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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.

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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 “internally-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).

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

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

that target detection incrementally improves with the amount of visual information provided by a cue (Hout & Goldinger, 2015; Vickery et al., 2005). According to the “guided search” model, detecting a predetermined target requires making the best match between stimulus features activated in a preparatory template and stimulus features presented in the environment (Wolfe, 1994, 2007; Wolfe et al., 1989), and the identity of a search cue, shown prior to the onset of a visual search display, may determine the visual contents of the preparatory template. An image cue that matches the target precisely is more effective in guiding search compared to a word cue (Castelhano & Heaven, 2010; Malcolm & Henderson, 2009, 2010; Nako, Smith, & Eimer, 2015; Spotorno, Malcolm, & Tatler, 2014; Wolfe, Horowitz, Kenner, Hyle, & Vasan, 2004), whereas an image representative of a target category (Yang & Zelinsky, 2009), or a word cue with a visually descriptive adjective (e.g., “red purse”), are both less effective than an exact image but more effective than a single word cue (e.g., “purse”; Schmidt & Zelinsky, 2009). This suggests that different cues may affect the ability to activate pictorial information prior to visual search, which contributes to the efficiency of target detection.

2.2. Interference

2.2.1. The Perky effect

One way to infer the pictorial nature of internally sourced visual representations is by the extent of their overlap with perceptual representations. Perceptual representations are undeniably sensory in nature, so an overlap between perceptual and internally sourced visual representations suggests a sensory component to nonretinal vision. Perhaps the best evidence that internally sourced and stimulus driven visual information share cognitive mechanisms comes from behavioral studies on the interference of VI with perception. Historically, the confusion of the two is called the “Perky effect” (coined by Segal & Nathan, 1964), following from results obtained in the first experimental study of VI (Perky, 1910). In this study, subjects were asked to imagine a colored object while staring at a fixation mark on what they thought to be a blank screen. In reality, faint colored shapes were projected onto the screen during VI. Perky found that all 24 subjects in the main experiment reported only imagining various objects, and none suspected that visual stimuli were actually presented to them. Segal and Nathan (1964) followed the basic structure of Perky’s experiment but also manipulated the intensity of the stimuli presented and asked subjects to report whether they perceived a stimulus or simply imagined it. Subjects in this study showed mixed confidence ratings about whether a stimulus was perceived or imagined when presented with low intensity images. Segal and Gordon (1969) suggested that VI introduces a source of internally generated noise to the detection of real visual stimuli (also see Segal & Fusella, 1970), and this noise is particularly due to an overlap in visuospatial representations, as evidenced by greater interference between perceived and imagined stimuli that are spatially overlapping (Craver-Lemley & Reeves, 1992).

2.2.2. Binocular rivalry

More recently, the interference between perceived and imagined stimuli has been studied in tasks of binocular rivalry, the process by which a single stimulus gains access to conscious awareness following the simultaneous presentation of a different stimulus to each eye: which of the two stimuli becomes dominant is a matter of competition for limited processing resources. Pearson, Clifford, and Tong (2008) used a binocular rivalry paradigm to investigate the effects of VI on perceptual stability (i.e., the extent to which one of two oriented gratings that dominated perception on one trial also reliably dominates on a successive trial). When subjects were instructed between trials to activate

VI of a grating that was previously suppressed, the likelihood of perceptual stability between the two trials decreased to chance level. Furthermore, activating VI of the originally suppressed grating disrupted perceptual stability as effectively as viewing a reduced-contrast percept of the suppressed stimulus. Finally, the authors found that both imagining and viewing a specific orientation prior to rivalry produced a similar gradient of ocular dominance depending on how precisely a rivalry stimulus matched the imagined or viewed orientation. A subsequent study found similar effects of imagined and perceived colors on dominance (Chang, Lewis, & Pearson, 2013), indicating the results are not stimulus specific. These studies showed that VI could impact stimulus dominance during binocular rivalry to a similar extent as viewing a weak percept. Furthermore, they demonstrated that VI has at least one behaviorally measurable component (precision) that can interfere with perception in different ways.

2.2.3. Perceptual priming

The dominance of stimuli that match recently imagined objects during binocular rivalry (also see Pearson, Rademaker, & Tong, 2011) could arguably be described as priming by VI, and indeed a more recent study has explicitly termed it as such (Bergmann, Genç, Kohler, Singer, & Pearson, 2015). Perceptual priming is typically defined as the implicit influence of a recently viewed stimulus on subsequent perception. There are currently mixed results concerning the extent to which imagined objects can produce priming effects. McDermott and Roediger (1994) found that VI of an object can increase identification speed of a subsequently presented image fragment of that object. However, a later study (Cabeza, Burton, Kelly, & Akamatsu, 1997) found no evidence for a priming effect of VI on perception, and instead suggested the earlier findings (1994) reflected a priming effect of VI on VI, because VI is required to mentally complete, and thus identify, fragmented images. In a further attempt to disentangle priming by VI and perception, Michelon and Zacks (2003) had different groups of subjects perform a word-picture matching task following VI or perception of various objects, half of which were congruent with the picture in the matching task. Subjects who previously viewed pictures of objects showed faster response times for the same items in the word-picture matching task compared to previously unseen items, but those who had studied the objects using VI did not show such a priming effect. The authors took this as evidence that VI and perception rely on different processing mechanisms, but an alternative explanation is that VI may recruit the same mechanisms as perception only if VI is sufficiently vivid, and this may depend on the extent to which subjects require vivid VI to perform a task. In line with this, Michelon and Koenig (2002) found that VI can prime a perceptual task specifically when the task requires subjects to imagine objects in detail. This study additionally demonstrated that individuals can change VI vividness depending on task demands, hinting at some amount of flexibility in the ability to represent pictorial information.

2.2.4. Dynamic visual noise

Another interference effect that has been used to assess the pictorial nature of VI and VWM is dynamic visual noise (DVN). DVN is classically used to disrupt working memory by presenting a grid of black and white pixels that change positions randomly during a stimulus retention interval. In the first study of this effect (Quinn & McConnell, 1996), DVN was found to effectively disrupt visual but not verbal working memory, suggesting selective interference of random perceptual noise with internally sourced visual representations. Subsequent studies did not find such a reliable effect (Andrade, Kemps, Werniers, May, & Szmalec, 2002; Avons & Sestieri, 2005), but this discrepancy could be due to a lack of overlap in the pictorial representations activated by perception of DVN

(random pixels) and the contents of VWM/VI. In line with this, Borst et al. (2012) argued that if VI and VWM are pictorial, and thus rely on representations that have a particular visuospatial layout of features, they should be more affected by the presentation of DVN with a similar visuospatial structure to the targets compared to DVN made up of random pixels. In their task, subjects were either required to generate VI of a previously learned language character (VI condition), or hold in mind a briefly presented novel language character during a retention interval (VWM condition), followed by an auditory cue prompting a visual feature judgment of that character (e.g., whether it contained diagonal lines). Subjects were instructed to make a “yes” or “no” response as quickly as possible following the cue while simultaneously viewing structured DVN that resembled language characters or unstructured DVN made up of a grid of randomly changing pixels. Structured DVN impaired accuracy to a greater extent than unstructured DVN in both the VWM and VI conditions, which provides evidence that VI and VWM may both be characterized by pictorial representations that are similar in their content to representations activated during visual perception.

2.3. Cortical evidence

It is clear from the above behavioral studies that research on VI, VWM, and preparatory templates provide an amalgamation of indirect evidence for an overlap between internally and externally sourced visual representations, contributing to the hypothesis that these representations both rely on pictorial content. Nevertheless, more direct evidence for this comes from the neurostimulation and neuroimaging literature. Several studies using these methods have found overlaps in the cortical regions recruited for both VI and perception.

Transcranial magnetic stimulation (TMS) is a neurostimulation method used to briefly disrupt normal neural function in a selective region of cortex by applying a transient magnetic field that elicits an electrical pulse in neurons. TMS can be used to establish causal links between brain and behavior. Kosslyn et al. (1999) found that stimulating occipital pole using rTMS impaired subjects' ability to mentally compare different properties (length, width, orientation, spacing) of imagined stripes, suggesting this region, typically involved in viewing low-level visual features, is also recruited to make visual judgments about imagined features. A recent study (Reeder, Perini, & Peelen, 2015: Experiment 2) found that double-pulse TMS over posterior temporal cortex (pTC), overlapping object-selective cortex (see Peelen & Kastner, 2011), impaired performance during preparation to search for object categories. This indicates that this region is not only involved in viewing object categories, but also activating them in a preparatory template.

