

cognition?” Gilles Rode, Sophie Jacquin-Courtois, Patrice Revol, Laure Pisella, Anne Sylvie Sacri, Dominique Boisson and Yves Rossetti review the current status on neglect research. They emphasize new findings suggesting an important influence low-level sensorimotor transformations can have on higher cognitive levels of space representation. Thus, they explain why cognitive deficits like neglect may be positively modulated by passive physiological stimulation such as caloric vestibular stimulation or via a prism adaptation procedure.

John Rauschecker has written a chapter (20) entitled “*Cortical processing of auditory space: pathways and plasticity*” in which he describes current knowledge on anatomical and functional auditory spatial processing. He presents the concept of a “where”- and “what”- stream in the auditory systems.

George Mangun and Sean Fannon highlight in their chapter (21) entitled “*Networks for attentional control and selection in spatial vision*” the special role attentional processes play in spatial vision. In particular, they focus on the neural mechanisms underlying voluntary visual spatial attention. They propose specialized neural mechanisms for voluntary spatial attention.

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Chapter 1

SPATIAL PROCESSING DURING MENTAL IMAGERY: A NEUROFUNCTIONAL THEORY

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Abstract:

Diverse methodologies, from animal research to neuroimaging, have begun to paint a coherent picture of the neural underpinnings of the human visual system. We outline a model that consists of seven coarsely defined processing subsystems. We begin with a discussion of the gating function of attention within a set of retinotopically mapped areas, which we call the visual buffer. This subsystem is implemented in the occipital lobe. Two major pathways lead forward, one going down to the inferior temporal lobe and the other up to the posterior parietal lobe. The functions of these systems are discussed, as are the roles of structures that integrate the two types of information and processes that use information to guide visual search. These same processes are used to generate visual mental images on the basis of stored information and to interpret patterns in images. We summarize a variety of types of evidence that support the putative role of each subsystem, as well as research investigating the anatomical localization of each subsystem.

Key words: vision; mental imagery; top-down processing; spatial processing.

SPATIAL PROCESSING DURING MENTAL IMAGERY: A NEUROFUNCTIONAL THEORY

Visual perception may be the best understood type of information processing in the brain, and thus it is fortunate that perception and mental imagery share many of the same neural systems. In this chapter we argue that visual mental imagery will become one of the best understood cognitive functions, in large part because it draws on mechanisms used in perception. Indeed, Ganis et al. (2004) estimated that the two functions rely on over 90% of the same brain areas.

Why is the study of perception such a "success story"? Consider five reasons. First, perception involves an easily observable stimulus-response relationship (even if the response is simply a report of the qualities of the observed stimulus). Because properties of the stimulus are easily controlled, it is relatively simple to measure and describe the stimulus-response relationship. Second, because several nonhuman species have visual systems similar to our own, the study of animal brains has greatly illuminated the neural mechanisms of perception. Third, the attempt to develop artificial visual systems has led to useful insights into the nature of vision per se (e.g., Marr, 1982). Fourth, methods from cognitive psychology have been used to study patients who have suffered focal brain lesions (e.g., see Farah, 1984). Finally, the advent of neuroimaging methodologies has allowed researchers to study the human brain in action. In the case of visual mental imagery, the confluence of these methods has underscored the parallels between visual imagery and visual perception, while at the same time highlighting the ways in which the two functions differ (Kosslyn et al., 2001a, 2006; Ganis et al., 2004).

The convergence of these methodologies has led to an emerging picture of many of the features of the visual system. We want to build on that understanding here, extending it to visual mental imagery processing. Not all aspects of perceptual processing are used in imagery. Rather, we can conceive of visual perception in terms of two phases. "Early" visual processing relies solely on signals from the eyes; "late" visual processing relies in part on information stored in memory. The fundamental idea underlying our theory is that visual mental imagery, which arises from stored knowledge, relies on many of the same mechanisms as late visual perception (Ganis et al., 2004; Kosslyn et al., 1997, 2001a, 2006). This chapter will provide an overview of the processing mechanisms that implement late visual perception and visual mental imagery.

SUBSYSTEMS OF LATE VISUAL PERCEPTION AND VISUAL MENTAL IMAGERY

The brain relies heavily on parallel processing to function effectively. Different areas of the brain have different processing functions, and various regions work together as systems to accomplish tasks. Studies of monkey neuroanatomy and neurophysiology have revealed at least 32 distinct visual areas in the monkey cortex, and there are probably still more to be discovered. Later visual processing and visual mental imagery can be divided into seven major components, as illustrated in Figure 1-1.

