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The Prefrontal Landscape: Implications of Functional Architecture for Understanding Human Mentation and the Central Executive [and Discussion]

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The prefrontal landscape: implications of functional architecture for understanding human mentation and the central executive

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SUMMARY

The functional architecture of prefrontal cortex is central to our understanding of human mentation and cognitive prowess. This region of the brain is often treated as an undifferentiated structure, on the one hand, or as a mosaic of psychological faculties, on the other. This paper focuses on the working memory processor as a specialization of prefrontal cortex and argues that the different areas within prefrontal cortex represent iterations of this function for different information domains, including spatial cognition, object cognition and additionally, in humans, semantic processing. According to this parallel processing architecture, the 'central executive' could be considered an emergent property of multiple domain-specific processors operating interactively. These processors are specializations of different prefrontal cortical areas, each interconnected both with the domain-relevant long-term storage sites in posterior regions of the cortex and with appropriate output pathways.

1. INTRODUCTION

The prefrontal cortex is the area of the brain most often associated with executive processes in humans. Concerning this venerated organ of mind, two points are rarely contested: first, that this large expanse of neocortex has a compartment organization based on its cytoarchitectonic subdivisions; and second, that injury to this cortex in humans and animals results in a diversity of behavioural abnormalities. One of the major questions confronted by our field is that of how function maps onto structure in association cortex. Do the different regions carry out distinctive functions, e.g. inhibitory control, motor planning and spatial memory, as argued at different times by numerous contributors to the prefrontal literature (e.g. Fulton 1950; Mishkin 1964; Brutkowski 1965; Fuster 1980; Pribram 1987)? Is there a hierarchical relationship between superior and inferior dorsolateral cortex as recently proposed by Owen *et al.* (1996)? Or is the prefrontal cortex organized into subregions according to informational domain with the different domains sharing a common specialization that can uniquely be identified with prefrontal cortex (Goldman-Rakic 1987)? According to this latter view, content, not function, is mapped onto major cytoarchitectonic fields. It would be premature to draw strong conclusions and firm answers to the questions that will be raised here. However, a field advances when discrete hypotheses can be generated, compared and eventually some of them falsified. Furthermore, an understanding of the 'functional map' in prefrontal cortex has direct implications for the nature and existence of a general purpose central executive (Baddeley & Hitch 1974; Baddeley 1986) and/or a supervisory attentional system (Shallice 1982), as well as for defining the concept of polymodal cortex, the nature of consciousness and the organization of mind. This essay addresses the landscape of prefrontal cortex anatomically and functionally, based on the premise that structure and function are inextricably related. And I would argue further, that every theory of cortical function should be integrated with knowledge of regional circuitry and physiology. This meeting has provided an opportunity to review different organizational schemes and suggest ways they may be harmonized and/or tested in future research.

2. TRADITION OF FUNCTIONAL DUALITY

A major organizing principle of prefrontal function since mid-century has been that of a duality between the dorsolateral and orbital cortices. An early example of this partition can be found in the Salmon Lecture delivered by John Fulton (1950). Fulton subdivided the prefrontal cortex into mesopallium – posterior areas 13 and 14 of Walker – and neopallium – Walker's areas 9, 10, 11 and 12, 46 and 8. The mesopallium was part of the visceral brain involved in emotion and affect while the neopallium was considered important for intellectual functions. The trend for orbital lesions, particularly posterior or mesopallial areas to produce selective impairments on tasks which evoke emotional or appetitive responses and for lateral lesions of the convexity to produce impairments on tests requiring integration of information has persisted in one form or another to the present day. The caudal regions of the orbital cortex have long been associated with the interceptive and palpable senses (Fulton 1950) and anatomical evidence is accumulating to show that the orbital areas subserving these functions are definable in terms of the relevant afferent inputs (e.g. Baylis *et al.* 1995; Carmichael & Price 1995). Dias *et al.* (1996) have shown deficits in reversing stimulus-reward associations following orbital lesions in the marmoset presumably attributable to connections with limbic areas. Finally, clinical studies reveal an autonomic pattern of deficits associated with orbital lesions (Damasio *et al.* 1991), although cognitive deficits have also been observed (Eslinger & Damasio 1985; Freedman & Oscar-Berman 1986).

