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Splitting the Spotlight of Visual Attention

Can the brain attend to more than a single location at one time? In this issue of *Neuron*, McMains and Somers report psychophysical and fMRI evidence showing that subjects can attend to two separate locations concurrently and that divided spatial attention leads to separate zones of attentional enhancement in early visual cortex.

Story has it that Elvis Presley enjoyed watching three TV programs at once. He bought three television sets, lined them up along the wall of the TV room in the Graceland mansion, and tried his best to monitor three different shows simultaneously (Figure 1). However, many scientists would argue that such feats of divided attention are impossible, even for the King of Rock 'n' Roll.

According to the spotlight theory of visual attention, people can attend to only one region of space at a time (Eriksen and St James, 1986; Posner et al., 1980). This metaphor of attention as a spotlight assumes a limited degree of flexibility. People can shift their spotlight of attention from location to location, independent of eye position, and adjust the size of the attended region like a zoom lens. However, the theory assumes that the attentional spotlight cannot be divided across multiple locations. If more than one object must be attended to at a given time—say multiple football opponents coming in for the tackle—then attention must serially shift from one location to another. The longstanding notion that spatial attention cannot be divided stems from the assumptions of early philosophers, such as Descartes, that consciousness itself is unitary and indivisible.

In this issue of *Neuron*, McMains and Somers (2004) challenge this longstanding notion by using fMRI to test whether attending to two separate locations leads to separate regions of neural enhancement in early retinotopic visual areas. The experimental design can be better understood in simplified form by considering Elvis's TV room (Figure 1). If subjects must fixate the middle TV while selectively attending to the TVs to the left and the right, what happens in visual cortex? (In the display from McMains and Somers, the "TVs" consisted of rapid serial sequences of letters and digits presented independently in the left and right locations and a task-irrelevant sequence of digits presented at fixation; the subject's task was to identify matching digits in the left and right locations.) According to the attentional spotlight hypothesis, attention cannot be divided and must spread across the middle region to encompass both the left and right stimuli. Instead, however, McMains and Somers found that attending to the separated left and right stimuli led to greater fMRI activity in corresponding retinotopic regions than when the stimuli were ignored or passively viewed, and critically, no attentional enhancement was found for the central foveal stimulus. These spatially separated attentional effects were pervasive throughout retinotopic visual cortex and were evident as early as primary visual cortex (V1).

The results provide neural evidence that subjects can attend to two separate regions of space and selectively modulate early visual activity in a top-down fashion. Perhaps, however, subjects were achieving this apparent split of attention by rapidly shifting a single spotlight from one location to the other.

To address the issue of attentional shifting, the authors performed a separate psychophysical study in which subjects viewed similar displays of letter/digit
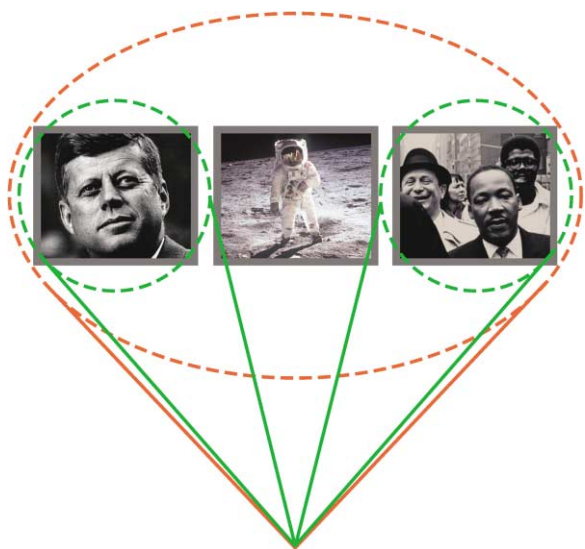

Figure 1. Schematic Diagram of Elvis's TV Room

According to the spotlight theory of attention, when subjects attend to the left- and rightmost items, attention must encompass the intervening region because the spotlight of attention cannot be divided (shown in red). Here, McMains and Somers show that subjects can attend to the left and right items independently (shown in green) while ignoring the intervening item and that this leads to separate regions of attentional enhancement in visual cortex.

sequences and had to identify digits in either a single location or two locations. Items were presented at varying rates (40–250 ms/item) to estimate the amount of time required to achieve a given level of performance for identifying digits. If subjects must shift attention from one location to the other to monitor two sequences of letters, then they should require at least twice the amount of time to identify a pair of letters in two locations than to identify a single letter in a single location. Subjects' performance (d′) on the task increased linearly as a function of presentation duration, indicating that greater processing time led to a steady improvement in performance. Remarkably, however, subjects were almost equally good at monitoring two locations as a single location at all presentation rates, indicating that subjects were able to attend to the two locations simultaneously with minimal cost. The results provided compelling evidence in favor of divided attention and extend the findings of previous psychophysical studies (Kramer and Hahn, 1995).

