Review

Illusory contours: a window onto the neurophysiology of constructing perception

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Seeing seems effortless, despite the need to segregate and integrate visual information that varies in quality, quantity, and location. The extent to which seeing passively recapitulates the external world is challenged by phenomena such as illusory contours, an example of visual completion whereby borders are perceived despite their physical absence in the image. Instead, visual completion and seeing are increasingly conceived as active processes, dependent on information exchange across neural populations. How this is instantiated in the brain remains controversial. Divergent models emanate from single-unit and population-level electrophysiology, neuroimaging, and neurostimulation studies. We reconcile discrepant findings from different methods and disciplines, and underscore the importance of taking into account spatiotemporal brain dynamics in generating models of brain function and perception.

Models of illusory contour processing

Illusory contours (ICs) constitute 'simple' stimuli for the investigation of vision (Box 1, Figure I). They have attracted considerable attention in the past for a number of reasons. First, ICs provide access to mental operations that link sensation and perception by generating experiences in the absence of physically present information. Second, ICs can be used to understand binding mechanisms (see Glossary) and their perceptual consequences, particularly because IC stimuli can be readily used in experiments across species, with clinical and developmental populations, and in artificial vision [1]. These features have been of interest to Gestalt psychologists for over a century (Box 1) and are still stimulating research in psychology, neuroscience, and computer science (Box 2).

Researchers are generally divided into three camps regarding the brain mechanisms responsible for IC perception based on the presumed role of feed-forward versus feedback activity, as well as the locus of neural sensitivity

Glossary

Binding:: (neurophysiologic) processes whereby different information is nonetheless coded to refer to the same object or event. Here, different information refers to spatially separated stimulus elements, such as inducers of ICs.

Bottom-up versus top-down processes:: bottom-up processes rely exclusively on feed-forward architectures, whereas top-down processes incorporate feedback and lateral architectures.

Event-related oscillation:: phase resetting of ongoing EEG activity within a given frequency band/bin (0–4 Hz, delta; 4–8 Hz, theta; 8–12 Hz, alpha; 12–30 Hz, beta; 30–80 Hz, low gamma; 80–200 Hz, high gamma). Stimulus-evoked oscillations are strictly phase-locked and sum over trials. Averaged across all frequencies, they constitute the ERP. Stimulus-induced oscillations vary from trial to trial in their phase with respect to stimulus onset and tend to cancel out in the ERP.

Event-related potential (ERP):: EEG activity that is time-locked and phase-locked to a stimulus [91]. Because this activity is often of low amplitude relative to background EEG, data from many trials are typically signal-averaged. The ERP consists of components defined by their latency and topography at the scalp. Source estimation methods, solving the electromagnetic inverse problem, identify brain regions generating the ERP [22,23].

Feed-forward versus feedback architectures:: feed-forward architectures are those that are constituted only by connections from input to output layers. Feedback projections go from output to input layers; lateral connections remain within a layer. These architectures can be differentiated by the laminar distribution of neuronal terminations: feed-forward to granular layers, feedback to supra-granular and infra-granular layers, and lateral to all layers [92].

Illusory contours (ICs):: perception of lines, forms, and volumes in the absence of physical support (e.g., luminance gradients). The first human experiments describing conscious perception of ICs date back to the early 20th century, with variations continually created [87–89,93].

Modal completion versus amodal completion:: modally completed ICs typically comprise at least three aspects: (i) perception of the borders, (ii) brightness enhancement of the illusory figure versus the background, and (iii) positioning of the illusory figure in the foreground in front of the inducer elements. Amodally completed ICs, by contrast, do not result in brightness enhancement, and the figure is perceived in the background behind the inducer elements.

Receptive field:: in the case of visual cortices, the receptive field of a neuron typically refers to that region of space from which a firing rate can be elicited beyond spontaneous activity levels. This space can alter dynamically [94], and influences on neural activity can extend spatially beyond the classical receptive field borders [95].

Salient region:: term borrowed from computer vision to refer to pixels the probably belong to the same surface or form without forcibly delineating their borders.

