A. Document Overview

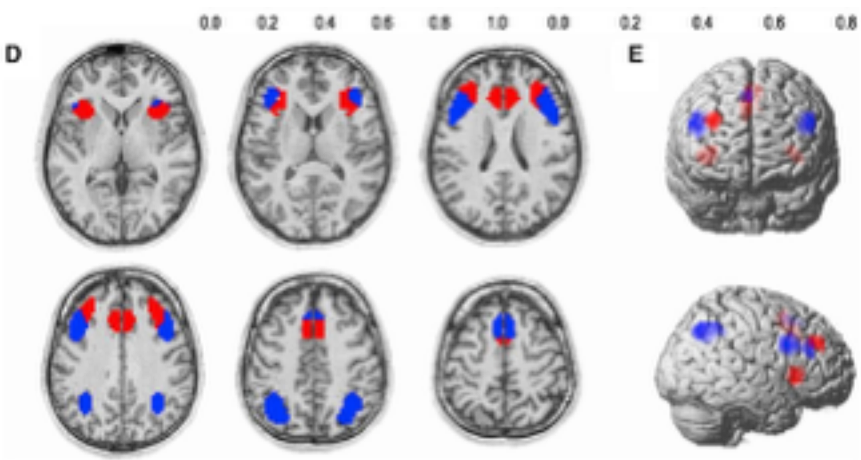
This document identifies the brain regions that have been linked with performance on each Cambridge Brain Sciences task. The information comes from studying how performance on the tasks is affected by factors such as injuries or disease, as well as studying healthy brains using functional brain imaging technologies like functional magnetic resonance imaging (fMRI) and positron emission tomography (PET).

When evaluating the core cognitive abilities measured by the Cambridge Brain Sciences tasks, brain regions are recruited to perform a specific task (e.g. manipulate items in memory), rather than deal with a specific type of information (e.g. words vs. numbers), ensuring that our abstract computerized tasks are suited to target particular cognitive abilities that apply across a wide range of contexts. Furthermore, all tasks (and indeed, most behaviors) require more than one function, such that performance requires a network of brain regions rather than a single region. "It is simply very hard to be precise about the function of a region when that region is important in such a diversity of behavior" (Duncan & Owen, 2000). Nonetheless, research has revealed brain regions that are associated with the cognitive abilities targeted by each task.

B. Brain Networks Behind the Cambridge Brain Sciences Tasks

In a landmark study published in *Neuron* (see Hampshire et al., 2012), we found that not only did performance tend to cluster into three cognitive domains—reasoning, short-term memory, and verbal ability—but each domain recruited distinct brain networks.

These networks within the frontal, parietal, and temporal cortices contribute to multiple tasks. That is, any given task can recruit from multiple networks to varying degrees—it is not the case that any task or real-world activity activates one specific brain region, but rather, mixes and matches from brain regions suited to the various requirements and stages of a complex task.



The short-term memory (STM) network (red) and reasoning network (blue).

Table 2. Task-Component Loadings from the PCA of Internet Data with Orthogonal Rotation

	1 (STM)	2 (Reasoning)	3 (Verbal)
Spatial span	0.69	0.22	
Visuospatial working memory	0.69	0.21	
Self-ordered search	0.62	0.16	0.16
Paired associates	0.58		0.25
Spatial planning	0.41	0.45	
Spatial rotation	0.14	0.66	
Feature match	0.15	0.57	0.22
Interlocking polygons		0.54	0.3
Deductive reasoning	0.19	0.52	−0.14
Digit span	0.26	−0.2	0.71
Verbal reasoning		0.33	0.66
Color-word remapping	0.22	0.35	0.51

The mapping of each task to each network, based on performance data. The numbers are called factor loadings, and indicate the correlation between the observed task score and the latent "cognitive domain" score associated with a specific brain network.

