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Individual differences shape the content of visual representations

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ABSTRACT

Visually perceiving a stimulus activates a pictorial representation of that item in the brain, but how pictorial is the representation of a stimulus in the absence of visual stimulation? Here I address this question with a review of the literatures on visual imagery (VI), visual working memory (VWM), and visual preparatory templates, all of which require activating visual information in the absence of sensory stimulation. These processes have historically been studied separately, but I propose that they can provide complimentary evidence for the pictorial nature of their contents. One major challenge in studying the contents of visual representations is the discrepant findings concerning the extent of overlap (both cortical and behavioral) between externally and internally sourced visual representations. I argue that these discrepancies may in large part be due to individual differences in VI vividness and precision, the specific representative abilities required to perform a task, appropriateness of visual preparatory strategies, visual cortex anatomy, and level of expertise with a particular object category. Individual differences in visual representative abilities greatly impact task performance and may influence the likelihood of experiences such as intrusive VI and hallucinations, but research still predominantly focuses on uniformities in visual experience across individuals. In this paper I review the evidence for the pictorial content of visual representations activated for VI, VWM, and preparatory templates, and highlight the importance of accounting for various individual differences in conducting research on this topic.

1. Introduction

Visual imagery (VI; Box 1), visual working memory (VWM; Box 2), and visual preparatory templates (Box 3) all require the representation of visual information in the absence of sensory stimulation. The prevailing stance in this review is that these "int ernally-sourced" (i.e., nonretinal visual) representations have a pictorial component to their contents and may recruit visual sensory regions. There is a debate spanning decades that dichotomizes internally sourced visual representations as either "depictive" (composed of visual information with a specific visuospatial relationship between features) or "descriptive" (composed of verbal or conceptual labels; see Kosslyn, Ganis, & Thompson, 2001 for a longer discussion on this distinction and Pearson, Naselaris, Holmes, & Kosslyn, 2015, for an updated state of affairs). Kosslyn used the term "depictive" to describe VI that has particular visuospatial properties, and suggested depictive VI is represented according to precise X,Y coordinates on an imaginary grid; however, the current review does not make specific claims for depictive representations, since the evidence for this is very limited (see Naselaris, Olman, Stansbury, Ugurbil, & Gallant, 2015; Pearson & Kosslyn, 2015). Rather, the review focuses on (the more generally defined) pictorial representations, which may not follow such rigorous visuospatial rules but are nevertheless visual in their contents. The most common way to infer pictorial content is by comparing the extent of overlap (both behavioral and cortical) between internally and externally sourced (i.e., sensory-driven) visual representations. This has been done across the different literatures on VI, VWM, and preparatory templates.

VI, VWM, and preparatory templates are all highly related; for example, activating a template for a task may require both tapping into long-term memory stores (e.g., during search for familiar objects) and holding in mind recently seen visual information that must be refreshed for each experimental trial (e.g., remembering the identity of a briefly presented cue). Thus, VI and VWM contribute to the contents of templates for such tasks. Recent studies and opinion papers have already encouraged linking VI and VWM in the study of the cognitive and neural mechanisms recruited for representing visual content (Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Borst, Ganis, Thompson, & Kosslyn, 2012; Keogh & Pearson, 2011, 2014; Tong, 2013). Here I add the preparatory template literature to this discussion (also see

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Box 1. Visual imagery. Up until the 20th century, VI has been discussed exclusively in a subjective, philosophical, and introspective sense – a black box that could not be touched by experimental science. But with the boom of psychophysical investigations in cognitive psychology following the long reign of behaviorism in the mid-20th century, VI finally became a serious topic of scientific investigation. From its earliest quantitative investigations, there has been much debate over its function, contents, and impact upon subjective perception. According to Stephen Kosslyn's model of VI (summarized in Kosslyn, Brunn, Cave, & Wallach, 1984), VI is the process by which one can depict in the ''mind's eye'' visual information that is retrieved from memory. VI can be used to simply generate pictorial representations, but it can also be used in a broader ''visual thinking''sense, such as inspecting and manipulating images for problem solving (e.g., mental rotation, following mental maps, mentally rearranging objects in a scene). Visual representations activated both by external (perception) and internal (VI) sources are activated in a ''visual buffer'' that has certain visuospatial restrictions; for example, images can only be contained within one's visual field, and lose resolution if they are represented too small or too far away. Furthermore, the resolution of VI begins to disintegrate immediately after initial activation without effortful retention.