A remaining question concerned whether divided attention across the two hemifields might be a special case, given that there is some evidence that each half of the brain may have its own attentional spotlight. For example, split-brain patients can search through bilateral displays twice as quickly as unilateral displays, suggesting that each hemisphere has its own attentional resources (Luck et al., 1989). Moreover, recent studies have found that people can attentionally track the movements of up to four dynamic objects in the visual field but can only track up to two objects in each hemifield (A. Alvarez and P. Cavanagh, unpublished data). Therefore, it is possible that divided attention is most effective when the stimuli are presented to separate hemispheres.

McMains and Somers conducted an additional experiment to test if the attentional spotlight can also be divided within a single hemifield. The basic experimental design can be understood as follows. Subjects fixated the rightmost stimulus (see Figure 1) and had to attend to the rightmost and leftmost stimuli while ignoring the intervening stimulus. Thus, all three stimuli were presented within a single hemifield (with the foveal stimulus extending into the other hemifield). The fMRI results again revealed attentional enhancement of early visual areas, including V1 and V2, for the two attended locations and significantly less attentional enhancement in the intervening region. These findings demonstrate that the attentional spotlight can also be divided within a single hemisphere.

Overall, the study provides compelling fMRI and psychophysical evidence demonstrating that the spotlight of visual attention can indeed be divided. Although we cannot know for sure whether Elvis could effectively attend to the left and right TVs while ignoring the middle one, the present findings demonstrate that people are capable of dividing their attention for certain displays and tasks.

However, it remains an open question as to why attention can be divided successfully in some situations but not others. Studies show that people can attentionally track the movements of up to four dynamic targets simultaneously and can efficiently detect changes to the attended targets but not the neighboring distractors

(Sears and Pylyshyn, 2000). However, other studies have found that, for certain demanding discrimination tasks, people can attend to visual information presented in one location or another but cannot simultaneously attend to both locations (Joseph et al., 1997; Reeves and Sperling, 1986). Attentional resources can be divided across separate regions of space, but sometimes this division of resources occurs at great cost and at other times it does not. Future research may reveal what factors determine the divisibility of attentional resources and what neural factors underlie these limits.

In particular, it remains to be discovered whether our capacity to attend to only a few locations or items is due to processing limitations in high-level areas, early visual areas, or as a consequence of the interaction between areas. Areas involved in eye movement planning, such as the frontal eye fields (FEF) and the lateral intraparietal sulcus (LIP), have been strongly implicated in top-down attentional selection. For example, electrical stimulation of FEF can lead to attentional modulations in corresponding regions of visual area V4, consistent with a spotlight enhancement effect (Moore and Armstrong, 2003). However, beyond the present study, it remains unknown as to how many separate spotlights can be sustained in a stable fashion in high-level attentional areas or early visual areas.

Another interesting question concerns why and how attentional selection takes place at the earliest stages of cortical processing, including primary visual cortex (V1). Many recent neurophysiological and neuroimaging studies have found that attentional selection occurs at least as early as V1, and related studies have found that V1 activity can be tightly linked to the conscious perception of a visual stimulus (Tong, 2003). Attentional bias signals in early visual cortex may serve not only to enhance the sensory gain of visual signals but may also contribute to a variety of perceptual processes, including figure-ground segmentation, object-based grouping, and saccadic target selection (Mazer and Gallant, 2003; Roelfsema et al., 1998; Zipser et al., 1996). Challenges for future research include investigating how high-level areas (e.g., FEF, LIP) interact with early visual areas to carry out the processes of visual selection, filtering of neighboring distractors, and the read-out of task-relevant information for the purposes of recognition, action, and awareness.