C. Summary Table of the Brain Regions Specific to Each Task

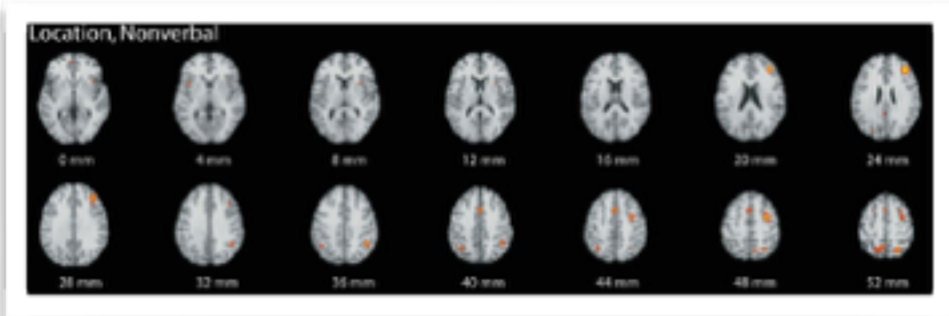
A table summarizing brain regions that correspond with each task are provided below. Detailed explanations are available in section D.

Task	Outcome Measure	Related Brain Regions
Monkey Ladder	**Visuospatial Working Memory**—the ability to temporarily hold information in memory, and manipulate or update it based on changing circumstances or demands..	• Prefrontal cortex / mid-dorsolateral prefrontal cortex • Premotor cortex • Posterior parietal cortex
Spatial Span	**Spatial Short-Term Memory**—the ability to temporarily store spatial information in memory.	• Right mid-ventrolateral area • Parieto-occipital regions
Token Search	**Working Memory**—The ability to temporarily hold information in memory, and manipulate or update it based on changing circumstances or demands.	• Frontal lobe • Temporal lobe • Amygdalo-hippocampal region • Mid-ventrolateral frontal cortex • Mid-dorsolateral cortex • Premotor cortex
Paired Associates	**Episodic Memory**—The ability to remember and recall specific events, paired with the context in which they occurred, such as identifying when and where an object was encountered.	• Left dorsolateral prefrontal cortex • Ventral and anterior left prefrontal cortex regions • Ventral prefrontal cortex • Ventral region of the parietal cortex
Rotations	**Mental Rotation**—The ability to efficiently manipulate mental representations of objects in order to make valid conclusions about what objects are and where they belong, which is a function of visual representation in the brain.	• Intraparietal sulcus • Medial superior precentral cortex
Polygons	**Visuospatial Processing**—The ability to effectively process and interpret visual information, such as complex visual stimuli and relationships between objects.	• Right dorsolateral prefrontal cortex • Right hemisphere

Task	Outcome Measure	Related Brain Regions
Odd One Out	**Deductive Reasoning**—The ability to apply rules to information in order to arrive at a logical conclusion.	• Anterior frontal cortex • Anterior insula / frontal operculum • Inferior frontal sulcus • Anterior cingulate • Presupplementary motor area • Intraparietal sulcus
Spatial Planning	**Planning**—The ability to act with forethought and sequence behaviour in an orderly fashion to reach specific goals, which is a fundamental property of intelligent behavior.	• Frontal lobe • Mid-dorsolateral frontal cortex • Caudate nucleus • Thalamus • Lateral premotor • Anterior cingulate
Grammatical Reasoning	**Verbal Reasoning**—The ability to quickly understand and make valid conclusions about concepts expressed in words.	• Frontal operculum • Posterior temporal lobe • Superior parietal lobe • Dorsal prefrontal cortex • Ventral prefrontal cortex
Digit Span	**Verbal Short-Term Memory**—The ability to temporarily store information in memory.	• Mid-ventrolateral prefrontal cortex
Feature Match	**Attention**—The ability to draw upon mental concentration and focus in order to monitor for a specific stimulus or difference.	• Mid-ventrolateral frontal cortex • Right inferior frontal gyrus
Double Trouble	**Response Inhibition**—The ability to concentrate on relevant information in order to make a correct response despite interference or distracting information.	• Right prefrontal cortex • Dorsolateral region