Many neuroimaging studies have found that activating internally sourced visual representations can recruit cortical areas typically involved in performing perceptual tasks, including early visual regions such as lateral geniculate nucleus (Chen et al., 1998), pulvinar (Chen et al., 1998), and V1 (Albers et al., 2013; Chen et al., 1998; Cichy, Heinzle, & Haynes, 2012; Goldenberg et al., 1989; Harrison & Tong, 2009; Klein et al., 2004; Kok, Failing, & de Lange, 2014; Kosslyn, Thompson, Kim, & Alpert, 1995; Kosslyn et al., 1993, 1999; Mazard, Tzourio Mazoyer, Crivello, Mazoyer, & Mellet, 2004; Pearson et al., 2008; Serences, Ester, Vogel, & Awh, 2009; Slotnick, 2005; Thirion et al., 2006); extrastriate regions such as visual association cortex (Albers et al., 2013; D'Esposito et al., 1997; Goldenberg et al., 1989; Harrison & Tong, 2009; Knauff, Kassubek, Mulack, & Greenlee, 2000; Roland & Friberg, 1985); and category-selective ventral temporal and occipitotemporal cortices (Cichy et al., 2012; Ishai, Ungerleider, & Haxby, 2000; Johnson, Mitchell, Raye, D'Esposito,

& Johnson, 2007; Mechelli, Price, Friston, & Ishai, 2004; Mitchell & Cusack, 2016; O'Craven and Kanwisher, 2000; Peelen & Kastner, 2011; Reddy, Tsuchiya, & Serre, 2010; Reeder, Perini, et al., 2015; Stokes, Thompson, Cusack, & Duncan, 2009a). Furthermore, several studies have found that activating visual representations from memory can recruit cortical regions that typically process particular classes of visual information, such as V1 for colors (Serences et al., 2009) and orientations (Albers et al., 2013; Harrison & Tong, 2009; Klein et al., 2004; Kok et al., 2014; Serences et al., 2009), lateral occipital complex (LOC) for object shape (Stokes, Thompson, Nobre, & Duncan, 2009b), the fusiform face area (FFA) for faces, and the parahippocampal place area (PPA) for places (Esterman & Yantis, 2010; Ishai et al., 2000; O'Craven and Kanwisher, 2000). A cortical overlap between internally and externally sourced visual representations provides evidence that internally sourced representations can have a pictorial or sensory component.

3. Similarities and differences between internally and externally sourced pictorial representations

Despite mounting neuroimaging evidence for a pictorial component of internally sourced visual representations, many studies have failed to find such evidence in either early (D'Esposito et al., 1997; Ishai et al., 2000; Knauff et al., 2000; Mellet, Tzourio-Mazoyer, & Bricogne, 2000) or extrastriate visual areas (Ganis, Thompson, & Kosslyn, 2004). Overlaps between internally and externally sourced visual representations are often found in frontal and parietal regions (Ganis et al., 2004), which are classically thought to be involved in directing attention to relevant stimulus information rather than representing visual content (but see Christophel, Hebart, & Haynes, 2012; Ester, Sprague, & Serences, 2015). Some studies have found frontal activity only during internally sourced visual tasks (Ishai et al., 2000; Mechelli et al., 2004). Inconsistencies across tasks, regions of interest, stimuli, analyses, and/or neuroimaging methods used are all factors that may contribute to these discrepant findings.

One fMRI study (Lee, Kravitz, & Baker, 2012) attempted to remove these inconsistencies to comprehensively study the overlap between internally and externally sourced visual representations in various regions extending across the visual system. First, the authors established a set of stimuli (photographs of real-world objects against a white background) that could be reliably decoded using classification methods during perception across the ventral visual system, extending from early (V1) to high-level (posterior LOC and anterior LOC, posterior fusiform; pFs) visually selective regions of cortex. The authors then compared the representation of these stimuli within and across the different visual regions during VI and perception.

Group-level results showed that the magnitude of responses were generally smaller during VI compared to perception across all regions analyzed, and only reached significance in extrastriate cortex (V2–V4). Classification results revealed that stimuli could be reliably decoded from VI in extrastriate cortex and LOC, but not V1. And whereas decoding accuracy decreased significantly from posterior to anterior parts of the visual hierarchy during perception, the opposite effect was found for VI when VI and perception decoding accuracies were directly compared. Furthermore, VI and perception shared the largest decoding overlaps, and the highest similarity in representation, in the highest region of the visual hierarchy tested (pFs; see Fig. 1). Representations activated during VI were found to be more uniform across the visual regions tested compared to perception, which showed larger distinctions between individual object images in early visual regions; despite these differences, VI and perception of individual objects showed

significant cross-decoding of representations all along the visual hierarchy. In sum, Lee and colleagues found that VI and perceptual tasks share many cortical overlaps and are represented similarly enough to be reliably decoded from the activity patterns elicited by one another. The key differences between them may be the generally weaker nature of VI representations compared to perceptual representations, particularly in early visual regions, and the direction of information flow (also see Mechelli et al., 2004).

The “weaker representation” account is further supported by several behavioral and neuroimaging studies (Chang et al., 2013; McDermott & Roediger, 1994; Pearson et al., 2008; Segal & Nathan, 1964). Region-wide blood oxygenation level dependent (BOLD) signal changes are often smaller and cover a smaller area for tasks that rely on internally sourced visual information compared to perception (Ishai et al., 2000). Furthermore, where standard univariate analyses have failed to find region-wide stimulus related BOLD signal changes, classification techniques have revealed evidence for pictorial content at the multivoxel level (Harrison & Tong, 2009; Riggall & Postle, 2012). This discrepancy may be due to the fact that internally sourced representations are weak and may not elicit large-scale BOLD increases, but may nevertheless show distinct patterns of activation within a region. Furthermore, we cannot assume that people represent internally sourced visual information in the same way (see the following section), and pattern classification techniques are better suited to account for individual variation (Davis et al., 2014).

VI of an expected stimulus has also been found to bias the emergence of visual information during binocular rivalry in a manner closely resembling the effects of viewing “weak” visual stimuli (around 40% of the luminance or 20% of the contrast of rivalry stimuli) but not “strong” visual stimuli (over 60% of the luminance/contrast of rivalry stimuli); both VI and weak visual stimulation facilitate the emergence of previously suppressed stimuli, whereas strong visual stimulation does not show such facilitation patterns (Pearson et al., 2008). A recent study has additionally found evidence that VI may elicit only a subset of object features represented during perception in occipitotemporal cortex, in line with this “weaker representation” account, but another factor the authors considered was that individual variability in the ability to represent visual features during VI may have contributed to inconsistencies in group-level analysis (Mitchell & Cusack, 2016).

4. Evidence for individual differences in pictorial representation

Within the broad scope of neuroscientific and psychological research, individual differences are not often the focus of studies of visual representation, but they nevertheless influence the interpretation of visual information both imagined and perceived. In the previous section, I suggested that there are some general differences between internally and externally sourced visual representations, but these differences alone do not adequately explain the discrepant findings observed in the literature concerning the pictorial nature of internally sourced representations. Researchers have been historically binary in their interpretations depending on the results they obtain – either pictorial representations are exclusive to visual perception, or they are not. I argue that individual differences are a large contributing factor to these discrepant findings, and that it is necessary to account for such differences to accurately interpret the contents of VI, VWM, and visual preparatory templates.