The neopallium or dorsolateral convexity in turn can also be further differentiated into functional territories. In an influential 1964 essay, Mishkin introduced a division of labour between dorsal and ventral portions of the neopallium according to which the dorsolateral convexity represented by the principal sulcus was concerned with spatial function, while the ventral part, or the inferior prefrontal convexity (including the cortex of the lateral orbital cortex) was associated with the maintenance of what was termed 'central sets' (Mishkin 1964). Although then, as now, impairment on delayed-response tasks defined the dorsolateral contribution, emphasis was placed more on its spatial nature and less in terms of the immediate memory process. The tradition of functional diversity was further elaborated by Fuster (1989) who expanded duality of function into the functional trinity of preparatory set, retrospective provisional memory and suppression of external and internal influences. In Fuster's system, the first two functions were associated with the dorsal prefrontal convexity; the last mentioned with the orbital prefrontal cortex. Importantly, however, these three functions were considered subordinate to the synthetic role of prefrontal cortex in 'the formation of temporal structures of behaviour with a unifying purpose or goal' (Fuster 1980, p. 126). With respect to memory, Fuster & Alexander (1971), Pribram and Tubbs (1967) and Goldman & Rosvold (1970) all placed emphasis on the temporal structuring of delayed-response tasks, considering their spatial properties as subsidiary. Further, Fuster considered the memory function of prefrontal cortex to be highly localized to one subarea of cortex which subserved both non-spatial as well as spatial processing. Depression of activity in the principal sulcus region by cooling produced both non-spatial and spatial impairments (Bauer & Fuster 1976). On the other hand, surgical removals of the dorsolateral and inferior convexity portions of the dorsolateral cortex have yielded evidence of dissociation between the spatial and non-spatial memory systems of the prefrontal cortex. Passingham, for one, found deficits on delayed colour matching task following inferior convexity lesions; delayed alternation was unimpaired by the same lesion. Conversely, lesions of the principal sulcus produce impairments on spatial delayed-response tasks and rarely on non-spatial tasks (for review, see Goldman-Rakic 1987). Nevertheless, the interpretation often given to this dissociation is that the inferior convexity plays a role in inhibiting or overcoming incorrect or prepotent response tendencies while the dorsolateral prefrontal cortex, exemplified by the salient delayed-response deficits, is central to the memorial programming of appropriate motor programmes.

More recent studies have offered additional views of prefrontal functional architecture. Petrides has advanced the idea of a two-stage hierarchical organization of prefrontal cortex according to which the midfrontal areas 9 and 46 carry out sequential processing and self-monitoring functions while the inferior convexity areas 45 and 47 (in humans) are engaged in a lower level function entailing 'comparison between stimuli in short-term memory as well as the active organization of sequences of responses based on conscious explicit retrieval of information from posterior cortical association systems'. In the Petrides model, each level can operate on either spatial or non-spatial information.

This brief review of the literature is intended to make one point – how widespread and deeply rooted is the view that the prefrontal cortex is a composite of functionally distinct or hierarchically arranged areas engaged respectively with the cardinal psychological processes of attention, affect, emotion, memory and motor aspects of behaviour. In this paper I will expand on another view that (1) the dorsolateral prefrontal cortex as a whole has a generic function – 'on-line' processing of information or working memory in the service of a wide range of cognitive functions; (2) that this process is iteratively represented throughout several and possibly many subdivisions of the prefrontal neopallium, and (3) that each autonomous subdivision integrates attentional, memorial, motor and possibly affective dimensions of behaviour by virtue of network connectivity with relevant sensory, motor and limbic areas of brain. This view is compatible with the diversity of behavioural deficits described for frontal lobe patients and animals with experimental lesions, and differs mainly with interpretations of data rather than with the data itself, which, in my view, is remarkably consistent (reviewed in Goldman-Rakic 1987).

3. WORKING MEMORY AND 'ON-LINE' PROCESSING

The tissue surrounding the caudal half of the principal sulcus (Walker's area 46; Brodmann's area 9) including portions of the frontal eye field (area 8) in the rhesus monkey qualifies as a mental sketch pad and central processor of visuo-spatial information. Lesions restricted to this region have been shown repeatedly to impair performance on spatial delayed-response tasks which tax an animal's working memory ability, i.e. to hold an item of information 'in mind' for a short period of time and to update information from moment to moment. The impairments are selective in two critical respects; performance on tasks which engage memory for objects such as visual discrimination object reversal, learning set, match-to-sample is not affected by the same lesions nor do these lesions impair performance which relies on associative memory (e.g. Jacobsen 1936; Goldman *et al.* 1971; Passingham 1975; Mishkin & Manning 1978) or sensory-guided responses (e.g. Funahashi *et al.* 1993*a*; Sawaguchi