D. Detailed Supporting Data

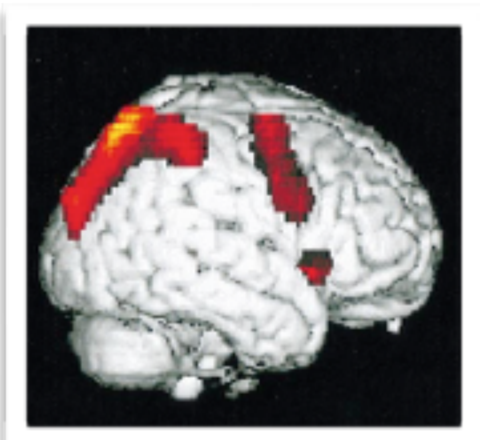
Monkey Ladder



Brain regions activated by nonverbal, location-based working memory tasks. (Owen et al., 2005)

Monkey Ladder involves the cognitive function of working memory, but also requires visuospatial functions. Imaging data has revealed the brain regions involved in working memory using nonverbal stimuli with a spatial component. Across studies using tasks of this type, the **prefrontal, premotor, and posterior parietal cortex** are found to be involved (see Owen et al., 2005, for further details). The **mid-dorsolateral prefrontal cortex**, in particular, plays a role in working memory regardless of whether or not there is a spatial component (Owen et al., 1998).

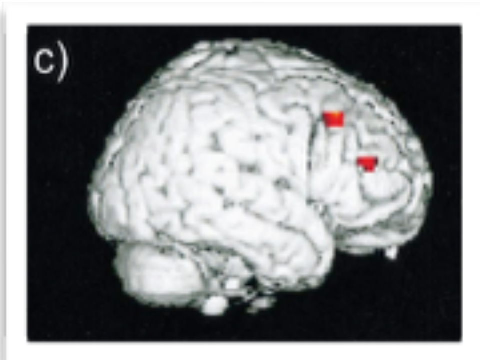
Spatial Span



Areas of the brain activated by spatial span, compared to simple visuomotor control. (Owen et al., 1999)

Spatial Span is a spatial short-term memory task that requires holding a spatial sequence in memory for a short time. An early imaging study (Owen et al., 1999) using Spatial Span found increased blood flow in the **right mid-ventrolateral** area during the task. In Spatial Span, information does not need to be manipulated in memory, so additional brain regions involved in similar working memory tasks (e.g., Token Search) are not involved in this simpler task. Damage to the **parieto-occipital regions** of the brain causes impairment in visuospatial tasks like Spatial Span, but those with frontal lobe damage tend to be more impaired if there is a planning component, rather than pure memorization.

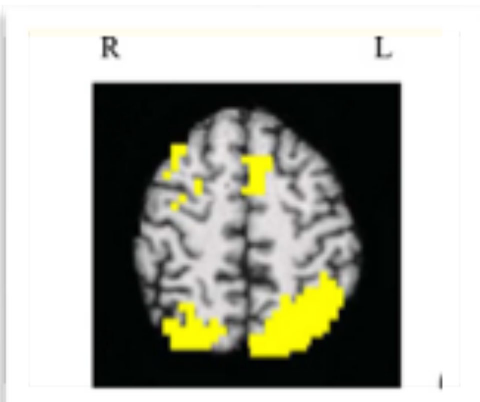
Token Search



Unique areas of the brain activated by a complex spatial working memory task, in comparison with a simpler Spatial Span task. (Owen et al., 1999)

Token Search combines several cognitive abilities: short-term memory, working memory, and a strategy / planning component. Patients with damage to the **frontal lobe** are impaired even on easy puzzles, despite performing well on simpler short-term memory tasks. This implies that the frontal lobe is particularly important for the strategy component of Token Search. Patients with lesions in the **temporal lobe** or **amygdalo-hippocampal region**, on the other hand, are impaired only on more difficult puzzles, implying that these regions are more responsible for the memory component of the task. Imaging studies confirm that the **mid-ventrolateral frontal cortex**, **mid-dorsolateral cortex**, and **premotor cortex** are all activated during this complex task (Owen et al., 1996).