Box 2. Visual working memory. Working memory is a term that was coined in the 1970s (e.g., Baddeley & Hitch, 1974) to delineate a type of short-term memory that is involved in both storing and actively processing information for cognitive tasks. Baddeley and Hitch (1974) wrote of working memory as a system with processing and storage limitations that can pass information into long-term memory stores with active rehearsal. Working memory was first thought to be a dominantly verbal process, but studies of VI in working memory (Paivio, 1969), particularly on the interference of VI with visual perception during working memory tasks (Baddeley & Andrade, 2000; Bruyer & Scailquin, 1998), soon led to the hypothesis that working memory has two component systems: a ''phonological loop'' for verbal information, and a ''visuospatial sketchpad'' for visual information, the latter of which was later simply termed visual working memory (VWM). The language used to describe models of VI and VWM are strikingly similar (e.g., active visual information is held in a ''visual buffer'' that requires rehearsal for successful retention), and indeed the active processing component of VWM is currently proposed to be synonymous with VI (Tong, 2013).

Box 3. Visual preparatory templates. For over 25 years, researchers have described the cognitive process of generating an internal preparatory representation of visual information that is used to bias selective attention toward matching items in the external world (Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Wolfe, Cave, & Franzel, 1989). There is some debate concerning whether such ''preparatory templates'' activated for visual tasks represent pictorial or semantic content (see Lupyan & Spivey, 2010; Moores, Laiti, & Chelazzi, 2003; Reeder, van Zoest, & Peelen, 2015; Vickery, King, & Jiang, 2005). Several studies provide evidence that the contents of preparatory templates are principally pictorial, and may range from precise representations of expected colors, feature locations, and viewpoints (e.g., searching for a familiar illustration in a book; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; van Moorselaar, Theeuwes, & Olivers, 2014), to a collection of target-diagnostic shape features impervious to changes in viewpoint, color, or precise location (e.g., during naturalistic search; Evans & Treisman, 2005; Peelen & Kastner, 2011; Reeder & Peelen, 2013; Reeder, Perini, & Peelen, 2015; Treisman, 2006).

Stokes, 2011) to provide a more comprehensive review of the evidence for internally sourced pictorial content. One major problem across these literatures is that there is conflicting evidence regarding the extent to which internally sourced visual representations are pictorial. I argue that discrepant findings may in large part be due to individual differences in pictorial representative ability.

Behavioral studies have found that individuals may differ in the vividness, precision, abilities, and strategies used to represent internally sourced visual information. Neuroimaging and neurostimulation studies have additionally revealed individual differences in the cortical regions recruited for various internally sourced visual tasks depending on self-reported and quantitatively measured imagery abilities. Individual differences in the surface area of visual cortex may also affect pictorial vividness and precision, and one's level of perceptual expertise for a particular category of objects may alter the pictorial representation of objects belonging to that category. Collectively, these differences may determine whether and to what extent pictorial content is activated in the absence of visual stimulation.

In this review, I will first provide an overview of the evidence for the pictorial content of visual representations activated for VI, VWM, and preparatory templates (section two). I will then report on the discrepancies in the literature concerning the extent to which these processes activate pictorial content (section three). In section four I will provide evidence that many of the discrepancies evident in section three could be explained by accounting for the various individual differences listed above. Finally in section five I will review specialized experiences influenced by pictorial abilities (including intrusive VI and hallucinations), which highlights the clinical significance of this topic for future studies.

2. Evidence for the pictorial representation of nonretinal visual information

2.1. Behavioral evidence

2.1.1. Contingent attention capture

Studies of contingent attention capture provide behavioral evidence for the pictorial nature of nonretinal visual representations. Contingent attention capture is the involuntary orienting toward task-irrelevant stimuli that share features with task-relevant stimuli. For example, when subjects are instructed to detect a particular color in a central display, the appearance of an irrelevant item of the same color in the periphery impairs central target identification, indicative of a capture effect by stimulus content (Folk, Remington, & Johnston, 1992). Contingent attention capture paradigms have recently been used to provide evidence that pictorial representations of target features are activated prior to the onset of visual stimulation. The sudden onset of an image that shares visual features with a search target produces a reliable capture effect; this occurs on trials when the capture stimulus appears in lieu of the expected search display (Reeder & Peelen, 2013). This suggests that visual features of impending targets are activated in preparation for search (also see Reeder, van Zoest, et al., 2015).

2.1.2. Visual search

There is also evidence for the pictorial nature of internally sourced representations in the wider visual search literature, in

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