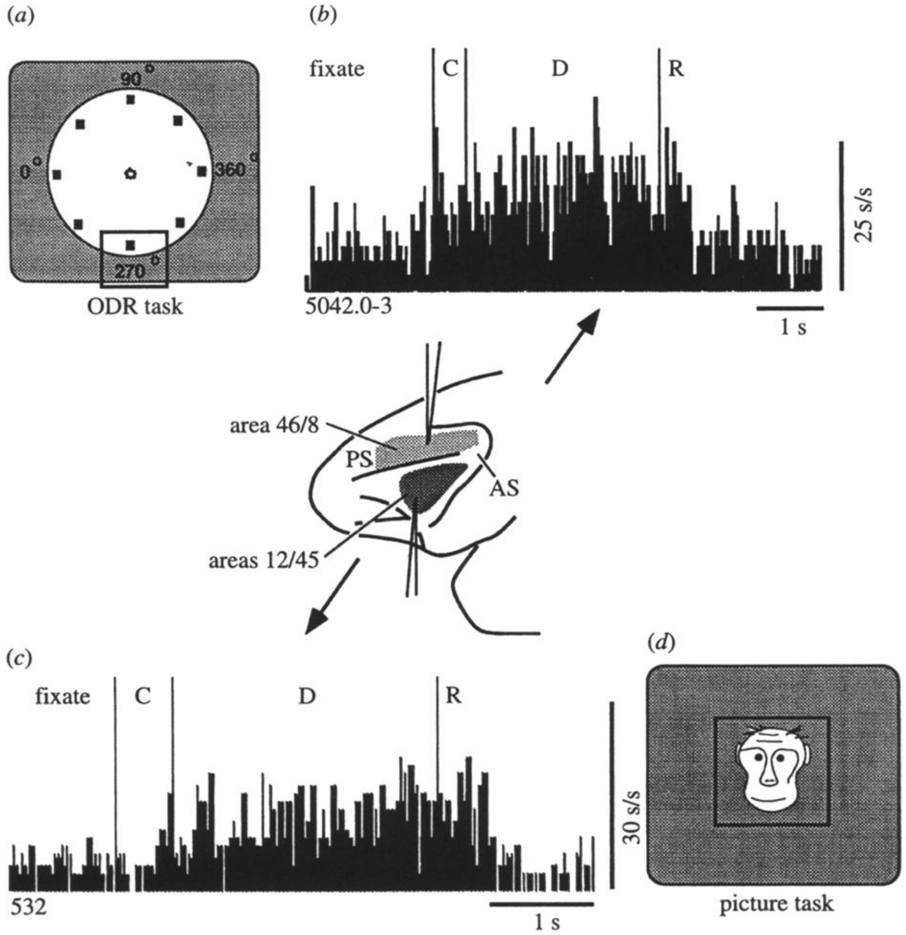

Figure 1. Multiple memory domains are illustrated in this diagram of the monkey prefrontal cortex. The dorsolateral area around the principal sulcus and anterior arcuate is important for spatial working memory; that for features or attributes of objects, in the inferior convexity of the prefrontal cortex. (*a*) Diagram of ODR task; (*b*) activity of a neuron recorded from area 46 during the ODR task. The neuron shown was activated in the delay whenever the monkey had to recall the target presented at the 270° location and at no other location; (*c*) a neuron activated in the delay whenever the stimulus to be recalled was a picture of a particular face during a picture working memory task; the same neuron was unresponsive to other memoranda or in relation to direction of response. (*d*) Diagram of picture working memory task. These results illustrate that prefrontal neurons can code selective aspects of or selected images in working memory. Modified from Funahashi *et al.* 1989 and Wilson *et al.* 1993.

& Goldman-Rakic 1993; Chafee & Goldman-Rakic 1994). In general, neither the consistent rules of a task nor its sensorimotor requirements cause a problem for the prefrontally lesioned animal. The monkey's difficulty lies in recalling information and using it to guide a correct response. Thus, on the basis of neuropsychological evidence, I have suggested that the brain obeys the distinction between working and associative memory, and that prefrontal cortex is pre-eminently involved in the former while other areas of the neopallium and hippocampus are likely the necessary critical substrates of memory consolidation and long-term storage (Goldman-Rakic 1987).

