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Visual Working Memory in Human Cortex

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Abstract

Visual working memory (VWM) is the ability to maintain visual information in a readily available and easily updated state. Converging evidence has revealed that VWM capacity is limited by the number of maintained objects, which is about 3 - 4 for the average human. Recent work suggests that VWM capacity is also limited by the resolution required to maintain objects, which is tied to the objects' inherent complexity. Electroencephalogram (EEG) studies using the Contralateral Delay Activity (CDA) paradigm have revealed that cortical representations of VWM are at a minimum loosely organized like the primary visual system, such that the left side of space is represented in the right hemisphere, and vice versa. Recent functional magnetic resonance imaging (fMRI) work shows that the number of objects is maintained by representations in the inferior intraparietal sulcus (IPS) along dorsal parietal cortex, whereas the resolution of these maintained objects is subserved by the superior IPS and the lateral occipital complex (LOC). These areas overlap with recently-discovered, retinotopically-organized visual field maps (VFMs) spanning the IPS (IPS-0/1/2/3/4/5), and potentially maps in lateral occipital cortex, such as LO-1/2, and/or TO-1/2 (hMT+). Other fMRI studies have implicated early VFMs in posterior occipital cortex, suggesting that visual areas V1-hV4 are recruited to represent information in VWM. Insight into whether and how these VFMs subserve VWM may illuminate the nature of VWM. In addition, understanding the nature of these maps may allow a greater investigation into individual differences among subjects and even between hemispheres within subjects.

Keywords

Visual Working Memory; Visual Field Maps; EEG; fMRI

Behavioral Measurements

Visual working memory (VWM) is the ability to maintain visual information in a readily available and easily updated state. Despite our rich visual experience, VWM has a limited capacity and represents only a small fraction of the available visual scene. Under the right conditions, one can miss changes happening across wide swaths of the visual scene (Simons & Ambinder, 2005). Even with a complete sensory trace of visual information, such as iconic memory, only a subset of the information can be accurately reported (Sperling, 1960). Many researchers have found evidence across a variety of tasks that VWM capacity is limited to representations of about 3 - 4 objects (Sperling, 1960; Pashler, 1988; Irwin, 1992; Luck & Vogel, 1997; Cowan, 2001; Vogel, Woodman et al., 2001; Awh, Barton et al., 2007; Scolar, Vogel et al., 2008; Zhang & Luck, 2008; Barton, Ester et al., 2009).

The most robust and now most popular of these tasks is the change detection task, which has three stages. The first is the encoding stage, where an array of objects is briefly presented (usually for a period between 100 and 500 ms), and the subject must encode as many of the objects as they can into VWM. Next, there is a short delay, generally about 1000 ms, when the subject must maintain the objects in VWM. Finally, the test array in which one object may have changed is presented, and the subject must indicate with a button press whether the test array is the same as or different from the sample array. A common variation probes a single object rather than displaying the entire array of objects at test, to reduce the likelihood of counting and grouping strategies (Figure 1).

The change detection task allows for the estimation of the number of objects that can be simultaneously held in VWM, using the k formula developed by Pashler (1988) and refined by Cowan (2001). The formula can be written as:

$$k = (\text{Hit Rate} + \text{Correct Rejection Rate} - 1) * \text{Set Size} \quad (1)$$

The k formula assumes that there are no limitations in the encoding or test portions of the task, such that errors are due only to the lack of objects being maintained in the maintenance stage. It is important to emphasize that there are other factors that could affect performance which would be interpreted as differences in VWM capacity k , but which in fact have nothing to do with VWM maintenance. As a result, one must be careful in interpreting values of k not to draw aberrant conclusions about VWM capacity.

Luck and Vogel (1997) employed the change detection task and k formula to great effect, showing that the number of objects the average human could maintain in VWM was 3 - 4. Furthermore, by presenting a variety of different numbers of features for each object, they also showed that the number of objects represented does not depend on the number of features attributed to each object, but only the number of objects maintained (Luck & Vogel, 1997). Neurological correlates to this number limit of VWM capacity show sustained cortical activity corresponding to the number of objects maintained in VWM and have been demonstrated in EEG (Vogel & Machizawa, 2004; Vogel, McCollough et al., 2005; Drew, McCollough et al., 2006; McCollough, Machizawa et al., 2007) and fMRI (Todd & Marois, 2004; Todd & Marois, 2005; Xu & Chun, 2006). In addition, individual differences in VWM number capacity have been demonstrated behaviorally (Awh, Barton et al., 2007), with EEG (Vogel & Machizawa, 2004; Vogel, McCollough et al., 2005), and with fMRI (Todd & Marois, 2005).