In the following section, I lay out the evidence that the overlaps and distinctions between internally sourced and stimulus driven visual representations can be explained in large part by individual differences (also see Olivetti Belardinelli et al., 2009), and that the

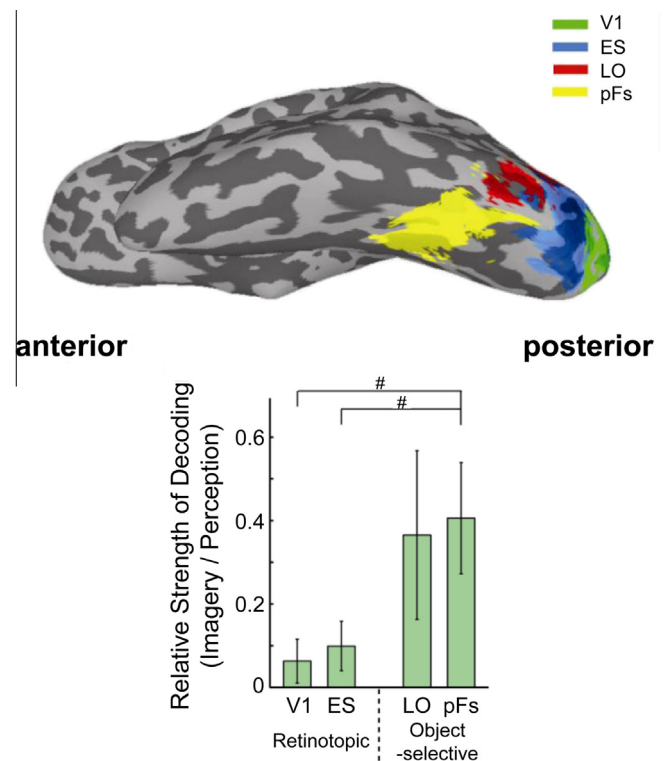


Fig. 1. (Top) The visual regions targeted for classification analysis. (Bottom) The extent of decoding overlap between VI and perception in each visual region tested; error bars represent standard error of the mean (SEM). Modified from Figs. 2 and 5 in Lee et al. (2012), reproduced with permission from Elsevier.

extent to which internally sourced visual representations are pictorial is dependent on the self-reported vividness of VI, the strengths and weaknesses in quantitatively measured VI abilities, the appropriateness of the strategy used to prepare for visual targets, the quantitatively measured precision of internally sourced representations, the level of perceptual expertise with the visual stimuli to be represented, and – as an anatomical factor – the surface area of visual cortex.

4.1. VI vividness

4.1.1. Behavioral evidence

Studies that argue against a simple “weaker representation” account for internally sourced visual representations have provided evidence that the extent to which this information is pictorial is correlated with self-reported measures of VI, such as the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973). Behaviorally, the degree to which VI primes perceptual dominance in binocular rivalry (i.e., the proportion of trials on which a rivalry stimulus that matches an imagined stimulus dominates perception) is reliably correlated with self-reported VI vividness ratings (Bergmann et al., 2015; Pearson et al., 2011) (note that $N = 20$ in this study); see Fig. 2). In addition to the VVIQ questionnaire (Fig. 2a), these studies took VI vividness ratings on every experimental trial following VI of a cued grating, prior to the presentation of a binocular rivalry display. They found that for trials on which higher vividness ratings were reported, a previously imagined stimulus was more likely to emerge dominant from the binocular rivalry display compared to the unimagined stimulus (Fig. 2b,c). These results collectively show that individuals can have generalized differences in VI vividness and that a single person can activate variably vivid VI over time, both of which significantly influence perception.

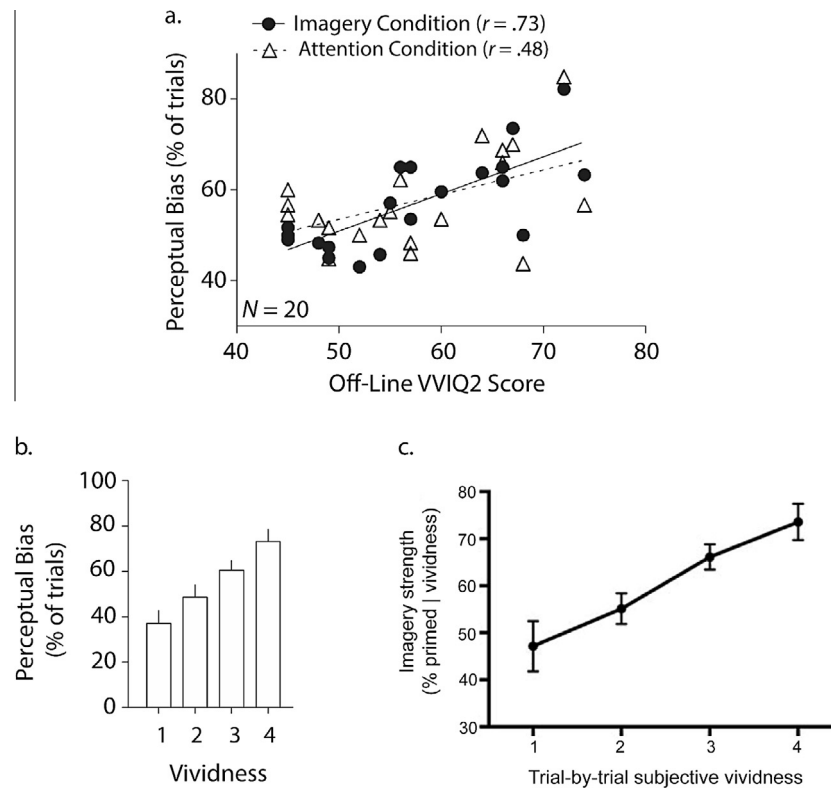


Fig. 2. (a) The correlation between general VI ratings on the VVIQ2 and perceptual bias by VI of a previously suppressed grating stimulus (VI strength) during binocular rivalry. The “Imagery condition” required VI of a to-be-remembered grating during the delay period and the “Attention condition” required attending to-be-remembered features of a grating presented during the delay period that contained both to-be-remembered and distractor features. (b) The relationship between online ratings of VI vividness and VI strength during binocular rivalry; error bars represent SEM. (a–b) Note $N = 20$. Modified from Figs. 1 and 3 in Pearson et al. (2011) reproduced with copyright permission from SAGE publications. (c) The correlation between online ratings of VI vividness and VI strength during binocular rivalry; error bars represent SEM. Modified from Fig. 2 in Bergmann et al. (2015) reproduced with copyright permission from Oxford University Press.

4.1.2. Neuroimaging evidence

Some studies have found evidence for internally sourced pictorial representations only as low in the visual hierarchy as occipitotemporal cortex, arguing that EVC recruitment is exclusive to representations activated by perception (D’Esposito et al., 1997; Ishai et al., 2000; Knauff et al., 2000; Mellet et al., 2000). This is, however, in contrast to the findings of many other neuroimaging studies. Individual differences in the vividness of representing pictorial content may have something to do with these discrepant findings (see Fig. 3). For example, Lee et al. (2012) found that target decoding accuracy during VI was generally higher in extrastriate and object-selective visual regions than in V1, but when VI vividness was taken into account, the authors found a correlation between vividness ratings and the extent to which VI and perception elicited similar patterns of activity in V1 (note that $N = 11$ in this study). Similar to this, Cui, Jeter, Yang, Montague, and Eagleman (2007) found a significant correlation between subjects’ scores on the VVIQ and the BOLD signal change elicited by VI in EVC (note that $N = 8$ in this study). Using a different scale of VI vividness, the Italian version of the Questionnaire upon Mental Imagery (QMI; Sacco & Reda, 1998, as cited in Olivetti Belardinelli et al., 2009), Olivetti Belardinelli et al. (2009) found that self-reported VI vividness was positively correlated with stronger BOLD signal in EVC (note that $N = 9$ in this study). When subjects were split into high- and low-VI groups, subjects who reported high VI vividness showed positive BOLD contrast in EVC whereas subjects who reported low VI vividness actually showed negative BOLD contrast, which the authors suggested was indicative of early visual deactivation, perhaps due to using a verbal rather than visual preparatory strategy.

Goldenberg et al. (1989 Experiment 2) conducted one of the earliest studies to find a link between regional cerebral blood flow (rCBF) and VI vividness using single photon emission computed tomography (SPECT). Subjects were asked to perform two tasks (VI task and control) during which the experimenters intravenously injected a radioactive tracer to visualize rCBF. In the VI task, subjects were prompted with an auditory cue to imagine previously viewed capital letters and report the number of corners for each one. In the control task, they were asked to report the number of characters that separated two given letters (e.g., “A to K”), if arranged in alphabetical order (e.g., 9). Following the experiment, subjects completed the VVIQ and a questionnaire reporting the strategies they used for the different tasks, with particular focus on whether they used VI for either task. Results showed a positive correlation between subjects’ VVIQ scores and reported vividness of the capital letter stimuli in the VI task. There was also a trend for more vivid imagers to report using VI in the control task. Importantly, vividness ratings on the VI task were negatively correlated with rCBF in frontal regions and positively correlated with rCBF in inferior temporal regions and to a lesser extent in inferior occipital regions.

