to divide the prefrontal lobe into five basic areas (first suggested in print in Faw, 2000a), each of which is massively connected to pre-motor/motor, posterior-cortical, subcortical, brain-stem, and spinal areas. This results in a “multiple domain...prefrontal functional architecture” (Goldman-Rakic, Scalaidhe, & Chafee, 2000, p. 739) involved in “circuit relationships with the posterior association cortices” (p. 733).

As an explicit organizing metaphor, memory aid, and conceptual framework, the prefrontal cortex may be viewed as a five-member *Executive Committee*, as the prefrontal-control extensions of five sub-and-posterior-cortical systems, with the dorsolateral prefrontal area (in a narrower definition than Fuster’s) having the role of executive committee *Chair* or *Coordinator* (Faw, 1999, 2000a, 2000b). This organizational metaphor expands terms already rampant in the literature, such as ‘executive,’ ‘executive control,’ and ‘executive functions’ (Baddeley, 1992, 1998; Fuster, 1999; Goldman-Rakic et al., 2000; Passingham, 1995). Expanding the term ‘executive’ to ‘executive committee’ shows the domain-specificity, yet interactivity, of distinct areas of the prefrontal lobe. Continuing the set of metaphors, each prefrontal member of the executive committee chairs a *sub-committee*—one of the five neural systems—each of which can do a lot of work on its own without committee approval, but can also make its case for taking over central control of conscious working memory, attention, and willed action.

This executive-committee metaphor suggests that the prefrontal-control portions of the five systems interact, ‘make decisions,’ and even ‘vote’; and that one committee member dominates in one situation and another in another situation, changing as a function of task and motivation. Further, the designation of the dorsal-lateral-prefrontal-cortex (DL-PFC) as the ‘Coordinator’ suggests that it dominates under at least some circumstances.

The use of the ‘executive committee’ metaphor does not at all, of course, imply a group of homunculi or a single dorsolateral prefrontal cortex (DL-PFC) homunculus. No one system is intelligent or conscious or engaged in planning—only the person is. Which system dominates at any one time is determined by the type of input, the type of processing necessitated by the output, the processing occurring just prior to the new input, responses conditioned to such inputs, memories triggered, and reigning motivational forces.

This paper will show various ways in which the ‘Coordinator’ (DL-PFC) is dominant in directing attention, working memory, and willed action. Let us begin with an excellent example of the ways in which the systems interact, ‘vote,’ ‘make decisions,’ and change dominance from situation to situation. This can be seen in the PET scan findings of Marshall, Halligan, Fink, and Wade (1997) from a patient with *hysterical paralysis* (called conversion disorder in DSM-IV-TR), who had not been able to move her left leg since a traumatic event, but had no known physiological reason to be paralyzed. Moving her good *right* leg activated the normal front-to-back *left* dorsal lateral prefrontal motor-control pathway, from dorsolateral prefrontal to premotor to motor areas, with no anterior cingulate or orbital-frontal

activation. Attempting unsuccessfully to move her ‘paralyzed’ *left* leg activated the *right* prefrontal-to-premotor portion, but not the right primary motor cortex. Instead, the right orbital frontal and right anterior cingulate cortex were significantly activated. Marshall and colleagues suggested that “these two areas inhibit prefrontal (willed) effects on the right primary motor cortex when the S tries to move her left leg” (p. B1). In the terms we will be using, the ‘*Motivator*’ (amygdala—ventral medial orbital prefrontal cortex) system sensed that there was great threat in moving that leg and the ‘*Attender*’ (hippocampus-anterior-cingulate) system recalled the traumatic incident that led to the paralysis. Together, they ‘outvoted’ the dorsolateral ‘*Coordinator*’ in its attempted willed action to move the left leg. We will see other, less dramatic, examples in this paper of the ways in which the five systems interact.

The ‘members’ of a sub-committee system include: (a) sub-cortical and posterior-cortical *input areas*; two sets of *working memory sequence-processing loops*; (b) long time-frame sequence loops from prefrontal → basal ganglia → thalamus → back to the prefrontal area (see Fig. 2); and (c) short time-frame sequence loops from pre-

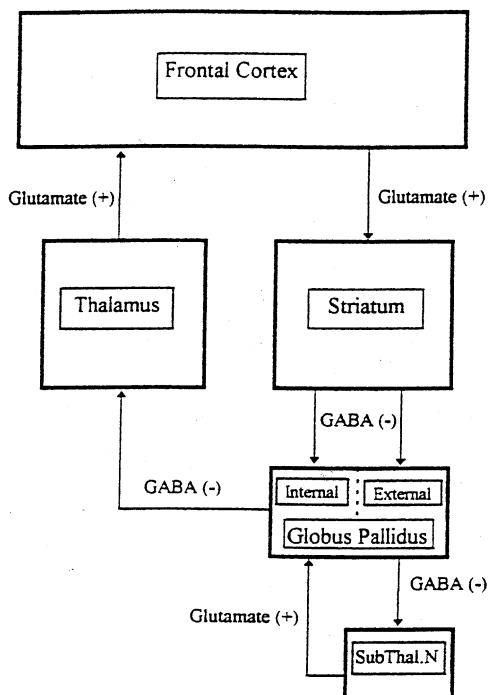


Fig. 2. Basal ganglia loops. The core system in frontal-subcortical circuits. Signals projecting from the striatum portions of the basal ganglia to the globus pallidus portion of the basal ganglia can be transmitted to the thalamus via a “direct” pathway, which is mediated by the internal globus pallidus and involves two inhibitory synapses, or via an “indirect” pathway, which is mediated by the external globus pallidus and subthalamic nucleus and involves three inhibitory synapses. The direct pathway produces disinhibition of thalamocortical transmission, whereas the indirect pathway produces inhibition of the thalamocortical pathway. From D. Feifel (1999), Guilford Press.

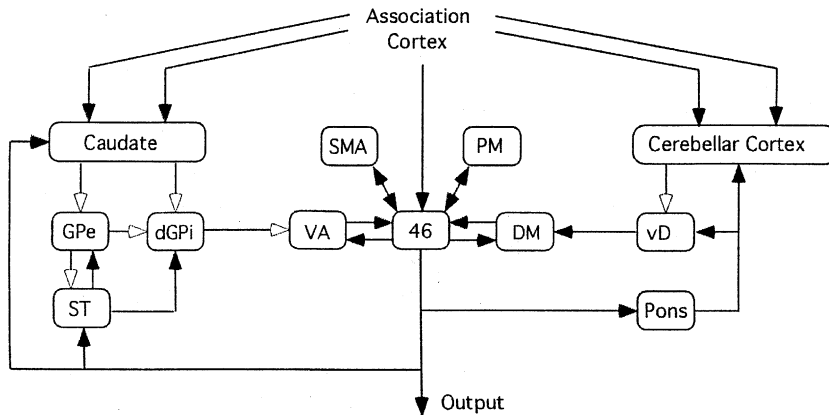


Fig. 3. Cerebellum loops linked with basal ganglia loops. Distributed processing module subserving, for example, dorsolateral prefrontal area 46. The subcortical channel through the basal ganglia consists of caudate, a dorsal zone of the internal globus pallidus (dGPi), zone of external globus pallidus (GPe), and subthalamus (ST). This channel loops back to primary Motor M1 through the ventral anterior nucleus of the thalamus (VA). The subcortical channel through the cerebellum includes a portion of the pontine nucleus (pons), a ventral zone of the dentate nucleus (vD) of the cerebellum and the cerebellar cortex. This channel loops back to M1 through the dorsomedial nucleus of the thalamus (DM). Other cortical areas are premotor (PM) and supplementary motor area (SMA). From J.C. Houk (2001), Guilford Press.

motor → pontine nuclei → cerebellum → thalamus → pre-motor and motor cortex (Fig. 3); and (d) a *response-control path* from prefrontal → supplementary/premotor → motor strip → brainstem or spinal cord to motor responses.

2. Defining the five systems

2.1. Introducing the executive committee members

There are various ways to divide pre-frontal areas. The easiest is Fuster's: To look at the three frontal surfaces of the curved triangle of each prefrontal lobe (Figs. 1 and 4): The curved lateral wall (parts or all of Brodmann areas (BA) 8, 9, 10, 11, 44, 45, 46, and 47—Brodmann, 1909), the flat floor orbital surface (parts or all of areas 10, 11, 13, and 47), and the flat medial wall (parts or all of areas 8, 9, 10, 11, 12, 25, and 32). Many of the numbered areas wrap around onto two or three surfaces. Throughout this paper, I will use BA to refer to Brodmann areas (such as BA 10 for Brodmann area 10).

Our 'Executive Committee' model suggests the following five 'subcommittees,' each of which will be more fully defined anatomically immediately following this list.

1. The '*Perceiver*' (bilateral but dominant-*right*-hemisphere ventral-lateral prefrontal cortex—*VL/PERC-PFC*) is the frontal extension of the ventral

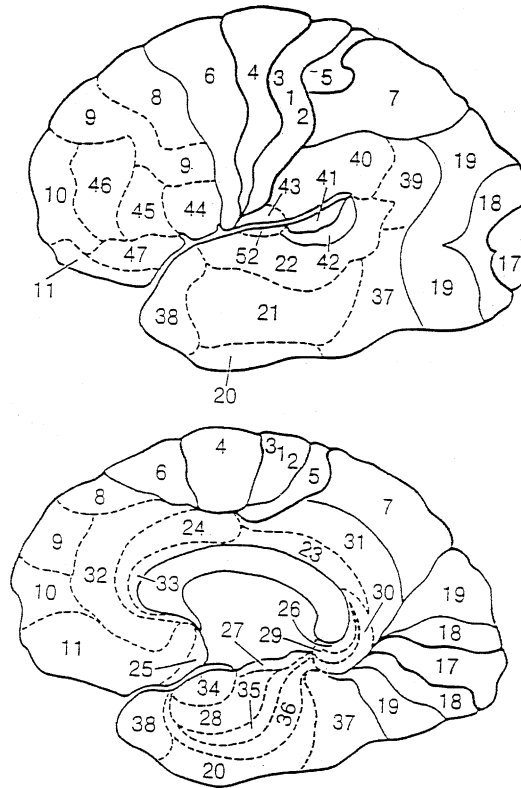


Fig. 4. Brodmann's (1909) areas.

- perceptual stream (the *VL/PERC system*) which represents the world and self in object coordinates. The pre-frontal portions of this system are found in ventral lateral pre-frontal areas BA 45 and 47, lateral orbital (lateral BA 11 and 13), aspects of the frontal pole (BA 10), and ventral third of dorsolateral area (ventral BA 46).
2. The 'Verbalizer' (bilateral but usually dominant-*left*-hemisphere ventral-lateral prefrontal cortex system—*VL/VERB-PFC*) is the frontal extension of the language stream (the *VL/VERB system*) which represents the world and self in language coordinates. This includes prefrontal areas BA 45 and 47. This could also be seen as the "Conceptualizer," "Symbolizer," or "Communicator" because this system is broader than "verbal language." As we will see, this system is involved in some aspects of arithmetic and in communicating sign language and written language, as well as speech. But these alternative phrases are much too broad, in that visual recognition of a face involves visual "concepts" and drawing pictures involves both "symbols" and "communication." Thus, we will err on the restrictive side in calling this the "Verbalizer."

3. The ‘*Motivator*’ (ventral/medial-orbital pre-frontal cortex—*VMO-PFC*) is the frontal cortical extension of a subcortical extended-amygdala stream (the *VMO system*) which represents the world and self in motivational/emotional coordinates. This includes medial-orbital areas BA 11–14.
4. The ‘*Attender*’ (dorsal-medial/anterior cingulate—*DM/AC-PFC*) is the frontal cortical extension of a subcortical extended-hippocampal stream (the *DM/AC system*) which represents the world and self in spatiotemporal coordinates and directs attention to internal and external events.
5. The ‘*Coordinator*’ (the dorsolateral prefrontal cortex—*DL-PFC*) is the frontal extension of the dorsal perceptual stream (the *DL system*) which represents the world and self in body- and eye-coordinates and controls willed action and working memory.

This tutorial review examines the interacting roles of these five systems in perception, working memory, attention, long-term memory, motor control, and thinking. These five prefrontal areas constitute the prefrontal ‘executive committee.’ The name of a full system will bear the initials listed in this paragraph, e.g., VL/VERB, while the name of the *prefrontal* area for a system will add “-PFC” to the system’s name, e.g., VL/VERB-PFC. I will include the anatomical abbreviation for a system (e.g., VL/VERB after the “Verbalizer”) the first time it is mentioned in a 2–3-paragraph section.

2.2. The ‘*Perceiver*’ and the ‘*Verbalizer*:’ Two ventral-lateral systems

What in other mammals is a wide bilateral ventral-lateral and basal-lateral system of object-processing perceptual posterior areas and their corresponding ventral-lateral and basal-lateral frontal areas, can be helpfully divided in humans into two ventral/basal-lateral ‘conscious-content’ systems: One retaining its broad task of processing *perceptual* objects for deliberate and precise responses and the other specializing in processing *verbal* “objects” for deliberate responses. These two systems are introduced together because they coexist in much the same topography of the brain—the ventral-lateral surface (folding around onto the basal surface) of both posterior and frontal lobes—with the *perceptual stream* being dominant in the *right* hemisphere, for most people, and the *verbal stream* being dominant in the *left*. Despite their respective dominant hemispheres, both streams are clearly bilateral (Grady, 1999).

Using an ‘executive committee’ analogy for the bilateral co-extensive nature of these two systems: they constitute two ‘subcommittees’ with basically the same members, like a congressional committee that handles both banking and tariff issues. The members on the right side of the chamber become most actively involved to process perceptual issues; while the members on the left side become most involved during verbal issues. The relations between the right and left hemispheres in both perception and language will be clarified during the body of this paper.

2.2.1. The ‘Perceiver’ (ventral-lateral/perceptual—VL/PERC) system

A basic finding in each of our five subcortical/posterior-cortical/frontal systems is that the subcortical and posterior-cortical portions *create the basic mental representations* for that system and then the frontal portions exert various forms of *executive control* over the representations for delayed and/or complex responses.

2.2.1.1. Posterior areas of the ‘Perceiver’. The concept of this multi-modal ‘Perceiver’ system is an extension of the ‘what is it?’ ‘ventral visual stream’ (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992; Underleider, 2000) projecting primarily from the retinal X-cells, through the parvocellular layers in the lateral geniculate nucleus of the thalamus (Hecker & Mapperson, 1997), through occipital BA 17 and ventral BA 18 and 19, inferior-and-basal temporal BA 37, 20, 21, and ventral BA 38. These inferior/basal temporal areas are found on the lower half of the lateral wall of the temporal lobe and continue down over much of the basal surface, including the fusiform and parahippocampal gyri—now famed for their early and medium-processing-level ‘face’ and ‘place’ areas (Kanwisher, 1999).

Cortical *auditory* processing projects from the medial geniculate nucleus of the thalamus to temporal-insula BA 41 and 42; continuing in the anterior and posterior parts of superior temporal BA area 22, and dorsal 38. Auditory input comes from three distinct posterior auditory processing areas to three distinct prefrontal areas. The first of these relates most directly to this perceptual prefrontal system: High level ‘what is it?’ auditory input travels in the lateral-frontal auditory pathway from the middle section of the superior temporal cortex (anterior BA 22), and projects to BA 10, 46, and dorsal 8 (Kaufer & Lewis, 1999). A second, less robust, auditory projection projects from the more limbic anterior superior temporal regions (BA 38) and to aspects of this ‘Perceiver’ system as well as to the ‘Motivator’ (VMO) and ‘Attender’ (DM/AC) systems (Barbas, 1992; Barbas & Pandya, 1991). The third auditory pathway projects from posterior superior temporal to the ‘Verbalizer’ (VL/VERB) system.

When you think about it, the well-established distinction between ventral (what is it?) and dorsal (where is it so I can respond?) in the *visual* system is counter-intuitive. It came as an unexpected empirical discovery. In contrast, a ‘what?’ versus ‘where?’ distinction in the *somatosensory* system is rarely addressed but intuitive, at least in part. The use of ‘fine touch’ to determine which coin one is holding is clearly a ‘what is it?’ sense; ‘crude touch’ is a ‘where is it?’ sense; while proprioception (the knowledge of where each body part is) is a ‘so I can respond’ (Goodale & Milner, 1992) sense. Pain and temperature have ‘where is it?’, ‘emotional/motivational arousal,’ and ‘so I can respond’ characteristics.