Single neuron recording has been used extensively to dissect the neuronal elements involved in working memory processes. This approach also can provide fresh insights into issues of functional allocation as well as deliver convergent validation of their essential nature. In the oculomotor delayed response paradigm utilized for this purpose, briefly presented visuo-spatial stimuli are remembered in order to provide guidance *from memory* for subsequent saccadic eye movements (figure 1*a*). The essential feature of this task is that the item to be recalled (in this case, the location of an object) has to be updated on every trial as in the moment-to-moment process of human mentation. The prefrontal cortex contains classes of neurons engaged respectively in registering the sensory cue, in holding the cued information 'on line', and in releasing the motor responses in the course of task performance whether the task is conducted in the manual (Fuster & Alexander 1971) or oculomotor (Goldman-Rakic *et al.* 1991) mode. In aggregate, dorsolateral prefrontal cortex contains a local circuit that encompasses the entire range of subfunctions necessary to carry out an integrated response: sensory input, through retention in short-term memory, to motor response. Thus, attentional, memorial and response control mechanisms exist within this one area of prefrontal cortex and need not be allocated to separate architectonic regions. Much remains to be learned about a dedicated area like the principal sulcus, including whether it has further functional subspecializations that have yet to be delineated.

Prefrontal neurons that express 'memory fields are particularly relevant to this discussion (see figure 1*b*). The concept of a 'memory field' is based on the finding that the same neuron appears to always code the same location and different neurons code different locations. Consequently, individual neurons capable of holding specific visuo-spatial coordinates 'on line' appear to be aggregated into a working memory system within an area of the prefrontal cortex. These aggregates likely form modular or columnar units defined by common visual-spatial coordinates but with the specialized subfunctions of cue registration, maintenance of the mnemonic trace and response preparedness allocated to different neurons within a column (Goldman-Rakic 1984). Again, much remains to be learned about these modules but, even at a microarchitectural level of cortical function, sensory, memorial and motor subfunctions are represented in the circuitry of the module. We have demonstrated that temporary inactivation of one or a few modules results in loss of 'on-line' memory for particular target locations (Sawaguchi & Goldman-Rakic 1991). Further, in instances where the memory field of a neuron is not maintained throughout the delay and the activity falters, the animal is highly likely to make an error (Funahashi *et al.* 1989). The finding that neuronal firing is content-specific and directly associated with accurate recall provides a dramatic example of a compartmentalized and constrained architecture for memory processing equivalent to that observed in sensory systems. Additionally, it has been shown that prefrontal neurons can code the direction of an impending response iconically, i.e. without reference to the direction of the response (Funahashi *et al.* 1993*b*). These and other results provide strong evidence at a cellular level for the theorized role of prefrontal neurons in working memory, i.e. maintenance of representational information in the *absence* of the stimulus that was initially present. Knowledge of these neuronal properties helps to provide an explanation for the observation that monkeys and humans with prefrontal lesions have little difficulty in moving their eyes to a visible target or reaching for a desired object; rather their problem is organizing and directing these same motor responses to *remembered* targets and objects. In the same vein, damage to the prefrontal cortex does not impair knowledge about the world or long-term memory; it impairs only the ability to bring this knowledge to mind and utilize it to guide behaviour.

4. WORKING MEMORY, MENTAL PROCESSING AND PERSEVERATION

Two issues have dominated thinking in the area of prefrontal localization. One already mentioned is the degree of dissociation between areas subserving motor control, disinhibition and perseveration on the one hand and memory processes on the other. Another related issue is the separate location of a temporary storage component and a processing component of working memory (Just & Carpenter 1985; Baddeley 1986). Both issues can be addressed in non-human primates to some degree with an anti-saccade task in which monkeys are trained to suppress the automatic or prepotent tendency to respond in the direction of a remembered cue and instead respond in the opposite direction, a transformation that is not particularly easy for human subjects (Guitton *et al.* 1985). The anti-saccade task could be viewed as a member of a class of tasks like the Stroop test, which require prepotent response tendencies to be overridden by opponent or unlike responses. In our experiment with monkeys (Funahasi *et al.* 1993), we implemented a compound delayed-response paradigm, in which, on some trials, the monkey learned to make deferred eye movements to the same direction signalled by a brief visual cue (standard oculomotor delayed-response (ODR) task), and on other trials, cued by a change in the colour of the fixation spot, to suppress that response and direct its gaze to the opposite direction (delayed anti-saccade task, DAS). The monkeys succeeded in learning this difficult task at high (85% and above) levels of accuracy, in itself an indication that monkeys are capable of holding 'in mind' two sequentially presented items of information – the colour of the fixation point and the location of a spatial cue and transforming the direction of response from left to right (or the reverse) based on a mental synthesis of that information. Approximately one-third of the task-related population coded the direction of the impending response, showing a pattern of activation in the delay period that presaged rightward or leftward responses. However, the majority (approximately 60%) of prefrontal neurons were iconic, i.e. their activity in the delay period reflected the location of the cue, whether the intended movement was toward or away from the designated target. These results, together with numerous other single unit studies of prefrontal neurons, establish the following two major points: (1) the same area of cortex harbours sensory, mnemonic and response coding mechanisms, thus supporting an integral localization of the functions of attention, memory and motor response; and (2) the very same neuron involved in commanding an oculomotor response is also engaged when opposing responses are suppressed and/or redirected. Thus prefrontal neurons engaged in directing a response from memory are at the same time part of the mechanism engaged to inhibit the immediate or prepotent tendency to respond. Based on these findings, we would interpret the common association of verbal fluency and Stroop-like deficits discussed in the recent study by Burgess & Shallice (1996) as a failure to suppress a prepotent response (naming the word) due to an inability to use working memory to initiate the correct response (naming the colour of the word based on recent instruction). Perseveration and disinhibition may be the inevitable result of a loss of the neural substrate necessary to generate the correct response.