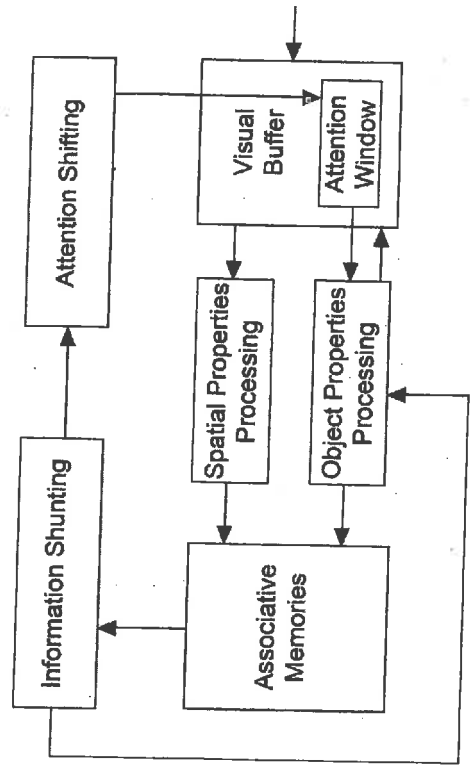


Figure 1-1. Subsystems of late visual processing.

THE VISUAL BUFFER

The neurons in the first visual area (known as V1, primary visual cortex, striate cortex, Area 17, and Area OC) are organized in a way that (roughly) preserves the spatial organization of the cells in the retina. This organizational structure is referred to as retinotopic mapping – the geometric layout of space in the real world is preserved in these first visual regions as it is on the retina. About half of the visual areas in the monkey brain have this organization. These areas may be grouped together as a single functional structure, called the *visual buffer*. In perception, such spatially organized cells detect edges and regions with like qualities (similar colors, textures, patterns, and so on; e.g., see Marr, 1982).

Perhaps the most dramatic evidence of the retinotopic structure of visual cortical regions was provided by Tootell et al. (1982). They trained a monkey to stare at the center of a bullseye-like pattern with spokes radiating from the center, consisting of staggered flashing lights. While the monkey looked at the stimulus, the investigators injected a radioactively tagged sugar (2-deoxyglucose) into its bloodstream. Tootell et al. sacrificed the animal to observe this marker of activity in the animal's brain while it looked at the pattern. The marker showed an image of the pattern essentially projected onto Area V1, the first cortical area to receive signals from the eyes. However, the image was a distortion of the original pattern, with greater cortical area devoted to the high-resolution foveal portion of the visual field.

Particularly strong evidence of retinotopic mapping in humans was initially provided by Fox et al. (1986), who used positron emission tomography (PET) to measure blood flow to Area V1 while participants looked at different types of visual patterns. Neuroimaging studies of visual imagery often document that retinotopically mapped areas are activated when one visualizes (Kosslyn and Thompson, 2003). Indeed, several studies have shown that the focus of activation in human V1 shifts when participants visualize patterns at larger sizes. In one study, for example, Klein et al. (2004) used event-related functional magnetic resonance imaging (ER-fMRI) to show that the pattern of activation in V1 mirrored the orientation of a shape. In this study, the vertical meridian of V1 was activated when participants visualized a flickering "bow-tie" pattern vertically, whereas the horizontal meridian was activated when they visualized the pattern horizontally. Moreover, when transcranial magnetic stimulation (TMS) is used to impair V1 temporarily, imagery for patterns is also impaired (Kosslyn et al., 1999).

However, not all studies have reported such effects during visual imagery. Meta-analyses indicate that activation arises in areas that implement the visual buffer when participants need to see "details" of shapes with high resolution, but not when images of spatial relations are processed (e.g., see Thompson and Kosslyn, 2000; Kosslyn and Thompson, 2003).

THE ATTENTION WINDOW

In perception, the visual buffer receives far more information than can be passed downstream for further processing. Therefore, there must be a mechanism for selecting certain information for further processing while (temporarily at least) ignoring other information. This selective aspect of processing is known as *attention*. The attention window functions the same way in both perception and imagery by selecting a pattern within the visual buffer to be processed in detail. The visual buffer's spatial organization allows the attention window to select information from contiguous locations for more detailed processing. Thus, properties of the attention window constrain the input received by each subsequent processing subsystem.