Cortical somatosensory processing receives input through the VPL nucleus of the thalamus from the body and VPM nucleus from the head. Thalamic input projects to several narrow strips which extend vertically down the most anterior part of the parietal lobe—collectively known as BA 3, 1, 2—the SI (somatosensory-one) area. This then projects to the SII (S-2) area in the insula (submerged ‘islands’ of nuclei in the furrow between the parietal and temporal lobe), to BA 5, to the anterior portion of BA 7 (7b) and then to the lateral orbital frontal area. In at least a functional sense, it is mainly the fine-touch-for-identification information that becomes part of our ‘Perceiver’ (VL/PERC) and ‘Verbalizer’ (VL/VERB) (as in the use of touch in Braille

reading) systems—processed in SI and SII, which links bodily sensations with memory traces.

Taste input comes from the tongue and mouth through the brainstem nucleus solitarius tract to the thalamic VPM nucleus and the hypothalamus and the Central Nucleus of the amygdala. The cortical primary taste area—gustatory-1 (G-I)—involved in *identifying* tastes (Pinel, 2000) is in the parietal insula (BA 43), just below the tongue and mouth representations of the somatosensory system. This projects via the centro-medial nucleus of the thalamus to the G-II area in orbital frontal area, and is involved in the *emotional response* to taste (Scott, 2000).

The *smell* system has its cortical reception in the entorhinal medial temporal BA 34 and 28 and through the MD nucleus of the thalamus to the ventral orbital lobe (BA 13) (Gilman & Newman, 1992). Both of these project to secondary and tertiary olfactory areas in posterior-lateral orbital frontal cortex. The posterior smell projection relates to *emotional* responses; while the orbital smell projections relate to smell *perception* and the *reward value* of smells (Rolls, 2000).

Transitional brain areas tend to be multi-modal, with groups of neurons that respond to some combination of visual, auditory, and somatic stimuli from the same point in space, at the junctures of their respective unimodal processing areas, such as in the superior temporal gyrus; BA 39 (angular gyrus) and BA 40 (supramarginal gyrus); temporal pole (BA 38) and the submerged insula, the predecessor to lateral cerebral cortex (Bennett & Netsell, 1999).

2.2.1.2. Frontal areas of the ‘Perceiver.’ The frontal area of this ‘Perceiver’ (VL/PERC) system receives middle-and higher-processed input from various unimodal and multimodal sensory areas (Grady, 1999; Passingham, 1995). The senses from the more primitive sensory association regions, smell and taste, project to the least-differentiated posterior-lateral orbital area; while the more developed somatosensory, auditory, and visual areas project to the more differentiated anterior-lateral orbital, frontal pole (auditory), and ventral BA 46 (visual and auditory—Kaufer & Lewis, 1999). This allows the frontal areas of this perceptual system to receive multiple parallel sensory projections from association cortices of different phylogenetic ages and with different functional relevances (Chow & Cummings, 1999).

The *frontal pole* (BA 10) is sometimes listed as part of the ‘Coordinator’ (DL-PFC) area, sometimes all alone, and sometimes as part of the anterior portions of the orbital frontal area. We will treat it *here* as part of the ‘Perceiver’ system because it receives some of the auditory projections. The ventral portion of BA 46 is normally included (along with the dorsal portion of BA 46 and area 9) as a major part of the ‘Coordinator.’ This *ventral* portion of BA 46 is included here as part of the ‘Perceiver’ system because it receives both visual and auditory projections that are object-related.

The *orbital surface* is the very bottom surface of the frontal lobe, shown as area BA 13 and orbital extensions of BA 10, 11, and 47. Some diagrams also show an area 14. Grady (1999) cites BA 11, 13, and 14 in the monkey as critical for recognition memory. Circuits associated with the orbital surface consist of a heteromodal sensory division and a paralimbic division Chow and Cummings (1999). The heteromodal sensory division represents the projection from every sensory system to the lateral orbital frontal area, and thus is a key component of our ‘Perceiver’ system.

The paralimbic division represents the projection from the amygdala and some other limbic areas to the ‘Motivator’ (VMO-PFC) area, and thus will be dealt with as part of that system.

2.2.2. The ‘Verbalizer’ (ventral-lateral verbal—VL/verb) system

This is one of the most specialized *human* pathways, handling various aspects of received and expressed language. While generally portrayed as being restricted to the dominant hemisphere, it is clear that the language pathway is bilateral—with somewhat distinct language aspects carried by each hemisphere.

In Section 2.2.1, we described three auditory pathways projecting from anterior—BA 22, 38, and posterior-22, respectively. The third auditory projection is crucial for our ‘Verbalizer’ system. It receives and synthesizes input from BA 41–42 and anterior-22. It originates from BA *posterior*-22, projects to inferior-parietal angular gyrus (BA 39) and supramarginal gyrus (BA 40), and then projects between the first two auditory pathways to the ‘Verbalizer’ frontal areas. The angular and supramarginal gyri are multimodal areas, responding to visual, auditory, and somatosensory stimuli. They, in turn, project through the arcuate fasciculus fibers, passing through the insula, to face-representation ventral premotor (PM) BA 6 and Broca’s area in the frontal operculum (BA 44 and 45 and 47) (Barbas, 1992; Barbas & Pandya, 1991).

The frontal areas incorporate portions of motor cortex (BA 4) involved in expressive language—*lips* and *tongue* areas, but also *hand* and *arm* areas involved in writing and sign language; then pre-motor (BA 6 and 44); supplementary motor (SMA) in dorsal-medial BA 6 and adjoining anterior cingulate (BA 24); and pre-frontal language areas (BA 45 and 47). In most language studies, analogous right hemisphere regions are also activated, but at a much lower level (Geschwind & Iacoboni, 1999). The PM BA 44 receives auditory-discrimination input from temporal BA 22 and word-meaning input from parietal BA 40. The monkey equivalent to human BA 6 and 44 (also called F-4) is involved in various grasping mechanisms in peri-personal space—the space around the person within reaching distance. Pre-frontal areas BA 45 and 47 are larger on the left, in humans, by a margin of 30% and 45%, respectively (Geschwind & Iacoboni, 1999). The monkey’s frontal area F-5 is equivalent to human BA 45, and is involved in grasp representations and action recognition, containing so-called ‘mirror neurons.’

2.3. The ‘Motivator’ and the ‘Attender.’ Two medial systems related to motivation and emotion

Now we examine two *medial* frontal systems that have major contact with limbic areas, representing two olfactory-centered ‘paralimbic trends.’ The ‘Motivator’ (ventral/medial-orbital frontal—VMO) system represents the ‘ventral amygdala-orbital frontal paralimbic trend,’ while the ‘Attender’ (dorsal-medial/anterior cingulate—DM/AC) system represents the ‘dorsal hippocampal-anterior cingulate paralimbic trend’ (Barbas & Pandya, 1991; Mesulam, 1985, 1997; Sanides, 1972). Our ‘Motivator’ and ‘Attender’ systems include the highest proportion of limbic inputs to the entire frontal lobe. The ‘Motivator’ is phylogenetically older—basically relating to paleocortical portions of the amygdala and nearby ‘bed nuclei’—and more involved

with the internal state of the organism, mediating information concerning the internal environment, than is the ‘Attender’ system (Chow & Cummings, 1999).

We noticed in Section 2.2.1 that a second auditory system comes from the more limbic anterior superior temporal regions (BA 38) and projects to the ‘Motivator’ and ‘Attender’ systems—to the orbital frontal region and medial frontal paralimbic BA 32 and 25 (Barbas, 1992; Barbas & Pandya, 1991). To further show the close ties between these two paralimbic systems, the ‘Motivator’ gets afferents from the amygdala within rostral areas of the anterior cingulate—the ‘emotional/affective cingulate’—and the amygdala also serves as a minor afferent for the ‘Attender’ anterior cingulate circuit (Chow & Cummings, 1999).

These two systems are visible on the medial surface where the two hemispheres connect—above and below the anterior arch of the corpus callosum. These streams deal with motivation, emotion, and attention. The ‘Motivator’ system takes the ventral (lower) pathway along the prefrontal medial surface while the ‘Attender’ takes the dorsal (upper) pathway.

2.3.1. The ‘Motivator’ (ventral/medial-orbital—VMO) system

The ‘Motivator’ (VMO) system represents the *ventral amygdala-orbital frontal paralimbic trend*. Paleocortical amygdala areas (central nucleus and its related bed nuclei of the stria terminalis) are found in all vertebrates (Banyas, 1999) and are involved in the production of *anxiety* and the development of *generalized anxiety emotional responses* (Davis, 2000). Archicortical amygdala areas (medial nucleus), begun in lower vertebrates and well developed in reptiles, birds, and mammals, are involved in the production of *rage* and the development of *angry responses* and seem to inhibit *fear* (Beatty, 1995; Faw, 2000a; Kalat, 1998; Klein, 2000). Neocortical amygdala (cortico-basolateral complex), found only in mammals and best differentiated in primates (especially in humans), is related to the production of *fear* and the development of *phobic responses* and seems to inhibit *anger* (Beatty, 1995; Faw, 2000a; Kalat, 1998; Klein, 2000). The neocortical basal-lateral nuclei project to both ‘Motivator’ orbital and ‘Attender’ anterior cingulate frontal areas.

The orbital frontal surface is the very bottom surface of the frontal lobe, shown as BA 13 and orbital extensions of BA 10 and 11. The prefrontal area can be defined as the most medial strip of the orbital frontal cortex, wrapping around into the ventral portion of the frontal medial wall, incorporating the medial portions of BA 11–14. The medial orbital frontal area sends prominent projections back to basolateral and basal accessory nuclei of the amygdala, while the posterior-lateral orbital frontal projects directly to the central nuclei of the amygdala.

2.3.2. The ‘Attender’ dorsal-medial/anterior cingulate (DM/AC) system

The ‘Attender’ (DM/AC) system represents the *dorsal hippocampal-anterior-cingulate paralimbic trend*, forming the posterior and superior portions of the paralimbic belt (Kaufer & Lewis, 1999). Phylogenetically newer than the ventral amygdala-orbital-frontal paralimbic trend, it relates to archicortical hippocampus and the neocortical parahippocampal gyrus. It receives information from the circuits of the hippocampal complex, posterior cingulate gyrus, and amygdala (to some extent). The amygdala and the hippocampus are deeply buried in the temporal lobe.

The *rhinal* (perirhinal and entorhinal) cortex is the basal and medial cortical surface covering the amygdala and anterior third of the hippocampus. The *parahippocampal* cortex (BA 26–30) covers the posterior two-thirds of the hippocampus.

Perceptual nuclei of the thalamus project both *directly* to the hippocampal complex and amygdala (short-latency perceptually responsive cells firing 25 ms after stimulus presentation) and *indirectly* through the higher perceptual processing of the cortex (higher order cells firing 200 ms—Wilson, Babb, Halgren, & Crandall, 1983). The basal forebrain projects acetylcholine axons to modulate the hippocampal complex (DeLuca, Schultheis, & Donofrio, 2000).

The posterior- and anterior-cingulate gyrus and surrounding parietal and frontal portions of this system constitute a *cortical mid-line strip* (Raichle, 2001), the posterior part of which includes the posterior cingulate, precuneus, and retrosplenial medial-parietal cortex. The cingulum is a major fiber strip running the length of the cingulate gyrus, connecting parts of it with the hippocampus and running through the posterior cingulate gyrus (BA 31 and 23).

The frontal extension of the cortical mid-line strip include the dorsal-medial prefrontal (BA 32, 25, 12, and parts of 11) and anterior cingulate gyrus (BA 24 and 33). Some of the dorsal-medial prefrontal cortex that relates to the anterior cingulate proper is in the para-cingulate sulcus, adjacent to the cingulate. While it is common to distinguish the anterior cingulate from the posterior cingulate, the anterior cingulate has also been divided into three parts: (1) the posterior portion, in dorsal-posterior BA 24, its *motor division* (Frith, 2001), contains some of the supplementary motor areas for some of our systems; (2) a middle (BA 24) portion called the *cognitive (AC-cd)* or *attentional division* and (3) a more rostral-inferior BA 32 anterior cingulate *affective division (AC-ad)*—in front of and curving below the corpus callosum (Frith, 2001; Gruzelić, 1998; LeDoux, Lang, Bradley, & Cuthbert, 1998).

2.4. The ‘Coordinator’ dorsal-lateral (DL) system

The ‘Coordinator’ (DL-PFC) is the frontal extension of the *dorsal perceptual stream* (Passingham, 1995)—the “where is it? (Underleider, 2000; Ungerleider & Mishkin, 1982) so I can respond” (Goodale, 2000) stream—which receives extensive somatosensory and visual-spatial processing from the parietal lobe.

I will be treating the ‘Coordinator’s’ prefrontal section (DL-PFC) as BA 46 and 9 and portions of 10 and 8. BA 8 can be divided into its ventral portion (8A) and its dorsal portion (8B). While The ‘Coordinator’ is heavily connected with its parietal sensory and motor areas, it is also heavily connected with other prefrontal areas, including connections with anterior and posterior cingulate gyrus, directly and indirectly with the latter’s major hippocampal feed, and with the ‘Attender’s’ (DM/AC) BA 32 (Barbas, 1992).

There are two quite distinct motor/pre-motor/supplementary-motor sub-systems under the primary control of the ‘Coordinator’ system: A somatic limb-and-body manipulation sub-system and an eye-head orientation sub-system (Passingham, 1995). Each motor sub-system receives input from its respective subcortical and parietal processing areas and is controlled by its own premotor and supplementary-motor areas. Each does some of its processing in cortical-subcortical loops.

2.4.1. The ‘Coordinator’s’ limb/body motor sub-system

Posterior cortical portions of this sub-system include a number of parietal lobe somatic and sensory-processing areas, each of which receives visual, somatic, and other types of stimuli. At least functionally, the somatosensory sub-strip within SI (BA 3, 1, 2) and BA 5 and 7b are most engaged in this ‘Coordinator’ (DL) system, as they involve one’s current bodily positions, body map, and feedback loops between motor control and new bodily positions. We find a lot of this processing in the intraparietal sulcus (IP) in the monkey. The ventral bank of the IP (the *VIP* area)—codes visual and bodily stimulus-location relative to the head (Behrmann, 2000), and is in circuit with ventral premotor area *F-4*, to control arm and mouth reaching. Anterior IP (*AIP*) is in circuit with rostral ventral premotor *F-5* for control of grasping (Chelazzi & Corbetta, 2000). The medial IP (*MIP*) codes stimuli within arm-reaching distance (Behrmann, 2000).

Primary somatosensory area (BA 3, 1, 2) is the main reciprocal connection with the primary motor area (BA 4); while the higher somatosensory processing areas are in reciprocal connection with the higher motor processing areas—pre-motor (PM), supplementary motor (SMA), and DL-PFC (Kaufer & Lewis, 1999). The limb/body *PM* area is in *lateral BA 6* on the lateral surface of the frontal lobe. It, as well as BA 3, 1, 2 and 4, has an inverted vertical body map. Lateral BA 6 receives input from the dorsal part of parietal BA 5 and 7b. It is in reciprocal connection with the limb/body primary motor area to its posterior and in reciprocal connection with the DL-PFC to its anterior, especially the pre-motor’s ventrolateral regions, corresponding to upper body representation (Passingham, 1995). The limb/body *SMA* is in *media BA 6*, on the superior medial surface of the lobe. It contains a horizontal body map. This medial BA 6 receives input from the medial part of parietal BA 5. These parietal areas also feed into DL-PFC BA 9 and 46. The limb/body *SMA* is also in reciprocal connection with DL-PFC in front and the limb motor area behind and motor centers in brainstem and spinal chord.

2.4.2. The ‘Coordinator’s’ visual (eye) motor system

The visual *dorsal* stream (Underleider, 2000; Ungerleider & Mishkin, 1982) begins with the magnocellular (large celled) ganglion cells in the retina (Hecker & Maperson, 1997), and then projects to the brainstem’s superior colliculus (SC), thalamic LGN and pulvinar, to BA 17, but also to dorsal BA 18 and 19 and to the posterior portion of parietal BA 7 (7a). The lateral surface of intraparietal sulcus (*LIP*) maps stimuli by retinal coordinates (Behrmann, 2000).

The eye primary-motor area is in BA 4c and/or the “frontal eye fields” (FEF) in BA 8. It has both ventral and dorsal stream input (Kaufer & Lewis, 1999; Passingham, 1995). The eye primary motor area is closely linked with the eye PM area—a ventral caudal part called BA 8a—which also receives input from the same visual areas. Prefrontal input to BA 8 is more restricted to dorsal regions along the prefrontal lateral convexity (Kaufer & Lewis, 1999). The eye primary-motor and PM areas have two main types of oculomotor output: preoculomotor areas in the midbrain and pons that activate cranial nerves III, IV, and VI, and deep levels of the superior colliculus. There is also an eye-SMA called the “supplementary eye field” (SEF). The SEF is just dorsal to BA 8, jutting into BA 6. It receives input from the

parietal LIP and visual movement-detecting areas MT and MST and projects to the same output areas. The eye PM and SEF areas are also reciprocally connected with the DL-PFC.