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Box 1. The phenomenology and psychophysics of IC sensitivity

When viewing ICs (Figure I) the human visual system perceives elements for which there exists no correlate in the real world. Psychologists have investigated which types of figures induce such illusions, typically instructing observers to indicate whether or not they perceived ICs depending on different aspects of the figure. Spatial factors affect the strength of perceived ICs in Kanizsa figures: (i) stimulus size, (ii) inducer size, and (iii) inducer spacing. For example, smaller retinal size results in clearer ICs [83]. Shipley and Kellmann independently varied inducer size, inducer spacing, and overall stimulus size of Kanizsa figures [84]. They found that only the inducer size and inducer spacing had an effect on the perceived intensity of the ICs. From this, they proposed integration of these two variables into a single metric that they called the support ratio, which is the ratio of the physically specified contour length to the total edge length of the figure; the larger the support ratio, the stronger is the illusion (although see [8,42]). Temporal factors also influence IC perception. Kojo *et al.* presented inducers of Kanizsa-type ICs sequentially rather than simultaneously and demonstrated that if the inducer disks are less separated in space they can be more separated in time and *vice versa* [85]. There is therefore a degree of spatiotemporal coupling in IC perception. Nonetheless, psychophysical data also support IC sensitivity occurring pre-attentively [73] and directing the allocation of spatial attention [74].

This pre-attentive aspect raises the question of the extent to which IC sensitivity requires higher cognitive functions. The observation of IC perceptual abilities across mammals, birds, and insects might provide one level of argument against such a necessity [1], as well as the observation of neural sensitivity to ICs despite anesthesia [15] (although in one study IC sensitivity originated in area V4 despite anesthesia [19]). Causal data linking neural activity and perceptual abilities in animals are scant. Studies of perceptual abilities in lesioned animals support the role of higher-tier visual cortices [76,77]. Developmental data may provide parallel arguments, addressing whether IC sensitivity constitutes an innate rather than learned capacity. EEG/ERP recordings from babies demonstrated that infants younger than 3 months of age do not show enhanced gamma-band oscillations when viewing Kanizsa figures, whereas older infants do [86]. This supports the notion that IC perception is an acquired ability of our brains, which in turn favors the involvement of higher cognitive functions.

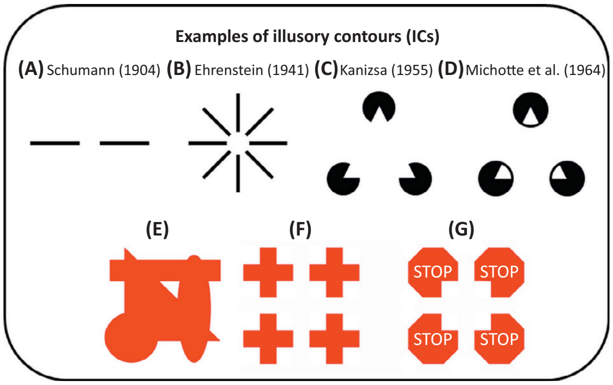

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Figure I. Examples of illusory contours. **(A,B)** ICs composed of lines. **(C)** IC composed of geometric figures. **(D)** The illusory figure is viewed through a white wall with three holes (amodal completion). **(E)** Four geometric shapes are overlaid in an ambiguous way. Any shape could be perceived as being in the foreground. **(F)** If an illusory figure is induced by unoccluded real-world shapes, it is perceived only weakly. **(G)** If the illusory figure can be explained by the occlusion of real-world shapes, it is perceived more vividly. Stimuli in all panels were redrawn here by the authors. Those shown in panels A–D were first described in [87], [88], [89], and [90], respectively.

that is specific to the IC versus other stimulus features (Figure 1). One model contends that IC sensitivity is an exclusively feed-forward process first apparent within the lowest levels of the cortical hierarchy (i.e., areas V1/V2) (Box 3) [2]. This model is predicated largely on the observation of contextual modulations of the activity of individual neurons by stimuli falling outside of their classical receptive fields [3]. However, in the case of ICs such contextual modulations in V1/V2 extend only out by $\sim 3^\circ$ and are always delayed relative to responses evoked by stimuli falling within the neuron's receptive field [3], such that individual neurons no longer exhibit IC sensitivity if the gap distance between inducers is too large [4]. In addition, and as evident from the examples shown in Box 1, ICs often span across large distances as well as the vertical meridian. These receptive field, temporal, and perceptual aspects, as well as advances in computational modeling (Box 2), have spurred proposals of alternative neurophysiological mechanisms that rely on neurons with large, often bilateral, receptive fields that extensively overlap across the neural population [5,6]. Such properties, particularly when considered alongside the rapidity of signal propagation through visual cortices (Box 3), in principle would allow for a predominant role of higher-level cortices, such as inferotemporal cortices in macaque monkeys and lateral occipital cortices (LOC) in humans, in mediating IC sensitivity. In light of such considerations, a second model also contends that IC sensitivity is mediated first by V1/V2, but this sensitivity is the consequence of feedback inputs from higher-order regions, such as LOC, that are not themselves sensitive to ICs [7]. A third model localizes IC sensitivity first in LOC and subsequently in V1/V2, mediated by feedback from LOC to V1/V2. Both areas receive modulatory top-down input from parietal cortex, which is sensitive to salient regions [8] and plays a role in visuospatial attention and state-dependent phase resetting of ongoing oscillatory activity in visual cortices [9].