Sperling (1960) and many other researchers have reported evidence supporting our inference of an adjustable attention window. Much of this research focuses on the covert shifting of attention. For example, participants can detect a target more quickly when its location is cued just before its presentation than when there is no cue (Posner et al., 1980), presumably moving the attention window to the cued location even before they can move

their eyes. Only about 30-50 milliseconds are required to shift attention covertly (without moving one's eyes).

Because the attention window functions within the visual buffer, it should be localized with the areas that implement the visual buffer. However, the size and location of the attention window may be dictated by structures elsewhere in the brain, such as the pulvinar nucleus of the thalamus. The pulvinar may gate outputs from the low-level visual areas to higher ones through its reciprocal connections to V4, the inferior temporal lobe (IT), and the posterior parietal lobe. Single cell recordings in rhesus monkeys have provided evidence for the pulvinar's role in delineating the attention window. Pulvinar neurons projecting to cortex "within the attention beam" show increased activity whereas pulvinar neurons projecting to other cortical areas show little or no response. However, the effect was found only in neurons in the dorsomedial pulvinar (projecting to dorsal areas in the posterior parietal cortex), but not in the inferior or lateral pulvinar (projecting to V1 and ventral areas) (Petersen et al., 1985).

During imagery, the attention window may underlie some types of image scanning. That is, numerous studies have shown that participants require more time to scan greater distances across an imaged object. However, the rate of scanning is the same when people scan between two locations that are "visible" initially as when they scan between a "visible" location to one that was "off screen" initially (Kosslyn, 1980). The attention window is confined to the visual buffer, and thus it cannot be shifted "off screen." Rather, the image may be shifted across the visual buffer, much as a picture is shifted across a TV screen when the camera pans across a scene. Nevertheless, the attention window may underlie scanning over images when only short distances must be traversed (Pinker, 1980).

THE VENTRAL AND DORSAL SYSTEMS

Patterns of activity in the visual buffer provide input to two major systems. The ventral system is a set of brain regions running from the occipital lobe through the inferior temporal lobe. The ventral system encodes object properties, such as shape, color, and texture. Some cells in these areas are so highly tuned that they respond to very specific stimuli, such as faces seen in profile. "Higher" cells in the system (i.e., those further down the processing pathway) have very large receptive fields and respond similarly to objects across a wide variety of locations and positions. Critically, the ventral system stores visual memories of shape and color. Some evidence suggests that such details are stored preferentially in the left cerebral hemisphere (Marsolek et al., 2002).

However, by processing information from various locations equivalently, the ventral system sacrifices information necessary for navigation and reaching. A second network of brain areas preserves this information. The dorsal system is a set of brain regions running from the occipital lobe through the parietal lobes. The dorsal system registers spatial properties of objects, such as location and size. The dorsal system also plays a key role in storing spatial information, not simply encoding it. Information is processed in the ventral and dorsal systems concurrently. These systems have sometimes been referred to, respectively, as the *what* and *where* systems (Levine, 1982; Ungerleider and Mishkin, 1982).

Levine (1982) reviews results from studies of brain-damaged patients. Damage to the occipital-temporal region leads patients to have difficulty recognizing and identifying objects, whereas damage to the occipital-parietal region results in difficulty in processing spatial information. PET and fMRI studies provide further support for the distinction between the two visual cortical pathways in humans. PET studies have shown occipital-temporal activation in recognition tasks, and occipital-parietal activation during spatial tasks (see Kosslyn et al., 2004).

Because one of the primary purposes of spatial information is to guide movements, it is not surprising that most neurons in the posterior parietal lobe are active either as a result of making a movement or in anticipation of moving. There is evidence that motor processes are also engaged during imagery, particularly during specific types of mental rotation. For instance, Kosslyn et al. (2001b) showed that motor cortex was activated when participants imagined mentally rotating figures manually but not when they imagined the figures being rotated by an external force. In addition, Wraga et al. (2003) asked one group of participants to mentally rotate Shepard and Metzler (1971) objects in two conditions and another group to mentally rotate pictures of hands in the first condition, and Shepard-Metzler objects in the second condition. When the second (i.e., object) conditions for each group were compared, motor areas were found to be activated only in the group that first imagined hand rotations, suggesting that these participants transferred a motor strategy to a non-motor rotation task. Moreover, Wraga et al. (2005) suggest that different motor areas are activated for imagined self versus object rotations.