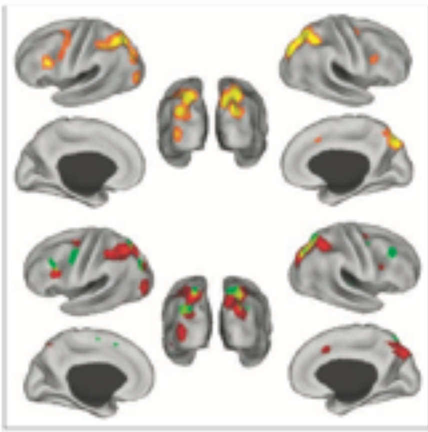
Paired Associates



Areas in the parietal cortex activated by an episodic memory task. (Hayes et al., 2004)

Paired Associates is an episodic memory task in which two items—such as object identity and location—must be paired in memory, then later recalled. The **left dorsolateral prefrontal cortex** is related specifically to encoding memories and using executive processes to create an organizational structure, which is required for performance in Paired Associates, and has also been observed in realistic recall of object locations (Hayes et al., 2004). More **ventral and anterior left prefrontal cortex regions** appear to be recruited for general episodic memory encoding (Fletcher, Shallice, & Dolan, 1998a). During retrieval of the encoded memories, the **ventral prefrontal cortex** and the **ventral region of the parietal cortex** are activated specifically during tasks with cued recall (as in Paired Associates; Fletcher et al., 1998b).

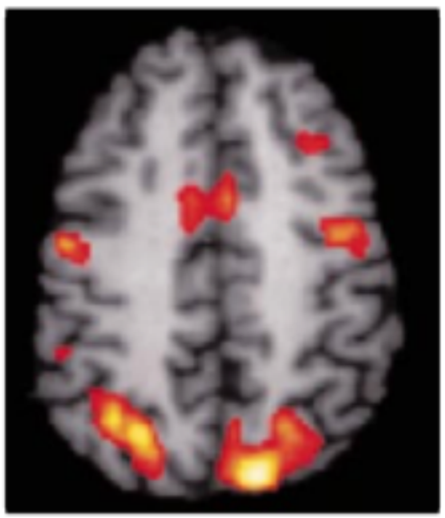
Rotations



Areas of the brain activated during mental rotation. (Zacks, 2008)

The Rotations task requires visuospatial processing, and specifically the ability to mentally rotate objects. A review of the literature (Zacks, 2008) found that mental rotation activates the **intraparietal sulcus** and adjacent regions—areas that contain spatially mapped representations, implying that a representation of objects is simulated and rotated in the brain in an analog manner. However, the **medial superior precentral cortex** is also activated—this is a motor area, implying that at least in some cases, a simulation of moving the object occurs in the brain. Damage to the brain can impair mental rotation; for example, patients with Parkinson's disease perform poorly, which extends to real-world difficulty with tasks such as learning and navigating routes (Uc et al., 2007).

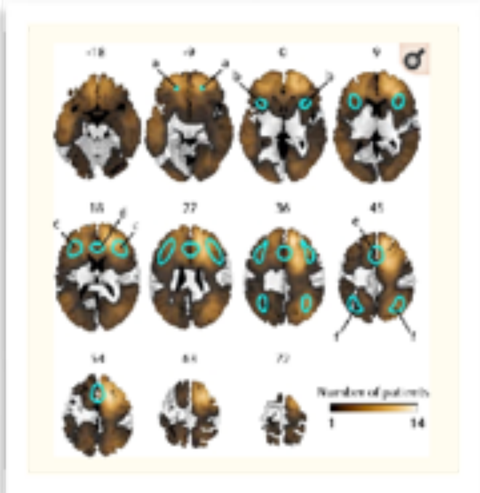
Polygons



Areas of the dorsolateral prefrontal cortex activated by visuospatial orienting. (Pollman & von Cramon, 2000)

Polygons requires quick visuospatial processing, object recognition, and reasoning in order to determine if the shapes are the same or different. Unlike some similar tasks, memory is not applicable to Polygons, as there is no delay between presentation of the shape and matching it to the other shape. One study (Pollman & von Cramon, 2000) found that the **right dorsolateral prefrontal cortex** activated when performing goal-directed visual search, but was not related to memory, suggesting this area is important for visuospatial processing. Damage to the brain can impair visuospatial function and attention, leading to poor performance on Polygons. In one study (Lee et al., 2008), nearly half of a sample of patients with acute **right hemisphere** strokes were impaired in an interlocking polygons task. Not only is visuospatial analysis generally impaired, but neglect of one side of the visual field can lead to failure to attend to one side of the polygon.