2.5. *Phylogenetic development of the prefrontal areas*

The two most primitive areas of the frontal lobe constitutes a *medial band* of paralimbic circuits, involved in cortical processing of motivational/emotional stimuli and responses: our ‘Motivator’ (*ventral-medial-orbital—VMO*) pre-frontal area, heavily connected with the amygdala and insula, and our ‘Attender’ (*dorsal-medial/anterior cingulate—DM/AC*) pre-frontal area heavily connected with the hippocampal system (Sanides, 1972). The three *lateral* frontal areas developed later and show more differentiation (Banyas, 1999). Our ‘Coordinator’ (*dorsolateral surface—DL*), in the narrower sense, and its premotor areas seems to have developed from the anterior cingulate (Banyas, 1999). Our ‘Perceiver’ (*perceptual ventral-lateral area—VL/PERC*) developed from the more basal and medial orbital area (Banyas, 1999). In humans, our ‘Verbalizer’ (*language ventral-lateral area—VL/VERB*) differentiated from the ‘Perceiver’ system.

3. **Basic executive-committee brain model**

3.1. *Five cortical systems and six cognitive functions*

Each of our five cortical systems (Perceiver, Verbalizer, Motivator, Attender, and Coordinator) plays a role in each of our six cognitive functions (perception, working memory, attention, long-term memory, motor control, and thinking). By examining each cortical system’s contribution to each cognitive function, we learn a lot about each system and about each function. We see how the five systems interact and how the six functions interact. Indeed, we gain a strong sense that psychological ‘faculties’ such as ‘attention’ and ‘working memory’ are at best operational definitions for what is assumed to be happening in particular experiments.

Five brain systems (by paper section) six functions					
	Perceiver	Verbalizer	Motivator	Attender	Coordinator
Perception	4.1	4.2	4.3	4.4	4.5
Working memory	5.1	5.2	5.3	5.4	5.5
Attention	6.1	6.2	6.3	6.4	6.5
Long term memory	7.1	7.2	7.3	7.4	7.5
Motor control	8.1	8.2	8.3	8.4	8.5
Thinking	9.1	9.2	9.3	9.4	9.5

Section 3 is a summary section of the Executive Committee brain model—and thus will not be studded with references. Sections 4–9 present the evidence for each cortical system's involvement in each of the six cognitive functions and will be amply referenced. When the contributions have been clarified for each of our five systems in perception, working memory, attention, long-term memory, motor control, and thinking, we might see something like the following.

3.2. *The cognitive function of perception: The five brain systems for bringing information on line*

Perception is the most basic of the six cognitive functions, in that representations of external and internal objects and events are allowed to come on line in real time. Working memory, attention, memory encoding and retrieval, voluntary motor responses, and thinking are all cognitive functions that then use the representations brought on line. Each of the five brain systems deals with some combination of *exteroceptive* (processing external stimuli), *interoceptive* (processing bodily stimuli), and *proprioceptive* (processing the position of all body parts) perceptual input, for both non-conscious and conscious processing. The five brain systems differ in what modalities and aspects of sensory input they process and what they do with the input.

The 'Perceiver' (VL/PERC) system receives very basic environmental-object information from each of the five exteroceptive systems and uses it to discriminate and identify objects and situations. The 'Verbalizer' (VL/VERB) system also receives environmental-object information from each exteroceptive modality, through the same basic pathways as the 'Perceiver' system, but uses the sub-set of information that relates to communication. The 'Motivator' (VMO) system receives basic environmental-object information, directly from the perceptual-thalamus, and well-processed information from the 'Perceiver' and 'Verbalizer' systems. The 'Motivator' also receives interoceptive, body-feeling, and emotional-response information, which it links with the environmental information. The 'Attender' (DM/AC) system receives basic and processed environmental-object information from the thalamus and 'Perceiver' system, environmental-spatial/location information from the posterior portions of the 'Coordinator' (DL) system, and processed interoceptive/emotional information from the 'Motivator' system. The 'Coordinator' system directly receives basic and processed environmental-spatial information and some environmental-object information from the 'Perceiver' system.

The posterior areas of ventral-stream 'Perceiver,' 'Verbalizer,' 'Motivator,' and 'Attender' carry the representations of attended or remembered *objects and events*; the dorsal stream parietal lobe carries the *spatial location* of the attended and remembered objects; and the frontal portions of all five streams "hold in mind" and process stimuli already in the system.

3.3. *The five systems for working memory*

Fuster lists 'perceptual working memory' as one of the cognitive executive operations of the pre-frontal lateral surface. In fact, in our three areas on the prefrontal lateral surface: the 'Coordinator' (DL-PFC), 'Perceiver' (VL/PERC-PFC), and

‘Verbalizer’ (VL/VERB-PFC), such delay cells have been found in monkeys, both in the posterior areas where the perceptual input arrives (and is ‘held’ in working memory) and in the prefrontal area that controls the delay.

It seems likely that *each* of our five prefrontal streams is actively involved in controlling working-memory delay functions with its respective posterior area, with the ‘Coordinator’ playing some role as executive-controller, so that each sub-region of our prefrontal executive committee is organized by informational/response domain, with each domain mediating on-line processing. For instance, working-memory tasks involving visual-spatial/location processing activate the ‘Coordinator’ and working-memory tasks involving object identification and processing involve the ‘Perceiver’ areas.

The ‘Perceiver’ system holds on line environmental object information and the mental imaging based on it; the ‘Verbalizer’ system holds environmental language-based information and verbal thinking; the ‘Motivator’ system holds inner-organism interoceptive and emotional information and bodily feeling imagery; the ‘Attender’ (DM/AC) system holds experientially processed information from the environment and inner world; while the ‘Coordinator’ system holds on line visual-spatial, somatic-spatial, and proprioceptive information and spatial- and motor-imagery.

The prefrontal working memory circuits activate ventral and dorsal sites and process the contents being held in circuits by delay cells. It is not clear whether: (1) the ‘Coordinator’ and/or ‘Attender’ prefrontal working memory circuits activate the relevant prefrontal area delay cells, that correspond to posterior-cortex-held information, *and* the posterior delay cells, that are holding the information—or (2) whether the activated prefrontal delay cells then activate their own corresponding posterior delay cells—or even whether (3) a widely dispersed working memory activates relevant prefrontal delay cells which then activate their own posterior delay cells.

If the ‘Coordinator’ is the only area that can initiate ‘delay cell’ activity, but causes delays in cells of other prefrontal areas and in the latter’s posterior areas (option 1), then the ‘Coordinator’ is the engine of working memory—the classic view. The fact that the ‘Coordinator’ has most reliably shown involvement in working memory tasks speaks for this option. Under option 2, the ‘Coordinator’ might control working memory by recruiting other prefrontal areas to activate their own posterior delay cells, because of ‘Coordinator’ control over the visual- and somatic-spatial/motor sub-systems. Since so many real-life and experimental working memory tasks lead to such responses, the ‘Coordinator’ system has taken over the general control of working memory.

Under option 3, the other prefrontal areas recruit the ‘Coordinator’ when the going gets tough, so that the ‘Coordinator’s’ specific tasks within working memory are blended with the specific tasks of the other prefrontal systems. This would predict that working memory tasks that are strictly a matter of keeping a percept or certain words or emotional feelings in mind—without demanding pointing, pushing a lever, tracking stimuli with one’s eyes, or grasping stimuli—would not recruit the ‘Coordinator,’ but would be handled competently by one or more of the other relevant prefrontal areas. Working memory tasks that demand some sort of somatic or eye-movement responses—usually in addition to some perceptual, verbal, or emotional processing—would involve the ‘Coordinator.’

Under this third option, the ‘Coordinator’ manages delays in “visual/somatic-spatial” networks; the ‘Perceiver’ and ‘Verbalizer’ ventral-lateral prefrontal areas manage delays in perceptual and language networks; and ‘Motivator’ ventral-medial-orbital and ‘Attender’ anterior cingulate areas somehow share the working memory/delay/control tasks for emotional and motivational networks. The fact that the latter two can ‘gang up against’ the ‘Coordinator’ and inhibit its control, speaks for this option. Options 2 and 3 would make the specific working memory function of the ‘Coordinator’ a complement to its role as the initiator of motor somatic/eye responses.

3.4. *The five systems for attention*

Intense new stimuli sharpen diffused-attention or grab attention away from currently attended stimuli by the direct intensity of their perceptual-thalamic input and their lateral inhibition of currently attended and other channels, through the gating grid surrounding the thalamus: the reticular nucleus. Both ventral-stream cells representing the new objects and dorsal-stream cells representing their spatial array increase in signal strength, while surrounding cells are inhibited.

Novel, unexpected, or meaningful stimuli (if not intense as well) need to be processed at least briefly by the amygdala for emotional valence, by hippocampus and prefrontal areas for unexpectedness, and by memory-storage-cortex for novelty. They then grab attention through reverberating circuits between their thalamic and cortical cells, with lateral inhibition using the thalamic reticular nucleus.

Object-perceptual, language, and emotional-perceptual posterior processing systems serve as attentional *sites*, containing the cortical cells whose activation is increased or decreased. For instance, in visual attention, the ventral stream (in the ‘Perceiver’ VL/PERC system) is the site for object-based attention, while the dorsal stream (in the ‘Coordinator’ DL system) is both the site for location-based attention and, because of its specialty in peripheral vision, the source for the corresponding object-based exogenous attention.

Various portions of the posterior/anterior cingulate midline strip (in the ‘Attender’ DM/AC system) select among competing perceptual, conceptual, and emotional stimuli, the specific strand of on-line information meriting endogenous-attentional shift. The anterior cingulate is involved in endogenous selective attention, especially when there is conflict or competition between different processing streams—such as between perceptual and verbal attention in the Stroop Task. The AC signals the ‘Coordinator.’

The ‘Coordinator’s working-memory signals ‘highlight’ potential locations of interest in the parietal map and cause these parietal areas to undergo sustained activation during a delay period for attention, potential coding into long-term memory, and possible motor response. The ‘Coordinator’ plans exploratory eye and hand movements toward the stimuli for possible motor response. The right-DL helps sustain attention. It may be that the ‘Coordinator’ signals the relevant prefrontal area dealing with the object-processing of the new center of attention (the perceptual, verbal, or emotional ventral streams), which then signals its corresponding posterior/

subcortical processing cells to increase firing. Or it may be that the ‘Coordinator’ directly contacts the posterior sites of the other prefrontal areas.

The ‘Coordinator’ signals the frontal eye fields (FEFs) to activate corresponding posterior parietal attention-cells to *disengage* attention from currently attended objects. The FEF concurrently signals the superior colliculus (SC) to *shift* attention. The SC then instructs the thalamic pulvinar as to which parietal cells to *engage*.

One can direct *covert attention* toward an object or situation, while keeping the eyes focused elsewhere. Such covert shifts—while attempting to maintain overt focus elsewhere—must involve very sophisticated forms of endogenous attention. Endogenous attention ‘willfully’ inhibits the normally exogenous eye-movement shift to the covertly attended object. This includes focusing attention independent of eye movements, counter-saccade tasks of deliberately glancing in the opposite direction to the cue, moving attention to different locations not activated by stimuli, and maintaining attention for a prolonged time to the same location. Presumably the ‘Coordinator,’ as the prefrontal extension of the parietal/frontal attentional mechanisms, is primarily involved in this for at least the attentional components of the motor systems under its control.

3.5. *The five systems for long term memory*

There are several ways in which our five brain systems are involved in memory. The same posterior-cortical higher-level uni-modal and multi-modal pathways involved in bringing information on line store the information and serve as attentional and working-memory sites for that information. The reactivation of these pathways helps mediate the comparison between new and stored information—leading to *recognition*.

The initial perceptual activation of these pathways seems to be sufficient to alter the pathways to store information to an *implicit* memory degree. Concurrent backward ‘potentiation’ of such cortical stimulation by the hippocampal complex seems to be crucial for more dramatic altering of the pathways needed for encoding semantic and episodic memory (perhaps using the rhinal cortex and hippocampus-proper, respectively). As such memories are being consolidated, the hippocampal complex areas initially store major portions of the memory content. After the memories are consolidated, the hippocampal complex likely stores certain links that bring back various elements of the contexts of restored memories, while the specialized pathways store the individual memory elements. The possibility of the hippocampal complex potentiating memory storage is greatly enhanced by frontal processes, including spatial attentional focus on the information carried by that pathway and the temporal enhancement of working-memory.

3.6. *The five systems for motor control*

Each system is involved in motor control, with prefrontal planning of movements, supplementary- (SMA) and pre-motor (PM) area preparation of movements, and primary motor and subcortical execution of movements. Posterior areas of the systems deliver feedback from movements just made, back to frontal areas. The frontal control steps allow for the comparison of predicted states with the feedback.

Each system differs in the motor systems under its control, with the ‘Coordinator’ (DL) having major control over somatic and eye motor systems; the ‘Verbalizer’ (VL/VERB) controlling expressive language (with some overlap with hand control); the ‘Motivator’ (VMO) controlling hormonal, autonomic, and basic brain-stem response systems; and the ‘Attender’ (DM/AC) involved in responses in endogenous attention and in SMA (preparation) processing for other systems. The ‘Perceiver’ (VL/PERC) system is least involved in motor control, specializing more in feeding its perceptual output to other systems. The ‘Coordinator’ is famed for being essential for willed action. The unique role of the ‘Coordinator’ in control of action may be as the primary controller of the somatic-manipulation and the eye-orientation motor systems, and as the predominant player in delaying responses.

3.7. *The five systems for verbal and imaginal thinking*

Finally, each brain system is involved in thinking and imagery. Posterior areas hold word thoughts and imagery content. Spontaneous non-language imaging is triggered directly by the memory-processing areas of the posterior perceptual systems. Spontaneous visual- and auditory-thinking is triggered directly by the language system in the posterior lobes. Frontal areas are involved in the controlled reflective use of imagery and verbal thought. The actual manipulation and control of such imagery and word-thought fit within the ‘mental’ aspects of the action-initiation and working-memory control of the frontal portions of the ‘Perceiver’ (VL/PERC) and ‘Verbalizer’ (VL/VERB) systems, in coordination with the ‘Coordinator’ (DL-PFC).

Each perceptual system within the ‘Perceiver’ system has its own *modality of imagery*; the ‘Verbalizer’ system has self-talk *verbal* imagery; the posterior portion of the ‘Coordinator’ system has *spatial*-imagery; the frontal portion of the ‘Coordinator’ system has *motor* imagery; and (presumably) the ‘Motivator’ (VMO) has *emotional* imagery. It is not clear what role the ‘Attender’ (DM/AC) system would play in this—except to shift attention to specific spontaneous images and to encode imaginal experiences. The ‘Verbalizer’ system is involved in pulling together verbal-thoughts in a semantically coherent way, while the ‘Coordinator’ system is involved in pulling together verbal-thoughts in an action-sequence coherent way.

To rehearse and plan, top-down sensory-like imaging and word-thinking needs to be employed. Some naturally poor visual imagers and some people after brain lesion say that they experience brief spontaneous images but can neither ‘hold’ or ‘transform’ them, nor generate them at will (Brain, 1954). A comparable deficit in controlled word-thinking and control over verbal imagery (hallucinations) is at the core of some symptoms of schizophrenia. Grady (1999) found bilateral activation in ‘Coordinator’ BA 9 in visual mental imagery; slightly dorsal to areas for auditory imagery.

3.8. *Relationships among the six cognitive functions*

Working memory is involved in various forms of *attention*. Working memory needs *selective* attention to control which of the many perceived, verbalized, valenced, and/or remembered objects are stored in working memory, because percep-

tion is much faster than working memory storage, the storage capacity of working memory is limited and the process of encoding an object into a durable form in working memory is slow and resource-demanding (Luck & Hillyard, 2000). Prefrontal working memory circuits notify and activate dorsal and ventral attentional sites and process the contents being held in circuits by delay cells. In turn, the *sustained* characteristic of both preparatory and maintenance attention is probably supplied by working memory; with the working memory specialty of *right*—‘Coordinator’ (DL-PFC) found in *preparatory* attention and *left*—‘Coordinator’ in *maintenance* attention.