In contrast, the ventral system uses object properties, including shape, color, and texture, to match input to information stored in visual memory. Such processing attempts to make the best match between a stored object and current input; if successful, the viewed object is recognized.

At this point, it is important to draw a distinction between *recognition* and *identification*. If visual input matches a representation in visual memory, one will know that the object is familiar, that is, will recognize it. However,

identification occurs only when the input goes on to access multimodal, conceptual information about the object; one identifies an object when one can access a full range of stored explicit information about it, such as its name, its preferred environment, its sounds, smells, and so on. Identification involves knowing more about the object than can be discovered from immediate input from the senses. The ventral system does not contain the structures and mechanisms needed for identification; rather it affords only recognition, by matching input with stored representations.

Turning to imagery, a critical fact is that visual memories are stored in the temporal lobe (in the ventral system) via a population code; they are not stored as topographic images. A second crucial fact is that there are rich connections running backwards from the inferior temporal lobe to the areas that comprise the visual buffer. Thus, according to our theory, when an image is recalled the information stored in the ventral system is—at least in some conditions—“unpacked” and made explicit as a depictive image in early visual cortex (in the visual buffer). This reconstructed pattern can then be reinterpreted, it can be “inspected” much as an actual object can be inspected during perception. In both imagery and perception, input from the attention window is compared to stored visual memories, and spatial properties are registered.

ASSOCIATIVE MEMORIES

Associative memory receives input from all of the modality-specific mechanisms that allow us to recognize objects. For example, we can recognize a dog by seeing it, hearing its bark, or petting its fur; and once we recognize it, using different “what” systems, we can identify it, using *long-term associative memory*. Outputs from the ventral and dorsal pathways converge in long-term associative memory. The mere fact that you can “picture” where certain items are in your kitchen cabinets is evidence that object representations are cross-indexed with spatial representations. Moreover, whenever we use landmarks to navigate, we are associating shape information with location information, and learning the layout of a building or the route to work requires storing such associations.

At the same time, the outputs from the ventral and dorsal systems converge in dorsolateral prefrontal cortex (DLPFC), in an area that appears to serve as a kind of short-term associative memory (e.g., see Wilson et al., 1993; Rao et al., 1997). Approximately half the neurons in this area conjoin shapes with specific locations, and keep this information “on line”. Such representations are important for guiding eye movements.

Long-term associative memory not only cross-indexes information from the different perceptual pathways (and multiple sensory modalities), but also organizes concepts that do not arise directly from the senses (mathematical truths, meanings of abstract nouns such as "love", categorical classifications, etc.). One type of associative memory representation researchers have hypothesized is called a "structural description", which specifies how parts are arranged to form an object. Inputs from both the ventral and dorsal systems are used to build up such representations. Computer vision researchers, especially, have argued that such representations are important for object identification, in large part because such a description will apply equally well to the various configurations of a flexible shape. For example, when one sees a gymnast performing a floor routine, the same structural description of a human form will apply to all her various contortions. In order to identify an object, a structural description is constructed on the basis of information from the dorsal and ventral pathways, and then compared with stored structural descriptions.

To construct a structural description, one must be able not only to recognize all the individual parts of an object, but also be able to compute relatively abstract spatial relations among those parts. The dorsal system can compute two distinct types of spatial relations representations. One *coordinate* type preserves metric information, and is useful for guiding movement; the other type discards metric information, and instead specifies only the broad category of the spatial relation (such as "attached to," "above," "left of"). Structural descriptions apparently rely on this second, *categorical*, type of spatial relation representation. Kosslyn et al. (2005) provide evidence that these two types of processing, categorical and coordinate, may be implemented in different hemispheres. They asked participants to generate mental images of patterns that they had learned in one of two ways. In one (categorical) condition, participants memorized verbal descriptions of how an object's parts were connected; in the other (coordinate) condition, participants viewed the object's parts sequentially, in specific locations, and had to mentally attach the pieces together. Comparison of the two imagery conditions using PET showed relatively more activation in the left hemisphere during the categorical condition and relatively more activation in the right hemisphere during the coordinate condition (although a majority of brain areas were activated in common across conditions, suggesting that both types of imagery also relied on the other subsystems described here).

Long-term associative memory plays two important roles in visual imagery. First, it stores descriptions of how parts are arranged into shapes. Such descriptions are used when one needs to construct a high-resolution image. Second, long-term associative memory stores "visual codes." These

codes are associated with all the other information about an object, and can be used to access specific stored memories in the ventral system. Thus, when given an object's name, the corresponding visual code is activated, which in turn can access the appropriate visual memory.