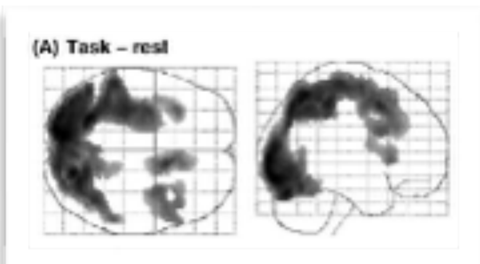
Odd One Out



Brain regions involved in deductive reasoning. (Woolgar et al., 2010)

Odd One Out is a task of deductive reasoning—a core cognitive ability often included in tasks of fluid intelligence. Engaging in difficult deductive reasoning results in a characteristic pattern of activity in several regions of the brain, including the **anterior frontal cortex, anterior insula / frontal operculum, inferior frontal sulcus, anterior cingulate, presupplementary motor area**, and **intraparietal sulcus**. One study (Woolgar et al., 2010) verified that these specific areas play a role in fluid intelligence by confirming that damage to these regions—but not outside of them—predicts poor performance in reasoning tasks, including items similar to Odd One Out.

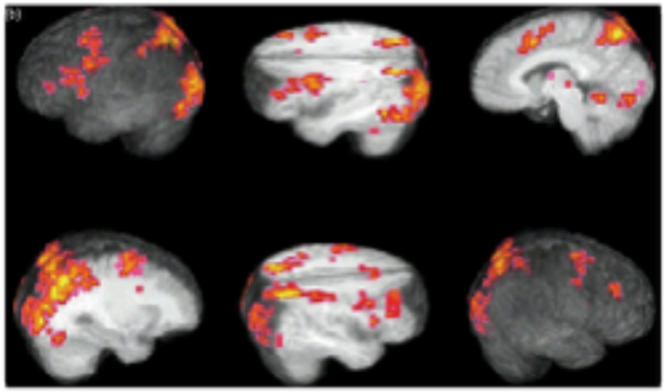
Spatial Planning



Areas of the brain activated by spatial planning, compared to a brain at rest.

Spatial Planning requires the brain's reasoning and forward-thinking abilities. Spatial working memory is also required in order to hold plans in memory long enough to execute. The **frontal lobe** is known for its involvement in these higher executive functions. Early imaging studies (e.g. Owen et al., 1996) found that the **mid-dorsolateral frontal cortex** was activated in various versions of Spatial Planning. The **caudate nucleus** and the **thalamus** were involved only in more difficult puzzles. A subsequent study (Dagher et al., 1999) added the **lateral premotor** and **anterior cingulate** areas to the network responsible for the visual processing and anticipation of movement required for spatial planning.

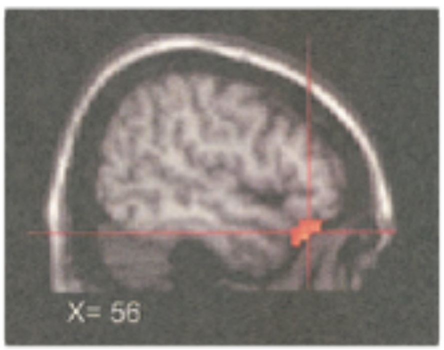
Grammatical Reasoning



Regions activated by difficult problems in a grammatical reasoning task. (Drummond et al., 2003)

Grammatical Reasoning primarily involves two cognitive processes: verbal-based reasoning to determine what the sentence should be describing, and comparison of this internally-generated answer with the image on the screen. One study (Drummond et al., 2003) found that engaging in these tasks recruited brain regions associated with rehearsal and language processing within the **frontal operculum and posterior temporal lobe** language areas, and the **superior parietal lobe** visuospatial processing region was also active. In more difficult problems, additional brain regions in the **dorsal and ventral prefrontal cortex** are recruited. Interestingly, regions associated with working memory do not seem to be involved, as previously thought. This reliance on verbal and reasoning abilities over working memory is confirmed by imaging and behavioral data in the context of the other eleven tasks (Hampshire et al., 2012).

