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SPECIAL ISSUE

Linking Hypotheses in Visual Neuroscience: A Tribute to Davida Teller

REVIEW ARTICLE

Linking brain to behavior for the visual perception of figures and objects

JEREMY D. FESI AND JANINE D. MENDOLA

Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

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Abstract

The dissociation of a figure from its background is an essential feat of visual perception, as it allows us to detect, recognize, and interact with shapes and objects in our environment. In order to understand how the human brain gives rise to the perception of figures, we here review experiments that explore the links between activity in visual cortex and performance of perceptual tasks related to figure perception. We organize our review according to a proposed model that attempts to contextualize figure processing within the more general framework of object processing in the brain. Overall, the current literature provides us with individual linking hypotheses as to cortical regions that are necessary for particular tasks related to figure perception. Attempts to reach a more complete understanding of how the brain instantiates figure and object perception, however, will have to consider the temporal interaction between the many regions involved, the details of which may vary widely across different tasks.

Keywords: Linking hypotheses, Figure perception, Segmentation, Contours, Object shape processing, Depth structure

Introduction

The dissociation of a figure from background is an important part of object perception. Figure processing is necessary for us to detect, recognize, and interact with objects and entities in our environment. Not surprisingly then, humans are extremely sensitive to figure information, detecting and discriminating shapes across multiple cue types such as regional contrast of luminance, texture, color, motion, and binocular disparity (Regan, 2000) (see Fig. 1). We are so sensitive to potential figures that even cue-impoverished stimuli such as Kanizsa's (1979) triangle nonetheless yield strong percepts of modally completed "illusory" figural contours (see Fig. 2A). Attempts to understand how the brain instantiates our perception of figures have collectively provided some important cortical regions of interest and their associated roles in figure processing.

At the heart of the field of neuroscience is an attempt to understand the relationship between an animal's nervous system and its behavior. Similarly, experiments in psychophysics seek to investigate the manner in which measures of perceptual discrimination reflect constraints of underlying neural mechanisms. In this spirit, Teller (1984) outlined five families of "linking propositions" that can be used to infer neurological substrates of psychophysical data. Although some researchers combine psychophysical and neurophysiological recording methods to explore these links directly, many experiments adhere to only one methodology. In this case, linking "hypotheses" may be formed by bridging separate studies to suggest possible behavior/brain relationships. With regard to figure processing in humans, some studies do combine a direct behavioral measure with neuroimaging data, whereas others use passive viewing methods. To date, the most common task is a simple figure detection task. This does not allow for a specific investigation of individual processes underlying figure perception, but does ensure participants' perception of relevant stimuli relative to distractors, as well as attentional engagement. While a similarly explicit link to behavior cannot be made with data from the passive viewing studies, in some cases, such comparisons of data from task-based *versus* passive viewing conditions have not differed (Murray et al., 2002; Bakar et al., 2008; Guzzon & Casco, 2011; Appelbaum et al., 2012), but see an exception in the case of peripheral viewing conditions (Bakar et al., 2008). More generally, we can consider that passive viewing experiments are nonetheless eligible to support links to related task-based neuroimaging and psychophysical studies by analogy. Studies on nonhuman animals such as monkeys and cats also examine direct links between behavioral and physiological data, and these can also be compared by analogy to the data of human subjects (see Tootell et al., 2003; Orban et al., 2004). Such comparisons ideally allow us to understand how single-unit spiking activity—reflective of neuronal action potentials—relates to the population level activity that underlies both VEP and fMRI signals for noninvasive human studies. Although the differences between the recording methodologies serve to qualify interpretations of findings with regard to figure processing, there are nonetheless

Address correspondence to: Jeremy D. Fesi, Department of Ophthalmology, McGill University, Montreal, Quebec H3A 1A1, Canada. E-mail: jeremy.fesi@mail.mcgill.ca

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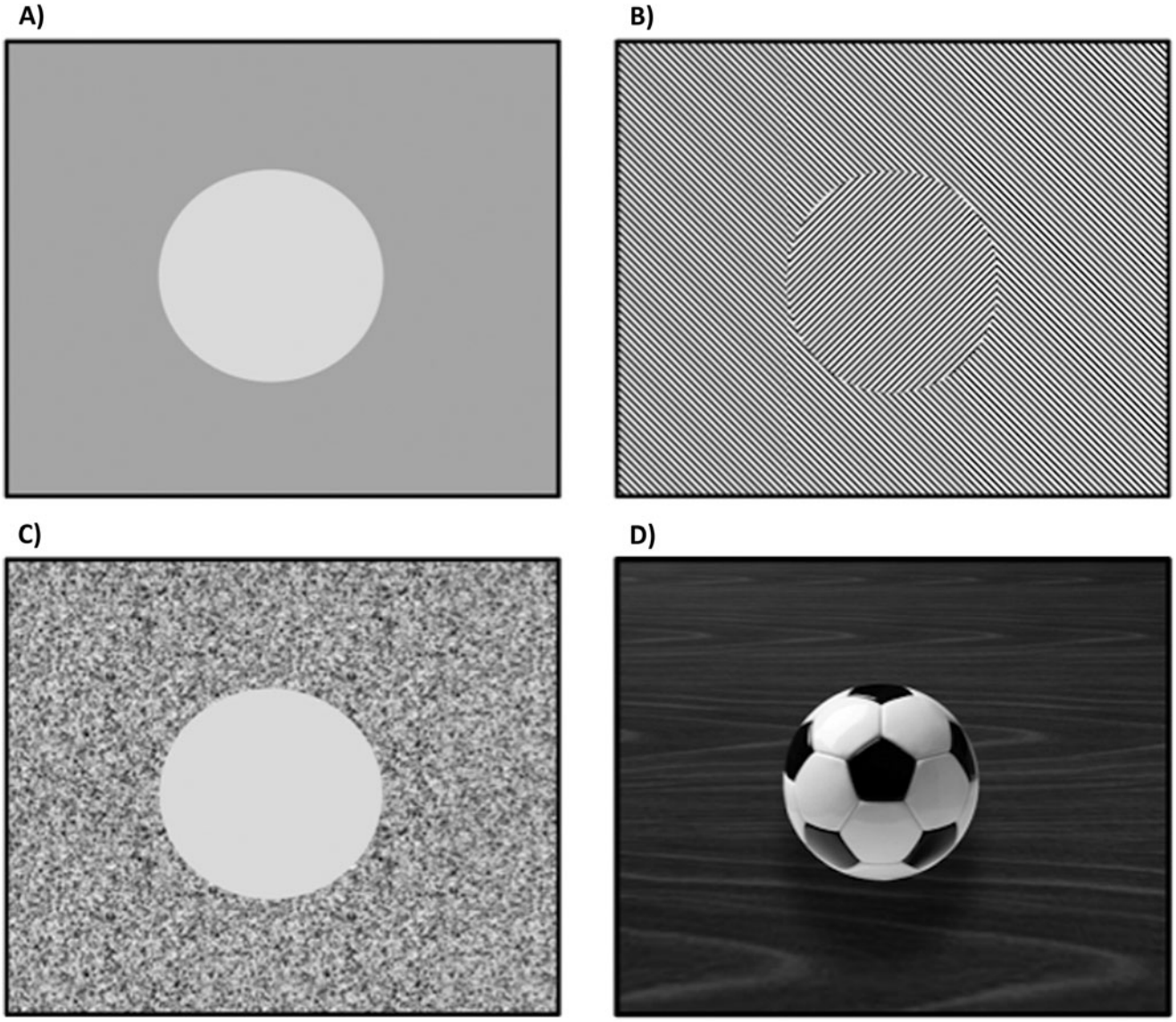


Fig. 1. Examples of figure contrast. Most experiments on figure contrast investigate sensitivity to only one type of contrast, such as (**A**) luminance or (**B**) texture, yet real figures are defined by multiple combined cues. (**C**) This schematic example shows a figure defined by texture, luminance, and spatial frequency contrast, whereas (**D**) shows a more realistic figure defined by luminance and texture contrast, plus some depth and shading cues.

encouraging similarities in their conclusions with regard to regions of interest and their functions (e.g., Kriegskorte et al., 2008).

The primate visual system is understood to be roughly hierarchical in organization, proceeding from striate cortex, to extrastriate regions, to increasingly higher-tier regions in lateral occipital (LO), temporal, or parietal cortex. This procession is not purely feed-forward, however, and feedback connections to lower visual areas have been shown to be very important for figure processing, as will be discussed. In fact, several proposed neural models of object and texture processing focus on statistical processing of natural image features rather than a hierarchically organized feed-forward circuit (e.g., Simoncelli & Olshausen, 2001; Naselaris et al., 2009). As an organizing principle for the contents of our review, however, we have opted to follow a somewhat conventional hierarchical scheme.

In Fig. 3, we propose a provisional model of distinct cortical processing stages related to figure perception. The stages of the model are not without controversy or disagreement, and these will be addressed accordingly, in turn, in the sections below. The first stage represents the processing of basic visual features at the local level of individual cells in primary visual cortex (V1); the second stage represents an early segmentation of a visual scene for salient regions; the third stage represents the interpolation of a two-dimensional figure surface, including the contours that distinguish the surface from surrounding regions; the fourth stage concerns selectivity for figure shapes, enabling discrimination and generalization; the fifth stage represents a volumetric interpolation of an object's surface; and the sixth represents a pair of parallel stages for volumetric shape categorization and detecting changes in the depth structure of a scene. Particular focus will be placed on the earlier stages of the model that relate most readily to two-dimensional figures, although the distinction of 2D from 3D image processing is not always clear, as will be made apparent.

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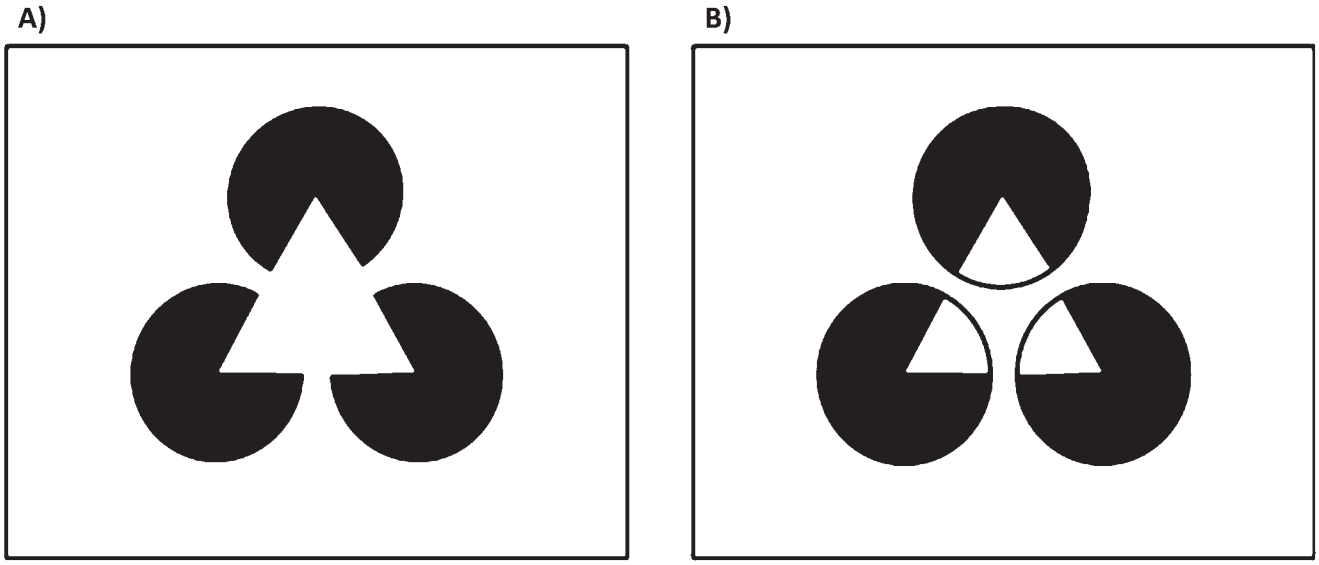


Fig. 2. Gestalt illusory shapes. In (**A**), the arrangement of the pacman inducers elicits the perception of an illusory white triangle occluding three black circles. The triangle results from modal completion of the gapped boundaries into a coherent figure contour, while the perception of the pacmen as occluded circles represents amodal completion of their hidden surfaces. In (**B**), the white triangle shape is completed amodally, and appears as if viewed from three holes in a wall.

