

Grossberg, S. & Pearson, L.

LIST PARSE MODEL SUPPLEMENTARY MATERIAL

Section 1: Localization of low-level inputs to the lateral prefrontal cortex

Posterior parietal association areas in (a) the inferior parietal lobule, (including the supramarginal and angular gyri) and areas of the sylvian fissure near the parietal-temporal boundary overlapping into the superior temporal sulcus (including area Spt; Hickok & Poeppel, 2004), and (b) Brodmann's areas 7a,c,ip,m are likely locations for high-level category storage operations for phonological (for review: Hickok & Poeppel, 2004) and spatial (for review: Goldman-Rakic, 1987; also see work on the dorsal "where" visual processing stream; Ungerleider & Mishkin, 1982) information, respectively.

More specifically, Brodmann's area 22 in the superior temporal gyrus (termed Wernicke's area in the left hemisphere of the human) and the phonological areas of the inferior parietal lobe project extensively through the arcuate fasciculus to portions of the ventrolateral prefrontal cortex (e.g., areas 44 and 45, including portions of anterior Broca's area in the left hemisphere of the human). In the monkey, visuospatial information from areas 7a,c,ip,m in the parietal lobe target largely *distinct and localized* portions of areas 9/46v,d and 46 (Petrides & Pandya, 1994) in and around the principal sulcus of the dorsolateral prefrontal cortex (for review: Goldman-Rakic, 1987).

The neural correlates of these specific regions in humans are somewhat less clear, but are suggested by cytoarchitectonic homologues to the areas in the monkey (Petrides & Pandya, 1994). Object (e.g., semantic) category information from auditory (for review: Hickok and Poeppel, 2004) and visual (e.g., the ventral "what" visual processing stream; Ungerleider & Mishkin, 1982) presentation are likely to involve the anterior superior temporal sulcus and inferotemporal region (e.g., areas TEO and TE) respectively. These areas are known to be reciprocally connected with ventrolateral prefrontal cortex (Brodmann's areas 47/12 and 45; for review: Barbas, 1992).

Regional localizations of the lower-level portions of the auditory and visual "What" and "Where" processing streams, which are collapsed across in Figure 1, are well established (Constantinidis & Procyk, 2004; Kandel, Schwartz & Jessel, 2000). Aside

from the consistent connectivity patterns, similar activity patterns between these areas and their prefrontal targets in a variety of protocols (e.g., Chafee & Goldman-Rakic, 2000; D'Esposito et al., 1998) are consistent with the hypothesis that, among other possible functions, these areas represent high-level categorical information which is then fed into lateral prefrontal cortical working memory centers.

Barbas and colleagues have demonstrated in a multitude of structures the importance of laminar definition in establishing the connectivity patterns between cortical areas (e.g., Barbas & Rempel-Clover, 1997; Dombrowski, Hilgetag & Barbas, 2001; Hilgetag, Dombrowski & Barbas, 2002; Rempel-Clover & Barbas, 2000). In particular, Barbas & Rempel-Clover (2000) established that projections from a range of prefrontal areas, particularly area 46, terminate primarily in the infragranular areas of anterior temporal lobe area TE, and resemble the feedback pathways in early sensory cortical areas. Confirmation of this pattern of hierarchical connectivity between the posterior parietal lobes and the lateral prefrontal cortex has been previously reported (Goldman-Rakic, 1987). Similar feedback pathways were reported to exist in the projections from prefrontal area 8 to posterior visual areas MT and MST (Cusick, Seltzer, Cola & Griggs, 1995). These frameworks of organization are generally consistent with the connectivity between the hierarchical layers of cognitive working memory in the LIST PARSE model (Figures 1, 2, and 10b).