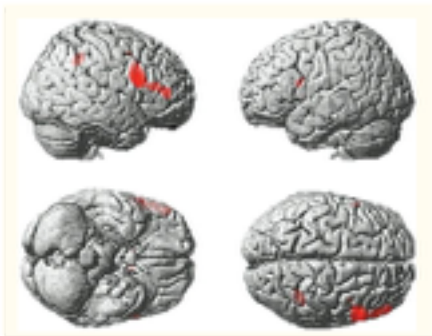
Digit Span



Averaged PET subtraction image of activation in the right hemisphere during forward digit span performance vs. control. (Owen et al., 2000)

Digit Span requires verbal (versus spatial) short-term memory. The frontal cortex is involved in tasks that require memorizing and recalling verbal information. More specifically, the **mid-ventrolateral prefrontal cortex**, primarily in the right hemisphere, is activated during verbal short-term memory tasks (Owen et al., 2000). This area of the brain is involved in tasks that require active, conscious retrieval and reproduction of stored information. Because Digit Span is a straightforward memorization task that does not require manipulation of items in memory (as in backwards digit span tasks and CBS working memory tasks, such as Token Search), it does not recruit additional brain regions involved in more complex tasks, such as the dorsolateral prefrontal cortex. Rather, the ventrolateral frontal cortex's general role is to enable the low-level encoding strategies required in Digit Span, such as rehearsal and initiation of intentional retrieval of information from memory.

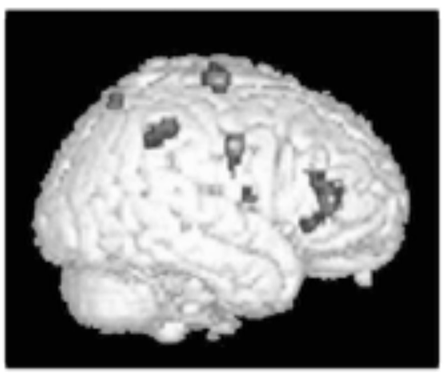
Feature Match



Activation in the inferior frontal gyrus and right inferior parietal cortex when a target (among distractors) is found. (Hampshire et al., 2010)

Feature Match is a perceptual task that requires the cognitive ability of tuning attention and monitoring for differences. The **mid-ventrolateral frontal cortex** is involved in functions targeted by Feature Match, such as deliberate, focused control of thought and action (Owen & Hampshire, 2009). Within this network, the **right inferior frontal gyrus (IFG)** in particular responds when a desired feature that is being monitored for (such as a difference) is found (Hampshire et al., 2009). This region adapts to activate in response to currently-relevant information— that is, it responds selectively to items that are most relevant to the task at hand, rather than any specific stimulus.

Double Trouble



Regions of the brain involved in attention, particularly in an unchallenging sustained attention task. (Manly et al., 2003)

Double Trouble is a task of sustained focused attention and response inhibition. The **right prefrontal cortex**, and in particular the **dorsolateral region**, is involved in tasks that require sustained focused attention, such as Double Trouble. Damage to these regions, common in cases of traumatic brain injury, may be responsible for the problems with attention that often follow injury, and impair performance on tasks like Double Trouble (Manly et al., 2003; Dimoska-Di Marco, 2011). Double Trouble is a task of sustained focused attention and response inhibition In addition to sustained attention, Double Trouble involves the cognitive ability of response inhibition—the ability to suppress making responses to task-irrelevant information (e.g., the meaning of a word, rather than its colour). This can be differentiated from simple attention or effort. Brain regions involved in this function, which is particularly prominent in Double Trouble's double-Stroop design, include the left inferior frontal gyrus (Taylor et al., 1997). The dorsal striatum has also recently been implicated as important for cognitive control, but not cognitive effort (Robertson et al., 2015).

E. References

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