Local feature sensitivity

The first stage in our model is the early processing of basic visual features, as occurring in primary visual cortex (V1) (Hubel & Wiesel, 1959, 1968). There is a large body of work that is impressive in its description of a retinotopically organized, multiplexed reduction of the visual image into simple features. At this early stage, local differences of luminance, color, orientation, or motion properties in the visual field excite the cells in V1 with receptive fields that correspond to the retinal area of stimulation. These local discrepancies provide "contrast" cues that are important for the detection of object edges (Livingstone & Hubel, 1988). While the most formative work on V1 is based upon single-unit recordings of cat and monkey cortex, fMRI studies on humans also demonstrate that area V1 is similarly important for early feature processing (e.g., Engel et al., 1997; Tootell et al., 1998; Schluppeck & Engel, 2002; Swisher et al. 2010). Additionally, lower visual cortex is important for the perception of figure contours. For instance, single-unit recording studies on monkeys have demonstrated for V1 neurons sensitivity to more global features such as a coherent *versus* incoherent Kanizsa shape (Lamme et al., 1993). Importantly though, the sensitivity to such stimuli has been shown to occur in V2 before V1, implying an early influence of feedback processing (Lee & Nguyen, 2001). Generally, the contribution of lower cortical regions to our detailed perception of figural contours is thought to depend upon feedback from higher visual areas (Grosof et al., 1993; Heider et al., 2000; Ramsden et al., 2001; Bauer & Heinze, 2002; Roelfsema et al., 2004; Li et al., 2006; Roelfsema et al., 2007; Likova & Tyler, 2008; Strother et al., 2012). This will be discussed in our section on figure contour interpolation. We argue, however, that there is a processing stage that is intermediate to local feature processing and contour interpolation. This stage is for the rough spatial segmentation of a scene into salient regions.

Scene segmentation of salient regions

After basic feature processing, the next stage of the model relates to the segmentation of a visual scene. In terms of its underlying neural processes, segmentation is largely thought to depend on a feed-forward progression from V1 to extrastriate regions (Appelbaum et al., 2012; Poort et al., 2012; Romeo et al., 2012), which exhibit progressively larger receptive fields (Tootell et al., 1988). Neural responses in regions V1–V4 to segmenting stimuli, most frequently figures defined by texture contrast, have been shown in to be unaffected by attentional demands, with differences between attention conditions being observed only among later responses in higher dorsal and ventral regions (Scholte et al., 2006; Martinez et al., 2007; Appelbaum & Norcia, 2009). Thus, scene segmentation has not been linked to conscious awareness but instead may operate early to cue attention and fixation for later conscious processing. Consistently, a behavioral study by Kimchi and Peterson (2008) found that altering the figure-ground information in the surround during a difficult task in central vision diminished performance, even without awareness of any alteration. Many researchers describe this early preattentive stage as "figure/ground segmentation," because, in most cases, the region of the scene that is segmented corresponds to a figure. However, we will avoid this description due to its association with continuous figure contours, a topic that will be addressed in the Figure contour interpolation section. Instead, like Stanley and Rubin (2003), we opt to use the term "salient region" as a cue for image segmentation, which may or may not result in subsequent figure contour interpolation.

Early work on texture segmentation focused on the "pop-out" properties of targets in complex displays (e.g., Julesz, 1981; Nothdurft, 1991), and this may relate more generally to early visual cueing to a region of a scene rather than specifically to figure surfaces. Similarly, Kanizsa illusory figures have been shown to exhibit pop-out salience in visual search tasks (e.g., Davis & Driver, 1994; Senkowksi et al., 2005), leading some researchers (Gurnsey et al., 1996; Stanley & Rubin, 2003) to investigate what aspect of the stimuli drives the pop-out effect. These experimenters each manipulated classic Kanizsa stimuli to diminish the perception of illusory contours (see Fig. 4 for an example) and found that pop-out salience was identical between the classic and the altered Kanizsa

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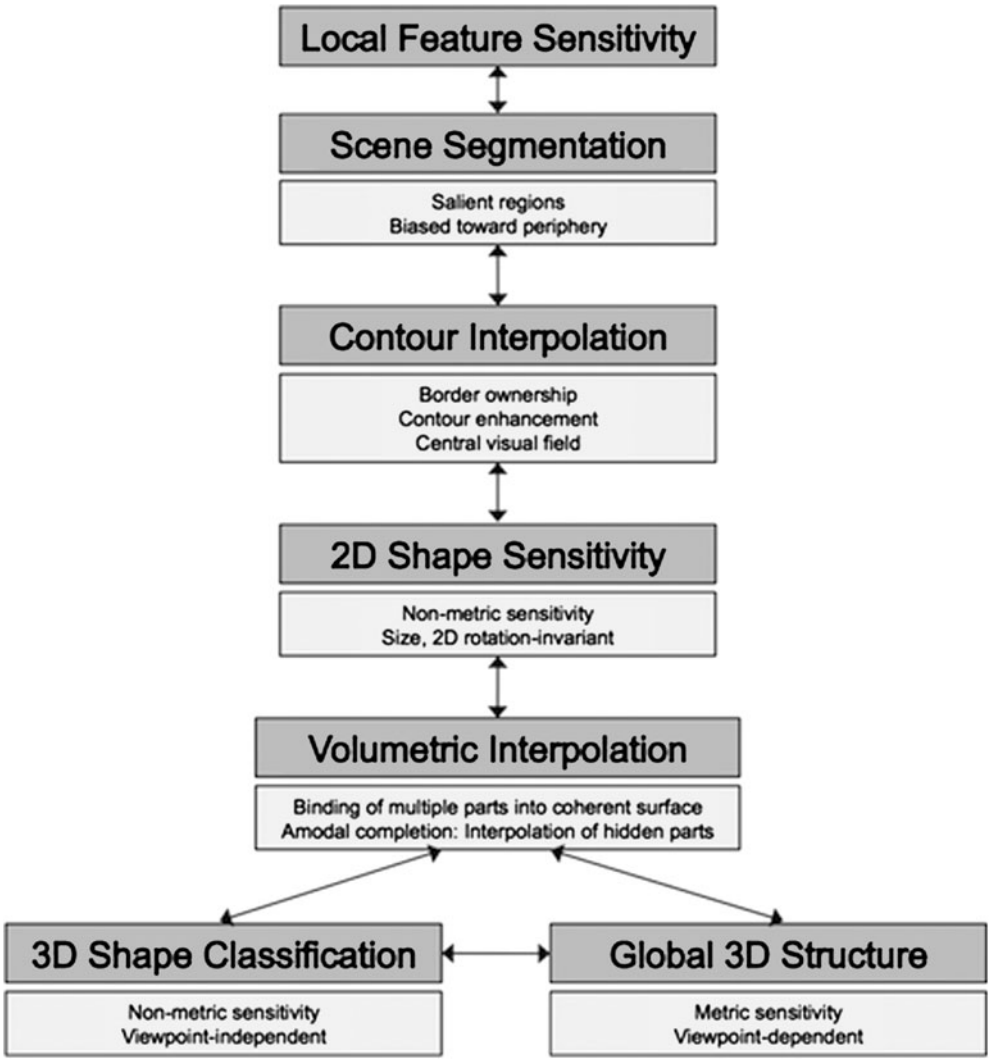


Fig. 3. Model of figure processing.

stimuli. Because the black inducers of the altered stimuli maintained their closed configuration, the stimuli served as "salient regions" for segmentation in a visual search, even though continuous illusory contours were not perceived. Thus, the sensitivity of the segmentation mechanism to the local features in the global configuration is broad, apparently not requiring the highest spatial precision.

This broad sensitivity to spatial configuration likely reflects a mechanism with low spatial frequency tuning and that is biased toward stimuli outside of central visual field. Psychophysical studies that directly investigated the effect of eccentricity on sensitivity to texture pop-out found that detection was optimal in the periphery (Fiorentini, 1989; Meinecke, 1989). Related to this, an eye-tracking study by Biber and Ilg (2008) found that pursuit initiation to illusory contour stimuli occurs before contour completion can take place, suggesting that segmentation facilitates fixation upon a salient region and that the perception of a figure's contours requires the high spatial precision afforded by central viewing (Hirsch & Curcio, 1989).

The role of different eccentricity biases across the visual cortex perhaps deserves more attention with regard to figure and object processing. Many studies on the neural correlates of segmentation (e.g., Roelfsema et al., 1998; Scholte et al., 2005, 2008; Appelbaum & Norcia, 2009; Appelbaum et al., 2012; Poort et al., 2012; Romeo et al., 2012) rely on fixed viewing conditions that require the subject to foveate on the center of a figure or on a figure's contour. (Scholte et al., 2006, 2008; Appelbaum & Norcia, 2009; Appelbaum et al., 2012). Others recorded from cells with receptive fields eccentric to a figure region (Roelfsema et al., 1998; Poort et al., 2012; Romeo et al., 2012), but the effect of eccentricity was not directly investigated. However, there are some important exceptions. For instance, McMains and Kastner (2011) investigated the effect of eccentricity on BOLD responses to Kanizsa shapes and some deformed variants. The authors found that the typical higher-level lateral occipitotemporal cortex responses to centrally placed coherent Kanizsa shapes were not observed when the shapes were presented outside of the central visual field. Eccentric stimuli activated lower-to-middle-tier extrastriate regions (V2–V4) instead.

Similarly, Caplovitz et al. (2008) found that the synchronized onset of four small circle stimuli in the near periphery (about 6° from fixation) activated areas V2 to V4, but not higher ventral regions; while Wong et al. (2009) employed a similar paradigm with central object viewing and did find significant activity in the LO complex, the group of areas in ventral visual cortex that have been found to respond selectively for coherent *versus* scrambled

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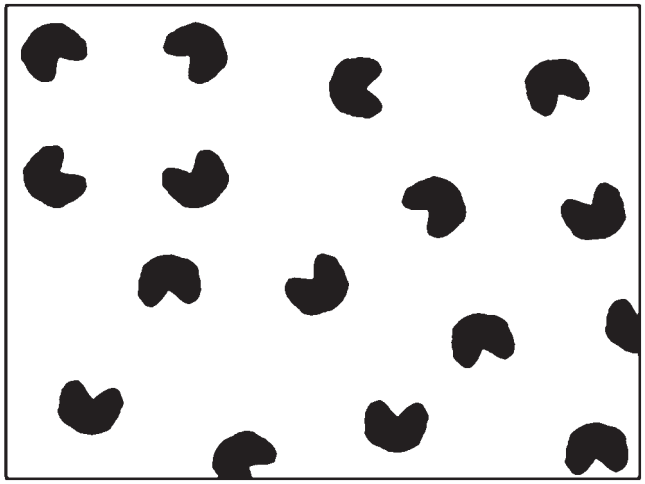


Fig. 4. A variant of the Kanizsa square with rounded, slightly misaligned inducers. Despite the absence of illusory contours, the salient region of configural closure is preserved. Because of this, it can be segmented from a scene of randomly oriented inducers.

object stimuli (Malach et al., 1995; Grill-Spector et al., 2001; Kourtzi & Kanwisher, 2001). Consistently, higher-tier ventral areas such as those in the LO complex have demonstrated a general sensitivity bias for stimulation in the central visual field, a bias that results from the higher spatial resolution of the fovea and is also shaped by visual experience (Levy et al., 2001; Hasson et al., 2002; Malach et al., 2002; Larsson & Heeger, 2006). Regions V1 to V3 (and possibly V4) may therefore be important for the detection of relevant stimuli in the peripheral or parafoveal visual field. The resulting scene segmentation may facilitate visual attention and foveal orienting that allows for a more precise interpolation of the figure *via* higher visual regions such as those in the LO complex.

Aside from the feed-forward progression of inputs from V1 to V4, another region that may play an important role in scene segmentation is the middle temporal area (MT) of macaques, known as V5 or hMT in humans (Born & Bradley, 2005). This crudely retinotopic area is thought to be crucial for the integration of local motion signals into globally coherent patterns (Adelson & Movshon, 1982; Newsome & Pare, 1988; Born & Tootell, 1992), but it has since been shown that MT may only integrate motion across regions of space rather than across the entire visual field (Majaj et al., 2007). The functional organization of some MT cell populations—namely, the opponent-tuning for center and surround receptive fields—has led investigators to conclude that the area is necessary for segmentation (Xiao et al., 1997; Masson et al., 1999; Born et al., 2000; Born & Bradley, 2005; Huang et al., 2007). Indeed, MT has demonstrated sensitivity to motion contrast stimuli (Marcar et al., 1995; Pack et al., 2004) and binocular disparity, a cue for object depth (Bradley & Andersen, 1998; Deangelis & Newsome, 1999; Krug & Parker, 2011). More specifically, however, the connective properties of MT—for example, direct connections to areas important for eye movements, such as the frontal eye fields, superior colliculus, and dorsolateral pons (Born & Bradley, 2005)—make the area a possible candidate for the initiation of ocular pursuit to a salient region of a scene. The precise contribution of MT to segmentation, however, remains to be fully understood, and the region will also be discussed with regard to contour interpolation and changing scenic depth structure.

Thus, after an initial, automatic feed-forward progression of object processing in visual cortex, the segmentation stage may lead to a more complex interaction between higher and lower cortical regions. The first stage of the model that depends on this complex interaction concerns the interpolation of a figure's surface contours, discussed below.