As a final note, the present study provides a rare example of how neuroimaging data can be gathered to test the predictions of a cognitive theory—an aim that should be more prevalent in cognitive neuroscience research. The results address a longstanding debate in the attention literature and inform our basic notions about the organization of the mind. Contrary to the claims of early philosophers, it seems that the human mind can be divided, at least in part, when selecting information from the external world for further processing.

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The Potion's Magic

During remembering, a perception of the past is constructed that includes sensory details of the original episode. In this issue of *Neuron*, Gottfried and colleagues provide evidence for selective piriform activation during recognition of visual cues previously paired with scents. These data provide evidence of sensory-specific reactivation of olfactory cortex during remembering.

Remembering is often accompanied by vivid perceptions of the past. Mnemonic perceptions can include diverse aspects of sensory experience, such as the sights at a baseball game, the tune of a song, or the fragrance of a recently encountered perfume. Titling their paper with a fitting allusion to Marcel Proust's classic, *Remembrance of Things Past*, Gottfried and colleagues used functional MRI (fMRI) in humans to explore how odors are represented during acts of remembering (Gottfried et al., 2004). Their results suggest that primary olfactory cortex is activated during the successful retrieval of past odors, complementing other findings that have shown visual, auditory, and motor cortex to be active during the retrieval of associated memory content.

Inquiry into how memories are represented during retrieval is quite old. William James (1890), by drawing insights from uncommon patients and his basic knowledge of the brain, suggested "that the cortical processes that underlie imagination and sensation are not quite as discrete as one at first is tempted to suppose." Since this early proposal, general consensus has emerged that brain regions participating in the perception of sensory events are utilized during memory retrieval and imagery (Kosslyn, 1994). Building from this consensus, three new

questions have been the focus of recent research. First, to what degree are different aspects of sensory content represented across different cortical networks? Second, within sensory-processing hierarchies, at what levels are regions recruited during the retrieval process? And finally, how is retrieval controlled such that sensory remnants of a specific episode can be accessed?

Gottfried and colleagues' study provides insights into two of these questions. Their fMRI paradigm consisted of subjects studying numerous pictures paired with one of nine distinct odors. During the scanned test, subjects were presented with the studied pictures intermixed with new pictures and were asked to indicate which were old and which were new. Comparison of recognized old pictures as compared to identified new pictures yielded the main finding of greater activity along posterior piriform cortex. Piriform cortex has been identified as responsive to olfactory stimulation and sniffing (Zatorre et al., 1992; Sobel et al., 1998), and thus, its presence is suggestive of modality-specific activation during retrieval. Gottfried et al. (2004) explored the specificity of piriform activation by contrasting their paired visual-olfactory study to that of a nonolfactory memory task that used similar procedures but did not activate piriform cortex.

Activation of piriform cortex during odor memory provides evidence for another sensory modality that is called upon during memory retrieval. Activation of sensory regions during the retrieval of visual and auditory cortex has been provided previously (e.g., Nyberg et al., 2000; Wheeler et al., 2000). The present study demonstrates, for the first time, selective activation of piriform cortex during retrieval of olfactory content in the absence of actual olfactory stimulation. This finding expands upon earlier demonstrations of the modulation of piriform cortex during the recognition of odors themselves (Dade et al., 2002). One important implication of the procedural differences between the prior work of Dade et al. and the present study is that evidence is provided that piriform cortex can be active in the absence of an olfactory cue and is selective for the retrieval of associated olfactory content. While too little data exist to draw strong conclusions, the present data are most consistent with representation of specific mnemonic content and not a general role in associative memory. One possibility is that piriform cortex may be the target, and not the origin, of associative mechanisms involved with memory.

An open debate about content-specific memory retrieval and mental imagery has centered on whether the earliest cortical sensory areas are active through top-down mechanisms. One possibility is that the primary sensory areas are active during retrieval (Kosslyn, 1994). An alternative possibility is that secondary areas in sensory hierarchies are recruited during retrieval to represent derived, high-level representations (Hebb, 1968; Roland and Gulyás, 1994; Wheeler et al., 2000). Activation of late sensory areas might reflect an efficient retrieval process that depends upon high-level sensory attributes rather than primitive response properties of primary sensory cortex. The present data suggest that, within the olfactory system, early cortical regions are involved.

What is left unspecified by the results of the present