Alvarez and Cavanagh (2004) then showed that the number of objects that can be maintained in VWM also depends on the complexity of the maintained objects. Using the change detection task and k formula with objects of varying levels of complexity, they showed that an independent method of assessing complexity (search rate among similar distracters) is strongly correlated with the estimation of the maximum number of objects of a certain type that could be maintained. Consequently, VWM number capacity was estimated to be lower for complex objects than simple ones. Neurological correlates that show sustained cortical activity corresponding to changes in the complexity of objects maintained

in VWM have similarly been demonstrated in EEG (Gao, Li et al., 2009) and fMRI (Xu & Chun, 2006).

These two disparate findings have been resolved by Awh, Barton, & Vogel (2007), who revealed that performance between simple and complex objects is identical, so long as the level of similarity between the test and sample object is large. Comparisons of simple objects are not limited by resolution because the sample and test are so dissimilar that the limiting factor is only k , the number of objects that can be held simultaneously in VWM. Normally, complex objects are limited by resolution, because they are so similar to one another within each category that the resolution of each object is too low to make accurate comparisons. If one makes the changes large enough such that resolution is no longer a limiting factor by making categorical changes between complex objects, performance is limited by k , as with simple objects (Figure 1). Thus, it appears that there are two limitations of VWM performance: the number of objects simultaneously held and the resolution at which those objects are represented.

Discrete or Flexible Resource Allocation?

The idea that a resolution resource exists for VWM begs the question: how is it allocated across maintained objects? Two scenarios arise as likely possibilities. The first is a flexible resource allocation model. In this model, resolution could be allocated differentially to objects of different complexity, such that a simple object might not be allocated much resolution, but an object of higher complexity, more demanding to represent, might be allocated more resolution. The second model is a rigid resource allocation model, in which objects up to a certain maximum, k , are represented with a certain resolution, regardless of complexity.

Recently, evidence favoring the discrete resource allocation model came when Zhang & Luck (2008) used a procedure that provides independent estimates of the number and resolution of representations in VWM to demonstrate that a subset of available objects are maintained and no information is retained about other objects. Further, they showed that giving a pre-cue to indicate which of the sample objects was most likely to change increased the likelihood that the cued object was encoded, but not the likelihood that it was allocated more resolution. The idea is that if resources could be flexibly allocated, subjects would have a large incentive to allocate more resolution to the pre-cued item. Barton, Ester, & Awh (2009) demonstrated complimentary results that argue in favor of a discrete resource allocation model. They presented arrays of objects to encode in a change detection task that varied in the amount of overall complexity in the display and found that change detection performance with any given object in the display did not depend on the complexity of the other objects in the display. Also in line with the predictions of a rigid resource allocation model, maintained object resolution plateaus after the item limit, k , is reached (Anderson, Vogel et al., 2011).

However, evidence in favor of a flexible resource allocation model came with the demonstration that drawing attention to an object with a flash changes the resolution at which it is encoded into VWM (Bays & Husain, 2008). Not only that, but it was

demonstrated that some of the error in the Zhang & Luck (2008) task was due to a mnemonic mismatch between color and location information, not simply random guessing (Bays, Catalao et al., 2009). Furthermore, other studies have found no evidence for a limit in the number of representations that can be held in VWM in general (Keshvari, van den Berg et al., 2013), or at least for certain conditions (Sligte, Scholte et al., 2008).

When directly compared, it appears that the discrete resource allocation model slightly more accurately fits the data of this study relative to the flexible resource allocation model (Rouder, Morey et al., 2008). Although much is made of the differences between these models, their similarities are often overlooked. It is agreed in general that resolution decreases as the number of objects maintained increases (Zhang & Luck, 2008; Barton, Ester et al., 2009; Bays, Catalao et al., 2009; Bays, Gorgoraptis et al., 2011). Both models propose that resolution decreases as set size increases, because the same amount of resources are split among many objects, but one proposes that those resources are evenly distributed across a limited number of discrete chunks, while the other proposes that the chunks are unlimited and their resolution can vary. Although one can imagine somewhat different predictions for neural implementation made by each model, it may be most useful for current questions of cortical organization to focus on their similarities and how the common features interact with the retinotopic organization of the visual system.