Figure contour interpolation

After the spatially rough segmentation of a scene, it is necessary to perceive certain regions within a scene as representing the surfaces of objects, including the contours that separate a figure from its background. The process is referred to here as "interpolation" because our perceptual construction of figure surfaces has been shown to occur readily even with limited visual information (e.g., Figs. 1 and 2). Nevertheless, in natural vision, objects can have clearly defined boundaries that separate the objects' surfaces from their surroundings. In uncluttered scenes, the contours of an object will close into a bounded two-dimensional image on the retina. These boundaries can be obscured, however, by occlusion in depth, which is discussed in the 2D shape sensitivity section. In addition to this information, objects provide a multitude of cues—such as regional contrast of luminance, color, texture, motion, and disparity—that consistently conform to, and thus reinforce, the spatial boundaries of their contours (Regan, 2000, Fig. 1).

From these many potential cues, the surface of a figure can be constructed by the visual system. Yet even in images that rely on only one or a few cues, there is a salient impression of continuous figure contours, even when there are local border discontinuities. Figure contour interpolation processes thus lead to the perceptual enhancement of an object's contours, which is also thought to be necessary for the illusory contours of a Kanizsa triangle (Fig. 2A). On the other hand, it is possible to find stimuli that have clearly defined line boundaries yet have ambiguous or competing "solutions" for different figure/ground relationships. Hence, the perceived ownership of the boundaries can be manipulated, or even shift from one rivalrous solution to another, as with Rubin's famous face/vase illusion (Fig. 5). We suggest that this reflects the same contour interpolation mechanism that contributes to perception of texture contrast displays and the Kanizsa shapes. In addition, these manipulations of border ownership (BOWN) perception reflect a mechanism that relies upon the global configuration of a scene for the assignment of a region as a figure, and the interpolation of the figure's surface boundaries, at least in two dimensions.

In principle, how might we identify a contour interpolation mechanism? First, it might exhibit identical response sensitivity across different figure cues. Given that figure cues from different types of figure contrast (e.g., Fig. 1) usually co-occur in natural images, a contour interpolation mechanism would likely show similar sensitivity to figure information across cue types, sometimes referred to as "cue invariance" (Albright, 1992; Sary et al., 1993). Aside from being cue-invariant, a mechanism that triggers contour interpolation might exhibit a response tuning across parametrically varied local contour strength that is nonmetric, but rather behaves in closer analogy with perceptual detection of figures. This would reflect an all-or-none process with a specific minimum value of figure size or contrast magnitude required to achieve interpolation. Naturally, such "categorical" tuning of responses to figure stimuli should be identical across cue types, as is generally the case behaviorally.

While there is some evidence that dorsal regions such as hMT+ may contribute to the processing of figure contours (see Likova & Tyler, 2008), their roles may be limited to dynamic figure contrast,

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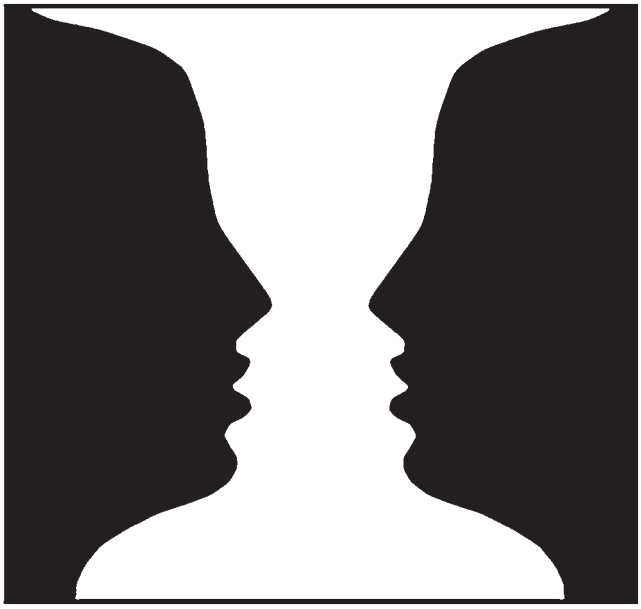


Fig. 5. Rubin's face/vase illusion. The image above can be seen as either a white vase in the center or two black faces to each side, but never both percepts at once. This is because the vase and the faces are defined by the same line boundaries and because the perception of any region as a figure requires the "ownership" of a boundary as the contours of the figure. Thus, the vase and faces compete for "border ownership," and the figure/ground organization changes with each perceptual shift in border assignment.

rather than serving as a general figure contour interpolation mechanism. In comparison, we do have evidence that more ventral areas in lateral visual cortex may be important for general object processing, as well as for figure contour interpolation. As mentioned above, the LO complex is a group of areas in human ventral visual cortex that have been found to respond selectively for coherent *versus* scrambled object stimuli (Malach et al., 1995; Grill-Spector et al., 2001; Kourtzi & Kanwisher, 2001). The complex includes the lateralmost parts of occipital cortex (called LO), as well as the likely homologue to monkey inferotemporal cortex (IT) and parts of the fusiform gyrus (Tanaka, 1997; Tootell et al., 2003; Orban et al., 2004; Preston et al., 2008). The anteriormost regions of LO complex such as the fusiform gyrus have been implicated in object processing that is more advanced than the extraction of simple figures from a scene. This includes the recognition of objects by a common category (e.g., Kriegskorte et al., 2008) and viewpoint-independent object shape sensitivity (e.g., James et al., 2002; Vanrie et al., 2002; Kim & Biederman, 2012), which will be discussed respectively in the 2D shape sensitivity and Volumetric surface interpolation sections.

In addition, there is evidence that the LO complex may also include a contour interpolation mechanism. In fMRI studies in monkeys (Sereno et al., 2002) and humans (Grill-Spector et al., 1998, 1999; Vinberg & Grill-Spector, 2008), for instance, the LO complex has demonstrated similar responses across different figure contrast cues, as well as for line-defined and illusory Kanizsa shapes, thus suggesting a cue-invariant sensitivity to figures. With regard to response tuning across parametrically varied object stimulus parameters, Mendola et al. (1999) and Altschuler et al. (2012) varied the size of Kanizsa figure stimuli, and both sets of authors observed response functions in the LO complex that were size-invariant. The responses were interpreted to reflect a categorical sensitivity to object information. Similarly, Fesi et al. (2011) compared VEP responses across types of motion contrast, as well as across contrast magnitudes, and found that responses in LO channels exhibited a categorical tuning function that likely reflected a threshold of figure contrast necessary to elicit a response, while dorsomedial channels showed a metric sensitivity that was similar across contrast cue types. In comparison, Thielscher et al. (2008) varied textural contrast, and argued that their results demonstrated a metric sensitivity to figure information in V4 and LO-complex. However, although the BOLD responses in these regions were parametrically ordered according to magnitude, we contend that the response functions reported by the authors are nonetheless quite compatible with an interpretation of categorical sensitivity rather than metric. Future research will be necessary to settle the matter, but it seems as if V4 and regions of the LO complex demonstrate sensitivity functions that support their consideration as possible mechanisms for contour interpolation.

In another line of evidence, the LO complex has shown responses to contour stimuli that are sustained and modulated by both spatial and object attention (Kourtzi & Huberle, 2005; Martinez et al., 2007), supporting its role as a top-down influence on lower visual areas for contour cues, as opposed to the more automatic nature of a scene segmentation mechanism (Appelbaum & Norcia, 2009; Keane et al., 2011). Interestingly, Stanley and Rubin (2003) argued that the LO complex is not important for contour interpolation but may instead be involved in scene segmentation. The authors found that BOLD responses in the LO complex were similar for classic Kanizsa shapes and altered variations with preserved salient regions (Fig. 4). The authors' conclusion, however, was based on separate analyses of scans for the classic and altered conditions, and so the pattern of BOLD activation for a direct comparison of the conditions remains to be formally addressed. Also, in terms of the temporal dynamics of the responses, Shpaner et al. (2009) conducted a similarly designed VEP experiment, and found that early evoked responses among LO channels were stronger for Kanizsa shapes than for the modified variants, while dorsomedial occipital responses were similar across the stimulus types, as were later LO channel responses. It remains likely then that regions in the LO complex are responsible for contour interpolation, while dorsal extrastriate areas might contribute to the faster low spatial frequency segmentation of a scene into salient regions (see also Knebel & Murray, 2012).

Might contour interpolation occur in a visual region lower than V4? Lower-to-middle-tier visual areas have also been implicated in figure contour interpolation, but their precise roles remain obscure. Traditional models of figure processing, inspired by single-unit studies of V1 and V2 response properties, relied on a feed-forward progression from striate to extrastriate cortex, to increasingly higher regions in lateral cortex. Yet full-scalp VEP experiments that explicitly compare the response properties of medial *versus* LO channels show that contour-specific responses in LO channels precede those in medial or dorsomedial channels (e.g., Halgren et al., 2003; Shpaner et al., 2009; Knebel & Murray, 2012). So, although cue-invariant sensitivity to figure contours has been observed in V2, V3, V3a, and V3b in monkeys (von der Heydt & Peterhans, 1989; Mysore et al., 2006; Sheth et al., 1996; Leventhal et al., 1998; Zeki et al., 2003; Peterhans et al., 2005; Zhan & Baker, 2006) and humans (Dupont et al., 1997; van Oostende et al., 1997; Kastner et al., 2000; Skiera et al., 2000; Zeki et al., 2003; Schira et al., 2004), this may not reflect contour interpolation *per se* but could be related to another cue-invariant process, such as scene segmentation.

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Indeed, there is evidence to suggest indirectly that MT+ and regions of the LO complex might be driving such cue-invariant sensitivity to figures in lower visual cortex. For instance, Welchman et al. (2005) demonstrated that BOLD responses in both hMT+ and the LO complex (but not lower-tier areas) respond more strongly to the combination of two different cues to the depth structure (in this case, binocular disparity and linear perspective) than to either cue presented in isolation. Additionally, Chandrasekaran et al. (2007) found that the same regions show BOLD response increases to the amount of global structural coherence in disparity-defined objects. Perhaps most intriguingly, fMRI studies by Ferber et al. (2003, 2005) compared the duration of participants' perceptual persistence of visually presented figure stimuli (i.e., subjective report of percept duration upon removal of the stimuli) with BOLD response duration. The authors found that perceptual persistence was linked to increased activity in LO cortex (and not hMT+), across different figure cues types. Wong et al. (2009) found a similar link between perceptual persistence of objects and BOLD response duration in the LO complex as well as lower areas such as V2, V3, and V4. However, a brief (50 ms) duration flash of the object stimulus was linked only to the LO complex. Because the temporal profile of responses in the LO complex corresponded with briefly flashed as well as persistent stimuli, the authors concluded that regions in the complex are responsible for figure interpolation, and recruit the lower- and middle-tier regions for contour salience and persistence of the object percept.

Although the full picture is far from clear, these studies collectively support the notion that it is the higher-tier ventral (and possibly dorsal) regions that are responsible for figure contour interpolation, partially through their influence on lower regions of visual cortex. However, beyond this conclusion, there is no one region that can be considered without a doubt as being responsible for contour interpolation. More direct comparisons of areas such as V4, MT, and LO cortex will be necessary to better understand their respective contributions to the figure processing circuit. One aspect that may shed some light in this respect is the progression from two-dimensional figure images to volumetric surface structures, which will be discussed below.

2D shape sensitivity

Studies that explore sensitivity to object features typically employ some type of shape or feature categorization task, and this largely engages areas in the ventral visual stream (Lehky & Sereno, 2007; Milner & Goodale, 2008). Within this cortical stream, sensitivity to shape has been observed to be roughly hierarchical (see Hegde & van Essen, 2007), with V4 and IT showing progressively more sensitivity to feature complexity than area V2 (Desimone et al., 1985; Kobatake & Tanaka, 1994; Rust & DiCarlo, 2010; Carlson et al., 2011).

Aside from being implicated in top-down contour interpolation processes, V4 is particularly important for 2D shape classification. Activity in V4 has been linked to shape discrimination in humans (Vinberg & Grill-Spector, 2008; Ales et al., 2012). Additionally, Denys et al. (2004) directly compared BOLD responses between monkeys and humans and found similar shape-selective response sensitivity in V4. How exactly does V4 contribute to shape processing? Single-unit recording studies on monkeys (Pasupathy & Connor, 2001, 2002; Rust & DiCarlo, 2010; Mysore et al., 2006; Carlson et al., 2011) indicate that individual cells in V4 respond preferentially to particular contour curvatures, with most cells exhibiting an orientation-specific tuning for either convex or concave curvature that is invariant across retinal position. Pasupathy and Connor (2002) have demonstrated that the orientation-specific curvature tuning of the individual cells likely represents a preference for object shape components and that the population responses of V4 can code for different shapes because of these response preferences. Because of this, V4 is regarded as a plausible mechanism for 2D shape coding.