5. MULTIPLE WORKING MEMORY DOMAINS

According to the working memory analysis of prefrontal function, a working memory function should be demonstrable in more than one area of the prefrontal cortex and in more than one knowledge domain. Thus, different areas within prefrontal cortex will share in a common process – working memory; however, each will process different types of information. Thus, informational domain, not process, will be mapped across prefrontal cortex. Evidence on this point has recently been obtained in our laboratory from studies of non-spatial memory systems in areas on the inferior convexity of the prefrontal cortex (O Scalaidhe *et al.* 1992; Wilson *et al.* 1992; Wilson *et al.* 1993). In particular, we explored the hypothesis that the inferior convexity of the prefrontal cortex comprising Walker's areas 12 and 45 may contain specialized circuits for recalling the attributes of stimuli and holding them in short-term memory – thus processing non-spatial information in a manner analogous to the mechanism by which the principal sulcus mediates memory of visuo-spatial information. The inferior convexity cortex lying below and adjacent to the principal sulcus is a likely candidate for processing non-spatial – colour and form – information, in that lesions of this area produce deficits on tasks requiring memory for the colour or patterns of stimuli (e.g. Passingham 1975; Mishkin & Manning 1978) and the receptive fields of the neurons in this area, unlike those in area 46 on the dorsolateral cortex above, represent the fovea (Mikami *et al.* 1982; Suzuki & Azuma 1983), the region of the retina specialized for the analysis of fine detail and colour – stimulus attributes important for the recognition of objects.

We recorded from the inferior convexity region in monkeys trained to perform delayed-response tasks in which spatial or feature *memoranda* had to be recalled on independent, randomly interwoven trials. For the spatial delayed-response trials (SDR), stimuli were presented 13° to the left or right of fixation while the monkeys gazed at a fixation point on a video monitor. After a delay of 2500 ms, the fixation point disappeared, instructing the animal to direct its gaze to the location where the stimulus appeared before the delay. For the picture delayed-response (PDR) trials, various patterns were presented in the centre of the screen (figure 1*d*); one stimulus indicated that a left-directed and the other a right-directed response would be rewarded at the end of the delay. Thus, both spatial and feature trials required exactly the same eye movements at the end of the delay; but differed in the nature of the mnemonic representation that guided those responses.