4.2. Appropriateness of preparatory strategy

Aside from VI vividness, it is also useful to consider VI strategy in studying individual differences in visual content representation; activating a vivid image of an inappropriate item (e.g., searching for the yellow Deutsche Post letter box in England) will nonetheless hinder visual task performance. Using TMS, my colleagues and I have previously found evidence for a link between the

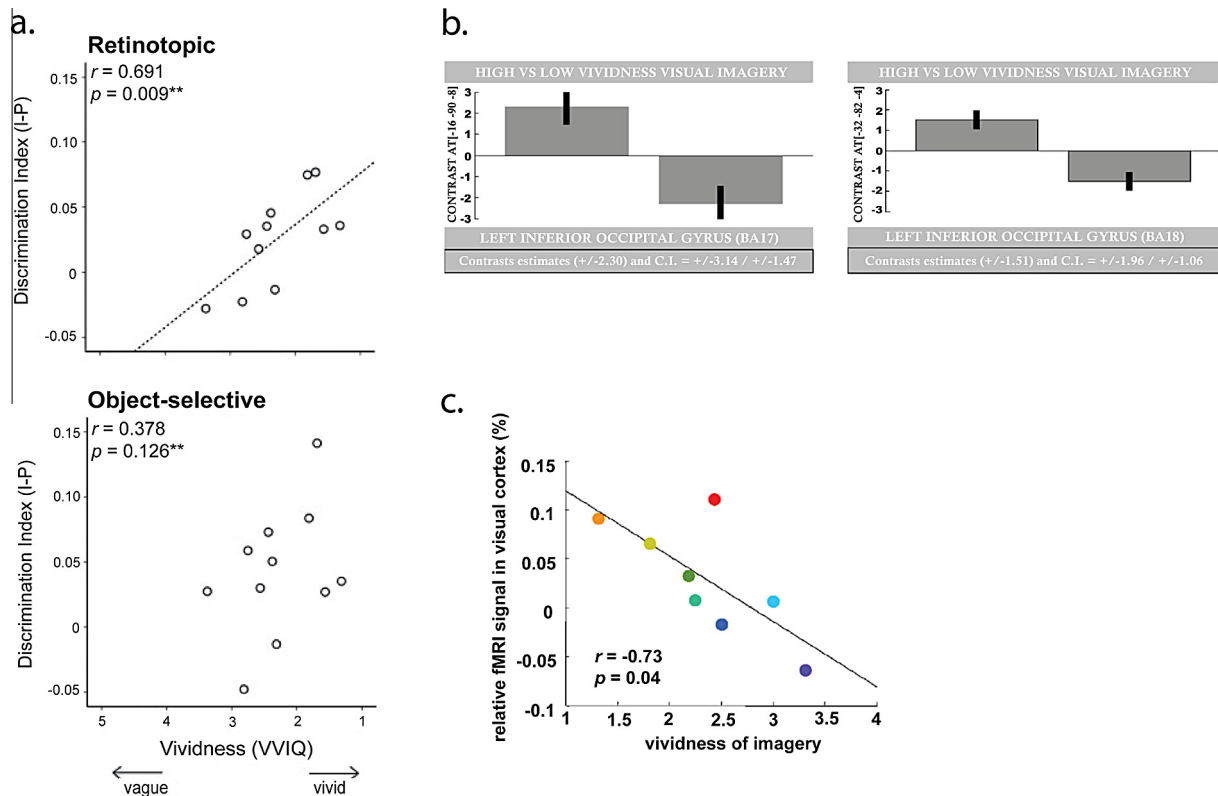


Fig. 3. (a) The correlation between VI vividness (VVIQ; lower scores denote more vivid VI) and the average classification accuracy of VI and perception of real-world objects in retinotopic visual cortex (V1–V3; significant) and object-selective cortex (posterior LOC and pFs; nonsignificant). Note $N = 11$. Modified from Fig. 8 of Lee et al. (2012) and reproduced with copyright permission from Elsevier. (b) Subjects in this experiment were split into high VI vividness and low VI vividness groups based on their scores on the Italian version of the QMI. High-vividness subjects showed positive BOLD contrast and low-vividness subjects showed negative BOLD contrast in Brodmann areas 17 and 18 corresponding to V1/V2 while listening to visually descriptive statements (e.g., “See a candle”); error bars represent 90% Confidence Interval (CI) for each region of interest. Note $N = 9$. Modified from Fig. 3 of Olivetti Belardinelli et al. (2009) and reproduced with permission from Elsevier. (c) The correlation between VI vividness (VVIQ) and visual cortex activity (BOLD signal in V1/V2 – BOLD signal over all gray matter) during VI of oneself or another person bench pressing or stair climbing. Different colors denote different subjects. Note $N = 8$. Modified from Fig. 1 of Cui et al. (2007) and reproduced with permission from Elsevier. Note the low sample sizes in the correlational analyses in panels (a) and (c). These results alone cannot be taken as strong or definitive evidence for a relationship between self-reported VI vividness and the overlap between internally and externally sourced visual representations.

cortical areas recruited for visual search and the extent to which individuals activate appropriate pictorial preparatory information for visual search (Reeder, Perini, et al., 2015; Experiment 1). In the task, subjects were cued to detect cars and people in photographs of naturalistic scenes. Just prior to target onset, we stimulated posterior temporal cortex (pTC), an area previously found to be involved in activating category-level visual information during preparation for search (Peelen & Kastner, 2011). Following experimentation, we collected self-reported preparatory strategy scores on a questionnaire (previously unpublished, but see Appendix A) that particularly targeted the contents of subjects’ templates activated in preparation for the search task. The questionnaire was split into “specific” and “general” VI strategy statements: for example, a “specific” statement would be, “After the [car] cue I looked out for one type of car (e.g., a sedan) at one location (e.g., in the center)” and a “general” statement would be, “After the [car] cue I anticipated detecting cars seen from multiple angles rather than from one angle”. From these reports alone, we found that individuals fall along a spectrum from being able to activate preparatory templates composed of high-level shape features diagnostic to the target object category (a “general” strategy), to activating no (or little) visual information in the template, or inappropriate templates composed of specific, low-level stimulus features (a “specific” strategy). A previous study found that subjects who reported to activate more general strategies on the same questionnaire performed more accurate real-world search than subjects who

reported to use more specific strategies (Peelen & Kastner, 2011 (note that $N = 14$ in this study); see Fig. 4a). When strategy was correlated with behavioral performance under TMS stimulation, we found that reporting a more general strategy correlated with a larger decrement in performance under stimulation to pTC compared to vertex in the preparatory period of visual search (note that $N = 16$ in this study; see Fig. 4b). These results collectively indicate that differences in self-reported preparatory representation strategies can affect both visual task accuracy and the visual regions recruited for the task.

Extending from this, neuroimaging studies have found that preparatory activity patterns elicited in high-level object selective cortex, such as LOC, correlate positively with category-level search performance (Peelen & Kastner, 2011; Soon, Namburi, & Chee, 2013); conversely, preparatory activity patterns in EVC correlate negatively with category-level performance (Peelen & Kastner, 2011 see Fig. 4c). In other words, high-level visual regions must be recruited to perform well on high-level visual tasks, suggestive of a high-level strategy, but some individuals may still recruit a specific strategy that relies on low-level visual cortex to their own disadvantage. In a study on the effects of VI vividness (as measured by the VVIQ) on mental rotation performance, high imagers (who recruited visual cortex to a greater extent than low imagers) were found to perform better than low imagers (who recruited the fronto-parietal control network to a greater extent than high imagers); this led the authors to suggest that being able to activate a