Moreover, *working memory*, *attention*, and *long-term memory* encoding and retrieval are closely related. The possibility of the hippocampal complex potentiating memory encoding is greatly enhanced by both *spatial* attentional focus on the information carried by that pathway and the *temporal* enhancement of working-memory. Bringing pathways that have stored experiences back on line may be all that it takes to retrieve memories.

There is a lot of overlap between *spatial attention* and *motor responses*. Brain scans show strong functional overlap between activation in parietal and frontal lobes during peripheral attention and saccadic eye movements, with more anterior prefrontal regions active during memory-guided or conditional saccades. All regions active for eye movement (FEF, SEF: medial frontal gyrus, and LIP/7a) are also active for attention (Chelazzi & Corbetta, 2000). The frontal eye fields are richly connected with parietal lobe ‘attention cells’ and the superior colliculus (SC) and the DL-PFC. The phenomenon of *covert attention* (in either selective or maintenance modes of attention) seems to differentiate motor commands and attention. But, the covert allocation of *attention* to a location may be closely related to the *intention* to move toward the same location. Thus neuronal signals for movements of attention may coincide with premotor preparatory motor signals, through either the oculomotor or somatic motor system (Chelazzi & Corbetta, 2000). In such cases, the ‘Coordinator’ might be sending parallel motor planning commands—one to overly look ahead and the other to covertly ‘look’ to the right.

Thinking is closely related to *perceptual processing* and *motor responses*. Indeed, such higher-order cognitive processes are likely ‘emergent properties’ of more basic sensory-motor systems. *Spontaneous* self-talk and mental imagery are spontaneous stream-of-consciousness forms of thinking closely linked with perceptual processes, triggered by posterior conceptual and perceptual areas. In turn, more *deliberative* controlled forms of verbal and imaginal thinking are closely linked with motor responses. Indeed, all forms of thinking might be seen as internally generated perceptual, verbal and motor responses.

3.9. *The rest of the paper*

In the rest of the paper, we will present the evidence for the conclusions drawn in Section 3, by examining in detail the cognitive functions of perception, working memory, attention, long-term memory encoding and retrieval, voluntary motor control, and thinking and imaging. Each major section will deal with one of these six cognitive functions, with sub-sections dealing with the participation of each of our

five brain systems in these functions. We will number subsections according to our five brain systems, such that “x.0” will be used in each of these sections for a general statement and “x.1” through “x.5” for our five cortical systems: The Perceiver, Verbalizer, Motivator, Attender, and Coordinator, respectively.

4. Bringing information on-line: The executive committee for perception

4.1. Bringing information on-line: Perception

Each of our five brain systems deals with perceptual input—with some combination of exteroception (what and where the environmental objects are), interoception (the perception of bodily aches, pains, hungers, and emotional feelings), and proprioception (where body parts are). The five systems differ in what modalities and aspects of sensory input they process and what they do with that input—whether they process it to identify objects, to locate objects, to respond in various ways to objects, to link environmental objects with internal emotional feelings, to process objects in verbal codes, or to encode objects into long term memory. Section 4 focuses on pre-memorial and pre-attentional aspects of perception.

Every area of the cerebral cortex is in extensive reciprocal connection with corresponding nuclei of the thalamus, to the extent that the thalamus can be considered a seventh layer of cortex (LaBerge, 2000). Ventral and posterior nuclei of the thalamus input ‘specific’ channels of sensory information, both for non-conscious action response through direct projection to the amygdala and hippocampus and for conscious action response through projection to cortical sensory areas (LeDoux, Iwata, Cicchetti, & Reis, 1988). The sensory input into these thalamic nuclei are mutually segregated (LaBerge, 2000). We will deal with a parallel ‘non-specific’ thalamic system when we deal with the cognitive function of attention.

4.2. The ‘Perceiver’ (ventral-lateral/perceptual) system for object perception

We are treating the ‘Perceiver’ (VL/PERC) system as a multi-modal expansion of the ‘ventral visual stream’ concept developed by Ungerleider and Mishkin (1982), and Underleider (2000), which receives sensory-input ‘for object recognition’ instead of ‘for location.’ This system helps drive ‘dorsal stream’ ‘location perception’ by an internal model of the world, allowing such things as identification, classification, attaching significance, and establishing causal relations (Goodale, 2000).

Each perceptual system begins with areas that process new perceptual information, involving pre-memory perceptual processing of separate features, the association of features, re-integration of the perceptual field, and the creation of perceptual constancies (Faw, 1987). Lesions here are responsible for such things as problems with color, depth, form, smell, taste, touch, or tone. The inability to determine the visual form of an object is called “visual *form* agnosia (not-knowing).” Other perceptual systems have comparable disabilities.

Even a brief 10–20 ms (millisecond) presentation of an object or word, if not followed by a mask, leads to a clear and reportable perception. It is not that the

10–20 ms is sufficient time for the full development of the genesis of the phenomenal experience (Bachmann, 2000; Faw, in press), but that a 10–20 ms input evokes a 100–350 ms process that leads to visible perception. The genesis of a simple and well-contrasted image takes 50–100 ms. The process may take 100–350 ms if there is visual noise or low subject alertness or the figure is ambiguous, complex or detailed—the process length depending upon the manipulation of these and other stimulus- and subject-variables. Representation of stimulus location matures faster than representation of contour, which precedes global form, which precedes local form, which precedes identification. It then takes dozens of seconds for perceptual representations to be relatively stabilized until attention shifts or a new object appears or there is efferent movement (Bachmann, 2000; Faw, in press).

4.3. The ‘Verbalizer’ (*ventral-lateral/verbal*) system for verbal perception

The ‘Verbalizer’ (VL/VERB) system is as much involved in picking up visual and auditory stimuli as the ‘Perceiver’ (VL/PERC) system. In fact, each sensory modality projects to the ‘Verbalizer’ system for naming and verbal-thinking. Where the two VL systems differ is in the types of auditory and visual stimuli they process and how they process them. The left hemisphere seems to specialize in ‘local’ fine-detail, type of processing, such as analyzing the features of unfamiliar faces (Faw, 1989), small details of visual mental imagery (Kosslyn, personal communication) and words and sentences. The right hemisphere seems to specialize in ‘global’ gestalt processing, such as recognizing familiar faces (Faw, 1989), global mental imagery outlines (Kosslyn, personal communication), some letter-form detection, the global nuances in communication, and bilateral body- and environment-maps. (The fact that both body-neglect and object-neglect tend to involve right hemisphere lesions suggests that the right hemisphere contains maps of both sides of the body and of space, while the left hemisphere contains maps of only the right side.) These ‘Verbalizer’ pathways have the task of bringing on line the objects and events of the outside world and one’s mental world in *language coordinates*.

Temporal Lobe BA 41–42 and 22 are seen as phonological-analysis areas, where auditory discrimination of simple auditory impulses, coding for pitch, loudness, and localization is made on both verbal and non-verbal sound (Jancke, Shah, Posse, & Grosse-Ryken, 1998). Anterior BA 22’s fibers from BA 41 and 42 are responsible for the turning of the head and eyes to follow sounds and for the interpretation and appreciation of intricate sounds.

Language-dominant hemisphere posterior BA 22 synthesizes input from BA 41–42 and anterior BA 22 into a comprehensive auditory language pattern: Translating heard sounds into well-learned words and phrases. Non-dominant posterior BA 22 seems to convert noises into complex meaningful sounds, such as alarm clock and wolf whistle. The emotional tone of speech sounds is mediated there.

Reading involves recognizing the objects called ‘letters’ and ‘words,’ but reading also requires sophisticated ‘magnocellular’ visual motion perception. Dyslexics show reduced brain activity in the latter (Demb, Boynton, & Heeger, 1998). The right hemisphere dominates in processing individual *letters* and the left hemisphere in processing *words* (Chialant & Caramazza, 1998; Hellige & Bauer Scott, 1997).

Language processing in inferior parietal BA 39 and 40 involve the ‘semantic’ (thus memorial) stages of processing. Areas in the frontal lobe generally involve memorial, thinking, working memory and motor response functions, all of which will be dealt with later. Yet, there is some evidence of *pre-semantic* visual and auditory projections to the frontal lobe (Geschwind & Iacoboni, 1999; Kohler, Swanson, Gur, & Mozley, 1998; Moreaud, Charnallet, & Pellat, 1998).

4.4. The ‘Motivator’ (*ventrallmedial-orbital—VMO*) system for emotional perception

Converging upon the *amygdala* are *external-world*-perceptual information input, *internal-world*-motivational–visceral information input and *anterior* motivational–autonomic *control output* (Aggleton, Burton, & Passingham, 1980). *Object recognition information* projects to the amygdala from visual, auditory, and somatosensory perceptual systems, individually and in combined forms; sending simple sensory input directly from perceptual thalamic and more complex sensory input from cortical areas and the hippocampus (LeDoux et al., 1988). The lateral nucleus of the amygdala receives this and passes it to the central nucleus both directly and indirectly via the basolateral and the accessory basal nuclei (LeDoux et al., 1988). *Motivational-visceral information* projects to the amygdala from the brainstem periacqueductal gray (PAG), intralaminar thalamic nuclei, septal area, and the reward circuits of the nucleus accumbens. *Anterior motivational/autonomic control* areas project to the amygdala from the temporal pole, anterior insula, orbital frontal and anterior cingulate gyrus, bringing in “social situation stimuli” (Carlson, 1992).

The ‘Motivator’ (VMO) prefrontal portion receives interoceptive bodily feelings, mood, and notification of threat or anger from the amygdala, entorhinal cortex, temporal pole (BA 38) and insula, and notification of rewards from the nucleus accumbens, a basal forebrain part of the dopamine reward circuits.

4.5. The ‘Attender’ (*dorsal-medial/anterior cingulate—DM/AC*) system for motivated perception

The *perirhinal cortex* receives input from the *ventral stream* sensory areas that code for vision, somatosensory, auditory and olfactory stimuli; while the *parahippocampal* cortex receives input from *dorsal stream* visual-spatial areas, such as posterior parietal cortex (Murray, 2000; Squire & Knowlton, 2000), that carry information about stimulus location, angle, and distance. These two sensory outputs then converge on the *entorhinal cortex*.

The frontal areas of this system receives information from the hippocampal complex, posterior cingulate gyrus, and, to a lesser extent, the amygdala, thus enabling the intentional selection of environmental stimuli based on the internal relevance of those stimuli for the organism (Chow & Cummings, 1999). The cingulate/para-cingulate cortical mid-line strip seems to be involved in various aspects of *awareness*, with: (a) posterior cingulate (and medial parietal cortex) involved in monitoring *pre-attentive peripheral vision* (Raichle, 2001); (b) posterior-portion of anterior-cingulate activated during *conscious motor functioning* (Frith, 2001); (c) middle-portion of anterior cingulate activated during *perceptual attention* (Frith,

2001; Raichle, 2001); and (d) anterior-portion of anterior cingulate (with ventral-medial prefrontal cortex) activated during *self-focused attention* upon one's internal feelings and emotions (Frith, 2001; Raichle, 2001). Object-attention tasks that activate (c), decrease (a) and (d) below baseline (Raichle, 2001). Posner and DiGirolamo (2000) conclude that the anterior cingulate is involved in subjective feelings of voluntary control of thoughts and feelings.

Conscious awareness of one's own mental states and reflection upon others' mental states (Theory of Mind—TOM) use overlapping portions of the 'Attender' (DM/AC-PFC) areas (Frith, 2001). Grady (1999) points out that PET scans that distinguished TOM tasks showed specific activation only in the medial portion of BA 8. The anterior cingulate is also involved in contributing to pain perception and the subjective (Posner & DiGirolamo, 2000) and/or the emotional aspects of pain (Kropotov, Crawford, & Polyakov, 1997), with the intensity of pain correlating with cingulate activation (Posner & DiGirolamo, 2000).

The *affective* cingulate and related medial prefrontal cortex seem to be involved in the *conscious experience of emotions*, such that damage here is associated with emotional blunting and abnormal skin conductance response changes to emotional visual scenes, lacking normal differentiation in consciously experienced emotional arousal (Kazsniak, in Watt, 1998). This is likely made possible by the minor amygdala feed to the anterior cingulate, as the 'Motivator' (VMO-PFC) area gets afferents from the amygdala within the so-called affective cingulate (Chow & Cummings, 1999). In turn, the middle-anterior *cognitivelattentional* cingulate area 24 is involved in the more cognitive aspects of emotional evaluation (Kazsniak, in Watt, 1998).

4.6. The 'Coordinator' (dorsolateral—DL) system for spatial perception

There is debate as to whether the 'Coordinator' (DL-PFC) represents the dorsal 'where?' stream or the re-integration of that with the ventral 'what?' stream (Kaufer & Lewis, 1999; Passingham, 1995; Vogeley, 1999). Visual input from both come to the eye-motor system in BA 8, which is a major part of our 'Coordinator' system. The dorsal system supplies the location-spatial dimension to the ventral system's visual-object discrimination (Chelazzi & Corbetta, 2000), but it is more complex than that. The ventral system is primarily fed sharply focused (foveal and para-foveal) input—the *figure* which you are viewing—while the dorsal visual-spatial system receives visual input primarily representing peripheral vision (from some 99% of the two retinas)—the *background* for the figure which you are viewing.

Both of the 'Coordinator's' motor systems are dependent upon visual, somatic, and other types of stimuli. For instance, the ventral, anterior, and medial intraparietal (VIP, AIP, and MIP) all draw from both visual and somatosensory stimuli (Behrmann, 2000), but then control different aspects of motor response.

There is some indication that the *left* 'Coordinator' (DL-PFC) may be more geared to objects and concepts, while the *right* DL-PFC may be more spatial. The more *ventral* part of BA 46 is part of the frontal extension of the ventral perceptual system for object recognition; while the *dorsal* portion of BA 46, BA 9, and at least portions of BA 8 and 10 are the frontal extension of the dorsal perceptual stream. Single-cell recordings in monkeys have shown that these parallel, segregated visual-

spatial and object-processing streams remain functionally and anatomically distinct in these respective prefrontal cortical regions (Wilson et al., 1983).

5. Holding information on line: The executive committee for working memory

5.1. *Holding information on line: Working memory*

5.1.1. *Holding information on line*

One of the best documented features of the pre-frontal area in general is its ability to hold information on line for finer perceptual discrimination and manipulation, to process the wider context of a situation, for delayed and novel responses rather than for reflex or learned responses, and for change in action or thinking as other input from other systems is selected. The development of prefrontal functions led to the human ability to respond independently of immediate external stimuli and to prepare for and think about the future and the consequences of one's actions (Goldman-Rakic et al., 2000).

5.1.2. *Cortical/basal-ganglia/thalamic/cortical loops*

The basic mechanism for working memory (LaBerge, 2000; Manoach, Gollub, Benson, & Meghan, 2000)—and thus involved in attention, long-term memory encoding and retrieval, motor control, and thinking—are two sets of loops involving the entire frontal lobe area, the thalamus, and either basal ganglia or cerebellum. Each of our five prefrontal systems uses such loops. There is some debate as to whether all areas of cortex except the primary sensory areas participate in the basal ganglia loops (Passingham, 1995) or if only the frontal lobe does (Clower, 2000) (see Figs. 2 and 3).

The caudate nucleus and putamen constitute the dorsal striatum, while the nucleus accumbens and its surrounds constitute the ventral striatum. The striatum and the internal and external globus pallidus constitute the basal ganglia. The basal ganglia 'direct loop' activates reverberating circuits, beginning with the given cortical area activating a specific part of the striatum, which then inhibits the *internal* portion of the globus-pallidus and the midbrain's substantia nigra pars reticulata, which is otherwise tonically inhibiting some portion of the thalamus. Thus, when the prefrontal area activates the striatum to inhibit the globus-pallidus' inhibition of the thalamus, the thalamus is reactivated, and it, in turn, activates the cortex (Alexander, DeLong, & Strick, 1986; Chow & Cummings, 1999).

An additional element turns it into an 'indirect loop' that inhibits reverberation. The cortical area activates the striatum, which inhibits the *external* segment of the globus pallidus, which inhibits the subthalamic nucleus (STN), which then activates the *internal* globus pallidus to increase its inhibition of the thalamus. Thus the thalamus' activation of the prefrontal area is greatly reduced (Chow & Cummings, 1999).

The loops from various cortical areas are parallel but basically segregated in terms of cortical area of derivation, the striatal area it connects to, and thalamic nuclei in their pathway (Alexander et al., 1986). Some of the input to prefrontal

areas comes directly; while other input projects to the basal ganglia or the thalamic components of the loops. This allows for the integration of information and the sequencing of information and cognitive and motor responses (Pickett, Kuniholm, Protopapas, & Friedman, 1998), making these loops essential for sequence skills rather than for the learning of unique pairings (Gabrieli, Stebbins, Singh, & Willingham, 1997), and involved in voluntary rather than reflexive action (Lasker & Zee, 1997).