We found that neurons were responsive to events in both delayed response tasks. However, a given neuron was generally responsive to the spatial aspects or the feature aspects and not both (Wilson *et al.* 1993). Thus, the majority of the neurons examined in both tasks were active in the delay period when the monkey was recalling a stimulus pattern which required a 13° response to the right *or* left. The same neurons did not respond above baseline during the delay preceding an identical rightward or leftward response on the PDR trials. Neurons exhibiting selective neuronal activity for patterned memoranda were almost exclusively found in or around area 12 on the inferior convexity of the prefrontal cortex, beneath the principal sulcus, while neurons that responded selectively in the SDR were rarely observed in this region, appearing instead in the dorsolateral cortical regions where spatial processing has been localized in our previous studies. In addition, we discovered that the neurons in the inferior convexity were highly responsive to complex stimuli, such as pictures of faces or specific objects. We subsequently used pictures of monkey or human faces as memoranda in a working memory task and demonstrated that such stimuli could indeed serve as memoranda in memory tasks (figure 1*a*, *c*). The same cells are unresponsive on trials when the monkey has to remember a different face or pattern nor do they code the direction of an impending response (Wilson *et al.* 1993). Finally, we have shown that the areas from which face or object selective neurons are recorded are connected directly with area TE in the inferiotemporal cortex which is a major relay of the ventral pathway for object vision (Mishkin *et al.* 1982) and an area rich in cells that respond to the features of visual stimuli, including faces (e.g. Rolls & Baylis 1986; Tanaka *et al.* 1991). Together with the evidence for dissociation of inferior prefrontal and dorsolateral prefrontal lesions *vis-à-vis* object processing (reviewed in Goldman-Rakic 1987), these several results establish that non-spatial attributes of an object or stimulus may be processed separately from those dedicated to the analysis of spatial location and vice versa. Furthermore, within inferior prefrontal cortex, different features appear to be encoded by different neurons (Wilson *et al.* 1993; and in preparation). Thus, feature and spatial memory – what and where an object is – are dissociable not only at the areal level but at the cellular level as well. Altogether these findings support the prediction that different prefrontal subdivisions represent different informational domains rather than different processes and thus, more than one working memory domain exists in the prefrontal cortex – one in and around the caudal principal sulcus concerned with spatial information and another on the caudal inferior convexity concerned with object information. If the inferior prefrontal cortex carries out temporal integration of information analogous to the spatial processing of the dorsolateral region, as we have proposed, then it will surely be engaged in 'comparison between stimuli in short-term memory as well as the active organization of sequences of responses based on conscious explicit retrieval of information from posterior cortical association systems' as formulated by Petrides an colleagues (Owen *et al.* 1996). The question to be decided in future research is whether this function is at a lower level of a hierarchical processing than the 'monitoring' function proposed by the same authors for superior prefrontal cortical areas. To decide this, the performance of monkeys with cortical lesions in superior areas will have to be directly compared to that of monkeys with inferior convexity lesions on the same set of tasks.

The functional architecture suggested by physiological and lesion studies in monkeys appear to be supported by findings from positron emission tomography and magnetic resonance imaging in humans. Thus, the middle frontal gyrus where area 46 is located

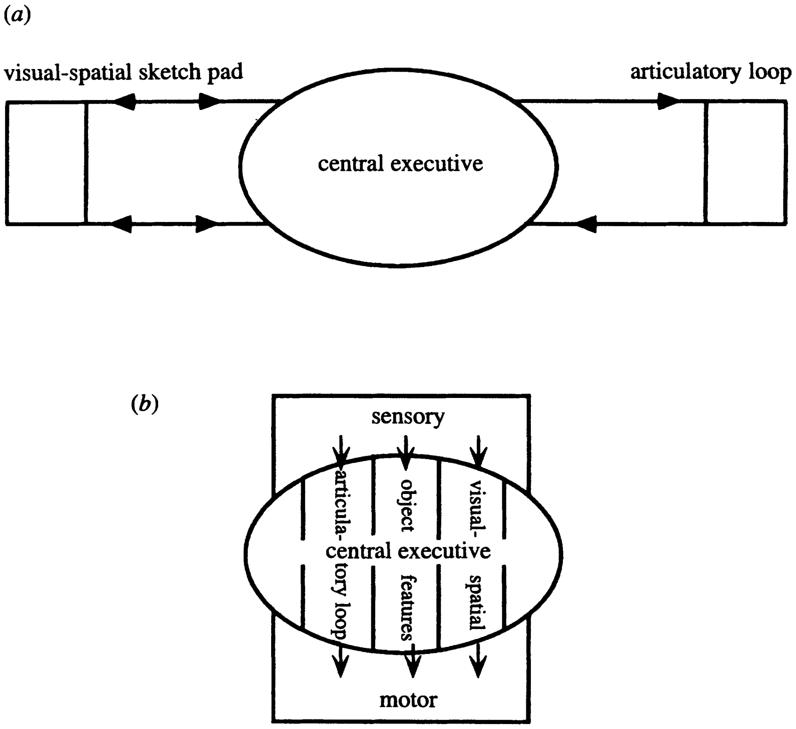

Figure 2. (*a*) Diagram of the central executive (psychologically based; Baddeley 1989). The model consists of a central executive and two slave systems – the phonological loop and the visuo-spatial sketchpad. The slave systems and central processor are presumed to be localized in separated regions of the cortex. (*b*) Model of the 'central executive' based on functional architecture elucidated in studies of non-human primates (Goldman-Rakic 1996). According to this neurologically based model, the central executive may be considered an emergent property of coactivated multiple domain-specific processors located in prefrontal cortex but interconnected both with the domain-relevant long-term storage sites in posterior regions of the cortex (sensory) and with appropriate motor pathways.