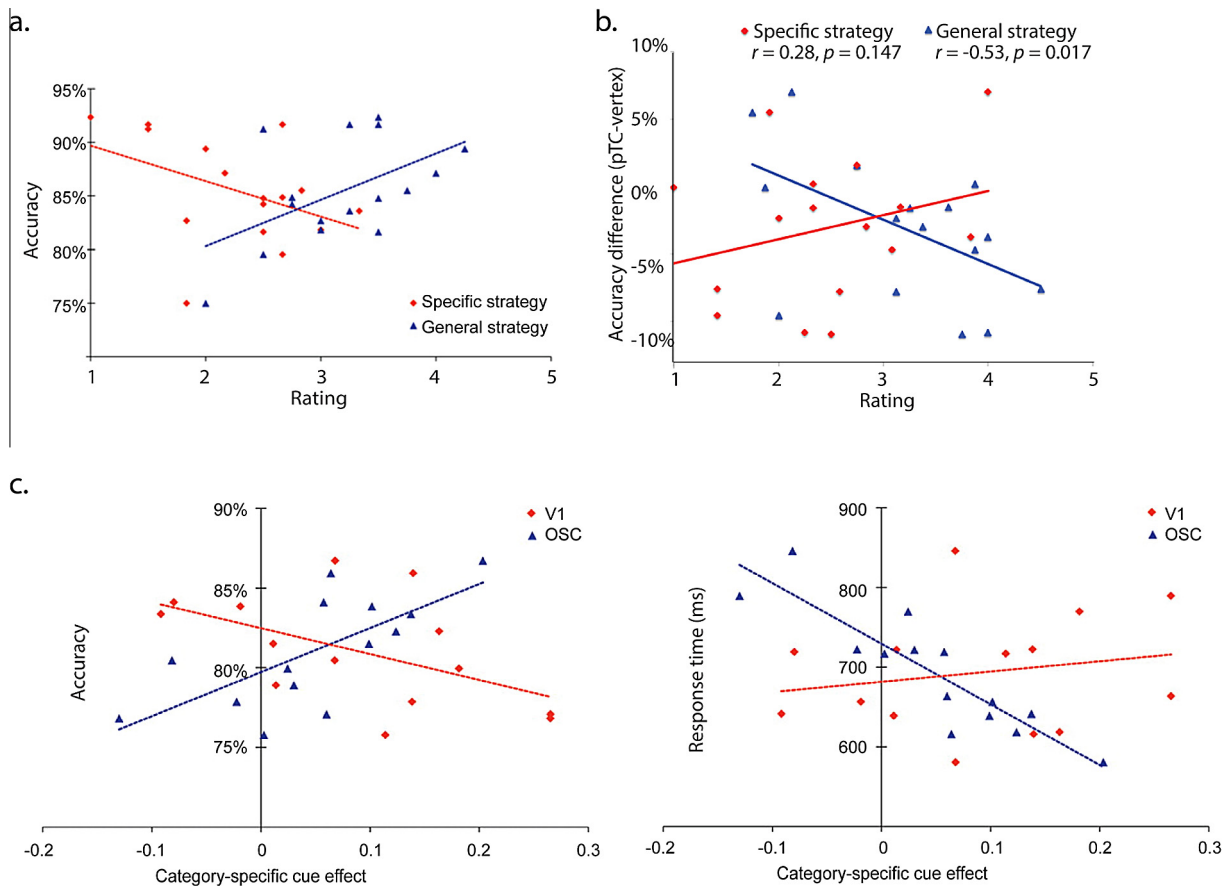


Fig. 4. (a) Peelen and Kastner (2011) found a positive correlation between real-world object detection accuracy and general preparatory representation strategy ratings. They found a negative, though nonsignificant, correlation between detection accuracy and specific strategy ratings. Note $N = 14$. This figure was modified from Fig. 5 in Peelen and Kastner (2011) and reproduced with permission from the National Academy of Sciences. (b) Negative differences in accuracy between pre-stimulus pTC and vertex stimulation correlated with higher general strategy ratings (more negative difference scores indicated a greater performance impairment under stimulation to pTC). More positive difference scores correlated, though nonsignificantly, with higher specific strategy ratings. Note $N = 16$. This figure was created from data collected by Reeder, Perini, et al., 2015. (c) Category-specific preparatory activity patterns in LOC correlate positively with detection accuracy (left panel) and negatively with response time (RT; right panel), whereas preparatory activity patterns in EVC correlate negatively with detection accuracy (left panel) and positively with RT (right panel). Note $N = 14$. This figure was modified from Fig. 4 in Peelen and Kastner (2011) and reproduced with permission from the National Academy of Sciences.

vivid image of the rotated object, above imagining the action of rotation, is necessary to perform well on the task (Logie, Pernet, Buonocore, & Della Sala, 2011). These studies provide evidence for individual differences in the neural regions recruited for different preparatory strategies, which ultimately lead to variations in visual task performance.

4.3. Quantitatively measured VI abilities

Simply adding VI questionnaires to the end of an experiment can account for a large amount of variability in the ability to activate internally sourced pictorial visual representations. However these measures are still subjectively assessed, and a more complete and accurate analysis of individual differences requires a combination of subjective and objective evidence. The importance of investigating individual differences in quantitatively measured VI abilities was comprehensively and succinctly discussed in a seminal paper by Kosslyn et al. (1984), in which the authors described the benefit of using experimentally testable methods along with introspective methods (e.g., VI vividness ratings) as measures of individual variability in internally sourced pictorial representations.

Adding a cushion of psychophysical batteries to the typical self-reported method was the first step toward systematically gauging VI abilities. Kosslyn and colleagues first created a composite list of

VI abilities that they had defined over the course of several previous studies: these include “picture” (the ability to activate detailed parts of objects in spatially appropriate locations to add resolution to an imagined form), “inspect” (the ability to make visual judgments about activated images), “maintain” (the ability to keep the resolution of an image steady through effortful image refreshing), and “manipulate” (the ability to change an image through mental rotation, parsing into features or parts, zooming in and out, panning in the depth dimension, and moving in imagined two-dimensional space). The authors hypothesized that different VI tasks rely on these abilities to different extents, and that individuals will perform better or worse on different tasks depending on their particular strengths and weaknesses in these abilities, which may be relatively independent from one another.

To test this, the authors first composed a battery of tasks that relied on different VI abilities and predicted the degree to which performance on different tasks would correlate depending on their overlap in the abilities needed for successful completion (see Fig. 5a). These tasks were: “acuity” (imagine a previously presented grating and mentally move it away from you until the lines begin to blur); “oblique effect” (mentally rotate a previously presented grating by 45 degrees and then perform the acuity task); “extent” (imagine two gratings moving away from each other and determine how far apart they can move before they blur); “mental rotation” (mentally rotate oriented characters to be

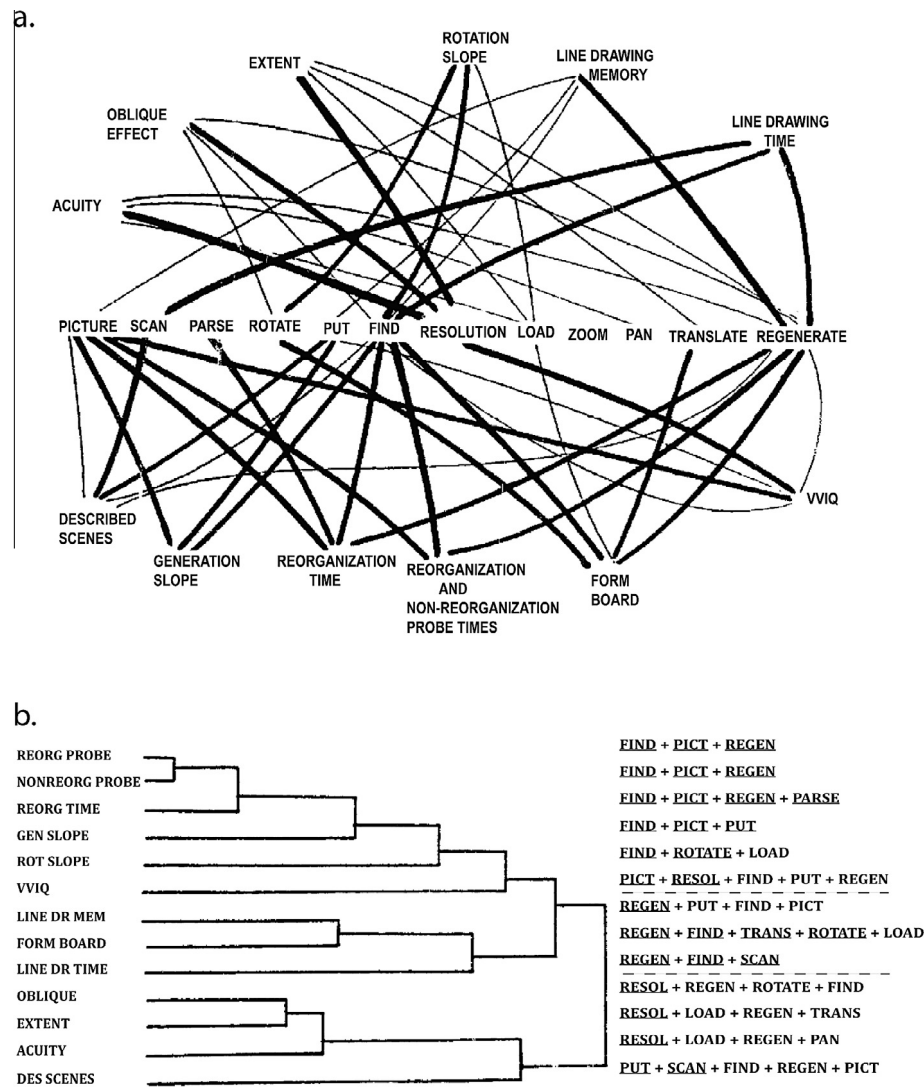


Fig. 5. (a) A comprehensive diagram of the psychophysical tasks performed for this study and hypothesized VI abilities required to perform them. Thicker lines denote a dominant VI ability for a task. (b) The results of the cluster analysis for all psychophysical tasks, clustered by the strength of their correlations with one another. The hypothesized VI abilities required to perform each task are listed on the right-hand side. This is evidence that tasks that recruit the same VI abilities show similar performance levels compared to tasks that recruit different VI abilities. Modified from Figs. 1 and 2 of Kosslyn et al. (1984) and reproduced with permission from Elsevier.