Projections to the thalamic relay cells from the globus pallidus can be selectively dis-inhibited by prefrontal working memory and preparatory attention mechanisms, allowing very specific cortical activation and processing, while other thalamocortical loops serving other frontal columns are being tonically inhibited, protecting against abrupt onsets of unattended stimuli. Thus, the frontal areas control the selection and amplification commands; while the thalamus contains the amplification circuit mechanisms (LaBerge, 2000). The midbrain substantia-nigra dopamine projection to the striatum also helps determine which specific loops are activated. Some brain areas, such as the amygdala, project to specific parts of the substantia-nigra to determine which loops it activates.

5.1.3. *Cortical/pontine nuclei/cerebellum/thalamic/cortical loops*

There is also debate among researchers as to whether cerebellar loops originate from parietal, motor cortex and somatic premotor but not visual premotor or prefrontal areas (Passingham, 1995); or whether there are cerebellar connections to prefrontal areas as well, via the thalamus (Clower, 2000). The basic circuit starts with cortical areas and projects to some motor nuclei in the brainstem pons, then to the cerebellum, to the thalamus, and then back to the cortex. Motor and pre-motor loops tend to project to the same thalamic nuclei in both basal ganglia and cerebellum loops, but with fairly unique pathways (Passingham, 1995). Such cerebellar loops are involved in prioritizing, processing, sequencing, and responding to information (Andreason, Paradiso, & O'Leary, 1998; Riva, 1998; Yamaguchi & Kobayashi, 1998). The prefrontal-basal ganglia loops seem to do the major processing and sequencing for initiating or stopping of deliberate action and for the deliberate working out of the action—like learning to drive a car or type—but then turn over more and more of the well-learned fast, fine, and split second sequencing to cortical-cerebellum loops (Passingham, 1995).

5.1.4. *Delay cells and brain scans*

The clearest pieces of evidence of a 'working memory' system seem to be that it has a network of delay cells/memory cells (Goldman-Rakic et al., 2000) and that various areas of the system show brain scan activation during specific types of working memory tasks (Faw, 2001). In monkeys, delay/memory cells have been found which either begin discharging when the sensory information arrives or at the off-set of the sensory cues—and continue discharging during the delay period between the off-set of the sensory cues and the preparation for response. (Goldman-Rakic et al., 2000; Passingham, 1995). Such delay cells would explain very brief pauses for working memory. Longer ranges of working memory presumably are arranged through the cortical/basal ganglia/thalamic/cortical loops.

5.2. The ‘Perceiver’ (*ventral lateral/perceptual*) system for object working memory

The ‘Perceiver’ (VL/PERC) system is involved in ‘object’ working memory (Tien, Schlaepfer, Orr, & Pearson, 1998), keeping relevant object information active so that an attentional search can be facilitated for the relevant object among an object array (Mangun, Jha, Hopfinger, & Handy, 2000). Miyashita (2000) has found *posterior delay cells* in the anterior ventral part of monkeys’ inferior temporal cortex (TE-av). These delay cells fire during the prospective-memory-type delay between the brief sight of a complex geometric figure and the selection of its associated figure. Goldman-Rakic et al. (2000) found the second part of the puzzle: *prefrontal delay cells*—precisely in monkey ventral lateral prefrontal BA 12/45, generally homologous to areas in both perceptual processing and human language—that fire during the delays in object-oriented working memory, processing nonspatial information, such as color, form, and patterns.

Goldman-Rakic et al. (2000) also reviewed human brain scan findings of working memory ‘object’ tasks and found right ventral-lateral prefrontal activation for these; while finding that working memory neurons responding to ‘location’ were clustered in our ‘Coordinator’ (dorsolateral prefrontal) areas. Grady (1999), also found that visual-spatial processing activates more dorsal prefrontal areas than does face perception. Petrides (1994) found that the ‘Perceiver’ (VL/PERC) or ‘Verbalizer’ (VL/VERB) prefrontal areas are activated in working memory, but only for simple retrieval of object identity or linguistic information.

5.3. The ‘Verbalizer’ (*ventral lateral/verbal*) system for verbal working memory

Most single-cell neuron recordings are performed in non-human animals, which do not show clear language use and, thus, no differentiation between ‘verbal’ and ‘perceptual’ ventral-lateral systems. Therefore, even though Miyashita’s (2000) and Goldman-Rakic and colleagues’ (2000), chapters show both right and left hemisphere diagrams for their delay cells, it is hard to show clear evidence of delay/memory cells in the human verbal system (Faw, 2001).

Nevertheless, there is considerable evidence from brain scans of verbal working memory in the frontal language strip (Goldman-Rakic et al., 2000; Miyashita, 2000). Stevens, Goldman-Rakic, Gore, and Fulbright (1998) found areas in the left inferior frontal cortex active on fMRI scans of verbal working memory tasks in controls, but dysfunctional in schizophrenic patients who have specific performance deficits in verbal but not nonverbal working memory. Stowe and colleagues (1998) found left inferior frontal cortex activation related to sentence complexity and lexical items. Lazar, Marshall, Pile-Spellman, and Hacein-Bey (1997) found that anesthetics injected into ‘prefrontal’ language areas decreased word-list generation, but retained comprehension.

There is evidence of two different types of verbal working memory performed by the ‘Verbalizer’ (VL/VERB) and the ‘Coordinator’ (DL) prefrontal areas. In a verbal working memory task that involved putting words together into sentences, Sirigu, Cohen, Zalla, and Pradat-Diehl (1998) found activation in the ‘Verbalizer’s’ Broca’s area when putting words together into a *well-formed sentence*; and in the ‘Coordi-

nator' PFC area when putting word groups together to form a *logical sequence of actions*.

5.4. The 'Motivator' (*ventral medial orbital*) system for emotional working memory

The 'Motivator' system and its 'Attender' (DM/AC) para-limbic counterpart send their basal-ganglia loop projections through the 'limbic' *ventral-striatum* portion of the working-memory circuits. Yet, at this time, the term 'emotional working memory' can be used only metaphorically because delay-cells have not been found there yet (Goldman-Rakic et al., 2000).

But behavioral and neuropsychological studies and brain-scan activation during natural working-memory tasks verify our 'Motivator' system's involvement in working memory. The *amygdala* is key to both stimulus evaluation of threat and the production of defensive responses. The *temporal-pole* participates in the evaluation procedure that invests *exterosensory* information with emotional significance, while the *anterior insular* participates in the evaluation procedure that invests potentially distressing cognitive and *interosensory* information with negative emotional significance (Reiman, 1997). Unchecked, these posterior portions of the 'Motivator' system determine that a new situation will get previously learned impulsive anger or fear responses, used in similar situations in the past (Passingham, 1995).

Then the *orbital-frontal cortex* allows one to break that pattern of response and give a new response to the current situation. It does this by somehow delaying the old response while it—with the total working-memory system—selects a more appropriate response. Patients with ventral medial prefrontal lesions have been described as having 'environmental dependency syndrome,' where their behavior is overly controlled by external stimuli, becoming stereotypical and stimulus bound (Grady, 1999). Delaying and controlling impulses seems to be a fundamental natural working memory task.

Another limbic aspect of working memory is the regulation of emotion and mood, with which the orbital frontal lobe helps. Left damage is far more likely to cause depression and right damage to cause mania (Geschwind & Iacoboni, 1999; see also Rauch, Savage, Alpert, & Fischman, 1997). This suggests that there are working memory delay-cells in this prefrontal area to be found, originating here or triggered and controlled by master delay-cells in the DL prefrontal area.

5.5. The 'Attender' (*dorsal mediallyanterior cingulate*) system for contextual working memory

There are *perirhinal* cells in the hippocampal complex that fire during delay periods, based on the expectation of, or the holding in working memory of, the stimulus characteristics to which they respond. This delay period firing is very similar to activity found in working memory prefrontal cells (Erickson et al., 2000), and thus are likely initiated by such prefrontal cells (Goldman-Rakic, personal communication). The same perirhinal cells lead to the suppression of the firing of cells to other stimuli in the visual field—an 'attentional' feature. In fact, direct and indirect pathways between the 'Coordinator' (DL-PFC) and hippocampus probably play a

role in maintaining contextual information on a moment-by-moment basis—that is, working memory (Goldman-Rakic, 1987).

While the posterior part of this system—the hippocampal complex—is central to explicit memory encoding, the anterior part—the anterior cingulate and surrounding dorsal medial prefrontal cortex—are central for endogenous shifts of attention and, thus, working memory.

5.6. The ‘Coordinator’ (dorsolateral) system as the coordinator of working memory

5.6.1. Frontal areas

It is the ‘Coordinator’ (DL) prefrontal area that has been long associated with working memory and ‘delay cells.’ There are DL-prefrontal neurons which increase firing rate during the delay period of a task where monkeys are rewarded for waiting to push a lever (manipulation motor system) or moving their eyes (orientation motor system) in response to the first signal until a second signal tells them to respond. Certain ‘location-memory field’ DL-PFC neurons are activated consistently each time the monkey must keep in mind a particular location. When the neurons lose their activation during the delay, the animal will likely make an error (Goldman-Rakic et al., 2000)—they forget where to reach or look. Each such working-memory neuron seems to be dedicated to a specific type of information, in fine synchrony with posterior-parietal visual-spatial systems. Neurons in the ‘Coordinator’ BA 46 and 8a seem especially involved in such delayed response to locations, so that every location in the visual field is represented by a group of neurons there (Goldman-Rakic et al., 2000).

Many researchers find a *left* ‘Coordinator’ (DL-PFC) specialty for *motor* and *conceptual* working memory, with a focus on internal representations, such as in letter- and category-based fluency tasks, listening to digits, verbal recall, holding in mind steps taken in solving puzzles, and strategy switching (Geschwind & Iacoboni, 1999). Left lesions are more likely to cause impaired recall of words, especially when the task is based on a search strategy internally generated through the mental effort of the subject (Geschwind & Iacoboni, 1999). We noted in Section 5.3 that the ‘Coordinator’s’ involvement in verbal working memory centers more on forming words into a logical sequence of actions, and the ‘Verbalizer’ (VL/VERB) system on forming words into well-formed sentences (Sirigu et al., 1998). *Right* ‘Coordinator’ PFC seems to be more related to *perceptual* working memory control (Bechara, Damasio, Tranel, & Anderson, 1998; Seki, Ishiai, Koyama, & Sato, 1998), including the categorization of perceptual objects and the use and representation of visual spatial data; design fluency tasks; and the active manipulation and monitoring of information (Geschwind & Iacoboni, 1999).

5.6.2. Posterior areas

The ‘Coordinator’ (DL-PFC) delay cells are in reciprocal connection with posterior-parietal delay cells, so that corresponding cohorts of parietal and DL-PFC neurons change their firing rate together during the cue, delay, and response periods of these tasks. For instance, prefrontal BA 8a neurons correspond with posterior parietal BA 7ip (inferior parietal sulcus) neurons (Goldman-Rakic et al., 2000).

Neurons in parietal LIP area are activated both when a monkey has to hold a location in mind for a delayed saccade task and for a preparatory attention task (Chelazzi & Corbetta, 2000).

6. Moving around on line: The executive committee for attention

6.1. *Moving around on line: Attention*

Attention can be seen both as an early sensory bottleneck and as a system for providing priority for motor acts, consciousness, and memory (Posner & DiGirolamo, 2000). There are several types or dimensions of attention (LaBerge, 2000). ‘Preparatory attention’ is sustained vigilance over the preparatory time between cue and target to aid response to anticipated events. ‘Selective attention’ determines what perceived, conceived, emotionally valenced, imagined, or remembered objects will be processed on line. ‘Maintenance attention’ is sustained focus on the objects or events already in attention, to process ongoing activity—such as listening to music or sorting out in one’s head the different meanings of attention.

The ‘source’ of attention refers to brain networks that control attention; while the ‘site’ of attention refers to the content-areas affected by attention (Posner & DiGirolamo, 2000). Generally, dorsal-stream attentional *source* mechanisms enhance, attenuate, or otherwise bias the stimulus-driven perceptual firing in ventral-stream perceptual/conceptual/emotional object-recognition systems for each sensory modality, which, in turn, act as *sites* for attentional effects (Posner & DiGirolamo, 2000; Underleider, 2000). Immediately after display onset, cells in the column sites representing both attended and unattended objects increase activity in response to their respective sensory input. Attention alters the firing, with enhancement of cellular firing and of performance at the target site and decay at distracter sites (LaBerge, 2000; Luck & Hillyard, 2000).

There has been a long-standing distinction between ‘involuntary attention,’ mediated by parietal lobe and its posterior-cortical/sub-cortical connections, and ‘voluntary attention,’ mediated by an interplay of the ‘Attender’ anterior cingulate gyrus and the ‘Coordinator’ DL-PFC cortex. It is better to use more philosophically neutral terms, such as ‘exogenous’ or ‘external-stimulus-produced’ attention versus ‘endogenous’ or ‘internal-stimulus-produced’ attention (Passingham, 1995). *Exogenous* shifts of attention can arise from several sources, such as sudden intense-stimuli, a novel stimulus, an unexpected development, or a personally meaningful object, word, or event grabbing one’s attention. *Endogenous* shifts and sustained attention result not from external stimulus changes but from motivational shifts in on-line working-memory processing.

6.2. *The ‘Perceiver’ (ventral lateral/perceptual) ‘sites’ of attentional effects*

6.2.1. *Posterior attentional sites*

Attentional modulation of pre-memory sensory processing begins about 60 ms after stimulus onset in the color/form-processing V-4 area, 70–90 ms in the inferior

temporal lobe, and 80–130 ms in the posterior fusiform gyrus (Mangun et al., 2000), before objects have been identified (Luck & Hillyard, 2000). There is then a significant attentional amplitude enhancement in the inferior temporal and other places from 160–180 ms, by which time object ‘recognition’ has occurred (Mangun et al., 2000). Cell assemblies representing objects which are being attended show greater sensory gain control than those representing objects in an unattended location, which show suppression of their firing at about 175 ms post onset (Mangun et al., 2000). This inhibition effect is even larger if both of the objects are within the receptive field of the same set of neurons. Similar attentional effects are found in the same locations with exogenous or endogenous attentional orienting (Mangun et al., 2000), but neural responses are greater if the response location has been ‘cued’—leading the individual to ‘expect’ where to direct attention.

6.2.2. *Core mechanism for attentional shifts*

We introduced the ‘Perceiver’ (VL/PERC) by mentioning the ‘specific’ thalamic nucleus pathways to the cortex. Parallel to these specific thalamic sensory pathways is a ‘non-specific’ thalamic system that acts as an on-off-loud-soft volume control for conscious processing by the cortex (Faw, 2000a). This non-specific system incorporates core nuclei of the thalamus, the *intralaminar-nuclei* (ILN), and a neural covering net of the thalamus, the *reticular-nucleus*, which acts as a ‘channel selector’ or ‘gating’ mechanism, allowing for the selecting of new channels of input for conscious attention. Specific and nonspecific systems interact at ‘gamma’ frequencies to create conscious and attentional integration (Bachmann, 2000).

Specific connections between the thalamus and the cortex must project through this net—like wires sticking through a fishnet, yet connected to the net—laterally inhibiting projections from adjacent areas of the thalamus. Reticular-nucleus cells increase their inhibitory influence on neighboring columns as the activity in the target columns increases (LaBerge, 2000). The small initial difference in firing rates between input that is enhanced and input that is inhibited can be magnified by a factor of 25 through the reticular nucleus net (LaBerge, 2000). This seems to be a core mechanism for *attentional shifts*.

Cortical columns project to relay cells in thalamic nuclei from pyramidal neurons in cortical layers V and VI (LaBerge, 2000). Neurons in cortical layer V fire in bursts of a few spikes at rates as high as 250 Hz, with inter-burst firing rates of 15 Hz. The thalamic nucleus projects back to layer VI of the original cortical area, facilitating the synaptic efficacy of layer V axons and thus potentiating the already strong bursts on the relay nuclei (LaBerge, 2000).

6.2.3. *Anterior attentional “source” involvement*

While the *right* ‘Coordinator’ *dorsal-lateral-PFC* area is generally seen as the vigilance-sustained-attention monitor (Posner & Rothbart, 1992), the *right* ‘Perceiver’ *ventral-lateral* frontal is also involved in this when object selection is crucial (Coull, Frackowiak, & Frith, 1998) and in shifts in perceptual experience in binocular rivalry studies (Chelazzi & Corbetta, 2000). Signals from this network bias neuronal activity in extrastriate visual area in object analysis, reflected in changes of

baseline firing prior to stimulus onset and modulation of the sensory-evoked responses. This leads to amplification and attenuation of neural signals.