Electroencephalography

Electroencephalography is the measure of the electrical activity originating in the brains of human subjects, recorded at numerous electrode sites placed on their scalps. EEG offers excellent insight into the temporal resolution (on the order of milliseconds) of electrical brain activity. However, many sources contribute to the activity recorded at each electrode, so its spatial resolution is coarse and generally relies on converging evidence (Clark, Fan et al., 1994; Luck, 1999; Luck, Woodman et al., 2000; McCollough, Machizawa et al., 2007).

A technique which has been applied to studies of VWM is a specialized form of the event-related potential (ERP) measurement. ERPs are very small electrical signals generated in cortical regions in response to specific events or stimuli (Blackwood & Muir, 1990; Sur & Sinha, 2009). The ERP related to a particular type of stimulus is measured by having subjects repeatedly respond to the stimulus hundreds or thousands of times, and then averaging the signal across trials and subjects in order to reveal a common waveform associated with the stimulus (Luck, 1999). A specialized ERP component used to study VWM is known as Contralateral Delay Activity (CDA) and measures sustained electrical activity during the delay period of a change detection task. The CDA requires objects to be presented in both hemifields, but held in VWM in one hemifield and not in the other. Then, the ERP waveform recorded from electrode sites in the posterior parietal, occipital, and occipital-temporal regions of the hemisphere ipsilateral to the remembered objects is subtracted from that of the contralateral hemisphere, resulting in a difference waveform, which constitutes the CDA (Vogel & Machizawa, 2004; Vogel, McCollough et al., 2005; Drew, McCollough et al., 2006; McCollough, Machizawa et al., 2007; Gao, Li et al., 2009).

Originally, the CDA revealed sustained activity commensurate to the number of objects represented in VWM. Using simple colored squares in a change detection task, the CDA activity increased as set sizes increased, until the subjects' working memory capacity was exceeded, at which point the CDA reached a plateau (Vogel & Machizawa, 2004; McCollough, Machizawa et al., 2007). More recently, the CDA has been shown to reflect the amount of resolution allocated to objects maintained in VWM. In a study comparing the CDA when simple or complex objects are maintained in a change detection task, electrode sites in posterior parietal, occipital, and occipito-temporal cortex showed greater activity for complex than simple objects (Gao, Li et al., 2009). While activity at the same electrode sites increased as the number of maintained simple objects increased, the activity remained indistinguishable between set sizes for complex objects. It is important to note that the VWM capacity estimate for these complex objects was measured to be two objects, so no difference is expected between set sizes two and four (Alvarez & Cavanagh, 2004). The authors interpreted these data as consistent with a flexible resource allocation model; however, the results can equivalently be explained by a rigid resource allocation model.

Functional Magnetic Resonance Imaging

When neurons are active, the ratio of oxygenated hemoglobin to deoxygenated hemoglobin in nearby blood increases after a few seconds (known as the hemodynamic response). Functional magnetic resonance imaging (fMRI) is a technique that takes advantage of such blood oxygen-level dependent (BOLD) activity in the brain by applying a strong magnetic field and encoding positions in space with slight differences in magnetic field strength and phase (Ogawa, Tank et al., 1992). This allows for a very specific spatial readout of brain activity (on the order of 1 mm³), but the hemodynamic response is on the order of seconds, which limits the ability of fMRI to distinguish fine temporal differences (Logothetis, Pauls et al., 2001; Logothetis & Wandell, 2004; Serences, 2004; Shmuel, Augath et al., 2006; Poldrack, Fletcher et al., 2008; Schridde, Khubchandani et al., 2008; Schummers, Yu et al., 2008; Chen & Parrish, 2009).

Initial fMRI studies of VWM focused on the role of the frontal lobe, in regions such as dorsolateral and ventrolateral prefrontal cortex (PFC). Much of the focus was trying to parcel out “spatial” vs. “non-spatial” VWM storage abilities, which returned mixed results that have since been reevaluated (Jonides, Smith et al., 1993; D'Esposito & Postle, 1999; Postle, Zarahn et al., 2000; Postle, Awh et al., 2004; Roth, Serences et al., 2006). These areas are now largely considered to be involved in the encoding-, manipulation-, and response-related aspects of VWM (Postle, Berger et al., 2000; Rypma, Berger et al., 2002) or attentional feedback control (Curtis & D'Esposito, 2003), operations normally ascribed to the “central executive” (Baddeley & Hitch, 1974; Baddeley, 1996; Baddeley, 2000; Baddeley, 2003). There is little evidence that these frontal areas, though vital to the VWM network, are the regions that give rise to the number and resolution limits on VWM capacity (Postle, 2006).