Proceeding beyond V4, the human LO complex shows robust sensitivity to shape information (Malach et al., 1995; Kanwisher et al., 1996; Altmann et al., 2004; Vinberg & Grill-Spector, 2008). In an attempt to localize areas of the brain with sensitivity to object shape, Grill-Spector et al. (1998) parametrically varied the spatial extent of phase-scrambling of object stimuli, and found that the LO complex was more selective for coherent object images than V4, which demonstrated a more intermediate sensitivity. This implies that, while V4 is important for object shape processing, the higher regions of ventral visual cortex encode the most global, orientation and position-invariant object shape information. How do the different regions within the LO complex contribute to shape processing? Lesions in posterior parts of the complex such as LOR have been linked to deficits in shape categorization tasks (James et al., 2003). This region exhibits limited position, and size invariance, in contrast to the more invariant-shape selectivity of more anterior parts, including IT (Denys et al., 2004; Sawamura et al., 2005; Stanley & Rubin, 2005; Larsson & Heeger, 2006). IT's robust and rotation-invariant sensitivity to 2D shapes has been well established *via* monkey single-unit studies (Ito et al., 1995; Fujita, 2003; Brincat & Connor, 2004; Lehky & Sereno, 2007). In fact, Baylis and Driver (2001) demonstrated that IT cells responded invariantly across luminance changes and mirror reversals of figure shapes, yet the cells were sensitive to stimuli that reversed in figure-ground arrangement, even though the contours of the stimuli remained unchanged. This offers convincing evidence that IT reflects a higher-level processing of object-based information across orientations and deformations than the more intermediate V4.

However, while shape processing is commonly thought to proceed hierarchically from V4 to areas of the LO complex, the actual dynamic network and its links to perception and task seem to be more complicated and variable. For instance, a VEP study employing cortical source localization methods (Ales et al., 2012) reported results that suggest a reverse order of processing. In their study, activity time locked to a shape discrimination task was first observed in the LO complex and then in V4. While this particular sequence of activation may be limited to tasks that require top-down strategies for performance, the results nonetheless serve to emphasize the point that cortical processing of figure and object perception is only roughly hierarchical and may vary greatly according to task. A challenge to the field, however, is to understand why some monkey studies have reported that IT lesions did not significantly affect object shape discrimination (Huxlin et al., 2000; Merigan & Saunders, 2004), although V4 lesions have resulted in considerable deficits (Walsh et al., 1992; Merigan & Pham, 1998; Girard et al., 2002).

Aside from the ventral stream regions discussed above, some dorsal stream regions have been consistently implicated in shape discrimination tasks, particularly V3A and parts of the IPS (Denys et al., 2004; Lehky & Sereno, 2007; Janssen et al., 2008; Klaver et al., 2008). Lehky and Sereno (2007) point out that dorsal stream shape sensitivity is much broader and weaker than regions such as IT and is likely not dependent upon input from the ventral stream.

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The role of these dorsal regions in object-related perception is controversial and will be discussed more extensively in the Discussion section.

Volumetric surface interpolation

In natural scenes, objects only very rarely cast perfectly symmetrical two-dimensional images on the retina. Instead their shapes can be more complex, they can be oriented in depth and can be obscured or partially hidden by other objects (known as "occlusion"). Thus, the visual system must interpolate coherent three-dimensional surfaces from the elements of a scene. This includes the binding of separate 2D image components into a surface and also completing surface edges that are hidden from view (sometimes both at once, see Fig. 6A).

An interesting question regarding the completion of occluded surfaces (amodal completion) is to what extent such completion differs in processing from the modal completion of illusory occluding surfaces like the Kanizsa triangle. Some researchers regard them as similar processes with shared mechanisms (e.g., Weil & Rees, 2011), yet others think of them as distinct (Singh, 2004; Zhou et al., 2008). Indeed, there are some indications that amodal completion may occur at a later processing stage than modal completion. For instance, human VEP experiments show that while the earliest responses among LO channels are similar for modal and amodal completion cues, negative potentials following a latency of about 250 ms are stronger and more sustained for amodal completion cues (Murray et al., 2004). Similar late negativity differences were observed by Brodeur et al. (2009), who found that the later responses were higher for amodal completion cues than modal completion cues. The authors argued that these later responses are inversely weighted to the perceptual saliency of the stimulus and that amodal completion requires more attentional processing to compensate for the ambiguity of surface cues. Moreover, when a stimulus with both modal and amodal cues was used to explore the competition of the two cue types, the perceptual difficulty-related negative evoked responses were largest for amodal targets with modal cue distractors (Brodeur et al., 2009).

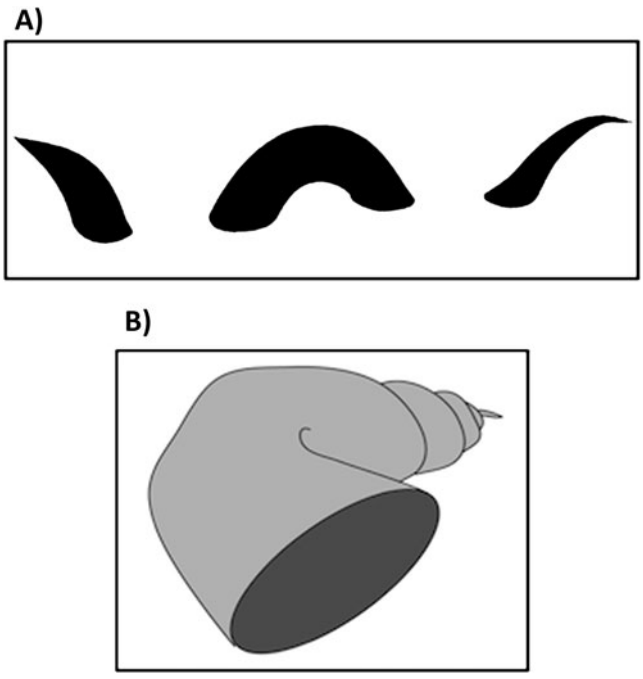


Fig. 6. Our own images of pictorially implied volume, inspired directly by Tse (1999). (**A**) Depicts a "sea monster" surface that requires the binding of multiple 2D components and the amodal completion of the monster's hidden parts. (**B**) Depicts a self-occluding object surface.

Thus, the comparison of modal and amodal completions suggests not only that the underlying interpolation processes may be different but also highlight the perceptual dominance of modally completed contours. After all, many experiments use the traditional Kanizsa images to investigate modal completion of the illusory "square" or "triangle" contours, rather than the amodally completed "circle" components. This may be because modal completion cues provide information about occluding objects, which in natural scenes are fully visible and closer to the observer than occluded objects. However, it may also be due to the perceptual ambiguity of objects that are partially hidden from view.

Our consideration of amodal completion, which concerns the interpolation of occluded surfaces, raises some more general questions concerning the processing of objects in depth. Does the perception of three-dimensional objects including complex self-occluding objects (Fig. 6B) as coherent volumetric surfaces simply depends on a hierarchical progression from 2D image sensitivity to 3D viewpoint-independent object recognition? Or is it more helpful to view all object interpolation processes in the brain as being biased toward volumetric surfaces, despite some observed sensitivity to unrealistic and impoverished 2D images used in experiments? Tse (1999) seems to argue for the latter interpretation, though the former is the more popular interpretation (see Kellman et al., 2005). While more research is needed to clarify the issue, the truth may exist somewhere in between a strict hierarchy from 2D to 3D *versus* an obligatory 3D analysis that applies to all images.

As mentioned earlier, real objects provide multiple overlapping cues, including cues to the three-dimensional structure such as shading and binocular disparity. Moreover, binocular disparity tuning is apparent already at the level of V1 (Poggio & Fischer, 1977; see also DeAngelis, 2000; Orban et al., 2006; Roe et al., 2007). Additional sensitivities are apparent in V2 and in V4, for example, a response preference for crossed disparities, indicating a bias for close objects (Hinkle & Connor, 2002, 2005). But are there cortical regions that code explicitly for a three-dimensional structure? The answer is yes, although the underlying processing may not reflect a classic hierarchical progression. It has been demonstrated that the brain regions involved in the processing of the 3D structure depend greatly upon the tasks employed to study the activity (e.g., Culham et al., 2003; Valyear et al., 2006; Cavina-Pratesi et al., 2007). For this reason, we will discuss, in separate sections, the brain regions implicated in 3D shape classification, requiring viewpoint-independent object sensitivity; and those involved in the computation of changing 3D scene structure, requiring viewpoint-dependent sensitivity.

3D shape classification

As mentioned earlier, the ventral visual system exhibits a roughly hierarchical progression of sensitivity to increasingly more complex object shapes. While sensitivity to image complexity is important, object features are not limited to the two-dimensional images they cast upon the retina. On the contrary, real objects must be recognized despite changes of the retinal image due to manipulations such as rotation in depth. Experiments concerned with contour interpolation and basic shape sensitivity typically rely on simple

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2D figure stimuli, but it is important to establish which regions of the cortex are merely sensitive to the shape of 2D retinal images, and which show viewpoint-independent sensitivity to object surface features, and are thus impervious to 3D transformations.

A few studies have directly compared 2D and 3D object cues. Regarding human subjects, Kourtzi et al. (2003) investigated fMRI adaptation responses in the LO complex to changes of 2D and 3D features. The authors reported, overall, that the LO complex did not demonstrate adaptation effects when objects had the same 2D contour shape but different 3D shapes (concave *vs*. convex in depth)—indicating a particular sensitivity to changes in the 3D structure rather than 2D image features. Moreover, there was a response adaptation when objects had similar 3D shapes but different 2D-outlined shapes (due to 3D rotation)—supporting the notion that the LO complex is primarily tuned to volumetric rather than 2D surface cues. Although the complex was found to collectively demonstrate preference for 3D structural cues, the authors subsequently localized response sensitivity to changes in 3D shape (convexity *vs*. concavity in depth) to anterior regions of the complex such as posterior parts of IT and fusiform gyrus, noting that posterior regions such as the lateral occipital region (LOR) did not exhibit such sensitivity to 3D shape change. Thus, although LOR does show sensitivity to depth cues, it is perhaps limited to image rather than object features.

Similar to the anterior LO complex, single-unit studies on monkey IT (Janssen et al., 2008; Yamane et al., 2008; Hung et al., 2012; Verhoef et al., 2012) show a sensitivity to 3D rather than 2D transformations, suggesting that the cells in the area respond to "inferred" 3D object cues from 2D displays rather than retinal image features. Moreover, somewhat resembling cells in V4 that exhibit differences in their preferred 2D contour curvatures (Pasupathy & Connor, 2001; Carlson et al., 2011), IT cells have been shown to differ in their preference for volumetric shape; these differences allow for the interpolation of a coherent viewpoint-independent representation of the object structure *via* the combination of cell responses to their respective preferred component shapes (Brincat & Connor, 2004; Yamane et al., 2008; Hung et al., 2012). These results seem compatible with a classic largely hierarchical theory for 3D shape processing such as that of Marr and Nishihara (1978), according to which object structures are perceptually derived from combinations of encoded structure components or "geons" (see also Beiderman, 2001).

Thus, hierarchical progression of invariant shape sensitivity is generally observed in the ventral visual stream for object categorization tasks, although the progression of sensitivity may be more of a graded one than a discrete step-wise progression (Hegde & van Essen, 2007; Rust & DiCarlo, 2010). IT perhaps represents a point in the processing hierarchy where object, rather than image, features are coded. This ultimately allows for the differentiation and generalization of object stimuli by categories such as "Animate" *versus* "Inanimate," or "Face" *versus* "Body"; an organizing principle that is similarly reflected in human fMRI and monkey single-unit recording studies (Tanaka, 2003; Kriegskorte et al., 2008; Haxby et al., 2011). Indeed, the number and structure of category representations remain a provocative question (e.g., Huth et al., 2012) as activity in regions such as the fusiform face area (FFA) is believed to instantiate the differentiation of exemplars within a shared category, most prominently demonstrated for face discrimination (Kanwisher et al., 1997; Grill-Spector & Malach, 2004; Loffler et al., 2005), but perhaps also for any fine-level within-category discrimination that is driven by training and expertise (Gauthier et al., 1999, 2000).

Yet this ventral circuit is not the only means in which the brain encodes the object structure. The Global 3D structure section discusses areas in the dorsal visual stream that calculate changes in the global depth structure of a visual scene, which is important for object tracking and manipulation rather than categorization.

Global 3D structure

While viewpoint-independent feature sensitivity is important for tasks related to categorization and recognition, sensitivity to image features that are viewpoint-dependent is important for tracking the spatial position and orientation of objects in relation to one another, as well as to the observer's own egocentric space. Such information is crucial for tasks requiring navigation, object pursuit, and object manipulation (Valyear et al., 2006; Milner & Goodale, 2008). Unlike object categorization, these types of tasks are primarily associated with activity in the dorsal visual stream (Haxby et al., 1991; Milner & Goodale, 2008). The overall function of the dorsal stream is somewhat controversial, as will be addressed later. However, we propose that dorsal regions sensitive to figure and object stimuli are important for processing the changing the *depth structure* of a scene, thereby allowing for viewpoint-dependent object sensitivity. Orban (2011) defines depth structure as "the variation of depth along the surface or edge of an object." Thus, object-sensitive regions in the dorsal stream process information about the three-dimensional surface layout of an observer's surroundings, particularly the continuous changes that arise from the object and observer movement (Borst et al., 2011).