6.3. The ‘Verbalizer’ (*ventral lateral/verbal*) ‘sites’ of attentional effects

The mechanisms of attention are as important in the verbal as in the perceptual system and involves the same basic mechanisms. You, the reader, may be starting to “glaze over” by this two-thirds point in this long paper. You may have read the last several paragraphs with minimal attentional focus. Suddenly you read these frank words and realize that you have been caught in the act. These words might exogenously grab your attention and endogenously convince you to commit sustained attention to the rest of this paper. In a similar way, your attention might wander during a conference lecture, but certain spoken words grab your attention back.

Not only do involuntary and voluntary attentional mechanisms operate with overt heard and read words, but also with covert words—word thinking. This is basic to modern cognitive therapy, where clients are asked to listen to their own ‘self talk’—to ‘hear’ their spontaneous inner speech when the exam is about to be administered or when they are walking up to give a class presentation or when they are sitting down for a job interview or involved in any situation that deepens their depression or agitates their anxiety (Beck, Emery, & Greenberg, 1985).

The clinical hypothesis is that we emit spontaneous self-talk pre-attentively or momentarily attentively. As we focus attention to our concurrent self-talk we can detect the ‘messages’ that we give ourselves that ‘subvert’ the rational course of our lives.

6.4. The ‘Motivator’ (*ventral medial orbital*) system for attention

The bulk of the research on attentional sites has individuals attending to objects, words or locations; thus implicating the perceptual, verbal, or dorsal-stream systems. There are three attentional features of this ‘Motivator’ (VMO) system that can be reported. Normal amygdala responses to fear stimuli occur in an astonishingly rapid 10–20 ms. The amygdala has ample connections with the ‘Motivator’ and the ‘Attender’ (DM/AC) to rapidly direct both exogenous and endogenous attentional shifts, to determine which 100–250 ms perceptual processes to bring to completion and which ones to decay. In addition, the most common response to electrical stimulation of the amygdala in alert animals is an ‘arrest’ reaction, in which spontaneous behaviors cease and the animal snaps to aroused attention, as the first phase of either fight (anger) or flight (fear) reactions (Carpenter & Sutin, 1983).

We have mentioned that Fuster (1999) used single-cell and pathological evidence to assign attention and motivation to the medial/cingulate surface and inhibitory control to the orbital surface. This suggests that the ‘Attender’ (DM/AC) chooses the object/location for attention and (directly or through the ‘Coordinator’—DL-PFC) signals the ‘Motivator’ (VMO) system to inhibit its amygdala-fed input. This would place the ‘Motivator’ with the ‘sources’ of attention by stifling the impulsive thinking and behavior that the amygdala uses, to break sustained attention.

6.5. The ‘Attender’ (dorsal mediallyanterior cingulate) system as selector for endogenous attention

6.5.1. Posterior areas and exogenous attention

The hippocampal complex helps compare new perceptions with memory traces of old experiences (Nadel & Moscovitch, 1998), by its retaining memory links from earlier experiences (Maquire, Henson, Mummery, & Frith, 2001). This comparison helps shift attention to novel, unexpected and meaningful stimuli. *Intense-stimulus* types of attention-grabbing events do not need to rely on memory—but operate from wired-in responses needed for survival—and are processed by the ‘Coordinator’ (DL) system. But, something grabbing one’s attention because it is novel, unexpected or personally meaningful does depend on memory. Attentional shifts to *unexpected* events imply some combination of working memory processing (e.g., you expected to see the answer 4 instead of 5, when you read your child’s mathematical calculation of 2 plus 2) and long-term memory storage (e.g., you were startled to see that the ‘horse’ in your neighbor’s yard today is really a zebra). Attentional shifts to *personally meaningful* events seem most tied to long-term memory (e.g., at a social event, you shift attention to a conversation about consciousness). These links with long-term memory may be why the hippocampal complex is involved. The hippocampus probably begins using short-latency thalamic and amygdala information for analyzing new perceptions for unexpected or meaningful new events and then incorporates long-latency temporal-lobe information for revisions in stimulus testing and for encoding new memories. Hippocampal situation-evaluation is used both for automatic posterior exogenous attention and for deliberate anterior endogenous attention.

6.5.2. Anterior cingulate directing endogenous attention

The mid-portion of the anterior cingulate gyrus (the ‘attentional’ or ‘cognitive’ cingulate) is best known currently as Posner’s ‘Anterior Attentional System’ (Rothbart and Posner, 1992) or his ‘midline attentional system’ (Posner & DiGirolamo, 2000). According to Posner, the anterior cingulate is activated when someone achieves a subjective experience of an object and when one needs to inhibit prepotent responses to focus on a target, presumably signaling the ‘Motivator’ (VMO) system to inhibit its amygdala-fed input (Fuster, 1999).

Thus the anterior cingulate is activated for tasks requiring conflict resolution between anatomically separate cognitive processing system, such as in the color/word conflict in the classic Stroop test, where the perceptual system competes with the verbal system. By analogy, Stroop-like effects have been found in many research paradigms, where any one processing system competes with another. Anterior cingulate activation is also found in dual-task situations, as with a sequencing task and a word-generation task, where both the cingulate and ‘Coordinator’ (DL-PFC) areas are very active. Both of these activations subside when performance is automated and attention is not needed. Then, when subjects are asked to focus attention on the well-learned sequence, these frontal areas are reactivated. Most brain scans show the anterior cingulate to be bilaterally involved in attention tasks (Benedict, Lockwood, Shucard, & Schucard, 1998), although it is hard to distinguish the closely situated

right and left cingulate (Geschwind & Iacoboni, 1999; Frith—personal communication).

Out of these conflict or dual-task situations, the anterior cingulate seems to select stimuli motivationally for attentional shift (Chelazzi & Corbetta, 2000). The anterior cingulate might directly trigger endogenous attentional shifts (Watt, 1998) or only instruct the ‘Coordinator’ DL-PFC which shifts to make (Chelazzi & Corbetta, 2000).

We noted in Section 6.2 that the thalamic *reticular-nucleus* (nRt), acts as a *channel selector* for selecting new input for conscious attention. This seems to be a common mechanism in shifts of perceptual/verbal attention, the posterior portions of which can be activated directly by competing stimuli in exogenous attentional shifts, and the anterior portions of which can be activated by frontal systems in endogenous attentional shifts. The anterior cingulate gyrus projects to vast portions of the anterior nRt thalamic gates (Watt, 1998)—about equal to the entire perceptual projection to the thinner posterior nRt gates—presumably to activate endogenous attention (Watt, 1998).

The *nucleus accumbens* in basal forebrain also projects to the nRt gates. The nucleus accumbens is a major part of the basal ganglia (ventral striatal) portion of both the ‘Attender’ anterior cingulate and ‘Motivator’ amygdala-orbital loops. According to Watt (1998), the nucleus accumbens also receives projections from the ‘Coordinator’ (DL) prefrontal lobe, the hippocampus and the amygdala. The accumbens may, thus, be a ‘gate’ for higher level input to the reticular nucleus along with the anterior cingulate direct projections to the reticular nucleus. This, presumably, allows the accumbens to tip the balance between present planning/working-memory ‘Coordinator’ (DL-PFC), past experience ‘Attender’ hippocampal/ anterior-cingulate and immediate threat ‘Motivator’ amygdala/medial-orbital prefrontal activation of attention (Watt, 1998). In contrast, Chelazzi and Corbetta (2000) prefer to see the ‘Attender’ cingulate as providing the motivational tone necessary for purposeful orienting, with the ‘Coordinator’ dorsolateral prefrontal doing the posterior-pathway biasing.

6.6. The ‘Coordinator’ (dorsolateral) system for directing exogenous and endogenous attention

6.6.1. Posterior areas

The dorsal visual-spatial system supplies the ‘location-spatial’ dimension to the ventral system’s ‘visual-object discrimination’—a *perceptual* task—at the same time that it continues its ‘sentry duty’ for new objects—an *attentional* task—noting the sudden appearance of intense stimuli like a bright light, loud sound, smell, or smoke, and activating exogenous attention cells within the midbrain colliculi and cortical perceptual areas.

This ‘orienting network’ involves the posterior parietal, superior colliculus (SC), and pulvinar. The *posterior parietal* lobe is involved in the spatial encoding of stimuli and in *disengaging* from the previous focus of attention. The *left* parietal lobe seems to disengage attention between objects, while the *right* parietal disengages attention within global aspects of a scene (Robertson & Rafal, 2000). Some cells in parietal areas LIP (lateral intraparietal parietal) and BA 7a are spatially selective attention

cells (Chelazzi & Corbetta, 2000), showing increased activation to unexpected stimuli and reduced activation when they represent non-attended or expected stimuli (Chelazzi & Corbetta, 2000). Neurons in parietal LIP area are activated both when a monkey has to hold a location in mind for a working memory delayed saccade task and for a preparatory attention task (Chelazzi & Corbetta, 2000).

Posterior parietal and the *frontal eye fields* both activate the SC which *shifts attention* (Posner & DiGirolamo, 2000) by sending a message to specific spatial-representative areas of the thalamic *pulvinar*, which then *engages* new attentional focus to the ventral visual pathway, to initiate and to enhance information at attended locations (Chelazzi & Corbetta, 2000; Posner & DiGirolamo, 2000). Thus, lesions in the pulvinar impair engaging attention at a new location, rather than in disengaging attention from a currently attended location. The pulvinar presumably delivers the control signals that modulate activity in the ventral stream (Chelazzi & Corbetta, 2000) and sends lateral inhibition to other pulvinar cells representing unattended locations, through the surrounding net-like reticular nucleus of the thalamus.

The pulvinar projects reciprocally to the SC and to visual areas in occipital, temporal, parietal and frontal lobes, with loops that preserve topographical relations (LaBerge, 2000). For instance, regions within the pulvinar contain cells that overlap in their connections to parietal area 7a, temporal lobe and the ‘Coordinator’ DL-PFC (LaBerge, 2000). The pulvinar increases firing to a visual stimulus that is a target of attention with or without an impending saccade. *Preparatory attention* seems to involve the *right* pulvinar (LaBerge, 2000).

6.6.2. *Anterior areas*

The frontal eye fields are richly connected with parietal lobe ‘attention cells and the superior colliculus, and with the DL-prefrontal area. The frontal eye fields are involved in the *preparation* of saccadic eye movements, but also signal whether the stimulus is a target or a distracter, even when eye movements to the target are not allowed—covert attentional’ tasks—or when a stimulus is detected through a manual response (Chelazzi & Corbetta, 2000).

The prefrontal portion of this ‘Coordinator’ system, DL-PFC, is more active in *sustained attention* for a substantial amount of time, a feat of endogenous attention, than in rapid shifts of attention, the latter being found more with the posterior exogenous attention system (Chelazzi & Corbetta, 2000). The *right* DL-PFC has some additional functions. Posner and Rothbart (1992) believe that it serves as a *vigilance attentional network* (preparatory attention), due to massive brain-stem locus ceruleus norepinephrine-system projection. This system is involved when one is holding oneself vigilant while waiting for the target to come, such as an air traffic controller needing to vigilantly focus on the radar screen for infrequent blips to occur. This vigilance attentional network will only be clearly activated on brain scans when the subject is giving rather intense focus (Posner, personal communication). This seems to involve maintaining vigilance on external objects and ‘clearing the mind’ of left DL-PFC thoughts (Posner & Rothbart, 1992). Lesions to the right DL-PFC lead to deficits in the ability to develop and maintain the alert state. The right frontal lobe has also been implicated in attention to extra-personal space (Grady, 1999), especially when exploratory motor movements are required.

7. Moving information off line and back on line: The executive committee for long term memory

7.1. Moving information off-line and back on-line: Memory processing

In Section 4.2 we used the term ‘perception’ for bringing information on line. In cognitive studies, the term ‘perception’ incorporates memorial tasks (such as recognizing objects) and attentional tasks, as well as the processing of basic form, sound, or taste stimuli. Moving information off line into storage is called ‘encoding’ into long-term memory. Bringing information back on line from storage is called ‘retrieval.’ We find each of our five systems involved, in different ways, in the encoding and retrieval of long-term memories.

The posterior perceptual areas contain the memory content and trigger spontaneous retrieval, while frontal areas are involved in effortful encoding and retrieval. Thus, ischemic vascular dementia patients (with considerable frontal damage) have poorer verbal fluency but better recall and recognition than Alzheimer’s patients (with damage to semantic storage areas) (Lafosse, Reed, Mungas, & Sterling, 1997).

7.2. The ‘Perceiver’ (ventral lateral/perceptual) system in memory processing

7.2.1. Basic memory terms and processes

Semantic memories represent a person’s general knowledge of the world (Tulving, 1991, 2000). *Perceptual semantic memories* represent the perceptual characteristics of objects. *Implicit perceptual semantic memories* represent perceptual characteristics that can potentially enhance, attenuate or otherwise bias later behavior but cannot be consciously retrieved (Tulving, 2000). *Explicit perceptual semantic memories* represent perceptual characteristics that can be consciously retrieved. Each new perceptual event presumably forms new posterior-cortex ventral-stream memory traces by just activating perceptual pathways, potentially creating an *implicit* memory (Murray, 2000; Squire & Knowlton, 2000).

Episodic memories represent somewhat-intact episodes and events and not just ‘facts.’ They mediate conscious access to the personally experienced past (Tulving, 2000). These often include the context and source of a past experience, in addition to its perceptual and verbal semantic content and entail some degree of a sense of ‘self involvement.’ Locke (1690/1967) linked the ‘unity of personal identity’ to our ability to place our current experiences within a string of episodic memories.

Contents of episodic memories are concurrently stored in their respective perceptual or language areas as *semantic* memories, which often linger long after the *episode* has slipped away. Presumably the blending of several episodic encounters with cows, for instance, leads to the formation of visual, auditory, and olfactory *categories* of ‘cow.’ Other times, some aspects of the episode remain long after specific semantic content has slipped away. Each sensory system projects to multi-modal areas that presumably store key unifying elements of such episodes, such as the temporal pole (Markowitsch, 2000) and the insular cortex.

The mere reactivation of parts of the pathway of *implicitly* stored memory traces by a new experience (Martindale, 1991) brings a non-conscious enhance-

ment, attenuation or biasing of performance, resulting in the need for less activation of ventral stream pathways to process current perceptions (Squire & Knowlton, 2000). The mere reactivation of *explicitly* stored memory traces by new experience brings a sense of ‘re-cognition’ or ‘recall’ of the stored memories (Rugg & Allan, 2000), with or without episodic and/or emotional context. Thus, if only visual memory traces of cows are activated, one experiences a visual-semantic memory retrieval; but if those same visual memory traces activate some stored multi-modal node from a specific experience with a cow, then one experiences the wider episode.

7.2.2. *Object agnosias*

Defects in object recognition, visual *object* agnosia, come from lesions in areas where memory representations are stored or severed links between intact pre-memory perceptual processing and perceptual memory storage (Faw, 1987, 1997). Obviously, lesions can involve both ‘form’ and ‘object’ processing areas, leading to non-pure forms of agnosia (Farah, 1990/1995; Faw, 1997). A person with visual object agnosia cannot name the objects, but also cannot show what the objects are used for (e.g., not being able to sit down on the chair to show you what it is used for). Other perceptual systems have similar disabilities. But agnosia is not an all-or-nothing disorder. Patients can lose their ability to recognize certain categories of objects, such as recognizing faces (prosopagnosia), living objects or non-living objects, suggesting the storage of visual memories in different areas.

7.2.3. *Anterior areas in memory control*

Ventral-lateral prefrontal areas and their temporal pole (area 28) connections seem to be involved in the retrieval of stored old episodic memories. The left DL-PFC is often involved in *encoding* into long-term memory, and the right DL-PFC in *retrieval*. Areas *ventral* to DL-PFC, the frontal portions of our ‘Perceiver’ (VL/PERC) and ‘Verbalizer’ (VL/VERB) systems also show brain activations during long-term memory. Holding information in working memory gives time for the encoding mechanisms to work. Bringing pathways that have stored experiences back on line may be all that it takes to retrieve memories.

7.3. *The ‘Verbalizer’ (ventral lateral/verbal) system for memory*

This ‘Verbalizer’ system also shows *implicit/priming* memory storage—called ‘conceptually driven’ implicit memory in contrast to the perceptual stream’s ‘data-driven’ implicit memory (Rugg & Allan, 2000). Learning the hidden grammar in one’s language and learning categories may be based on such priming mechanisms (Squire & Knowlton, 2000). Even a single activation of a ventral pathway may alter the pathway in such a way that implicit testing shows some biasing of further activation of that pathway.