In the search for regions which subserve VWM capacity limits, researchers have observed three regions of cortex whose activity during a VWM task is commensurate with either the number of or the resolution required to represent objects in VWM. The first region identified

spanned the intraparietal sulcus (IPS) in the dorsal parietal cortex bilaterally and was shown to have BOLD signal modulation positively correlated with the number of objects maintained in VWM during the delay period of a change detection task (Todd & Marois, 2004; Todd & Marois, 2005).

Further research led to the discovery that inferior IPS in both hemispheres showed activity dependent upon the number of maintained objects, but superior IPS and part of the lateral-occipital complex (LOC) in both hemispheres responded instead to the complexity of maintained objects (Xu & Chun, 2006). These regions were identified using either simple or complex objects in a change detection task. Behavioral VWM capacity was estimated for simple and complex objects, and then BOLD modulation was compared to behavioral estimates across LOC, superior and inferior IPS. Superior IPS and LOC were shown to have BOLD signal modulation corresponding to the behavioral measurements of VWM capacity. Inferior IPS showed activity corresponding to the number of objects presented, regardless of complexity.

The authors argue that inferior IPS is an area of object individuation based on location, leading to the VWM number capacity limit found in simple change detection tasks. In contrast, they argue, superior IPS and LOC are areas responsible for object identification and binding, such that a smaller number of complex objects can be represented than simple objects, in favor of a two-stage, flexible resource allocation model (Xu & Chun, 2006; Xu & Chun, 2007; Xu & Chun, 2009). However, it is also possible that the results could be equivalently explained by a slightly altered version of the discrete resource allocation model.

Recent studies have also implicated V1-hV4 in VWM processing, perhaps representing information that is related to the sensory information processed in each map (Harrison & Tong, 2009; Sligte, Scholte et al., 2009; Ester, Anderson et al., 2013). Studies such as these call into question the idea that a particular location of cortex is responsible for VWM, but rather it is likely that VWM is a distributed aspect of the entire visual system. Perhaps, like the visual system, representations of different types of information are represented in different portions of cortex.

Visual Field Maps

Visual information first enters primate cortex in primary visual cortex (area V1), located in the posterior occipital lobe, for low-level processing of visual details (Tootell, Hadjikhani et al. 1998). From there, visual information is sent to other visual areas, which can be differentiated by their unique cytoarchitectonic structures, connectivity, visual field maps (VFMs), and functional processing (e.g., (Van Essen, Newsome et al., 1984; Felleman & Van Essen, 1991; Wandell, Dumoulin et al., 2007; Brewer & Barton, 2012)). Many visual areas were first identified in monkey using primarily single and multiple unit recording techniques, and since, many homologues have been discovered in human (e.g., (Brewer, Press et al., 2002; Sereno & Tootell, 2005; Wandell, Dumoulin et al., 2007; Kolster, Peeters et al., 2010)). The most compelling evidence for visual areas in humans are VFMs, often called retinotopic maps, because they follow the organization of the retina. That is, nearby

neurons within a VFM analyze properties of nearby points of an image on the retina (e.g., (Wandell, 1999; Wandell, Dumoulin et al., 2007; Brewer & Barton, 2012)).

VFM are routinely measured using standard traveling wave methods (Engel, Rumelhart et al., 1994; Sereno, Dale et al., 1995; DeYoe, Carman et al., 1996; Engel, Glover et al., 1997; Wandell, 1999; Wandell, Dumoulin et al., 2007; Brewer & Barton, 2012). In this method, subjects view a periodic stimulus that moves smoothly through the visual field, which creates a traveling wave of activity within retinotopic VFMs. From the fMRI response time series, the position of the stimulus within the visual field that is optimal for evoking a response from each cortical location can be identified. Retinotopic VFMs are measured with respect to two visual field dimensions: eccentricity and polar angle. Rotating wedge and expanding ring stimuli consisting of high contrast, flickering checkerboard patterns are typically used to measure gradients of visual field polar angle and eccentricity, respectively.