Because Mishkin et al. (1983) famously observed that large lesions along the dorsal stream were found to affect a monkey's ability to detect an object's position in space, the stream is often thought to be necessary for spatial vision, including depth. However, depth processing is much more complicated than the classic dichotomy suggests, and it involves both visual streams. For instance, Neri et al. (2004) used fMRI to compare activity in dorsal and ventral regions to absolute and relative binocular disparity. Relative disparity—or the angular difference in binocular disparity between two objects—can provide cues to the respective depths of multiple objects. The authors concluded that ventral stream regions were more sensitive to relative disparity information than dorsal stream regions, which appeared as particularly sensitive to absolute disparities. However, several subsequent studies indicate that regions in the dorsal stream do indeed process relative disparity. For instance, Cottereau et al. (2011, also see 2012a, 2012b) observed that human V3A was particularly sensitive to relative disparity defined by a center-surround configuration of dot stimuli with distinct binocular disparities for center *versus* surround. In fact, the gain modulation of the V3A response was found to be proportional to the disparity difference. This metric sensitivity to relative disparity was also found in V3 and V3A of macaque *via* single-unit and multiunit recordings (Anzai et al., 2011). A separate single-unit study on monkeys by Krug and Parker (2011) varied relative disparity values of transparent overlapping "planes" of moving dots and found that cells in MT+ are tuned to relative, as well as absolute, disparity. What might account for the discrepancy of findings between these studies and Neri et al. (2004)?

As mentioned in the Global 3D structure section, the ventral stream is largely associated with stimulus classification, and a look at the tasks employed in the above studies seems to support this interpretation. While Anzai et al. (2011) and Cottereau et al. (2011) both relied solely on passive subject fixation, Neri et al. (2004) employed a depth discrimination task. Krug and Parker (2011) interleaved a similar discrimination task within their viewing protocol to assess the monkeys' performance, but the spiking data

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reported were taken only from the passive viewing trials. Moreover, a single-unit study on monkeys by Shiozaki et al. (2012) linked the response thresholds of V4 cells for relative disparity to the monkeys' discrimination thresholds in a psychophysical task. Collectively, these results are compatible with our interpretation of ventral stream regions as being linked to tasks involving classification. While the ventral stream has been shown to respond to relative disparity information, it may be primarily limited to categorical judgments of relative depth such as a disparity discrimination task. In an fMRI study by Preston et al. (2008), the authors endorse a similar conclusion. In the study, figures of varying disparities were presented to subjects as they performed an unrelated task to ensure attentive viewing. The authors found that dorsal areas such as V3A, V3B, V7, and intraparietal sulcus were found to exhibit a metric sensitivity to absolute disparity, while regions of the LO complex instead showed categorical sensitivity to "depth sign," in which a disparity-defined plane was either "behind" or "in front of" the fixation point. The study focused on absolute rather than relative disparity cues, but the results suggest that binocular disparity as processed in the ventral stream may have less to do with depth computation *per se* and more to do with qualitative object attributes. This is consistent with the interpretation of ventral stream processing as being primarily for viewpoint-independent categorization.

Thus, in contrast to the ventral stream, dorsal stream areas seem to show a metric sensitivity to changes in scenic depth structure, which includes figures defined against a background. Although midlevel dorsal regions such as V3A and V3B have previously been interpreted as specifically important for figure contour interpolation (Dupont et al., 1997; van Oostende et al., 1997; Zeki et al., 2003; Schira et al., 2004), studies that have explicitly compared responses in these regions across different depth cues indicate instead that they are particularly sensitive to cues to 3D structure (Beer et al., 2002; Tyler et al., 2006; Preston et al., 2009; Ban et al., 2012). Ban et al. (2012) in particular highlight the distinct sensitivity of V3B to combined depth structure cues (motion contrast and disparity), specifically when the cues offer compatible indexes of structure in depth. In this light, we propose that the metric sensitivity of dorsal areas such as V3A and V3B to disparity and motion contrast information (e.g., Preston et al., 2008; Anzai et al., 2011; Fesi et al., 2011; Cottereau et al., 2011) should be thought to reflect sensitivity to scene structure cues. Such a metric sensitivity to the changing global depth structure of a scene is consistent with the interpretation of the dorsal stream as generally important for viewpoint-dependent object processing (Gauthier et al., 2002; James et al., 2002; Vanrie et al., 2002; Kim & Biederman, 2012). This type of information would allow for the visual tracking of object features in depth (Caplovitz & Tse, 2007), as well as observer–object interactions such as grasping (Culham et al., 2003; Valyear et al., 2006).

Discussion

The experiments reviewed above offer important insight into the neural mechanisms of figure perception, either by directly exploring linking hypotheses between physiological and psychophysical data or by allowing us to construct less specific links by analogy. In this article, a processing model was proposed to provide a contextual framework for the experiments, with stages that proceed hierarchically according to function. The earliest stage of cortical processing is one of the best established in vision research, and concerns basic visual features. The second stage represents the segmentation of salient regions in a scene. This is followed by the interpolation of a figure's contours, which allows for the identification of the figure's shape. The fifth stage concerns volumetric surface interpolation, which allows for subsequent shape classification of three-dimensional surfaces, and the tracking of objects as they, as well as the observer, move in depth.

Our model and the surrounding literature review clearly serve as robust examples of the brain/behavior correlation claims that Teller (1984) sought to evaluate *via* families of linking propositions. We note in passing that several of the propositions and their implications are manifest here. In particular, our emphasis on neural responses that are invariant to cue type (contour interpolation), size, position, and rotation (2D shape sensitivity), or rotation in depth (3D shape classification) all represent strategic information loss that leads to a mapping between stimuli and brain states that is many:1, within the Identity family. Second, implicit in our discussion of metric *versus* categorical neural responses for contour strength or for 3D depth is the idea of a Similarity family in which continuous "monotonic variation in neural activity implies a monotonic variation in sensation and vise versa." Third, Teller cited bistable figures (and in our current context, the associated border ownership) as an example of the Mutual Exclusivity family of propositions in which percepts would have mutually exclusive brain states. Finally, her concept of the "bridge locus"—the set of neurons whose activities form the immediate substrate of (conscious) visual perception—is as relevant as ever. Teller's ideas seem to us to often be testable in principle and might motivate future experiments.

The current consensus regarding the neural substrates of our model's processing stages can be mapped out very roughly in terms of cortical regions, but the precise details of the underlying circuits remain unknown. For instance, the point in the circuit at which feed-forward processing of object information first cues top-down processes *via* feedback connections has yet to be clearly determined and is probably task dependent. As discussed above, this likely happens in lateral regions of occipital cortex for contour interpolation, yet the extent to which a midlevel area such as V4, as opposed to a somewhat higher region such as LOR, contributes to contour interpolation and 2D shape processing is not clear. Dissociating the functions of these regions will therefore be essential to understanding the dynamics of the circuit, especially the transition from 2D to 3D feature processing.

Generalizing beyond specific cortical regions, it may be important to understand figure processing in the larger context of the dorsal and ventral visual streams. These are thought to be functionally dissociable, with the ventral stream conventionally interpreted as important for the categorization and discrimination of the permanent features of objects, irrespective of the observer's viewpoint, whereas the dorsal stream is thought to instantiate the visual control of an observer's actions and is therefore more sensitive to changes related to an observer's viewpoint of objects (Mishkin et al., 1983; Haxby et al., 1991; Kobatake & Tanaka, 1994; Passingham & Toni, 2001; James et al., 2002; Sereno et al., 2002; Vanrie et al., 2002; Cox et al., 2005; Valyear et al., 2006; Milner & Goodale, 2008). Studies that highlight the categorical response properties of ventral areas *versus* the metric response properties of dorsal areas (Preston et al., 2008; Thielscher et al., 2008; Fesi et al., 2011; Altschuler et al., 2012; Cottereau et al., 2011) can be seen to support such a functional dissociation of the two processing streams.

Despite the usefulness of the two-stream model, there are researchers who argue that a conceptualization of the dorsal and ventral streams as functionally dichotomous—be it "what *versus* where," "what *versus* how," or "action *versus* perception,"—to be overly simplistic, obscuring important details of the visual system. For instance, in their review of functional and anatomical evidence

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from monkey cortex, Kravitz et al. (2011) argued that there are at least three pathways within the dorsal stream—the parieto-middle temporal, parieto-prefrontal, and parieto-premotor pathways—each important for distinct functions. Schenk and McIntosh (2010) stressed the extensive connections and interactions between the dorsal and ventral streams. Similarly, both *dorsal* hMT and *ventral* LO complex have been implicated in top-down processing related to figure contours (Kourtzi & Huberle, 2005; Likova & Tyler, 2008) and have shown similar response sensitivity to object coherence (Chandrasekaran et al., 2007) and the combination of depth cues (Welchman et al., 2005).

One unresolved controversy that is pertinent to linking hypotheses for figure processing concerns this dorsal stream and its contribution to conscious visual perception. The data primarily come from experiments using a method of dichoptic image presentation known as "continuous flash suppression." In this paradigm, an object stimulus is presented to a participant's nondominant eye, and a distractor grating is presented to the dominant eye, resulting in prolonged periods during which the participant reports no percept of the object. Despite the lack of object awareness, activity in the dorsal stream shows a robust object response, indicating that it is dissociated from conscious object perception (Fang & He, 2005; Almeida et al., 2008; Sakuraba et al., 2012). However, others argue that by using an objective assessment of perceptual sensitivity, such as the two-alternative forced choice (2AFC) method, rather than subjective reports, a neural link to conscious object perception is revealed that is similar for both ventral and dorsal stream regions (Hesselmann & Malach, 2011; Hesselmann et al., 2011). Regardless, data from multiple lesioning studies has lead Milner (2012) to conclude that, although activity in dorsal regions can sometimes be linked to tasks related to conscious perception, perhaps due to connections to other areas in the brain, the stream itself has limited access to conscious perception.

As was the case for our description of the automatic segmentation of scenes into salient regions, an unconscious process could still be regarded as an important influence on our behavior (Kimchi & Peterson, 2008). Indeed, in general, human behavior is no doubt affected strongly by many unconscious influences, in which neural activity is impactful but is not reflected in the contents of awareness. However, typically, linking hypotheses are intended to formalize the neural activity that is directly positively (or negatively) correlated with a conscious behavioral threshold or outcome. Therefore, in the case of the proposed dorsal stream dissocation from object-related awareness, it is important to consider both the presence and the absence of specific brain/behavior correlations in order to form a comprehensive understanding of how a region or circuit of the brain contributes to conscious visual perception (i.e., the bridge locus). A second implication of Milner's (2012) conclusion is that linked relationships of neural activity and behavior depend greatly upon the methods and tasks employed and may not necessarily reflect a constant overall function of a region or network.

Indeed, this controversy concerning the dorsal stream points to the more general issue of how individual linking relationships are constrained by the tasks and recording methods used to explore them. Brain–behavior links are often investigated within a limited range of tasks, such as onset detection or feature discrimination. It has been noted before that certain studies found no significant differences in responses for detection tasks and passive viewing conditions (Murray et al., 2002; Bakar et al., 2008; Guzzon & Casco, 2011; Appelbaum et al., 2012), yet the generalizability of the links across different tasks was not formally investigated. Studies that have directly compared links across tasks for similar stimuli include those that support a functional dissociation of the dorsal and ventral streams for grasping/tracking and categorization tasks, respectively (e.g., Culham et al., 2003; Valyear et al., 2006; Cavina-Pratesi et al., 2007). For instance, Cavina-Pratesi et al. (2007) directly compared BOLD responses to real 3D objects viewed passively or presented for grasping and reaching tasks as well as size and pattern discrimination tasks. The authors found activity in both dorsal and ventral regions in the passive viewing condition. However, the tasks each yielded distinct activation patterns, with BOLD activity in intraparietal cortex being linked to grasping and reaching, and LOR being linked to the feature discrimination tasks. Thus, if we wish to obtain a comprehensive understanding of how the visual system contributes to figure perception, a thorough investigation of how linking relationships are constrained by task will be necessary.

Much has been discovered with respect to how the brain instantiates our perception of figures, and we look at the prospects for future insights into relevant linking propositions with great optimism. We already know of many regions of interest thought to be important for figure perception. Now it is important to understand the dynamics of the circuit underlying figure detection, classification, and tracking, especially how the processes may vary from task to task. Also, the ongoing exchange between human and invasive nonhuman experiments will be vital for understanding mechanisms at the single-neuron level. Finally, we hope to eventually be able to describe how this circuit changes with age and experience and explain how such changes reflect important differences of perception.

References

Adelson, E. & Movshon, J.A. (1982). Phenomenal coherence of moving visual patterns. *Nature* **300**, 523–525.