right-side-up); “line drawings memory” (connect lines one at a time in an instructed configuration and report whether the final line is located above or below the starting line); “imagine described scenes” (determine whether you must scan left or right from one object of focus to another in a described scene); “image generation” (imagine different combinations of geometric figures to form composite images); “reorganization” (parse an image from the “image generation” task into a different configuration); and “image inspection” (determine whether an image from the “image generation” task contains a particular geometric figure or whether a geometric figure is symmetric along a given axis).

Results showed that performance on different psychophysical tasks correlated to different extents with each other; tasks that were hypothesized to use the same VI abilities (e.g., “acuity” and “extent” both require the ability to activate imagery with high resolution) correlated strongly with one another, whereas tasks that were hypothesized to use different abilities (e.g., “acuity” and “mental rotation”) correlated weakly with one another. There was also a significant positive correlation between predicted and observed performance depending on the VI abilities required for the different tasks. Using cluster analysis, the authors further

found that tasks that showed within-subject correlations also relied on the same VI abilities (see Fig. 5b), confirming that individual differences in task performance are largely associated with differences in quantitatively measurable VI abilities. Kosslyn et al. (1984) concluded that variations in VI can be compartmentalized into individual differences in various quantitatively measured VI abilities.

4.4. VI precision and visual cortex size

Measuring individual variability in the surface area of visual cortex is a particularly recent and unique approach to studying differences in the pictorial content of internally sourced representations. Bergmann et al. (2015) used binocular rivalry to first quantitatively determine the strength and precision of VI. VI strength was determined as the extent to which an imagined Gabor with a particular color (activated prior to the onset of a rivalry display) matched a subsequently dominant rivalry stimulus, coupled with a self-reported measure of VI vividness. VI precision was measured as the extent to which incrementally larger differences between the imagined and perceived orientation and visual

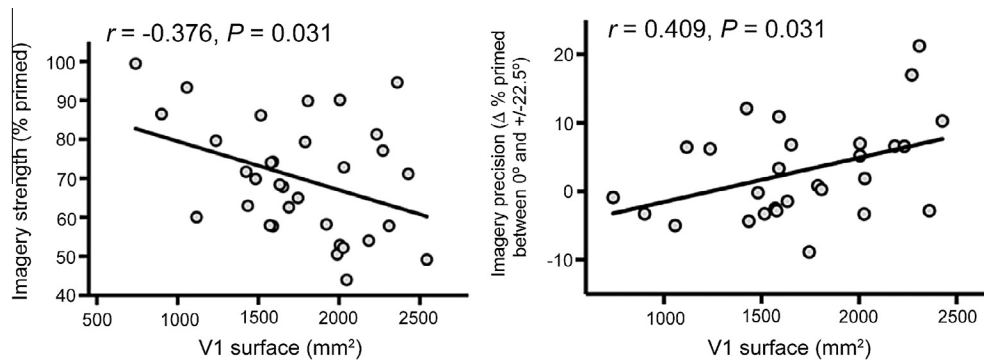


Fig. 6. (Left) The correlation between V1 surface area and VI strength. (Right) The correlation between V1 surface area and VI precision. Modified from Figs. 2 and 4 in Bergmann et al. (2015), reproduced with permission from SAGE publications.

field location of a Gabor affected ocular dominance during rivalry. Stronger dominance effects with more precise matches between imagined and perceived stimuli indicated higher VI precision. Prior to the binocular rivalry task, the experimenters acquired retinotopic maps of areas V1–V3 in each subject to determine the surface area of visual cortex. Results showed that subjects had high variability in both visual cortex anatomy and binocular rivalry performance. VI strength was negatively correlated with V1 surface area, whereas VI precision was positively correlated with V1 surface area (perhaps, as the authors suggested, because VI precision is a better analog to perceptual acuity than VI strength; see Fig. 6). Central V1 surface area showed the most reliable correlations with VI precision, and there were no other correlations between behavioral performance or VI vividness ratings and V2–V3 anatomy. These results provide further evidence that VI abilities are not only multifaceted (with stronger imagers tending to have a smaller V1 surface area, but more precise imagers tending to have a larger V1 surface area), but also that much can be gained from uniting investigations of several aspects of brain and behavior when assessing individual differences in pictorial representations.

4.5. Perceptual expertise

Thus far in the discussion of individual differences in internally sourced pictorial content, I have provided evidence for a range of representation abilities and strategies within the general population and their association with behavioral task performance, cortical regions recruited, and brain anatomy. Another interesting avenue of research on this topic is to study the pictorial representations of individuals who have an expert level of experience with viewing a particular class of objects.

There is already evidence that perceptual expertise, marked by an enhanced ability to discriminate visual features of a particular object class, changes the way that objects are processed during perception. For example, there seems to be a shift toward recruiting specialized cortical regions for processing exemplars of perceptual expertise compared to other classes of objects (McGugin, Gatenby, Gore, & Gauthier, 2012; McGugin, Newton, Gore, & Gauthier, 2014; McGugin, Van Gulick, Tamber-Rosenau, Ross, & Gauthier, 2015; McKeef, McGugin, Tong, & Gauthier, 2010). Behaviorally, experts show just as high subordinate-level (e.g., “Golden Retriever”) as basic-level (e.g., “dog”) categorization ability for the expert object category (Bukach, Phillips, & Gauthier, 2010; Gauthier, Williams, Tarr, & Tanaka, 1998; Tanaka & Curran, 2001; Tanaka, Curran, & Sheinberg, 2005; Tanaka & Taylor, 1991). Furthermore, objects of expertise dominate awareness during binocular rivalry (Stein, Reeder, & Peelen, 2016), and a higher level of expertise (as assessed by perceptual discrimination ability) correlates with more accurate detection of objects of expertise in nat-

uralistic search environments (Reeder, Stein, & Peelen, 2016 see Fig. 7a).

An important question following from these studies is whether the perceptual improvements observed here are linked to differences in the internally sourced pictorial content activated for objects of expertise vs. other object classes, and if so, in what ways? These studies do not directly study the contents of visual representations of objects of expertise, but they could benefit from such investigations. For example, as part of our study on the correlation between perceptual expertise and category-level search accuracy for cars (Reeder et al., 2016) we also gave subjects the preparatory strategy questionnaire detailed in Appendix A. 32/34 experts from the published study completed the questionnaire following experimentation. In an as yet unpublished analysis (see Appendix B), we found that subjects who reported to activate more specific images of cars in preparation for category-level search (in which the target exemplar could be one of hundreds of different cars) was negatively correlated with car discrimination performance (see Fig. 7b). This suggests that representing an inappropriately specific image of a car in preparation for category-level search could be a particular strategy of car enthusiasts with less expertise for discriminating car models than high-level experts. To flip it around, perhaps high-level car discrimination experts do not need to rely on visual templates composed of a set of restricted or “prototypical” features of cars, and this may contribute to better category-level search performance (as observed in the published results). These results demonstrate that the contents of internally sourced visual representations may be different depending on an individual's level of expertise with an object category. In other words, learned expertise (or more generally, extensive experience and exposure) for a particular class of objects may qualitatively alter the contents of pictorial representations compared to more casual experience with that class of objects, although this must be studied more explicitly in the future.