The progressive development of these models and the data supporting them in many regards highlight what may be considered a general tendency in neuroscience research over the past 30 or so years, namely, progression from an interest in characterizing the responses of individual neurons to the discrete localization of brain functions to quantifying the contribution of both spatial and temporal dynamics to emergent properties of distributed systems (Box 3). In what follows, we provide a review of these developments as they pertain to the mechanisms subserving IC perception and use this as an example to improve our understanding of the neural bases of perception.

Single-unit studies

Psychology differentiates sensation from perception (Box 1). Sensation reflects the neural representation of physical properties of stimuli, whereas perception refers to conscious experiences of the world that are sometimes inaccurate representations of physical stimuli. Sensory–perceptual interplay was noted by William James when

Box 2. Computational models of IC sensitivity

Neurophysiological studies of ICs cannot explain the precise mechanisms leading to increased neural firing in the absence of stimuli located within the classical receptive field of a neuron. Computational modeling describes circuits that can engender IC sensitivity. These new models firmly reject strictly feed-forward architectures without lateral or feedback connections and instead favor multi-layer architectures comprising mixtures of feed-forward, feedback, and lateral interactions (Figure I) [96,97].

Some of the original propositions based on neurophysiological observations included such interactions [98]. In strictly feed-forward architectures, neurons would only fire if there were real (i.e., luminance-defined) contours in their receptive field. However, models including lateral and feedback connections offer a mechanistic explanation of IC sensitivity. Neurons that receive stimulation with real contours in their receptive fields respond with an increase in their firing rate that would 'spread' in the case of lateral connections to excite neurons that do not 'see' real contours. However, this mechanism alone would result in ICs around every real contour. Bipolar cells that receive input from two collinearly aligned receptive fields fire only if a real contour is present or if both adjacent neurons fire and thus solve the problem [99]. These models were based on neurons that output only a spike rate rather than single spikes. Models that implement biologically plausible learning rules at their synapses require single spikes. Incorporation of both spiking neurons and lateral connections and bipolar cells results in a realistic model for IC processing [61]. More recent neurophysiologic data, however, suggest that feedback from higher-tier visual areas is required to perceive ICs, which has led to a Bayesian-based feedback model comprising multiple sets of selective and invariant layers that is effective in size-invariant stimulus disambiguation only after recursive processing between layers and, by extension, the spatiotemporal interplay of neural populations [96,97]. Key features of this type of computational model are the redundancy and overlap in feedback inputs from a higher layer involved in invariance to a lower layer involved in selectivity, which in turn are only effective over time [96]. These features parallel the neurophysiological properties of IT neurons.

IC sensitivity is just one of myriad examples in which the brain must complete missing information or generate perception from incomplete information. The identity hypothesis states that one neural mechanism is responsible for the completion of both ICs and occluded objects [100]. A recent modeling study was able to achieve both perceptual tasks in one biologically plausible network architecture [101]. This further supports the identity hypothesis and the importance of using IC sensitivity as a general phenomenon for application to other domains of visual perception.

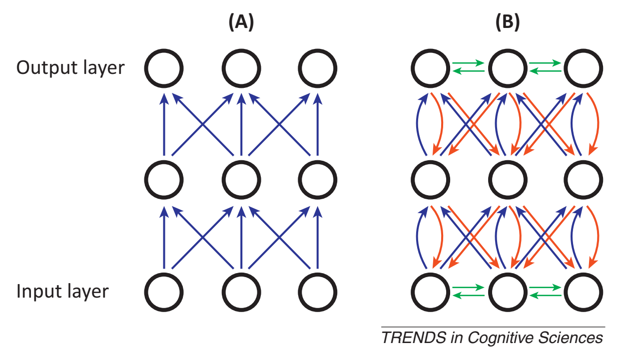

Figure I. Architectures for computational modeling. **(A)** Illustration of feed-forward connections (blue) in a network of artificial neurons (black circles). **(B)** Illustration of feedback (red) and lateral connections (green).

he wrote 'Whilst part of what we perceive comes through our senses from the object before us, another part (and it may be the larger part) always comes out of our own head.' [10]. Illusions have been thought to reflect perceptual or even 'cognitive' processes, because they do not reflect the physical properties of the outside world [11]. Neurophysiological studies use stimulus material from psychological experiments to elucidate sensory–perceptual interplay. The assumption is that low-level, early-latency processes represent exclusively sensation, whereas 'higher' visual cortices, as well as temporal and frontal cortices, are responsible for perception [12].