Each of the first few VFMs (V1, V2, and V3) can be identified as containing a representation of a full hemifield of visual space, with each hemisphere representing the contralateral hemifield (Wandell, 1999; Dougherty, Koch et al., 2003; Wandell, Dumoulin et al., 2007; Brewer & Barton, 2012). VFM V1 and the adjacent VFMs V2 and V3 contribute to a confluent foveal representation at the occipital pole (Schira, Tyler et al., 2009). All of these areas have a lower visual field representation located on the dorsal part of the posterior occipital lobe and an upper visual field representation on the ventral surface. Beyond these early VFMs in the posterior occipital lobe, visual cortex is loosely organized into anatomically distinct dorsal and ventral “streams” (Morel & Bullier, 1990; Baizer, Ungerleider et al., 1991). Several dorsal and ventral human VFMs have been mapped using fMRI, and they contain abutting upper and lower visual field representations and distinct foveal representations (Tootell, Mendola et al., 1997; press, Brewer et al., 2001; Wade, Brewer et al., 2002; Brewer, Liu et al., 2005).

Beyond the dorsal lower vertical meridian representation of V3 lies a string of hemifield maps running from the transverse occipital sulcus (TOS) up along the medial wall of the intraparietal sulcus (IPS). The first maps bordering V3d are V3A and V3B, which share a discrete foveal representation within the TOS (Tootell, Mendola et al., 1997; Smith, Greenlee et al., 1998; Press, Brewer et al., 2001). A series of recently described maps extend from IPS-0 (also called V7 (Tootell, Hadjikhani et al., 1998)) along the medial wall of the IPS, reversing smoothly into several hemifields from IPS-1 to IPS-5 (Sereno, Pitzalis et al., 2001; Silver, Ress et al., 2005; Swisher, Halko et al., 2007; Wandell, Dumoulin et al., 2007; Konen & Kastner, 2008). Weak foveal representations for each map fall along the fundus of the IPS.

In addition, two sets of VFMs (LO-1, LO-2, TO-1, and TO-2) positioned on the dorsal part of lateral occipital cortex anterior to V3d were recently described (Larsson & Heeger, 2006; Amano, Wandell et al., 2009). LO-1 and 2 share the confluent foveal representation with V1, 2 and 3, while TO-1 and 2 share a distinct foveal representation. LO-1 and 2 overlap with part of object-selective LOC, while TO-1 and 2 overlap with motion-selective areas MT and MST, respectively. Additional VFMs TO-3 and TO-4 have recently been described just inferior to TO-1 and TO-2 (Kolster, Peeters et al., 2010). Several recent studies and

reviews can provide more extensive details on the current state of visual field mapping (Brewer & Barton, 2012), the travelling wave methodology (Engel, 2012), population receptive field modeling for VFM measurements (Dumoulin & Wandell, 2008), and the history of VFM measurements (Wandell & Winawer, 2011).

The recently discovered IPS VFMs are strongly modulated by attention, and they appear to overlap with the superior and inferior IPS regions reported by Xu & Chun (2006) to subserve VWM. Also, it is likely that the region of lateral occipital cortex implicated in VFM falls within one or several of the lateral VFMs (LO-1/2, TO-1/2) (Barton & Brewer, 2010). If these regions do overlap, the retinotopic organization of the VFMs has important implications for the functional properties of these VWM areas. Indeed, studies of early VFMs suggest that VWM is represented in a retinotopic fashion in the early visual system, so it is likely that this relationship is maintained throughout the visual hierarchy.

Individual Differences

In the search for behavioral effects, ERP signatures, and brain regions corresponding to VWM capacity limits, individual differences are often overlooked as noise in the data that is muddying an otherwise clean study. If published, reports on individual differences of VWM capacity are usually relegated to less prestigious journals after the primary findings have snagged the lion's share of the attention. However, individual differences in VWM capacity continue to arise and are becoming more and more important in the ongoing debates of VWM capacity limitations (Vogel & Machizawa, 2004; Todd & Marois, 2005; Vogel, McCollough et al., 2005; Awh, Barton et al., 2007).

Much of the debate over VWM capacity limitations ignores the dissociation between the ability to maintain a number of objects in VWM and the ability to allocate resolution to those objects. Awh et al. (2007) revealed that performance across independent number-limited change detection tasks is strongly correlated within subjects. Correspondingly, performance on independent resolution-limited tasks is highly correlated. However, performance on number-limited tasks does not correlate with performance on resolution-limited tasks. Together, these results suggest that there are two independent abilities being tested in these tasks, one for number and one for resolution, which vary within and between subjects.