is consistently activated as human subjects access visuo-spatial information from long-term storage and/or immediate experience through representation-based action (e.g. McCarthy *et al.* 1994; Nichelli *et al.* 1994; Baker *et al.* 1996; Gold *et al.* 1996; Goldberg *et al.* 1996; Owen *et al.* 1996; Smith *et al.* 1996; Sweeney *et al.* 1996). In contrast, working memory for the features of objects or faces engages anatomically more lateral and inferior prefrontal regions (Adcock *et al.* 1996; Cohen *et al.* 1994; Courtney *et al.* 1996; McCarthy *et al.* 1996) and semantic encoding and retrieval as well as other verbal processes engages still more inferior, insular and/or anterior prefrontal regions (Paulesu *et al.* 1993; Raichle *et al.* 1994; Demb *et al.* 1995; Fiez *et al.* 1996; Price *et al.* 1996). The superior to inferior localization of spatial, object and linguistic processing in imaging studies of human cognition support a multiple domain hypothesis of prefrontal functional architecture and indicate that there may be a common bauplan for their network organization.

As to the remaining expanse of prefrontal areas, less is known. The evidence from recent studies of the orbital surface indicate that this general region of the frontal lobe may be similarly compartmentalized as to informational domain, though it is not yet clear that these regions have domain-specific 'on-line' memory functions. However, Rolls in this meeting has mapped a taste area in the caudolateral orbitofrontal cortex near an area concerned with olfaction (Tanabe *et al.* 1974), together providing sensory definition to the mesopallial map. Certainly, the studies of Rolls and others (Tanabe *et al.* 1974; Baylis *et al.* 1995; Carmichael & Price 1995) clearly define gustatory and olfactory regions in the mesopallial areas. What lies in between these and the dorsolateral regions – in the ventromedial and ventrolateral expanse of the orbital cortex – remains to be explored as do the dorsomedial and medial areas of the prefrontal cortex. Studies of orbital lesions in humans have revealed an autonomic pattern of deficits (Damasio *et al.* 1991) as well as subtle executive deficits in real world social contexts (Grattan *et al.* 1994; Eslinger *et al.* 1995).

6. LEVELS OF PROCESSING: DISTRIBUTED NETWORKS SUBSERVE SENSORY, MOTOR, LIMBIC AND MNEMONIC COMPONENTS CONSTRAINED BY INFORMATIONAL DOMAIN

Although the prefrontal cortex has a pre-eminent role in working memory functions, it does so as part of an integrated network of areas, each dedicated to carrying out specialized functions. Each working memory domain is embedded in and supported by a distinct and essentially independent network of cortical areas; thus networks are functionally integrated by domain. For example, the prefrontal areas engaged in spatial working memory are interconnected with portions of posterior parietal cortex (Cavada & Goldman-Rakic 1989), while the feature working memory areas of the inferior prefrontal cortex are interconnected with area TE in the temporal lobe

(Barbas 1988, 1993; Bates *et al.* 1994; Rodman 1994; Webster *et al.* 1994; Carmichael & Price 1995). A network is comprised of sensory association (temporal and parietal), premotor (cingulate motor areas, pre-SMA) and limbic (retrosplenial cingulate, parahippocampal or perirhinal) areas at a minimum and virtually all of the connections within a network are reciprocal (Selemon & Goldman-Rakic 1985). Thus, this model of prefrontal network organization contrasts with other theories of prefrontal organization which distribute attention, affect, memory and motor action among the different cytoarchitectonic regions of the prefrontal cortex. The multiple domain model distributes these functions among the cortical areas within networks defined by informational domain.

Allocation of function within a widespread cortical network is a subject currently under examination by a number of laboratories. Here I give two examples from our own work with respect to the spatial cognition network (Selemon & Goldman-Rakic 1988). Posterior parietal regions carry directionally specific information in all phases of the delayed response task (cue, delay and response) and thus, neurons in posterior parietal cortex mirror those in prefrontal cortex (Chafee *et al.* 1989; Chafee & Goldman-Rakic 1994). In contrast to the parietal cortex, neuronal activity in posterior cingulate cortex is, in general, not directionally tuned but rather posterior cingulate neurons appear to be engaged in a non-specific form of activation related to response anticipation (figure 2; Carlson *et al.* 1993). Both the single unit studies described here and a series of 2-deoxyglucose metabolic imaging studies in the literature (e.g. Friedman & Goldman-Rakic 1994) indicate that when spatial memories are activated, parietal, cingulate and prefrontal components of the spatial cognition network are coactivated, though each area may be essential for different aspects of the task in question.