Albright, T.D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science* **255**, 1141–1143.

Ales, J.M., Appelbaum, L.G., Cottereau, B.R. & Norcia, A.M. (2012). The time course of shape discrimination in the human brain. *NeuroImage* **67**, 77–88. doi: 10.1016/j.neuroimage.2012.10.044.

Almeida, J., Mahon, B.Z., Nakayama, K. & Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 15214–15218. doi: 10.1073/pnas.0805867105.

Altmann, C.F., Deubelius, A. & Kourtzi, Z. (2004). Shape saliency modulates contextual processing in the human lateral occipital complex. *Journal of Cognitive Neuroscience* **16**, 794–804. doi: 10.1162/089892904970825.

Altschuler, T.S., Molholm, S., Russo, N.N., Snyder, A.C., Brandwein, A.B., Blanco, D. & Foxe, J.J. (2012). Early electrophysiological indices of illusory contour processing within the lateral occipital complex are virtually impervious to manipulations of illusion strength. *NeuroImage* **59**, 4074–4085. doi: 10.1016/j.neuroimage.2011.10.051.

Anzai, A., Chowdhury, S.A. & DeAngelis, G.C. (2011). Coding of stereoscopic depth information in visual areas V3 and V3A. *The Journal of Neuroscience* **31**, 10270–10282. doi: 10.1523/JNEUROSCI.5956-10.2011.

Appelbaum, L.G., Ales, J.M. & Norcia, A.M. (2012). The time course of segmentation and cue-selectivity in the human visual cortex. *PLoS One* **7**, e34205. doi: 10.1371/journal.pone.0034205.

Appelbaum, L.G. & Norcia, A.M. (2009). Attentive and pre-attentive aspects of figural processing. *Journal of Vision* **9**, 1–12. doi: 10.1167/9.11.18.Introduction.

Bakar, A.A., Liu, L., Conci, M., Elliott, M.A. & Ioannides, A.A. (2008). Visual field and task influence illusory figure responses. *Human Brain Mapping* **29**, 1313–1326. doi: 10.1002/hbm.20464.

Ban, H., Preston, T.J., Meeson, A. & Welchman, A.E. (2012). The integration of motion and disparity cues to depth in dorsal visual cortex. *Nature Neuroscience* **15**, 636–643. doi: 10.1038/nn.3046.

https://doi.org/10.1017/S0952523813000266 Published online by Cambridge University Press

Bauer, R. & Heinze, S. (2002). Contour integration in striate cortex. Classic cell responses or cooperative selection? *Experimental Brain Research* **147**, 145–152. doi: 10.1007/s00221-002-1178-6.

Baylis, G.C. & Driver, J. (2001). Shape-coding in IT cells generalizes over contrast and mirror reversal, but not figure-ground reversal. *Nature Neuroscience* **4**, 937–942. doi: 10.1038/nn0901-937.

Beer, J., Blakemore, C., Previc, F.H. & Liotti, M. (2002). Areas of the human brain activated by ambient visual motion, indicating three kinds of self-movement. *Experimental Brain Research* **143**, 78–88. doi: 10.1007/s00221-001-0947-y.

Biber, U. & Ilg, U.J. (2008). Initiation of smooth-pursuit eye movements by real and illusory contours. *Vision Research*, **48**, 1002–1013. doi: 10.1016/j.visres.2008.01.021.

Biederman, I. (2001). Recognizing depth-rotated objects: A review of recent research and theory. *Spatial Vision* **13**, 241–253.

Born, R.T. & Bradley, D.C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience* **28**, 157–189. doi: 10.1146/annurev.neuro.26.041002.131052.

Born, R.T., Groh, J.M., Zhao, R. & Lukasewycz, S.J. (2000). Segregation of object and background motion in visual area MT: Effects of microstimulation on eye movements. *Neuron* **26**, 725–734.

Born, R.T. & Tootell, R.B. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature* **357**, 497–499. doi: 10.1038/357497a0.

Borst, G., Thompson, W.L. & Kosslyn, S.M. (2011). Understanding the dorsal and ventral systems of the human cerebral cortex: Beyond dichotomies. *The American Psychologist* **66**, 624–632. doi: 10.1037/a0024038.

Bradley, D.C. & Andersen, R.A. (1998). Center-surround antagonism based on disparity in primate area MT. *The Journal of Neuroscience* **18**, 7552–7565.

Brincat, S.L. & Connor, C.E. (2004). Underlying principles of visual shape selectivity in posterior inferotemporal cortex. *Nature Neuroscience* **7**, 880–886. doi: 10.1038/nn1278.

Brodeur, M., Lepore, F., Bacon, B.A. & Debruille, J.B. (2009). Simultaneous completions of modal and amodal figures: Visual evoked potentials reveal asymmetrical interference effects. *Visual Cognition* **17**, 632–654. doi: 10.1080/13506280802003640.

Caplovitz, G.P., Barroso, D.J., Hsieh, P.-J. & Tse, P.U. (2008). FMRI reveals that non-local processing in ventral retinotopic cortex underlies perceptual grouping by temporal synchrony. *Human Brain Mapping* **29**, 651–661. doi: 10.1002/hbm.20429.

Caplovitz, G.P. & Tse, P.U. (2007). V3A processes contour curvature as a trackable feature for the perception of rotational motion. *Cerebral Cortex* **17**, 1179–1189. doi: 10.1093/cercor/bhl029.

Carlson, E.T., Rasquinha, R.J., Zhang, K. & Connor, C.E. (2011*a*). A sparse object coding scheme in area V4. *Current Biology: CB* **21**, 288–293. doi: 10.1016/j.cub.2011.01.013.

Carlson, T., Hogendoorn, H., Fonteijn, H. & Verstraten, F.A.J. (2011*b*). Spatial coding and invariance in object-selective cortex. *Cortex* **47**, 14–22. doi: 10.1016/j.cortex.2009.08.015.

Cavina-Pratesi, C., Goodale, M.A. & Culham, J.C. (2007). FMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. *PLoS One* **2**, e424. doi: 10.1371/journal.pone.0000424.

Chandrasekaran, C., Canon, V., Dahmen, J.C., Kourtzi, Z. & Welchman, A.E. (2007). Neural correlates of disparity-defined shape discrimination in the human brain. *Journal of Neurophysiology* **97**, 1553–1565. doi: 10.1152/jn.01074.2006.

Cottereau, B.R., McKee, S.P., Ales, J.M. & Norcia, A.M. (2011). Disparity-tuned population responses from human visual cortex. *The Journal of Neuroscience* **31**, 954–965. doi: 10.1523/JNEUROSCI.3795-10.2011.

Cottereau, B.R., McKee, S.P., Ales, J.M. & Norcia, A.M. (2012*a*). Disparity-specific spatial interactions: Evidence from EEG source imaging. *The Journal of Neuroscience* **32**, 826–840. doi: 10.1523/JNEUROSCI.2709-11.2012.

Cottereau, B.R., McKee, S.P. & Norcia, A.M. (2012*b*). Bridging the gap: Global disparity processing in the human visual cortex. *Journal of Neurophysiology* **107**, 2421–2429. doi: 10.1152/jn.01051.2011.

Cox, D.D., Meier, P., Oertelt, N. & DiCarlo, J.J. (2005). "Breaking" position-invariant object recognition. *Nature Neuroscience* **8**, 1145–1147. doi: 10.1038/nn1519.

Culham, J.C., Danckert, S.L., DeSouza, J.F.X., Gati, J.S., Menon, R.S. & Goodale, M.A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research* **153**, 180–189. doi: 10.1007/s00221-003-1591-5.

Davis, G. & Driver, J. (1994). Parallel detection of Kanizsa subjective figures in the human visual system. *Nature* **371**, 791–793.

DeAngelis, G. (2000). Seeing in three dimensions: The neurophysiology of stereopsis. *Trends in Cognitive Sciences* **4**, 80–90.

Deangelis, G.C. & Newsome, W.T. (1999). Organization of disparity-selective neurons in macaque area MT. *The Journal of Neuroscience* **19**, 1398–1415.

Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Peuskens, H., Van Essen, D. & Orban, G.A. (2004). The processing of visual shape in the cerebral cortex of human and nonhuman primates: A functional magnetic resonance imaging study. *The Journal of Neuroscience* **24**, 2551–2565. doi: 10.1523/JNEUROSCI.3569-03.2004.

Desimone, R., Schein, S.J., Moran, J. & Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. *Vision Research* **25**, 441–452.

Dupont, P., DeBruyn, B., Vandenberghe, R., Rosier, A., Michiels, J., Marchal, G. & Orban, G. (1997). The kinetic occipital region in human visual cortex. *Cerebral Cortex* **7**, 283–292.

Engel, S.A., Glover, G.H. & Wandell, B.A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex* **7**, 181–192.

Fang, F. & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience* **8**, 1380–1385. doi: 10.1038/nn1537.

Ferber, S., Humphrey, G.K. & Vilis, T. (2003). The lateral occipital complex subserves the perceptual persistence of motion-defined groupings. *Cerebral Cortex* **13**, 716–721.

Ferber, S., Humphrey, G.K. & Vilis, T. (2005). Segregation and persistence of form in the lateral occipital complex. *Neuropsychologia* **43**, 41–51. doi: 10.1016/j.neuropsychologia.2004.06.020.

Fesi, J.D., Yannes, M.P., Brinckmann, D.M., Ales, J.M., Norcia, A.M. & Gilmore, R.O. (2011). Distinct cortical responses to 2D figures defined by motion contrast. *Vision Research* **51**, 2110–2120.

Fiorentini, A. (1989). Differences between fovea and parafovea in visual search processes. *Vision Research* **29**, 1153–1164.

Fujita, I. (2003). The inferior temporal cortex: Architecture, computation, and representation. *Journal of Neurocytology* **31**, 359–371.

Gauthier, I., Hayward, W.G., Tarr, M.J., Anderson, A.W., Skudlarski, P. & Gore, J.C. (2002). BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron* **34**, 161–171.

Gauthier, I, Skudlarski, P., Gore, J.C. & Anderson, A.W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience* **3**, 191–197. doi: 10.1038/72140.

Gauthier, I, Tarr, M.J., Anderson, A.W., Skudlarski, P. & Gore, J.C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature Neuroscience* **2**, 568–573. doi: 10.1038/9224.

Girard, P., Lomber, S.G. & Bullier, J. (2002). Shape discrimination deficits during reversible deactivation of area V4 in the macaque monkey. *Cerebral Cortex* **12**, 1146–1156.

Grill-Spector, K., Kourtzi, Z. & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research* **41**, 1409–1422.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y. & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* **24**, 187–203.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y. & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron* **21**, 191–202.

Grill-Spector, K. & Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience* **27**, 649–677. doi: 10.1146/annurev.neuro.27.070203.144220.

Grosof, D.H., Shapley, R.M. & Hawken, M.J. (1993). Macaque V1 neurons can signal "illusory" contours. *Nature* **365**, 550–552.

Gurnsey, R., Pearson, P. & Day, D. (1996). Texture segmentation along the horizontal meridian: Nonmonotonic changes in performance with eccentricity. *Journal of Experimental Psychology. Human Perception and Performance* **22**, 738–757.

Guzzon, D. & Casco, C. (2011). The effect of visual experience on texture segmentation without awareness. *Vision Research* **51**, 2509–2516. doi: 10.1016/j.visres.2011.10.006.

https://doi.org/10.1017/S0952523813000266 Published online by Cambridge University Press

Halgren, E., Mendola, J., Chong, C.D., & Dale, A.M. (2003). Cortical activation to illusory shapes as measured with magnetoencephalography. *NeuroImage* **18**, 1001–1009. doi: 10.1016/S1053-8119(03)00045-4.

Hasson, U., Levy, I., Behrmann, M., Hendler, T. & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron* **34**, 479–490.

Haxby, J.V., Grady, C.L., Horwitz, B., Ungerleider, L.G., Mishkin, M., Carson, R.E., Herscovitch, P., Schapiro, M.B. & Rapoport, S.I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United states of America* **88**, 1621–1625.

Haxby, J.V., Guntupalli, J.S., Connolly, A.C., Halchenko, Y.O., Conroy, B.R., Gobbini, M.I., Hanke, M. & Ramadge, P.J. (2011). A common, high-dimensional model of the representational space in human ventral temporal cortex. *Neuron* **72**, 404–416. doi: 10.1016/j.neuron.2011.08.026.

Hegdé, J. & Van Essen, D.C. (2007). A comparative study of shape representation in macaque visual areas V2 and V4. *Cerebral Cortex* **17**, 1100–1116. doi: 10.1093/cercor/bhl020.

Heider, B., Meskenaite, V. & Peterhans, E. (2000). Anatomy and physiology of a neural mechanism defining depth order and contrast polarity at illusory contours. *The European Journal of Neuroscience* **12**, 4117–4130.

Hesselmann, G., Hebart, M. & Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during "blindsight" in normal observers. *The Journal of Neuroscience* **31**, 12936–12944. doi: 10.1523/JNEUROSCI.1556-11.2011.