Section 2: Functional localization within the lateral prefrontal cortex

One possible anatomical substrate of the non-spatial cognitive working memory in the primate is in the ventrolateral prefrontal cortex, whereas spatial cognitive working memory may be localized to the principal sulcus, and motor working memory may be located in the dorsolateral prefrontal cortex (in particular, outside of and likely dorsal to the principal sulcus in the monkey) and medial premotor cortex (e.g., supplementary motor area (SMA) and pre-SMA).

Given the extensive interconnectivity among all regions of prefrontal cortex (for review: Barbas, 2000) and between these higher-level association cortices, neurons responsive to multiple modalities and category-types are found in all of these locations

(e.g., Rao, Rainer & Miller, 1997). However, lesions to the areas of prefrontal cortex receiving extensive bottom-up projections or the areas projecting to them would effectively cut off a majority of the direct category-specific information to the prefrontal cortex and would be expected to result in category-type selective impairments to working memory functionality.

In fact, lesion studies provide a compelling source of evidence for these functional localizations (for reviews: Curtis & D'Esposito, 2004; Goldman-Rakic, 1987; Passingham, 1993). Monkeys with dorsolateral prefrontal lesions show severe *specific* impairment in a wide range of tasks that require monkeys to retain spatial information in memory over a delay period (Goldman & Rosvold, 1970; Goldman, Rosvold, Vest & Galkin, 1971; Jacobsen, 1936; Levy & Goldman-Rakic, 1999; Mishkin, 1954; Mishkin & Pribram, 1954, 1955, 1956; Mishkin, Vest, Waxler & Rosvold, 1969; Petrides, 1991, 1995, 2000a; Pribram & Mishkin, 1956), particularly for stimuli presented in the contralateral visual field (Funahashi, Bruce & Goldman-Rakic, 1993). However, lesions confined to the principal sulcus typically produce deficits in spatial working memory of similar severity to much larger dorsolateral lesions (which include the principal sulcus) while lesions to areas of dorsolateral prefrontal cortex which leave the depths of the principal sulcus intact do not produce the spatial working memory specific impairments (e.g., Goldman & Rosvold, 1970; Goldman, Rosvold, Vest & Galkin, 1971; Petrides, 2000a). These studies, and the localized projections of dorsal “where” stream centers to areas in and around the principal sulcus (e.g., Goldman-Rakic, 1987), specifically implicate the principal sulcus in the maintenance of spatial information (in particular, stimulus cues) across a delay. This finding has been even further supported by numerous electrophysiological recording studies during oculomotor working memory tasks (e.g., Funahashi et al., 1989, 1990, 1991).

The dorsolateral prefrontal cortex (outside the principal sulcus) has been implicated by numerous electrophysiological recording studies in the representation of prospective movement sequences based upon past reward experience (Barraclough, Conroy & Lee, 2004; Averbeck, Sohn & Lee, 2006). Lesions to the mid-dorsolateral prefrontal cortex that specifically spare the depths of the principal sulcus produce deficits in both spatial and non-spatial object tasks that require complex “monitoring” (e.g., updating of working

memory representations), rather than simple maintenance, of information in working memory (Petrides, 1991, 1995, 2000a). In particular, the self-ordered task that is often used to demonstrate deficits in non-spatial tasks from dorsolateral prefrontal lesions (Petrides 1991, 1995) typically requires the monkey to remember its previous *movements*.

The medial premotor cortex (e.g., SMA and pre-SMA) has been linked in electrophysiological recordings to the preparation of motor response sequences based upon stimulus cues and/or the selection of motor responses maintained in working memory (Shima & Tanji, 1998, 2000). In addition, several studies have found serial order dependent-firing for movements within an eventual sequence among wide cross-sections of cells in both pre-SMA and SMA (e.g., Clower & Alexander, 1998; Isoda & Tanji, 2004; Shima & Tanji, 2000). Some subset of these cells may provide a substrate for explicit positional coding of some nature that is strongly suggested by secondary error effects like across-trial and within-trial across-temporal-group positional intrusions, but which are not modeled herein (for reviews: Henson, 1998b, 2001).