7. THE SUPERVISORY ATTENTIONAL SYSTEM, THE CENTRAL EXECUTIVE AND THE DOMAIN-SPECIFIC SLAVE SYSTEMS

One of the most powerful and influential ideas in cognitive psychology is Baddeley's working memory model (Baddeley 1986). This tripartite model of cognitive architecture invokes a supervisory controlling system called the 'central executive' and two slave systems, the 'articulatory loop' and the 'visuo-spatial scratch pad' or 'sketch pad', specialized for language and spatial material, respectively (figure 2). The model recognizes the separation of informational domains for lower level tasks handled by the 'slave' systems but retains the traditional notion of a general purpose, panmodal processor in the central executive that manages control and selection processes, similar to the supervisory attentional system of Shallice (1982). The findings reviewed above provide an alternative model in which the expression of central executive processing is a result of the interaction of multiple independent information processing modules each with its own sensory, mnemonic and motor control features. This multiple domain model reduces but does not necessarily eliminate 'the residual area of ignorance' called the central executive but it does open the question of how these independent systems cooperate to result in an integrated behavioural script.

Our view is that the central executive may be composed of multiple segregated special purpose processing domains rather than one central processor served by slave systems converging to a central processor; and that each specialized domain consists of local and extrinsic networks with sensory, mnemonic, motor and motivational control elements (figure 2; Goldman-Rakic 1987). This process-oriented view explains the dysexecutive syndrome – disorganization, perseveration and distractibility – as a default in one or more independent working memory domains. The working memory specialization of the prefrontal cortex is especially suited to retrieve information from long-term memory and process it 'on line'. It is possible to view the coactivation of multiple working memory domains and their associated cortical networks as a well designed parallel processing architecture for the brain's highest level cognition.

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Discussion

A. R. Cools (*Department of Psychoneuropharmacology, University of Nijmegen, P.O. 9101, 6500 HB Nijmegen, The Netherlands*). Your elegant studies on the prefrontal cortex have led you to make a discrimination between two systems, namely a system encompassing areas 49 and 9 and a system encompassing areas 45, 12 and 8. The first system is suggested to deal with spatial features, whereas the second one is suggested to deal with features of objects. Taking into account your observations that cells of the first system fire when the monkey orientates itself towards a particular spot in space in contrast to cells of the second system, which start to fire when the monkey 'spontaneously' moves its head, the question arises whether we may consider the possibility that one is actually dealing with an 'allocentric-egocentric' rather than a 'spatial-object' dichotomy. In other words I would like to suggest that the first system becomes active as soon as the 'movement to be made' has to be coded in allocentric coordinates in contrast to the second system that becomes active as soon as the 'movement to be made' has to be coded in egocentric coordinates. Would you like to comment on this possibility?

P. S. Goldman-Rakic. I appreciate the opportunity to clarify the task conditions, as apparently there is some confusion. In both the spatial and object working memory paradigms that we have employed, neurons are activated in the delay period. In both conditions, the head is fixed in position and fixation on a central spot is required throughout all phases of the task, that is, during cue presentation and during the delay period when the neurons show the tonic activity that we associate with recall of the relevant memorandum. It is therefore not the case that, in one circumstance the neurons fire when the monkey physically orientates towards a particular spot in space, and in the other, when the monkey spontaneously moves its head. In our experiments, therefore, neuronal activation is not triggered by what the animal is doing, as your question implies, since in both spatial and nonspatial paradigms the monkey is doing the same thing (fixating a central spot on the video monitor). The response requirements in the two tasks are also identical, both involving directional eye (but not) head or arm movements. Studies of how prefrontal neurons code direction of eye movements indicate that they are coded in retinotopic co-ordinates, which are considered egocentric.

K. Srivastava. How do primacy and recency relate to the working memory domain in experimental animals as well as humans?

P. S. Goldman-Rakic. That is an interesting question and one that we have not studied sufficiently, though we are currently examining this question with human subjects. Kesner has studied this issue in rodents and Petrides examined the effect of prefrontal lesions on order memory in monkeys. Generally, it is believed that all items in a list of reasonable length (7 digits according to George Miller's classical study) as well as their order can be held in a working memory buffer and arguably that middle items are more vulnerable because only they are subject to both proactive or retroactive interference. Baddeley has argued that the recency effect reflects the operation of passive storage processes which I assume are similar to those in delayed-response tasks.