But, there is some evidence in the language ventral-stream, at least, that frequently activating ventral pathways per se—even without hippocampal/rhinal involvement—might eventually develop memory traces that can become available even

to conscious memory. Markowitsch (2000) mentions that the classic amnesic patient H.M. eventually learned about the shooting of President Kennedy and the death of his parents through such repetition.

One gets the sense of *implicit* memory traces being like deer trails being formed in thick grasslands. After a single or a few deer runs, the path can be detected only by very subtle measurements. After frequent runs, the path begins to look like a path to the human eye. *Explicit* memory traces laid down with hippocampal/rhinal reinforcement might be like forming paths through the same thick grass using a lawn mower. The implicitly measured deer-run path-making is a slow and very limited way to etch such memories, but not totally different in kind from the explicitly measured lawn mower paths.

Even the *recognition* of heard words or read letters and words implies memory. The inferior temporal cortex (BA 37 and 21) continues visual object-recognition processing from the prestriate areas. Left inferior temporal cortex seems to have a special role in the processing of words specific to a sentence context (Stowe, Broere, Paans, & Wijers, 1998).

There are several dissociations in this system: such as between pre-semantic and semantic/memorial processing and between visual and auditory processing. For instance, Hall and Riddoch (1997) report on a patient with impaired auditory comprehension of words because of a faulty auditory-to-meaning link, not due to pre-semantic auditory processing or to faulty visual-to-meaning link. He could read and write words that he could not understand when hearing them.

Recognizing letters, words, and phrases entails conceptual semantic memory encoding, storage, and retrieval of 'verbal objects' in our 'Verbalizer' (VL/VERB) system. Again, within verbal memory, there are category-specific naming abilities, similar to those within perceptual memory, suggesting separate storage areas for the names of living and non-living objects (Cappa, Frugoni, Pasquali, & Perani, 1998; Laiacina, Capitani, & Barbarotto, 1997); the names of familiar persons (Papagno & Capitani, 1998); but also for the names of body parts (Shelton, Fouch, & Caramazza, 1998). Nouns seem to be stored in posterior cortex, and verbs in frontal areas.

A major technique in reading is *sounding out* read words; whether overtly (vocalization) or covertly (subvocalization). Subvocalization implies a visual-to-auditory translation stage between the letter-meaning and the word-meaning stage. This has generally been related to the left angular gyrus (Kaneko, Uno, Kaga, & Matsuda, 1998) linking the read word to the auditory imagery voice synthesizer, which is probably in the left superior temporal auditory-processing network (Ramsey, Horwitz, Donohue, & Nace, 1997).

Visual object *naming* is distinct from both the task of knowing the meaning of words and visual object recognition. A person with pure anomia (=not naming) without agnosia can recognize the object and show you what to do with it and may give approximate names for it (semantic paraphrasis), but cannot name it. The prefrontal portion of the 'Verbalizer' system is involved in effortful encoding (Bellgowan, Binder, Swanson, & Hammeke, 1998; Wagner, Schacter, Rotte, & Koutstaal, 1998) and in effortful retrieval (Lafosse et al., 1997; Lamar, Podell, Carew, & Cloud, 1997; Maguire, Frackowiak, & Frith, 1997).

7.4. The ‘Motivator’ (*ventral medial orbital*) system for memory

The convergence of environmental-object and interoceptive/emotional information allows the *amygdala* to *associate objects with rewards*, bestowing upon stimuli, motivational and emotional significance—determining whether this object, that is now being seen or heard, warrants fight, flight, approach, or indifference. Such processing determines how the individual will respond to the present situation and contributes to memories that help determine future responses. Thus, Rhesus monkeys with bilateral amygdectomy are markedly impaired in object-reward associations; object or place discrimination (Jones & Mishkin, 1972); and the acquisition of conditioned avoidance, conditioned suppression, matching to sample, and learning sets; all of which suggest ‘psychic blindness’ a polysensory emotional agnosia (Jones & Mishkin, 1972). Cutting the perceptual projections to the amygdala or the control output from the amygdala causes the same defect (Spiegler & Mishkin, 1981).

But, bringing external stimuli and internal stimuli on line together does not necessitate that the two will be linked in memory—just as playing two discordant notes on the piano at the same time does not mean that the piano will, on its own, play them together again. The amygdala is essential for encoding the emotional context of semantic and episodic memories (Murray, 2000) and enhancing memory storage. The ‘Motivator’ (VMO-PFC) system provides the only major prefrontal projection to entorhinal cortex to influence medial temporal lobe memory functions (Chow & Cummings, 1999).

In addition to the amygdala’s task of checking current sensory input for its emotional valence, autonomic nervous system arousal feedback activates the amygdala via norepinephrine pathways from the Vagus Nerve (cranial nerve #10). The amygdala then supercharges the hippocampus to encode emotional episodes. Emotional responses to simple stimuli can be conditioned in mammals through the direct thalamic input to the amygdala (Carlson, 1992).

Monkeys with lesioned *orbital-frontal* area are also markedly impaired in the learning of reversed object-reward and place-reward associations, as are those with amygdaloid lesions. But, the amygdala associates *objects* with rewards/threats, while the orbital-frontal area associates *responses* with rewards/threats (Passingham, 1995). That is, the amygdala determines that this new situation will get the ‘same old’ impulsive/well-learned anger or fear response given in similar old situations; but the orbital-frontal allows one to break that pattern of response and give a new response to the current situation.

7.5. The ‘Attender’ (*dorsal mediallyanterior cingulate*) system for memory

7.5.1. Encoding explicit semantic memories: *Rhinal cortex*

With the involvement of the *rhinal cortex* (linking multimodal object and spatial information) and (often) prefrontal working memory areas, the memory trace formed in the ‘Perceiver’ (VL/PERC) system, becomes an *explicit* semantic memory that can potentially be consciously recalled (Erickson et al., 2000; Miyashita, 2000; Murray, 2000). Monkeys with both perirhinal and entorhinal cortex removed show no object recognition even after a mere minute memory delay (Murray, 2000).

In encoding semantic memory, rhinal cortex undergoes rapid modification of synaptic connectivity and provides massive backward signals to modality-specific perceptual areas such as the inferior temporal, in order to guide reorganization of forward-neural circuits there (Miyashita, 2000). Stripping individual monkey inferior temporal neurons of the backward signals from rhinal cortex retains forward signals from visual stimuli but disrupts the forming of associative codes of the inferotemporal neurons between visual paired associates (Miyashita, 2000). In human amnesics with rhinal damage, semantic knowledge is disrupted (Murray, 2000), while those with damage restricted to the hippocampal/fornix system have minimal recognition deficits and are able to acquire a large amount of general knowledge about the world.

7.5.2. *Encoding explicit episodic memories: Hippocampus proper*

With the involvement of the hippocampus proper, the memory trace can become an explicit *episodic* memory. Damage to the hippocampus leads to severe *spatial* learning deficits in animals. Such ‘place memory’ may be a monkey equivalent of episodic memory—which for humans involves a great deal of verbal recall as well as place context. Humans with early damage restricted to the hippocampus have profound deficits in event memory, but can acquire extensive semantic knowledge (Murray, 2000). In contrast to Murray, Squire and Knowlton (2000) maintain that the hippocampus proper is crucial for both spatial and nonspatial memory and for both fact and event memory. In either case, the *left* hippocampal complex is especially activated in brain scans during *verbal encoding* tasks (Bellgowan et al., 1998), while the *right* hippocampal complex is activated in scans during complex *navigation* in large-scale spatial environments (Maguire et al., 1997).

7.5.3. *Cellular mechanisms for encoding semantic or episodic memories*

The hippocampal complex activates *long term potentiation* (LTP) through its massive backward signals to cortical areas to guide reorganization of forward-neural circuits there (Miyashita, 2000). In the process, AMPA-glutamate-receptor neurons potentiate the firing of NMDA-glutamate-receptor neurons (Pinel, 2000; Rosenzweig, Leiman, & Breedlove, 1999). This potentiation changes the structures and adhesion of the synapse itself, affecting the forward-projecting information being transmitted and future transmission (Lynch, 2000).

LTP has variants lasting for minutes, hours, days, and perhaps weeks and longer, called consolidation periods for newly formed memories. During these periods the new memories are easily erased, but after them they are extremely stable (Lynch, 2000). This suggests that as such memories are being consolidated, the hippocampal complex areas initially store major portions of the memory content. Miyashita (2000) has found patches in the ventral surface of inferior temporal cortex of some of the chemicals involved in the induction of LTP, expressed for paired-associate and visual discrimination learning.

While the hippocampus is essentially involved in the *encoding* of episodic memories, it seems to be involved in episodic *retrieval* also, perhaps in its role of comparing new experiences with episodes of the past. This suggests that after the memories are consolidated, the hippocampal complex stores certain links that bring

back various elements of the contexts of restored memories, while the specialized pathways store the individual memory elements. The possibility of the hippocampal complex potentiating memory storage is greatly enhanced by frontal processes, including *spatial* attentional focus on the information carried by that pathway and the *temporal* enhancement of working-memory.

We have noted that the basal forebrain projects acetylcholine to the hippocampal complex. Acetylcholine in the hippocampal complex rises during learning and falls during habit. DeLuca and colleagues (2000) suggest that the hippocampal complex monitors the environment, while the basal forebrain tells the hippocampal complex what to monitor.

7.5.4. *Anterior cingulate attentional selection and memory*

While the hippocampal-complex portion of our ‘Attender’ (DM/AC) system supplies the basic engine for the encoding of semantic and episodic memories, the attentional or cognitive division of the AC plays a directing role in long-term memory encoding and retrieval through its moment-by-moment selection of what input and working-memory-information-pathways to attend to. New information that is attended and held in working memory has more opportunity for long-term-potential encoding to occur. On the other end of the process, information stored in pathways has a better chance of being retrieved if it is attended and kept activated in working memory.

7.6. *The ‘Coordinator’ (dorsal-lateral) system for memory*

The ‘Coordinator’ (DL-PFC) and areas ventral and anterior to it—the polar orbital BA 10—have been implicated in encoding and storing episodic memories (Eustache, Desgranges, Petit-Taboue, & de la Sayette, 1997; Maguire et al., 1997; Markowitsch, 1995). The *encoding* of episodic memory seems to be a function of the *left* lateral prefrontal cortex (though not in BA 8: Grady, 1999). The *retrieval* from episodic memory seems more linked with the *right* lateral areas (Gur, Ragland, Mozley, & Mozley, 1997; Markowitsch, 1995, 2000; Tulving, 1991), especially when one has had personal involvement in the episode, one has retrieval success and one is recalling, rather than recognizing (Vogele, 1999). Not all episodic-memory retrieval is performed by the *right* prefrontal areas. The left DL-PFC is involved in word retrieval (Eustache et al., 1997)—presumably because of its close link with the verbal processing left language circuits—and in complex retrieval—likely because of its role in working memory.

8. Responding to information on line: The executive committee in motor control

8.1. *Responding to information on-line: Motor control*

The frontal lobes as a whole control voluntary actions through the *planning* of movements in prefrontal areas and their basal-ganglia loops, *preparation* of movements in supplementary motor areas (SMA) and premotor (PM) and their basal-

ganglia and cerebellum loops, and *execution* of movements in primary motor and sub-cortical areas (Fuster, 1995). Specific types of posterior- and sub-cortical input are reciprocally related to each frontal part of the system, and the frontal parts of each system are reciprocally connected within a hierarchy: PM/SMA areas are reciprocally connected with their sensory areas and motor areas posterior to them and with their prefrontal areas anterior to them.

Both PM and the SMA play a role in the preparation and selection of manipulative movements, showing greater PET activation when subjects need to select between movements rather than just repeat a movement, when subjects learn or relearn conditional tasks, and when they retrieve the movement that is appropriate to the context (Passingham, 1995). But the SMA areas seem more involved in self-initiated movements and in selecting or preparing movements based on *internal* cues (cues held in memory), while the PM areas seem more involved in selecting movements or preparing movements based on *external* cues or prompts (Passingham, 1995).

8.2. The 'Perceiver' (*ventral lateral/perceptual*) motor systems

The 'Perceiver' (VL/PERC) system seems to be linked to motor output only after being processed by memory, semantics, spatial reasoning, planning, and communication (Goodale, 2000), feeding information into various forms of cognitive processing and then into other prefrontal systems to allow them to respond, based on precise sensory information. But there may be a series of distinct motor systems related to specific lateral orbital areas, such as a 'feeding behavior system' relating to the posterior lateral orbital portion (Carmichael & Price, 1995). The *lateral* orbital frontal strip also shares with the 'Motivator' (VMO) *medial* orbital frontal strip reciprocal connection with the amygdala and thus some control over the extensive hypothalamic and brainstem motivational motor systems (Passingham, 1995).

8.3. The 'Verbalizer' (*ventral lateral/verbal*) motor systems

The 'Verbalizer' (VL/VERB) system is well known for its anterior motor functions. Frontal language areas seem more involved in producing verbs than nouns, a pattern found at least in English, German, Italian, and in Chinese (Chen & Bates, 1998; Semenza, Luzzatti, & Carabelli, 1997). The utterance of nouns initially precedes activity in frontal language areas (Sasaki, Nambu, Tsujimoto, & Matsuzaki, 1996).

The arcuate fasciculus links comprehension of heard/read language to what one wants to express in response. Cutting this connection leads to conduction aphasia, where one has good comprehension of what one hears and reads and one can speak spontaneously, but one is very poor in repeating what one hears (Geschwind & Iacoboni, 1999).

Ventral portions of BA 6 and 44 make up the 'Verbalizer' ventral pre-motor (PM) area (Passingham, 1995), which is activated during the motor planning component of word generation—the more words, the greater the activation (Karbe, Herholz,

Weber-Luxenburger, & Ghaemi, 1998). This ventral PM area mediates speech based on *external cues* (Passingham, 1995). A portion of medial BA 6, just anterior to the somatic-supplementary motor area (SMA) is a supplementary language area which mediates speech based on *internal cues* (Passingham, 1995) and the production of fluent speech not restricted to word position (Van Borsel, Van Lierde, Van Cauwenberge, & Guldemont, 1998). The left anterior SMA may be specialized in fluent speech versus stutter (Fried, Wilson, MacDonald, & Behnke, 1998; Van Borsel et al., 1998). BA 45 and 47 are seen as the ‘Verbalizer’s’ pre-frontal area, selecting competing but unambiguous verbal responses. Grady’s (1999) review of PET scans notes more activations from semantic processing and language in BA 47 than in any other region in the left hemisphere.

The left hemisphere has a bias to process natural languages independently of the modality through which language is perceived, for both speaking and the fluent use of American Sign Language (ASL) (Bavelier, Corina, Jezzard, & Clark, 1998). PET scans in humans in BA 45 show a left bias for an observation/execution matching system of grasping actions—suggesting that primate gestures might be the precursors of human language and that the ‘grammar’ of communicative gestures would be represented in nonhuman primate equivalent to BA 45. Human activation is also found there when a subject is required to grasp objects, imagine grasping objects or observing others grasp objects. Activation is also found with silent lip reading, where no acoustic or language-receptive areas are activated, suggesting that *visual* information feeds forward to Broca’s area in the left hemisphere (Geschwind & Iacoboni, 1999).

The *right* frontal homologue to Broca’s Area is dominant in the production of melodic components of prosody, the expression of the emotional content of language (Geschwind & Iacoboni, 1999), and various aspects of language ‘pragmatics.’ American Sign Language also strongly recruits right hemisphere structures, whether native signers are deaf or hearing (Loew, Kegl, & Poizner, 1997), showing that the specific processing requirements of the language also in part determine the organization of the language systems of the brain.

8.4. The ‘Motivator’ (*ventral medial orbital*) motor systems

Our ‘Motivator’ (VMO) system has at its disposal several sub-cortical motor pathways, through orbital-frontal projections back to various nuclei of the amygdala. The amygdala activates three main categories of emotional responses: (1) amygdala projections to the upper brainstem’s PAG activate emotional *behaviors* such as startle, flinching, and freezing (Kalat, 1998); (2) amygdala projections to the lateral hypothalamus activate *autonomic* responses, such as increasing heart beat, BP, and adrenaline rushes; and (3) amygdala projections to the bed nucleus of the stria terminalis control medial hypothalamic activation of *hormonal* responses, such as stress, sexual, and parental responses (Adrianov, 1996). We have noted that activation of the amygdala can lead to an “arrest” response, where all spontaneous activity is stopped and the animal becomes hyper-vigilant (Carpenter & Sutin, 1983)—both an attentional and a motor maneuver.