Todd & Marois reported group data (Todd & Marois, 2004) and individual differences (Todd & Marois, 2005) for their change detection measurements that revealed BOLD modulation in IPS corresponding to the number of objects maintained in VWM. Todd & Marois (2005) reported that the difference in BOLD modulation in relevant regions between the set size at which a subject's VWM number capacity is reached and set size 1 correlates with each subject's VWM capacity estimate. In other words, subjects with a larger VWM capacity as measured behaviorally also show larger BOLD modulations in cortex in response to the VWM task. This finding demonstrated that the BOLD signal can be used as a marker for VWM number capacity in individual subjects.

VWM number capacity limits have further been shown to correlate with limits of the number of objects one can track in a multiple object tracking (MOT) task. Also, it has been

reported that similar regions of cortex respond in a load-based manner during MOT and VWM tasks, and thus MOT may be subject to the same number capacity limit (Culham, Brandt et al., 1998; Culham, Cavanagh et al., 2001; Culham & Kanwisher, 2001; Cavanagh & Alvarez, 2005). The MOT task is similar to a change detection task, except that subjects must actively track objects rather than maintain them between the sample and test (Pylyshyn & Storm, 1988; Drew & Vogel, 2008). Interesting evidence has been presented using MOT tasks that show differences in the number of objects that can be tracked depending on whether the objects span both hemifields or are contained in one hemifield (Cavanagh & Alvarez, 2005). If one takes the assumption of a shared number capacity limit between VWM and MOT tasks, this is strong evidence that the total capacity limit is divided between the two hemispheres. In that case, one would expect that there may be individual differences between hemispheres within a subject.

Finally, what if there were little to no variability in the VWM capacity number limit among individuals or within hemispheres? It is possible that some unaccounted-for effect may underlie what appear to be individual differences in the estimation of VWM capacity number limit. Vogel et al. (Vogel, McCollough et al., 2005) had a very intriguing study using the CDA, where they compared subjects with high and low VWM capacity number limits. Using a change detection task with simple colored squares, they presented two or four target objects to remember, or two target objects and two distracter objects. They found that subjects with high capacity VWM showed equivalent CDA amplitude for two targets and two targets with two distracters, but subjects with low capacity VWM showed equivalent amplitude for four targets and two targets with two distracters. In an even more striking manipulation, they asked subjects to remember two targets for half of the delay period, and then either add two targets (append red) or exclude two distracters (exclude green) that appear during the delay period. High capacity subjects successfully appended targets and excluded distracters, whereas low capacity subjects successfully appended targets, but also appended distracters. Together, these results suggest that perhaps lower estimates of VWM number capacity may actually be due to an inability to deal with irrelevant objects, and not a lower maximum number of maintained objects. Based on this work, it is possible that all subjects have very similar VWM number capacities, but have trouble with other aspects of the task, such as successfully locking onto a manageable number of objects to maintain.

Conclusion and Future Directions

VWM capacity has been defined by two factors: the number of objects maintained and the resolution at which those objects are represented. The number of objects the average human can maintain seems to be about 3 - 4, and the resolution allocated to each of those objects declines as the number of objects maintained increases. Resolution appears to be allocated in a rigid manner, such that resolution is evenly distributed across maintained objects, regardless of those objects' complexity. Although a flexible resource allocation model has also gained traction, we suggest that the two models have more similarities than differences, and it is those similarities which should drive future research into the neural underpinnings of VWM.

These capacity limits have been demonstrated in a variety of behavioral measures, and the CDA reveals patterns of electrical cortical activity that show dissociable indices of number and resolution. Functional MRI results suggest that the number capacity limit arises in inferior IPS, while the resolution capacity limit arises in superior IPS and LOC, though other aspects of these objects (e.g., color) may be represented in other parts of visual cortex. The cortical regions involved with capacity limitation overlap with several recently-discovered VFMs, indicating that they are retinotopically organized. Thus, the limitations measured in VWM tasks may arise from the properties of the underlying organization of these VFMs. This idea also presents intriguing evidence that VWM may recruit the visual system to represent objects.