5. Specialized experiences associated with pictorial abilities

5.1. Intrusive VI

Only a few studies have delved into the relationship between pictorial abilities and the propensity to experience involuntary or intrusive VI. Intrusive VI may be a neutral or enjoyable experience (e.g., experiencing the sensation of color during reading in the case grapheme-color synaesthesia; Rich, Bradshaw, & Mattingley, 2005), or it could be disturbing, as in the case of various psychological and anxiety disorders such as obsessive-compulsive disorder (OCD) or post-traumatic stress disorder (PTSD; Çili & Stopa, 2015).

Synaesthesia is a phenomenon characterized by intrusive VI in one modality triggered by sensation in another modality. For

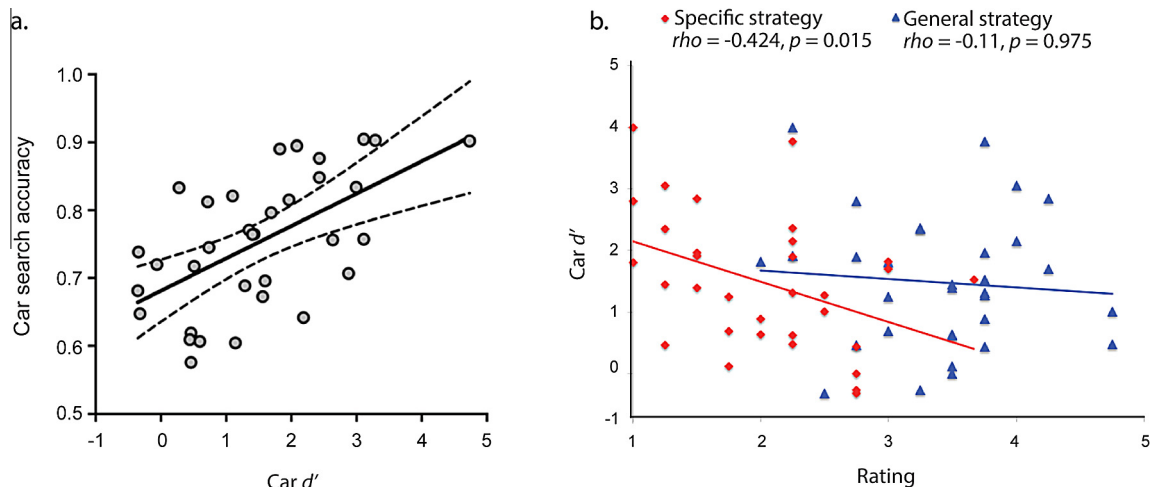


Fig. 7. (a) The correlation between car discrimination performance (d') and car search accuracy in a real-world detection task; dashed lines represent 95% CI. Modified from Fig. 3 in Reeder et al. (2016) and reproduced with permission as the author of the original article in *Psychonomic Bulletin & Review* under the Creative Commons license (<http://creativecommons.org/licenses/by/4.0/>). (b) The correlation between self-reported preparatory strategy ratings and car discrimination performance (d'). Higher specific strategy ratings showed a significant negative correlation, whereas higher general strategy ratings showed no correlation. This figure was created from data collected for Reeder et al. (2016).

example, a grapheme-color synaesthete may involuntarily experience the color red every time he or she sees the letter “T”, regardless of the objective color of the letter (Rich et al., 2005). Experiences may range from a strong feeling that there is an association between two modalities (e.g., feeling that a “T” should be red), to mentally projecting one modality onto another (e.g., reporting to project the color red onto the letter “T” in the real world; Ward, Li, Salih, & Sagiv, 2007). Synaesthesia in the visual modality and VI are tightly coupled; synaesthetic experiences are rarely confused with external stimulation (as in the case of hallucinations), and they are often reported to occur in the “mind’s eye” (Rich et al., 2005). It is therefore not surprising that synaesthetes report more vivid VI compared to non-synaesthetes (Barnett & Newell, 2008; McErlean & Banissy, 2016; Price, 2009).

Although intrusive VI in synaesthesia is often reported to be an enjoyable experience (Rich et al., 2005), intrusive VI is more often a symptom of psychological illness and may be unpleasant or upsetting. This includes distorted images of the self (e.g., visualizing oneself as unattractive or disfigured) in body dysmorphic disorder, social anxiety disorder, and bulimia nervosa; disturbing situational images (e.g., making a fool of oneself in public, experiencing graphic violence, or being covered in germs or toxins) in agoraphobia, PTSD, or OCD, respectively; or persecutory images (e.g., being poisoned) in delusional disorders, among many other types of VI across various conditions (Çili & Stopa, 2015). What these all seem to have in common is that patients who experience intrusive VI as a symptom of their disorder compared to patients who do not experience intrusive VI, show higher pictorial or VI abilities (Pearson & Westbrook, 2015).

One question that stems from the above findings is whether naturally better VI abilities correlate with a propensity to experience intrusive VI, or whether the onset of intrusive VI “exercises” and improves VI abilities as a side effect of the condition. There seems to be an association between VI ability and the experience of intrusive VI, but the nature of this relationship is unclear, and leaves much to be explored for future research.

5.2. Hallucinations

Hallucinations are defined as perception in the absence of visual stimulation (Abbot, Connor, Artes, & Abadi, 2007), and are some of the most puzzling of perceptual dysfunctions. Little is known about

the cognitive and neural mechanisms involved in hallucinations, or why they appear to some people and not others. VI may be involved in the experience of hallucinations, but there has been considerable debate concerning their relationship (Böcker, Hijman, Kahn, & de Haan, 2000; ffytche et al., 1998; Mast, 2005; Sireteanu, Oertel, Mohr, Linden, & Singer, 2008). ffytche et al. (1998) asserted that hallucinations are different from VI in that they are attributed to an external source, are as vivid as real percepts, and are involuntary. However, subjects who obtain high scores on self-reported measures of VI vividness have claimed that their mental images can manifest in as much detail as external stimuli (Aleman, Nieuwenstein, Bocker, & de Haan, 2000; van de Ven & Merckelbach, 2003); additionally, VI may be involuntary in various psychological disorders (Hackmann & Holmes, 2004; Çili & Stopa, 2015) and synaesthesia, as previously discussed. Perhaps the distinction between VI and hallucinatory experience is solely dependent on whether imagined content is attributed to internal or external sources, regardless of vividness or conscious control.

Self-reported VI vividness has been found to correlate with hallucination proneness (Aleman et al., 2000; van de Ven & Merckelbach, 2003). Aleman et al. (2000) and others (Brébion, Ohlsen, Pilowsky, & David, 2008) have found behavioral evidence for a higher correlation between VI and perception in hallucinating compared to non-hallucinating individuals, and one fMRI study (Gonsalves et al., 2004) found evidence for a greater cortical overlap between these processes in hallucinating individuals, as well. These findings indicate that the cognitive and neural mechanisms used for VI and perception may be less discrete in those who are prone to hallucinate. Furthermore, in a study of patients with Parkinson’s disease, patients who experienced hallucinations showed a stronger VI bias during a binocular rivalry task compared to patients who did not experience hallucinations and healthy controls (Shine et al., 2014). The link between VI, perception, and hallucinations is rarely studied, but further research on this topic is necessary to improve our understanding of hallucinatory experience, which is of particular clinical significance, and could add another necessary component to the study of pictorial visual representation.

6. Conclusions

The purpose of this review was twofold: first, I encouraged investigations into the pictorial content of visual representations

activated in the absence of visual stimulation, with particular focus on visual imagery (VI), visual working memory (VWM), and visual preparatory templates. I demonstrated that the literatures on VI, VWM, and preparatory templates could be united in building evidence that internally sourced visual representations can be pictorial in their content. Behavioral evidence for this includes interference between VI and perception (as seen in studies of the Perky effect, binocular rivalry, perceptual priming, and dynamic visual noise), attention capture by features that match visually to a preparatory template, and better search performance when subjects can prepare for precise visual features of targets. I further provide neurostimulation evidence that preparing to detect different objects recruits different visual cortical regions, similar to perception, and neuroimaging studies have additionally found evidence for overlaps in the cortical regions recruited for tasks that require internally and externally sourced visual representations. Nevertheless, there may be some general differences between these processes; internally sourced representations tend to be weaker in impacting behavior and in the extent to which visual regions are recruited compared to sensory driven representations, and these processes also require different directions of information flow through the brain. However, these differences cannot fully account for the discrepancies in the literature concerning the extent to which internally sourced visual content is pictorial. Instead, the discrepancies observed could be better explained by individual differences in content representation, which brings us to the major purpose of this review.