Hesselmann, G. & Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is "stream- invariant" in the human visual system. *Cerebral Cortex* **21**, 2829–2837. doi: 10.1093/cercor/bhr085.

Hinkle, D.A. & Connor, C.E. (2002). Three-dimensional orientation tuning in macaque area V4. *Nature Neuroscience* **5**, 665–670. doi: 10.1038/nn875.

Hinkle, D.A. & Connor, C.E. (2005). Quantitative characterization of disparity tuning in ventral pathway area V4. *Journal of Neurophysiology* **94**, 2726–2737. doi: 10.1152/jn.00341.2005.

Hirsch, J. & Curcio, C.A. (1989). The spatial resolution capacity of human foveal retina. *Vision Research* **29**, 1095–1101.

Huang, X., Albright, T.D. & Stoner, G.R. (2007). Adaptive surround modulation in cortical area MT. *Neuron* **53**, 761–770. doi: 10.1016/j.neuron.2007.01.032.

Hubel, D.H. & Wiesel, T.N. (1959). Receptive fields of single neurones in the cat's striate cortex. *Journal of Physiology* **148**, 574–591.

Hubel, D.H. & Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology* **195**, 215–243.

Hung, C.C., Carlson, E.T. & Connor, C.E. (2012). Medial axis shape coding in macaque inferotemporal cortex. *Neuron* **74**, 1099–1113. doi: 10.1016/j.neuron.2012.04.029.

Huth, A.G., Nishimoto, S., Vu, A.T. & Gallant, J.L. (2012). A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron* **76**, 1210–1224. doi: 10.1016/j.neuron.2012.10.014.

Huxlin, K.R., Saunders, R.C., Marchionini, D., Pham, H.A. & Merigan, W.H. (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cerebral Cortex* **10**, 671–683.

Ito, M., Tamura, H., Fujita, I. & Tanaka, K. (1995). Size and position invariance of neuronal responses in monkey inferotemporal cortex. *Journal of Neurophysiology* **73**, 218–226.

James, T.W., Culham, J., Humphrey, G.K., Milner, A.D. & Goodale, M.A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain* **126**, 2463–2475. doi: 10.1093/brain/awg248.

James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S. & Goodale, M.A. (2002). Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron* **35**, 793–801.

Janssen, P., Srivastava, S., Ombelet, S. & Orban, G.A. (2008). Coding of shape and position in macaque lateral intraparietal area. *The Journal of Neuroscience* **28**, 6679–6690. doi: 10.1523/JNEUROSCI.0499-08.2008.

Julesz, B. (1981). Textons, the elements of texture perception, and their interactions. *Nature* **290**, 91–97.

Kanizsa, G. (1979). *Organization in Vision: Essays on Gestalt Perception*. New York: Praeger.

Kanwisher, N.G., Chun, M.M., McDermott, J. & Ledden, P.J. (1996). Functional imaging of human visual recognition. *Cognitive Brain Research* **5**, 55–67.

Kanwisher, N., McDermott, J. & Chun, M.M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience* **17**, 4302–4311.

Kastner, S., De Weerd, P. & Ungerleider, L.G. (2000). Texture segregation in the human visual cortex: A functional MRI study. *Journal of Neurophysiology* **83**, 2453–2457.

Keane, B.P., Mettler, E., Tsoi, V., & Kellman, P.J. (2011). Attentional signatures of perception: Multiple object tracking reveals the automaticity of contour interpolation. *Journal of Experimental Psychology: Human Perception & Performance* **37**(3), 685–698.

Kellman, P.J., Garrigan, P. & Shipley, T.F. (2005). Object interpolation in three dimensions. *Psychological Review* **112**, 586–609. doi: 10.1037/0033-295X.112.3.586.

Kim, J.G. & Biederman, I. (2012). Greater sensitivity to nonaccidental than metric changes in the relations between simple shapes in the lateral occipital cortex. *NeuroImage* **63**, 1818–1826. doi: 10.1016/j.neuroimage.2012.08.066.

Kimchi, R. & Peterson, M.A. (2008). Figure-ground segmentation can occur without attention. *Psychological Science* **19**, 660–668. doi: 10.1111/j.1467-9280.2008.02140.x.

Klaver, P., Lichtensteiger, J., Bucher, K., Dietrich, T., Loenneker, T., & Martin, E. (2008). Dorsal stream development in motion and structure-from-motion perception. *NeuroImage* **39**(4), 1815–1823.

Knebel, J.F. & Murray, M.M. (2012). Towards a resolution of conflicting models of illusory contour processing in humans. *NeuroImage* **59**, 2808–2817. doi: 10.1016/j.neuroimage.2011.09.031.

Kobatake, E. & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology* **71**, 856–867.

Kourtzi, Z., Erb, M., Grodd, W. & Bülthoff, H.H. (2003). Representation of the perceived 3-D object shape in the human lateral occipital complex. *Cerebral Cortex* **13**, 911–920.

Kourtzi, Z. & Huberle, E. (2005). Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation. *NeuroImage* **28**, 440–452. doi: 10.1016/j.neuroimage.2005.06.017.

Kourtzi, Z. & Kanwisher, N.G. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science* **293**, 1506–1509.

Kravitz, D.J., Saleem, K.S., Baker, C.I. & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews. Neuroscience* **12**, 217–230. doi: 10.1038/nrn3008.

Kriegeskorte, N., Mur, M., Ruff, D.A., Kiani, R., Bodurka, J., Esteky, H., Tanaka, K. & Bandettini, P.A. (2008). Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron* **60**, 1126–1141. doi: 10.1016/j.neuron.2008.10.043.

Krug, K. & Parker, A.J. (2011). Neurons in dorsal visual area V5/MT signal relative disparity. *The Journal of Neuroscience* **31**, 17892–17904. doi: 10.1523/JNEUROSCI.2658-11.2011.

Lamme, V.A., Van Dijk, B.W. & Spekreijse, H. (1993). Contour from motion processing occurs in primary visual cortex. *Nature* **363**, 541–543. doi: 10.1038/363541a0.

Larsson, J. & Heeger, D. (2006). Two retinotopic visual areas in human lateral occipital cortex. *The Journal of Neuroscience* **26**, 13128–13142. doi: 10.1523/JNEUROSCI.1657-06.2006.

Lee, T.S. & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 1907–1911. doi: 10.1073/pnas.031579998.

Lehky, S.R. & Sereno, A.B. (2007). Comparison of shape encoding in primate dorsal and ventral visual pathways. *Journal of Neurophysiology* **97**, 307–319. doi: 10.1152/jn.00168.2006.

Leventhal, A.G., Wang, Y., Schmolesky, M.T. & Zhou, Y. (1998). Neural correlates of boundary perception. *Visual Neuroscience* **15**, 1107–1118.

Levy, I., Hasson, U., Avidan, G., Hendler, T. & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience* **4**, 533–539. doi: 10.1038/87490.

Li, W., Piëch, V. & Gilbert, C.D. (2006). Contour saliency in primary visual cortex. *Neuron* **50**, 951–962. doi: 10.1016/j.neuron.2006.04.035.

Likova, L. & Tyler, C.W. (2008). Occipital network for figure/ground organization. *Experimental Brain Research* **189**, 257–267. doi: 10.1007/s00221-008-1417-6.

Livingstone, M. & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science* **240**, 740–749.

https://doi.org/10.1017/S0952523813000266 Published online by Cambridge University Press

Loffler, G., Yourganov, G., Wilkinson, F. & Wilson, H.R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience* **8**, 1386–1390. doi: 10.1038/nn1538.

Majaj, N.J., Carandini, M. & Movshon, J.A. (2007). Motion integration by neurons in macaque MT Is local, not global. *The Journal of Neuroscience* **27**, 366–370. doi: 10.1523/JNEUROSCI.3183-06.2007.

Malach, R., Levy, I., & Hasson, U. (2002). The topography of high-order human object areas. *Trends in Cognitive Sciences* **6**(4), 176–184.

Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R. & Tootell, R.B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 8135–8139.

Marcar, V.L., Xiao, D.K., Raiguel, S.E., Maes, H. & Orban, G.A. (1995). Processing of kinetically defined boundaries in the cortical motion area MT of the macaque monkey. *Journal of Neurophysiology* **74**, 1258–1270.

Marr, D. & Nishihara, H.K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London. Series B, Biological Science* **200**, 269–294.

Martinez, A., Ramanathan, D.S., Foxe, J.J., Javitt, D.C. & Hillyard, S.A. (2007). The role of spatial attention in the selection of real and illusory objects. *The Journal of Neuroscience* **27**, 7963–7973. doi: 10.1523/JNEUROSCI.0031-07.2007.

Masson, G.S., Mestre, D.R. & Stone, L.S. (1999). Speed tuning of motion segmentation and discrimination. *Vision Research* **39**, 4297–4308.

McMains, S. & Kastner, S. (2011). Interactions of top-down and bottom-up mechanisms in human visual cortex. *The Journal of Neuroscience* **31**, 587–597. doi: 10.1523/JNEUROSCI.3766-10.2011.

Meinecke, C. (1989). Retinal eccentricity and the detection of targets. *Psychological Research* **51**, 107–116.

Mendola, J.D., Dale, A.M., Fischl, B., Liu, A.K. & Tootell, R.B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *The Journal of Neuroscience* **19**, 8560–8572.

Merigan, W.H. & Pham, H.A. (1998). V4 lesions in macaques affect both single- and multiple-viewpoint shape discriminations. *Visual Neuroscience* **15**, 359–367.

Merigan, W.H. & Saunders, R.C. (2004). Unilateral deficits in visual perception and learning after unilateral inferotemporal cortex lesions in macaques. *Cerebral Cortex* **14**, 863–871. doi: 10.1093/cercor/bhh045.

Milner, A.D. (2012). Is visual processing in the dorsal stream accessible to consciousness? *Proceedings of the Royal Society of London. Series B, Biological Science* **279**, 2289–2298. doi: 10.1098/rspb.2011.2663.

Milner, A.D. & Goodale, M.A. (2008). Two visual systems re-viewed. *Neuropsychologia* **46**, 774–785. doi: 10.1016/j.neuropsychologia.2007.10.005.

Mishkin, M., Ungerleider, L.G. & Macko, K.A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences* **6**, 414–417. doi: 10.1016/0166-2236(83)90190-X.

Murray, M.M., Foxe, D.M., Javitt, D.C. & Foxe, J.J. (2004). Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *The Journal of Neuroscience*, **24**, 6898–6903. doi: 10.1523/JNEUROSCI.1996-04.2004.

Murray, M.M., Wylie, G.R., Higgins, B.A., Javitt, D.C., Schroeder, C.E. & Foxe, J.J. (2002). The spatiotemporal dynamics of illusory contour processing: Combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *The Journal of Neuroscience* **22**, 5055–5073.

Mysore, S.G., Vogels, R., Raiguel, S.E. & Orban, G.A. (2006). Processing of kinetic boundaries in macaque V4. *Journal of Neurophysiology* **95**, 1864–1880. doi: 10.1152/jn.00627.2005.

Naselaris, T., Prenger, R.J., Kendrick, N.K., Oliver, M., & Gallant, J.L. (2009). Bayesian reconstruction of natural images from human brain activity. *Neuron* **62**(6), 902–915.

Neri, P., Bridge, H. & Heeger, D.J. (2004). Stereoscopic processing of absolute and relative disparity in human visual cortex. *Journal of Neurophysiology* **92**, 1880–1891. doi: 10.1152/jn.01042.2003.

Newsome, W.T. & Pare, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *The Journal of Neuroscience* **8**, 2201–2211.

Nothdurft, H.C. (1991). Texture segmentation and pop-out from orientation contrast. *Vision Research* **31**, 1073–1078.

Orban, G.A. (2011). The extraction of 3D shape in the visual system of human and nonhuman primates. *Annual Review of Neuroscience* **34**, 361–388. doi: 10.1146/annurev-neuro-061010-113819.

Orban, G.A., Janssen, P. & Vogels, R. (2006). Extracting 3D structure from disparity. *Trends in Neurosciences* **29**, 466–473. doi: 10.1016/j.tins.2006.06.012.

Orban, G.A., Van Essen, D. & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Sciences* **8**, 315–324. doi: 10.1016/j.tics.2004.05.009.

Pack, C.C., Gartland, A.J. & Born, R.T. (2004). Integration of contour and terminator signals in visual area MT of alert macaque. *The Journal of Neuroscience* **24**, 3268–3280. doi: 10.1523/JNEUROSCI.4387-03.2004.

Passingham, R.E. & Toni, I. (2001). Contrasting the dorsal and ventral visual systems: Guidance of movement versus decision making. *NeuroImage* **14**, S125–S131. doi: 10.1006/nimg.2001.0836.

Pasupathy, A. & Connor, C.E. (2001). Shape representation in area V4: Position-specific tuning for boundary conformation. *Journal of Neurophysiology* **86**, 2505–2519.