Parts of the superior, posterior temporal lobes and temporal-parietal-occipital junction area (near the junction of the angular gyrus and Brodmann's Area 19; see Kosslyn et al., 1995) may be the seat of long-term associative memory. The first sources of evidence that these areas are crucial for long-term associative memory are studies of area STP (short for superior temporal polysensory) in the monkey. This area is in the posterior superior temporal lobe of the monkey. Long-term associative memory requires input from visual, auditory, and somesthetic systems, and cells in monkey STP have such connections (from IT, superior temporal auditory cortex, and from posterior parietal cortex). Furthermore, more than half the neurons in STP respond to input from multiple modalities, and studies have shown STP to be implicated in shifting attention. STP's role in associative memory is further supported by its connections from AIT (the anterior part of IT) and Area 7a (in the parietal lobe, via the hippocampus), which may facilitate coordination of activity in the two visual pathways. Finally, STP has connections to the frontal lobes; the importance of connections between associative memory and the frontal lobes will be discussed shortly.

Although STP is a bilateral area of the monkey brain, and is not found in the human brain, it may be related to what has classically been called Wernicke's area (in the left posterior, superior temporal lobe of the human brain); this area implements processes used in language comprehension. In addition, nearby cortex in Area 19 and the angular gyrus may also play a role in implementing long-term associative memory in humans. Research with brain-damaged patients also provides support for the role of the posterior, superior temporal lobe or nearby cortex in implementing human long-term associative memory. For example, Warrington and Taylor (1978) and others have found evidence of long-term associative memory deficits in patients with left posterior lesions. For a more extensive review of the brain lesion literature with respect to visual imagery and perception, see Ganis et al. (2003).

INFORMATION SHUNTING

During perception, activated visual and spatial memories (from the ventral and dorsal systems, respectively) often are sufficient to identify an object. However, this is not always the case. For instance, if one glances briefly at an up-ended card table with folded legs, leaning against a door,

there may not be a good match in visual memory. It is likely that only certain parts or characteristics could be matched. In this case more information is needed.

If the input to long-term associative memory does not result in object identification, one does not randomly look around to acquire more information. Certain properties of the object, in particular motion or intensity changes, can serve to redirect our attention. In addition, one can use the stored information that is partially activated in long-term associative memory to guide a search. We treat the activated information as a hypothesis, and use this hypothesis to guide further processing by seeking information that has direct bearing on the hypothesis. Part of this process involves priming the expected distinctive property or shape in the ventral system. Indeed, there are direct connections between the regions of the frontal lobes that are the likely site of the information shunting system and the inferior temporal lobes, allowing rapid transmission of information from stored memories, as needed (Naya et al., 2001). The use of stored information to direct further encoding is called *top-down processing*.

According to the present theory, visual mental images arise when stored visual memories, in the ventral system, are activated. At least in some cases, these memories are activated so strongly that activation propagates backwards from the temporal lobes and an image representation is formed in the areas that compose the visual buffer. At the same time, an "object map" is constructed in the dorsal system. This object map is a spatial representation that indicates where specific details and parts belong on an object (or objects belong in a scene). At least in some tasks, this spatial representation alone is sufficient and an image of high-resolution details need not be reconstructed in the visual buffer. The representations in the visual buffer are spatially indexed to the object map. Thus, scanning images "off screen" (to parts that were not initially "visible" in the image) is accomplished by activating adjacent parts of the object map, in the dorsal system, which — if the task requires interpreting high-resolution details — in turn modulates activation in the ventral system so that images of different portions of the stimulus are activated in the visual buffer.

The DLPFC plays a crucial role in hypothesis generation and testing. Patients with damage to this area often show "perseveration" — they have difficulty stopping an on-going activity and initiating a new one (which may reveal a problem in accessing stored information, both about when to stop and what to do next). In addition, PET studies have shown activation in the DLPFC when participants are asked to seek specific information in memory (e.g., Petersen et al., 1988). Kosslyn et al. (1993) and Kosslyn et al. (1997) also found left-hemisphere activation of DLPFC in an imagery task where participants were asked to decide whether an "X" mark would or would not

cover a letter in a grid if the letter (which they were cued to visualize) were in fact present. This task is likely to have required categorical spatial relations processing because the participants used the grid as their guide to place the individual segments of the letters. In this context, it makes sense that left-hemisphere DLPFC would be activated (see also Laeng et al., 2003). It is also of interest that some patients with frontal lobe damage do not perform targeted eye movements, which suggests that they have a deficit in directing top-down search. In addition, PET results have provided evidence for the notion that the information shunting system and long-term associative memory work together (for example, see Kosslyn et al., 1995).