8.5. The ‘Attender’ (dorsal medial/anterior cingulate) motor systems

The mechanisms of the ‘Attender’s’ anterior cingulate internal-cue-evoked *attentional* shifts can be seen as a response system. The anterior cingulate shares control with the ‘Motivator’ (VMO) system over the autonomic nervous system through output to the amygdala and hypothalamus. Stimulation of the anterior cingulate and amygdala leads to the inhibition of spontaneous movement (Passingham, 1995). As we have noted, through some such means, the ‘Attender’ anterior cingulate and the ‘Motivator’ can ‘gang up’ to inhibit the ‘Coordinator’ dorsolateral cortex’s powerful motor control over the somatic pre-motor to motor system in ‘hysterical paralysis’ (Faw, 2000a, 2000b; Marshall et al., 1997). The ‘Motivator’ and ‘Attender’ inhibitory effect seems to be directly on the primary motor cortex. This suggests that these other prefrontal areas have some control over the somatic motor output system related to the ‘Coordinator’ dorsolateral prefrontal cortex.

8.6. The ‘Coordinator’ (dorsolateral) motor systems

Each of the ‘Coordinator’ (DL) motor systems receives input from its respective subcortical and posterior-cortical processing areas and is controlled by its own premotor and supplementary-motor areas. Each does some of its processing in cortical-subcortical loops. Activity of the neurons in the various intraparietal areas are specifically related to one or another type of motor behavior being planned—such as eye movements, reaching, or grasping (Chelazzi & Corbetta, 2000).

8.6.1. Somatic limb/body motor system

The limb/body motor system controls bodily responses to situations, including reaching and grasping, walking or running, or moving one’s body to contact or avoid objects. Posterior cortical portions of this system involve a number of parietal lobe somatic and visual processing areas. In monkeys, at least, this somatic motor system overlaps ventral-lateral motor areas found in human language processing. The parietal *VIP* (ventral intraparietal sulcus) area, which codes stimulus location relative to the head, is in circuit with ventral premotor BA 44/F4, to control arm and head (mouth) reaching. The *AIP* (anterior intraparietal sulcus) area is in circuit with rostral ventral prefrontal BA 45/F5 for control of grasping (Chelazzi & Corbetta, 2000); while the *MIP* (medial intraparietal) area codes stimuli within arm-reaching distance (Behrmann, 2000).

This motor system has its primary motor area in BA 4. The lips and tongue are used for speech, eating, and many other things, and so also participate in motor systems mentioned already in perceptual and verbal streams. The primary motor area is the principle activator of the *pyramidal motor system* which produces voluntary motor responses, especially fine movements of the fingers and mouth, by projecting to motor neurons in the brainstem and spinal cord, which in turn constrict muscles.

The limb/body PM area in lateral BA 6 has cells that fire when limb movements are based on *external cues* (Passingham, 1995). Lateral BA 6 receives input from the dorsal part of parietal BA 5 and BA 7b. The limb/body SMA in medial BA 6, has

cells which fire when limb movements are not based on external cues—thus on *internal cues* or *working memory* (Passingham, 1995). Small portions of the left anterior SMA serve as SMA in the speech motor system of the ‘Verbalizer’ (VL/VERB) system. In addition to helping set up the contra-lateral motor responses of the pyramidal system, PM and SMA areas participate in a bi-lateral *extra-pyramidal* motor system, helping to coordinate broader bodily responses needed for precise muscle movement.

8.6.2. *Visual (eye) motor system*

The LIP (lateral intraparietal sulcus) area maps stimuli by retinal coordinates (Behrmann, 2000). The eye primary-motor area has both ventral stream and dorsal stream input (Kaufer & Lewis, 1999; Passingham, 1995). The eye-pre-motor (PM) processes eye movements based on external cues. The ‘supplementary eye field’ (SEF) is activated when one is planning to make an eye movement (Behrmann, 2000). It process eye movements based on internal working memory cues (Passingham, 1995). Through these connections, the ‘Coordinator’ (DL-PFC) controls voluntary eye saccades and smooth pursuit motions.

The eye primary-motor and PM areas have two main types of oculomotor output: preoculomotor areas in the midbrain and pons that activate cranial nerves III, IV, and VI, which together move the eyes and deal with visual reflexes; and deep layers of the superior colliculus which coordinate eye movement responses with necessary head, shoulder, and bodily responses—and visual input with other sensory input leading to such responses.

8.6.3. *Willed action*

In its motor control, the ‘Coordinator’ (DL-PFC), itself, sets up a ‘*movement related potential*,’ beginning some 1000 ms prior to movement; and then the PM and SMA/SEF areas show the ‘*readiness potential*’ about 500 ms prior to action—setting up the motion and helping send parallel extra-pyramidal motor commands, as the motor cortex sends the basic pyramidal motor commands (Fuster, 1999). Both left and right ‘Coordinator’ (DL-PFC) can enact willed action contralaterally (Marshall et al., 1997), but the left DL-PFC seems to be the more definitive initiator for willed actions (Cummings, 1998; Lasker & Zee, 1997; Spatt & Goldenberg, 1997). The left DL-PFC is most important in programming strategies, control of executive functions, and motor responses (Geschwind & Iacoboni, 1999).

9. Processing information on line: Executive committee for thinking and imagination

9.1. *Processing information on line: Thinking and imagination*

Each of our five systems has as much to do with *mental* processing and responses as it does with *perceptual* processing and *motor* responses, so that higher cognition can be seen as an “emergent property” of the more primitive sensory and motor systems (Iacoboni, 2000, p. 524). Each of the five systems also seems to be involved with *mental-imaging systems*, in that mental imagery is found in each sensory form as

well as in verbal, emotional, motivational, and motor form. When both perception or motor control and imagery are disordered in a given patient, the problems are usually—but not always—of the same type (Farah, 1984; Faw, 1997). Mental imaging is itself involved in many aspects of perceptual and verbal presenting, working memory, attention, long-term memory, motor preparation, and emotional responding.

9.2. The ‘Perceiver’ (*ventral lateral/perceptual*) system in imaginal thinking

Much mental imaging arises when the perceptual systems activate stored memory traces, yielding a cognitive sense of recognition and/or a full conscious ‘perceptual’ mental picture. The *imaginal* representations formed are then as apt to be encoded into implicit, semantic, and episodic memory as are *perceptual* representations. Imaging systems help *perception* by completing partially perceived figures, clarifying ambiguous figures, and helping match new percepts to stored memories (Faw, 1997). Miyashita (2000) assumes that monkeys keep the *working memory* of the complex geometric figures as visual images. *Memorial* mental imaging allows perception to match present objects with objects perceived in the past and expected in the future (Miyashita, 2000).

Non-verbally triggered imaging can be seen as ‘pre-language thinking,’ related to Tolman’s animal cognitive mapping and Piaget’s human late-sensory-motor stage of cognition. It also represents a type of thinking available for pre-lingual/pre-signing congenitally deaf children.

9.3. The ‘Verbalizer’ (*ventral lateral/verbal*) system for verbal thinking

Both auditory and visual *language* input can be converted into both auditory and visual *imagery*. Verbally triggered word-thoughts and verbally triggered visual-images can be seen as two interacting ‘language modes of thinking’ (Faw, 1997). Bookheimer, Zeffiro, Blaxton, and Gaillard (1998) found PET scan activation in auditory-language areas and in visual areas when their subjects listened to meaningful phrases. Dominant BA 39 (or an area just posterior) translates the *words* that you read or hear into *visual images* conjured up by the words—e.g., creating the mental image of a cow—or of the visual image of the word ‘cow’—when you read or hear the word ‘cow’ (Farah, 1984; Faw, 1997).

Generating words *covertly* that begin with particular letters (Friedman, Kenny, Wise, & Wu, 1998) or the covert naming of visually presented objects codes (Zelkowitz, Herbster, Nebes, & Mintun, 1998) activates left posterior visual areas and left anterior language areas, suggesting that the inferior temporal lobe is important for visual-semantic processing and the frontal cortex for word generation of even *thought* words. The frontal language circuits are activated on PET scans during tasks such as memorizing a running line of text, counting a certain letter in the words or in nonsense letter sequences (Medvedev, Bekhtereva, Vorob’ev, & Rudas, 1997).

Goel, Gold, Kapur, and Houle (1998) ran PET scans during *deductive reasoning* categorical syllogisms, involving either spatial relational items or nonspatial relational items. Each reasoning condition evoked activation confined to the left

hemisphere ‘Verbalizer’ (VL/VERB) system and a portion of left ‘Coordinator’ (DL) prefrontal (BA 46). This ‘Verbalizer’ prefrontal area may be involved primarily in *putting together correct sentences* in reasoning, while the ‘Coordinator’ (DL) prefrontal area seems involved in putting word groups together to form a *logical sequence of actions* (Sirigu et al., 1998). There is strong evidence that a major right hemisphere language role is in maintaining alternative word senses (Faust & Chiarello, 1998; Titone, 1998), non-literal figurative language (Mariotti, Iuvone, Guilia, & Silveri, 1998) and metaphors (Anaki, Faust, & Kravetz, 1998).

9.4. The ‘Motivator’ (ventral medial orbital) system for self-coordinate thinking

The ‘Motivator’ (VMO) area is activated when people make ‘gut decisions,’ as in the Gamblers’ Game Dilemma, or make decisions in other difficult situations in which there is no clear-cut best answer (Adolphs, 2001; Bechara et al., 1998). Interestingly, making decisions in difficult situations in which there is one right answer activates ‘Coordinator’ (DL) prefrontal areas.

Related to this is the fact that the ‘Motivator’s’ amygdala is essential, in monkeys (Klüver, 1939) and in humans, for recognizing *fear* (Broks, Young, Maratos, & Coffey, 1998; Morris et al., 1996) and perhaps *anger* (Adolphs, Tranel, & Damasio, 1998) in the faces of others. This stream helps interpret social situations and make social judgments (Adolphs et al., 1998), so that persons with orbital lesions tend to have difficulty in appreciating and integrating relatively subtle social and emotional cues (Cicerone & Tanenbaum, 1997). Intact ‘Motivator’ orbital-frontal circuits seem necessary for the acquiring of social or moral knowledge (Adolphs, 2001; Faw, 2000b), so that children with early orbital frontal damage never acquire social and moral knowledge, while adults with later damage have already acquired it and can thus intellectually know what is socially or morally right, even though they don’t ‘feel’ it (Adolphs, personal communication). Grady (1999) notes that these changes tend to involve BA 11 and ventral medial portions of BA 10. The right hemisphere of this area seems to be crucial for ‘social inferring’ (Vogeley, 1999). The ‘Motivator’ may be the most important area in differentiating people according to basic personality traits (Soloff, 1998; Viinamaki, Kuikka, Tiihonen, & Lehtonen, 1998).

9.5. The ‘Attender’ (dorsal mediallyanterior cingulate) system for contextual thinking

We have examined the role of various portions of the cortical mid-line strip in monitoring pre-attentive peripheral vision, conscious motor functioning, perceptual attention, and self-focused attention upon one’s internal feelings and emotions; in the subjective and/or emotional aspects of pain; and in the conscious experience of emotions and ‘emotional evaluation.’ This last process of *emotional evaluation* would represent one way in which the ‘Attender’ anterior cingulate sub-system is involved in thinking.

Alexithymia, a rare clinical disorder representing the lack of emotional experiences or a difficulty in discriminating between one’s emotions (an ‘emotional blindsight’) is also linked to the ‘Attender’ anterior cingulate (Kazsniak, in Watt, 1998), perhaps resulting from a dissociation between the ‘affective’ and the ‘cognitive’

cingulate. Gruzelier (1998) found fMRI activation in the ‘affective division’ during an emotional counting Stroop paradigm (where subjects dealt with ‘negative’ words) and activation in the ‘cognitive’ division during a more cognitive version of the Stroop.

The anterior cingulate has been implicated in various other cognitive involvements, such as enabling the use of conditioned response rules (Everitt & Robbins, 1997) and error detection (Gruzelier, 1998; Posner & DiGirolamo, 2000). In the latter, anterior cingulate cortex is activated when the person is consciously aware of the error, suggesting that the anterior cingulate is directly related to one’s awareness of one’s planned behavior (Posner & DiGirolamo, 2000). Finally, extensive bilateral lesions of anterior cingulate and aspects of its basal ganglia loops can lead to the *global abulic state*, in which there is no cognitive activity, or to *akinetie mutism*, in which there is mutism and an almost total lack of any response.

9.6. The ‘Coordinator’ (dorsolateral) system for action thinking

Deficits from lesions in the ‘Coordinator’ (DL-PFC)—constituting the ‘frontal syndrome’—are among the best documented in clinical neuropsychology. Persons are especially impaired in planning and in changing a course of action or thinking, find it almost impossible to respond after delay or in unexpected appropriate ways to stimuli, and are impaired in motivation.

We have noted that making decisions in difficult situations in which there is one right answer activates the ‘Coordinator’ (DL) prefrontal cortex, while making decisions in difficult situations in which there is no clear cut best answer activates the ‘Motivator’ (VMO) cortex. One might say that the ‘Motivator’ system underlies self-coordinate thinking, while the ‘Coordinator’ underlies object/event-coordinate thinking.

Yet, the ‘Coordinator’ (DL) system’s role in ‘willed action’ suggests some sense of *self-as-agent*. A ‘sense of agency’ might be related to each of the five prefrontal systems, or it might be what makes the willed action associated with the ‘Coordinator’ unique, with a sense of agency possible only with DL-PFC involvement. Our ‘conviction to act freely’ may be based on the intuitive sense of agency accompanying ‘free’ actions, which might be related to the ‘motor imagery’ related to ‘movement related potentials and ‘readiness potentials’ (Pauen, in Vogeley, 1999), which are most clearly seen in the ‘Coordinator’ (DL-PFC).

In contrast, *passivity phenomena* such as thought insertion, ‘made’ movements, and hallucinations in schizophrenia seem to show the loss of agency or ownership (Fletcher, in Frith, 2001; Vogeley, 1999). This reaches an extreme in *Cotard Syndrome* in which there are such nihilistic delusions that the sufferer may deny that he or she exists, perhaps representing the complete absence of the self-construct (Cabeza, Kapur, Craik, & McIntosh, 1997). It may well be that such disruption in a conscious sense of agency might represent a disconnect between the agency-action-commands by the ‘Coordinator’ (DL-PFC) and the awareness of motor responses by the ‘Attender’s’ ‘motor cingulate gyrus.’

The *right* ‘Coordinator’ (DL-PFC) has been strongly linked to the ability to *monitor* and to have insight into one’s abilities and disabilities (Miller & Cummings,

1999; Starkstein et al., 1995; Vilkki, Servo, & Surma-aho, 1998; Young, Zakzanis, Bailey, & Davila, 1998)—the deficit in the latter is called *anosognosia* (Greek = not-ailment-knowing). Petrides (1994) links monkey ‘Coordinator’ (DL-PFC) BA 9 and dorsal 10 to tasks that draw heavily on self-monitoring and planning of behavior.

Posner and Rothbart’s (1992) suggestion that our right ‘Coordinator’ (DL-PFC) is involved in maintaining vigilance to external objects and in ‘clearing the mind’ of left ‘Coordinator’ thoughts is extremely interesting. It might be that the *left* ‘Coordinator’ sorts through the spontaneous ‘mental’ responses of the individual to determine when and where the *right* ‘Coordinator’ should sustain attentional focus to external events, so the individual can give further *left* hemisphere internal-world processing to external world situations for more adaptive motor responses.

One of the many ways in which the executive-committee model needs to be developed in later writings is for an updated review of the interconnections among the five prefrontal areas involved—showing both activating and inhibiting pathways. In concluding this paper, I will mention only a couple of examples. This paper is already long enough.

Kaufer and Lewis (1999) show the dominating role of our ‘Coordinator’ (DL-PFC) in its major reciprocal connections with the ‘Attender’ cingulate (medial frontal), ‘Motivator’ medial orbital frontal cortex, and ‘Perceiver’ lateral orbital frontal cortex, but do not show connections among the cingulate, medial-orbital frontal and lateral orbital frontal areas, nor do they indicate what connections are activating and what inhibiting.

As another example, Bernstein, Stiehl, and Bickle (2000) are developing neural-network programs based on circuitry between the ‘Attender’ anterior cingulate and the ‘Coordinator’ dorsolateral prefrontal areas in the control of saccadic eye movements. They cite studies showing excitatory input from the anterior cingulate to frontal regions including the DL-PFC and orbital areas, and ways in which sub-cortical input to various locations in the anterior cingulate dis-inhibit cingulate activation of specific parts of prefrontal regions.

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