Pasupathy, A. & Connor, C.E. (2002). Population coding of shape in area V4. *Nature Neuroscience* **5**, 1332–1338. doi: 10.1038/nn972.

Peterhans, E., Heider, B. & Baumann, R. (2005). Neurons in monkey visual cortex detect lines defined by coherent motion of dots. *The European Journal of Neuroscience* **21**, 1091–1100. doi: 10.1111/j.1460-9568.2005.03919.x.

Poggio, G.F. & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *J Neurophysiol* **40**(6), 1392–1405.

Poort, J., Raudies, F., Wannig, A., Lamme, V.A., Neumann, H. & Roelfsema, P.R. (2012). The role of attention in figure-ground segregation in areas V1 and V4 of the visual cortex. *Neuron* **75**, 143–156. doi: 10.1016/j.neuron.2012.04.032.

Preston, T.J., Kourtzi, Z. & Welchman, A.E. (2009). Adaptive estimation of three-dimensional structure in the human brain. *The Journal of Neuroscience* **29**, 1688–1698. doi: 10.1523/JNEUROSCI.5021-08.2009.

Preston, T.J., Li, S., Kourtzi, Z. & Welchman, A.E. (2008). Multivoxel pattern selectivity for perceptually relevant binocular disparities in the human brain. *The Journal of Neuroscience* **28**, 11315–11327. doi: 10.1523/JNEUROSCI.2728-08.2008.

Ramsden, B.M., Hung, C.P. & Roe, A.W. (2001). Real and illusory contour processing in area V1 of the primate: A cortical balancing act. *Cerebral Cortex* **11**, 648–665.

Regan, D. (2000). *Human Perception of Objects: Early Visual Processing of Spatial Form Defined by Luminance, Color, Texture, Motion, and Binocular Disparity* (1st ed.). Sunderland, MA: Sinauer Associates Inc.

Roe, A.W., Parker, A.J., Born, R.T. & DeAngelis, G.C. (2007). Disparity channels in early vision. *The Journal of Neuroscience* **27**, 11820–11831. doi: 10.1523/JNEUROSCI.4164-07.2007.

Roelfsema, P.R., Lamme, V.A. & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature* **395**, 376–381.

Roelfsema, P.R., Lamme, V.A. & Spekreijse, H. (2004). Synchrony and covariation of firing rates in the primary visual cortex during contour grouping. *Nature Neuroscience* **7**, 982–991. doi: 10.1038/nn1304.

Roelfsema, P.R., Tolboom, M. & Khayat, P.S. (2007). Different processing phases for features, figures, and selective attention in the primary visual cortex. *Neuron* **56**, 785–792. doi: 10.1016/j.neuron.2007.10.006.

Romeo, A., Arall, M. & Supèr, H. (2012). Noise destroys feedback enhanced figure-ground segmentation but not feedforward figure-ground segmentation. *Frontiers in Physiology* **3**, 274. doi: 10.3389/fphys.2012.00274.

Rust, N.C. & Dicarlo, J.J. (2010). Selectivity and tolerance ("invariance") both increase as visual information propagates from cortical area V4 to IT. *The Journal of Neuroscience* **30**, 12978–12995. doi: 10.1523/JNEUROSCI.0179-10.2010.

Sakuraba, S., Sakai, S., Yamanaka, M., Yokosawa, K. & Hirayama, K. (2012). Does the human dorsal stream really process a category for tools? *The Journal of Neuroscience* **32**, 3949–3953. doi: 10.1523/JNEUROSCI.3973-11.2012.

Sary, G., Vogels, R. & Orban, G.A. (1993). Cue-invariant shape selectivity of macaque inferior temporal neurons. *Science* **260**, 995–997.

Sawamura, H., Georgieva, S., Vogels, R., Vanduffel, W. & Orban, G.A. (2005). Using functional magnetic resonance imaging to assess adaptation and size invariance of shape processing by humans and

https://doi.org/10.1017/S0952523813000266 Published online by Cambridge University Press

monkeys. *The Journal of Neuroscience* **25**, 4294–4306. doi: 10.1523/JNEUROSCI.0377-05.2005.

Schenk, T. & McIntosh, R.D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience* **1**, 52–62. doi: 10.1080/17588920903388950.

Schira, M.M., Fahle, M., Donner, T.H., Kraft, A. & Brandt, S.A. (2004). Differential contribution of early visual areas to the perceptual process of contour processing. *Journal of Neurophysiology* **91**, 1716–1721. doi: 10.1152/jn.00380.2003.

Schluppeck, D. & Engel, S.A. (2002). Color opponent neurons in V1: A review and model reconciling results from imaging and single-unit recording. *Journal of Vision* **2**, 480–492.

Scholte, H.S., Jolij, J., Fahrenfort, J.J. & Lamme, V.A. (2008). Feedforward and recurrent processing in scene segmentation: Electroencephalography and functional magnetic resonance imaging. *Journal of Cognitive Neuroscience* **20**, 2097–2109. doi: 10.1162/jocn.2008.20142.

Scholte, H.S., Witteveen, S.C., Spekreijse, H. & Lamme, V.A. (2006). The influence of inattention on the neural correlates of scene segmentation. *Brain Research* **1076**, 106–115. doi: 10.1016/j.brainres.2005.10.051.

Senkowski, D., Röttger, S., Grimm, S., Foxe, J.J. & Herrmann, C.S. (2005). Kanizsa subjective figures capture visual spatial attention: Evidence from electrophysiological and behavioral data. *Neuropsychologia* **43**, 872–886. doi: 10.1016/j.neuropsychologia.2004.09.010.

Sereno, M.E., Trinath, T., Augath, M. & Logothetis, N.K. (2002). Three-dimensional shape representation in monkey cortex. *Neuron* **33**, 635–652.

Sheth, B.R., Sharma, J., Rao, S.C. & Sur, M. (1996). Orientation maps of subjective contours in visual cortex. *Science* **274**, 2110–2115.

Shiozaki, H.M., Tanabe, S., Doi, T. & Fujita, I. (2012). Neural activity in cortical area V4 underlies fine disparity discrimination. *The Journal of Neuroscience* **32**, 3830–3841. doi: 10.1523/JNEUROSCI.5083-11.2012.

Shpaner, M., Murray, M.M. & Foxe, J.J. (2009). Early processing in the human lateral occipital complex is highly responsive to illusory contours but not to salient regions. *The European Journal of Neuroscience* **30**, 2018–2028. doi: 10.1111/j.1460-9568.2009.06981.x.

Simoncelli, E.P. & Olshausen, B.A. (2001). Natural image statistics and neural representation. *Annu. Rev. Neurosci.* **24**, 1193–1216.

Singh, M. (2004). Modal and amodal completion generate different shapes. *Psychological Science* **15**, 454–459. doi: 10.1111/j.0956-7976.2004.00701.x.

Skiera, G., Petersen, D., Skalej, M. & Fahle, M. (2000). Correlates of figure-ground segregation in fMRI. *Vision Research* **40**, 2047–2056.

Stanley, D.A. & Rubin, N. (2003). FMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron* **37**, 323–331.

Stanley, D.A. & Rubin, N. (2005). Functionally distinct sub-regions in the lateral occipital complex revealed by fMRI responses to abstract 2-dimensional shapes and familiar objects. *Journal of Vision* **5**, 911. doi: 10.1167/5.8.911.

Strother, L., Lavell, C. & Vilis, T. (2012). Figure-ground representation and its decay in primary visual cortex. *Journal of Cognitive Neuroscience* **24**, 905–914. doi: 10.1162/jocn_a_00190.

Swisher, J.D., Gatenby, J.C., Gore, J.C., Wolfe, B.A, Moon, C.H., Kim, S.G. & Tong, F. (2010). Multiscale pattern analysis of orientation-selective activity in the primary visual cortex. *The Journal of Neuroscience* **30**, 325–330. doi: 10.1523/JNEUROSCI.4811-09.2010.

Tanaka, K. (1997). Mechanisms of visual object recognition: Monkey and human studies. *Current Opinion in Neurobiology* **7**, 523–529.

Tanaka, K. (2003). Columns for complex visual object features in the inferotemporal cortex: Clustering of cells with similar but slightly different stimulus selectivities. *Cerebral Cortex* **13**, 90–99.

Teller, D.Y. (1984). Linking propositions. *Vision Research* **24**, 1233–1246.

Thielscher, A., Kölle, M., Neumann, H., Spitzer, M. & Grön, G. (2008). Texture segmentation in human perception: A combined modeling and fMRI study. *Neuroscience* **151**, 730–736. doi: 10.1016/j.neuroscience.2007.11.040.

Tootell, R.B., Hadjikhani, N., Hall, E.K., Marrett, S., Vanduffel, W., Vaughan, J.T. & Dale, A.M. (1998). The retinotopy of visual spatial attention. *Neuron* **21**, 1409–1422.

Tootell, R.B., Switkes, E., Silverman, M.S. & Hamilton, S.L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *The Journal of Neuroscience* **8**, 1531–1568.

Tootell, R.B., Tsao, D. & Vanduffel, W. (2003). Neuroimaging weighs in: Humans meet macaques in "primate" visual cortex. *The Journal of Neuroscience* **23**, 3981–3989.

Tse, P.U. (1999). Volume completion. *Cognitive Psychology* **39**, 37–68. doi: 10.1006/cogp.1999.0715.

Tyler, C.W., Likova, L.T., Kontsevich, L.L. & Wade, A.R. (2006). The specificity of cortical region KO to depth structure. *NeuroImage* **30**, 228–238. doi: 10.1016/j.neuroimage.2005.09.067.

Valyear, K.F., Culham, J.C., Sharif, N., Westwood, D. & Goodale, M.A. (2006). A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study. *Neuropsychologia* **44**, 218–228. doi: 10.1016/j.neuropsychologia.2005.05.004.

Van Oostende, S., Sunaert, S., Van Hecke, P., Marchal, G. & Orban, G.A. (1997). The kinetic occipital (KO) region in man: An fMRI study. *Cerebral Cortex* **7**, 690–701.

Vanrie, J., Béatse, E., Wagemans, J., Sunaert, S. & Van Hecke, P. (2002). Mental rotation versus invariant features in object perception from different viewpoints: An fMRI study. *Neuropsychologia* **40**, 917–930.

Verhoef, B.E., Vogels, R. & Janssen, P. (2012). Inferotemporal cortex subserves three-dimensional structure categorization. *Neuron* **73**, 171–182. doi: 10.1016/j.neuron.2011.10.031.

Vinberg, J. & Grill-Spector, K. (2008). Representation of shapes, edges, and surfaces across multiple cues in the human visual cortex. *Journal of Neurophysiology* **99**, 1380–1393. doi: 10.1152/jn.01223.2007.

Von Der Heydt, R. & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *The Journal of Neuroscience* **9**, 1731–1748.

Walsh, V., Butler, S.R., Carden, D. & Kulikowski, J.J. (1992). The effects of V4 lesions on the visual abilities of macaques: Shape discrimination. *Behavioural Brain Research* **50**, 115–126.

Weil, R.S. & Rees, G. (2011). A new taxonomy for perceptual filling-in. *Brain Research Reviews* **67**, 40–55. doi: 10.1016/j.brainresrev.2010.10.004.

Welchman, A.E., Deubelius, A., Conrad, V., Bülthoff, H.H. & Kourtzi, Z. (2005). 3D shape perception from combined depth cues in human visual cortex. *Nature Neuroscience* **8**, 820–827. doi: 10.1038/nn1461.

Wong, Y.J., Aldcroft, A.J., Large, M.E., Culham, J.C. & Vilis, T. (2009). The role of temporal synchrony as a binding cue for visual persistence in early visual areas: An fMRI study. *Journal of Neurophysiology* **102**, 3461–3468. doi: 10.1152/jn.00243.2009.

Xiao, D.K., Raiguel, S., Marcar, V. & Orban, G.A. (1997). The spatial distribution of the antagonistic surround of MT/V5 neurons. *Cerebral Cortex* **7**, 662–677.

Yamane, Y., Carlson, E.T., Bowman, K.C., Wang, Z. & Connor, C.E. (2008). A neural code for three-dimensional object shape in macaque inferotemporal cortex. *Nature Neuroscience* **11**, 1352–1360. doi: 10.1038/nn.2202.

Zeki, S., Perry, R.J. & Bartels, A. (2003). The processing of kinetic contours in the brain. *Cerebral Cortex* **13**, 189–202.

Zhan, C.A. & Baker, C.L. (2006). Boundary cue invariance in cortical orientation maps. *Cerebral Cortex* **16**, 896–906. doi: 10.1093/cercor/bhj033.

Zhou, J., Tjan, B.S., Zhou, Y. & Liu, Z. (2008). Better discrimination for illusory than for occluded perceptual completions. *Journal of Vision* **8**, 1–17. doi: 10.1167/8.7.26.Introduction.

https://doi.org/10.1017/S0952523813000266 Published online by Cambridge University Press