Future lines of research should address specifically which of the VWM areas fall into which of the retinotopically-organized VFMs. It is possible that some of the VWM areas fall near retinotopic maps and not within them, but it is difficult to tell at this point because these regions have not been compared for overlap within individual subjects across visual cortex. In addition, most of the VWM capacity limitation literature ignores individual differences within and between subjects, and there is a wealth of opportunity to demonstrate just how subjects differ in their capacity limitations.

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B.B. wrote the manuscript, which was then revised by B.B. and A.A.B.

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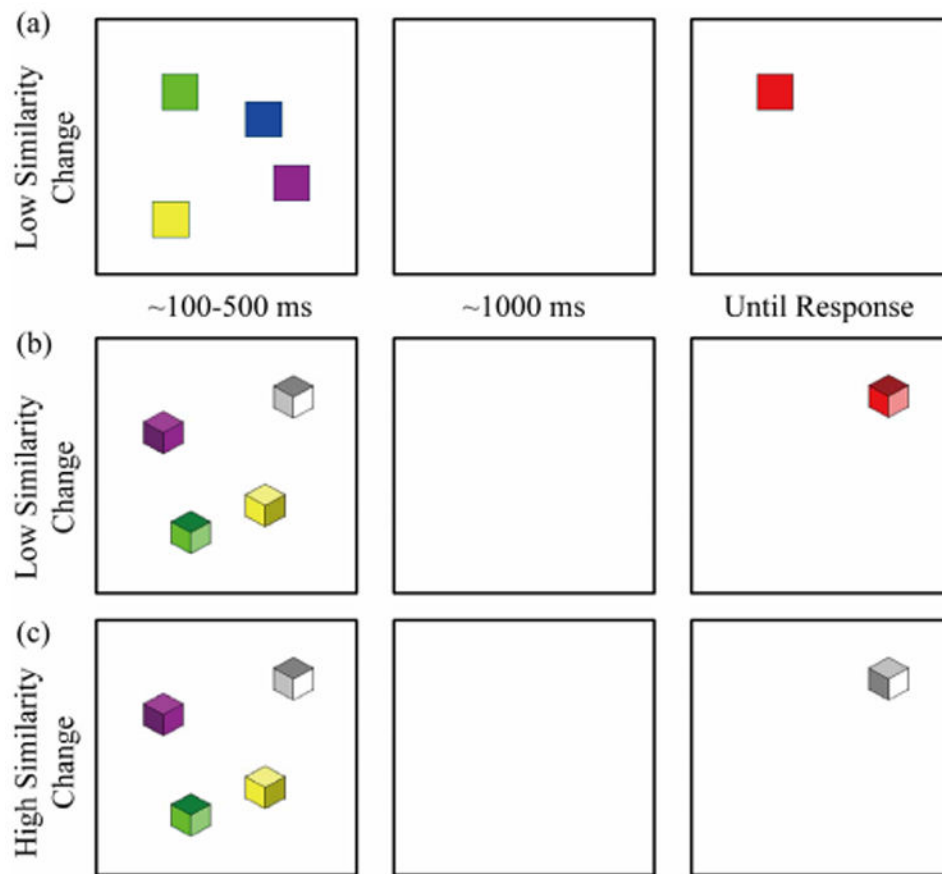


Figure 1.

Change detection with simple and complex objects. Typical change detection tasks are two-alternative forced-choice tasks in which a subject is presented with an array of objects to encode into VWM (usually for $\sim 100 - 500$ ms), maintains those representations once they are no longer visible (usually for ~ 1000 ms), and is then asked whether one probed object is the same or different from the sample object in the same position (usually until the subject responds, or for $\sim 1000 - 2000$ ms). Here, a set size of four and a probe array of one are represented. However, set size is often varied, and entire arrays are often presented at the probe, although still only one test object can change. (a) Simple colored square stimuli, typically drawn from about 6 distinct hues. Changes are always low in similarity (e.g., a green square changes to red), and thus require low resolution to make an accurate comparison. Complex stimuli adapted from Barton & Brewer (2010) are displayed in (b) and (c), which have both one of 6 or so overall hues like the colored squares, but the sides of each cube have three shades, creating 6 possible shading patterns as well. Thus, a change in overall hue (b) results in equivalent performance as with colored squares (a), because both are low similarity changes. In contrast, a change of shading pattern, but not overall hue (c), results in worse performance, because higher resolution is required to make an accurate comparison between the sample object and test probe.