Here I showed that individual differences in pictorial content may have a profound impact on experimental results and the interpretation of those results, and are predominantly overshadowed by studies that seek to generalize their conclusions to the population level. In the second half of this paper, I presented many factors that contribute to individual differences in pictorial content activated for visual tasks, namely: between- and within-subject differences in self-reported VI vividness, differences in quantitatively measured VI abilities, appropriateness of the preparatory strategy recruited for a task, variations in visual cortex surface area, and level of perceptual expertise with an object category.

VI vividness ratings are thus far the most widely used method of measuring individual differences in pictorial content. These ratings are reliably correlated with various neuroimaging and behavioral effects associated with between-subject differences in pictorial content, such as the extent to which VI primes ocular dominance during binocular rivalry and the extent to which early visual cortex (EVC) and object-selective cortex are recruited during VI. Not controlling for these differences may lead to recruiting a sample composed of predominantly vivid (or non-vivid) imagers, which could determine whether tasks requiring internally sourced representations are found to recruit visual cortex, or whether there are significant behavioral influences of these representations on visual perception. Quantitative measures of VI abilities are less widely studied but provide further convincing evidence that individual differences affect the extent to which internally sourced representations are pictorial. These include using a set of behavioral tasks to gauge different VI abilities (picturing, inspecting, maintaining, manipulating), investigating the extent to which different cortical regions are recruited for VI, and measuring differences in visual cortex anatomy.

One behavioral study of individual differences in quantitatively measured VI abilities by Kosslyn et al. (1984) was given particular focus in the current review for two reasons: first, it demonstrates many ways in which individuals may differ in representative abilities and how these differences can affect task performance in a predictable way; however, since its publication in 1984, only three (two mentioning individual differences specifically; Brandimonte

& Gerbino, 1993; Cornoldi & Vecchi, 2004; Ranganath, Cohen, Dam, & D'Esposito, 2004) of its 215 citations link these findings to VWM,¹ and none to preparatory templates. This is a striking example of the shortcomings of compartmentalizing neuroscientific research into specialized themes. The literature on visual content representation would benefit greatly from a pooling of knowledge from various literatures that have been historically uncommunicative.

There are only a few studies that have used a combination of VI vividness ratings and quantitative measures of VI ability to study individual differences in pictorial content. One promising quantitative measure that is also reliably correlated with vividness ratings is the degree of interference of VI with perception during binocular rivalry. Combining multiple measures, both subjective and objective, provides a more accurate picture of how pictorial content may vary between subjects and tasks, and future studies would benefit by adopting various self-reported and quantitative measures of internally sourced visual content (see McAvinue & Robertson, 2007 for another review on this topic).

Controlling for individual differences in studies of internally sourced pictorial content is often as easy as tacking questionnaires onto the end of an experiment. A questionnaire method could appeal to a broad range of studies, particularly those that have long exhibited discrepant findings, such as neuroimaging studies concerning the extent to which visual cortex is recruited for representing internally sourced pictorial content. Questionnaires are also a convenient option for studies with time constraints that require lengthy preparation or multiple sessions (such as fMRI, TMS, or psychophysical designs), or for studies in which the main purpose is not to measure individual differences but which would nevertheless benefit from the additional correlational analyses. For studies in which individual differences are a point of focus, it is important to account for various types of differences for the sake of comprehensibility. I have now shown that individual differences in pictorial content can take many forms (strategy, vividness, precision, etc.), and it would benefit future studies to keep these things in mind when designing new visual tasks or determining which of various VI abilities to measure, as Kosslyn et al. (1984) so aptly demonstrated (also see Dean & Morris, 2003). Because pictorial abilities are also associated with intrusive VI and hallucinations, it is of particular clinical significance to conduct thorough investigations on this topic.

In sum, it is important to consider individual differences in the study of the contents of visual representations in the absence of visual stimulation. This can be done using methods stemming from research into visual imagery, visual working memory, and visual preparatory templates. Future investigations would benefit from accounting for various self-reported and/or quantitative measures of pictorial ability. This will ultimately lead to a better understanding of the ways in which visual information activated by internal sources affect subjective visual perception.

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¹ I performed a Google Scholar keyword search within the list of citations for “visual working memory”, which retrieved 17 results, and “template”, which retrieved 14 results. Two were not in English. I performed another keyword search within each of the remaining 29 articles for the reference to the Kosslyn et al., 1984 article. 23 referenced this paper exclusively in the context of VI. One paper related VI to visual short-term memory (Brandimonte & Gerbino, 1993). Two related VI to VWM and cited the paper in the context of individual differences (Cornoldi & Vecchi, 2004; Ranganath, Cohen, Dam, & D'Esposito, 2004).

Acknowledgments

I would like to acknowledge Philipp Ruhnau and Stefan Pollmann for volunteering their time to provide helpful comments and suggestions for this review.

Appendix A. The visual preparatory strategy questionnaire given to subjects in the study by Reeder and colleagues (2016) following a visual search task. This questionnaire was not reported in the published study

Thank you for participating in this first part. We would like to ask you a few questions about how you performed the task. There are no right or wrong answers!

Try to remember what you did after you saw the cue (“M” or “P”) but BEFORE the scene appeared, and indicate the extent to which you agree with the following statements.

Answer each question on a scale from 1 (fully disagree) to 5 (fully agree)

1. After the “M” cue I looked out for cars at the multiple locations where they may appear in the scene	1	2	3	4	5
2. After the “M” cue I looked out for horizontal objects that were about the size of a car	1	2	3	4	5
3. After the “M” cue I looked out for one type of car (e.g., a sedan) at one location (e.g., in the center)	1	2	3	4	5
4. After the “M” cue I vividly imagined a car, as if I could almost see it in front of me	1	2	3	4	5
5. After the “M” cue I anticipated detecting cars seen from multiple angles rather than from one angle	1	2	3	4	5
6. After the “P” cue I thought about one particular individual, for example a person I saw on a previous trial	1	2	3	4	5
7. After the “P” cue I formed a general idea of what a person in the scene may look like	1	2	3	4	5
8. After the “P” cue I imagined persons with a prototypical posture as seen from the front	1	2	3	4	5
9. After the “P” cue I looked out for persons, but I didn’t have a vivid mental image of a person	1	2	3	4	5
10. After the “P” cue I looked out for vertical objects that were about the size of a person	1	2	3	4	5

Appendix B. Methods and results for the correlational analysis between car discrimination (d') reported in Reeder et al. (2016) and preparatory strategy ratings, the latter of which is previously unreported

B.1. Methods

Thirty-four self-proclaimed car experts (two women) participated in the study for payment. Participants were between the ages of 19 and 63 (mean age = 26.0 years) and had normal or corrected-to-normal vision. Participants performed a car discrimination task that assessed their level of expertise, followed by a

visual search task where they were required to search for cars (category of interest) and people (Reeder et al., 2016) embedded in photographs of real world scenes. Thirty-two of the thirty-four experts completed a visual imagery (VI) strategy questionnaire following the visual search task.

The results section below reports correlations between car discrimination performance (d') and VI strategy used for the visual search task. In the VI strategy questionnaire, statements 1, 5, 7, and 9 corresponded to a “general” strategy, and statements 3, 4, 6, and 8 corresponded to a “specific” strategy. Statements 2 and 10 corresponded to a “horizontal/vertical” strategy, which were not included in the following analyses. Each subject’s “general” and “specific” ratings were computed as the average reported strength of agreement with the 4 respective statements. “General” and “specific” scores were further broken down into “car” (1, 3, 4, and 5)- and “person” (6, 7, 8, and 9) statements (see Appendix A).

B.2. Results

Correlational analyses did not show any relationship between expertise (car discrimination d') and “general” VI ratings on the questionnaire ($p = 0.975$), but instead there was a significant negative correlation between expertise and “specific” VI ratings (Spearman’s $\rho = -0.424$, $p = 0.015$). With the hypothesis that these results were mainly driven by VI ratings for cars and not people, the latter of which represented the control category in the search task, a multiple regression analysis was run to determine the extent to which rating high on “specific” VI statements for each category contributed to these results. VI ratings on the “specific” statements significantly predicted subjects’ car discrimination performance ($F(2,29) = 3.343$, $p = 0.049$, $R^2 = 0.187$). As expected, these results were driven by VI ratings reported for cars ($t(31) = -2.063$, $p = 0.048$) but not people ($p = 0.352$).

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