ATTENTION SHIFTING

When testing a hypothesis, one must seek additional information. When the visual system uses top-down processing during perception to seek characteristics of a hypothesized object, information about the size and location of the object must be considered. The attention-shifting system is loosely defined as the set of mechanisms responsible for computing the direction and degrees that attention must be shifted, and for actually sending the commands to make the appropriate eye, head, and attention window movements. Posner et al. (1987) decomposed this system into three subsystems; one disengages attention from its current fixation; another shifts attention; and a third engages attention at the new location.

According to our theory, this system operates similarly in perception and imagery, except that during visual mental imagery it is sufficient to move the attention window in order to shift attention (the eyes and head are not required to move). In addition, at the same time that the attention window is shifted to the location of an important part of the imaged object, the "visual code" of the object (stored in long-term associative memory, along with the locations of important parts and characteristics) is activated. This code in turn primes the part or characteristic as seen in perception — and primes it so strongly during imagery that a pattern of activation is induced in the visual buffer.

During imagery the attention shifting subsystem may help to create the object map representation. Outputs from the pulvinar may send signals to the posterior parietal cortex, setting the regions of space to be attended to. This pointing of attention may be thought of as the general layout of the image to which more complete details may later be filled in; thus, attention allocation may be considered a crucial step in the formation of a high-resolution visual image. These pointed-to positions may then be stored within posterior parietal cortex (see Sereno et al., 2001). The object map may permit the real

world to be used as a type of external store (see O'Regan and Nöe, 2001). Knowing where an object is located in world space, we can return for another look. Kosslyn et al. (1993), using PET, showed that the pulvinar is more activated during an imagery task than a corresponding perception task (Experiment 1). This makes sense; attention allocation may play a primary role in the formation of the general layout of a mental image. In perception, with the object's boundaries already defined, there would be no need for the pulvinar to be activated in setting attention to the locations of space delineating the layout of the object in space.

CONCLUSIONS

To summarize: The image-formation process can be used iteratively, to construct very detailed images. To do so, all of the subsystems must work together.

For example, we've several times discussed a methodology in which participants were asked to form images of block letters within an empty grid (a task that features both spatial and depictive components and requires attentional allocation). An X was presented in one cell of the grid, and the participants were asked whether the X would cover part of the letter if the letter were in fact present. No matter where the X was presented, participants required comparable amounts of time to make this decision if they were allowed to form the image fully before the X appeared (Kosslyn et al., 1988). However, if the X was presented at the outset, the participants required different amounts of time to evaluate whether it would have fallen on the letter, depending on the location of the X. In fact, the times were predicted by the order in which the segments of the letter are typically drawn; the more segments that had to be drawn to reach the location of the X, the more time participants required to evaluate it.

This finding is as expected if the letters were visualized a segment at a time, using a description of how they are arranged to direct attention to the location of each successive segment – at which point an image of the segment would be generated. According to our theory, the description is stored in long-term associative memory, and the information shunting system looks up this description. The attention shifting subsystem would then shift attention to each successive location while the information shunting subsystem sends a visual code to the ventral system. The ventral system in turn would create a pattern of activation in the visual buffer to depict each segment. To test this theory, Kosslyn et al. (1997) asked participants to perform this task while their brains were scanned, using PET. They found activation in brain areas corresponding to each of the

subsystems described above, as predicted (see Thompson and Kosslyn, 2000, Kosslyn and Thompson, 2003, for meta-analyses providing further evidence for the general theory).

Late vision and visual mental imagery are complex capabilities, and the brain has adopted a strategy of "divide and conquer" for such functions. Rather than trying to accomplish a complex process in a single step, multiple subsystems each carry out specialized aspects of the processing, and the subsystems work together to accomplish the entire task. Although we do not know the specific workings of each component subsystem, nor have the neural substrates been completely delineated, a varied set of converging evidence suggests that it is useful to organize late level vision into seven distinct subsystems. These subsystems play a role both in visual perception and visual mental imagery. If nothing else, this emerging framework allows us to focus on more precise and detailed questions than was possible previously.

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