Neurophysiological experiments with ICs challenge this view. In their seminal study, von der Heydt *et al.* moved either illusory or real contours across the receptive fields of neurons in area V2 of awake, fixating monkeys [4]. Surprisingly, neurons fired when an IC moved across its receptive field, despite no physical stimulus change within the receptive field (Figure 2). Neurons in area V1 did not respond to ICs, although subsequent work provides (controversial) evidence of such responses [2,13,14] ([15] also provides data from cats). These types of results were taken as support for feed-forward mechanisms of IC sensitivity in V1/V2.

However, an unequivocal interpretation of data from these and other single-unit studies is not forthcoming for several reasons. First, and despite the exquisite spatial resolution of the technique, the timing and laminar distribution of effects have typically not been reported or quantified. Second, spatial sampling has thus far been highly restricted; measurements were obtained in low-level areas (V2/V1) or higher-level areas (V4 or IT), but not (yet) in both regions and elsewhere in the same animal (Box 3). Consequently, network dynamics remain unknown (Box 2). Third, stimulus parameters across studies often widely vary, including but not limited to the spatial distance across which the ICs were induced. One potential importance of this last point is that it is not yet determined to what extent (if any) mechanisms of IC sensitivity differ according to whether the induced perception is a line versus a form (Box 4).

One notable exception is the study by Lee and Nguyen [16], who recorded from both superficial and deep layers in areas V2 and V1 of awake monkeys. Aside from firing rates, these authors also examined the timing of differential responses and observed the earliest effects within the superficial layers of V2 at ~70 ms after stimulus onset, followed by effects at ~100 ms within deep layers in V2 and superficial layers in V1. The latest effect was observed at 120–190 ms after stimulus onset in deep layers of V1. In addition to these data concerning IC processing as a result of modal completion, Lee and Nguyen likewise measured responses to amodally completed ICs and luminance-defined contours. Responses in all measured areas and layers were stronger to modally versus amodally completed ICs. In some of their recordings from V2 neurons, responses were in fact stronger to the control stimuli (outwardly rotated Pacmen that did not form an IC) than to amodally completed ICs. Likewise, responses were weaker and delayed by ~55 ms for ICs (both modally and amodally

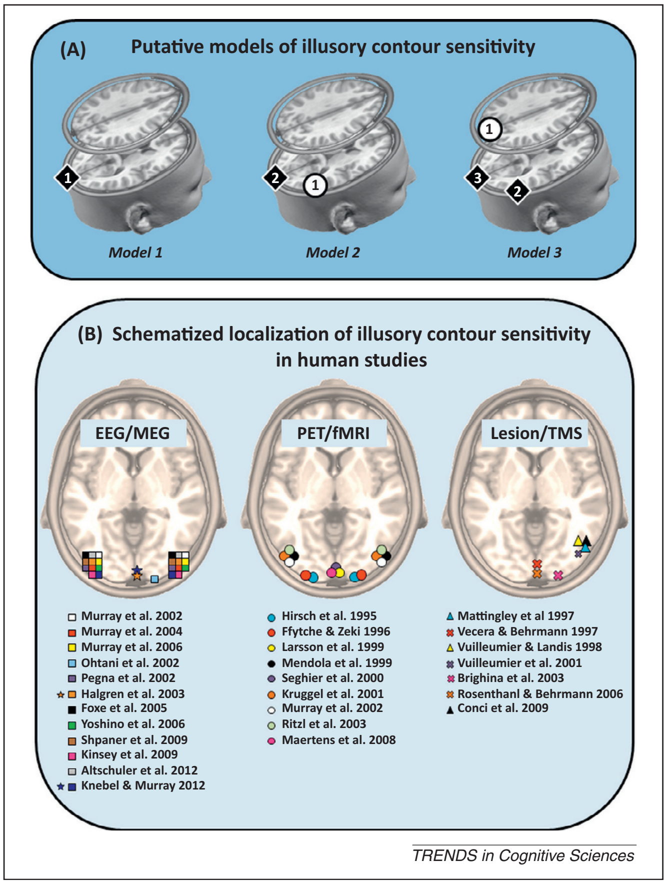

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Figure 1. Brain areas involved in illusory contour (IC) sensitivity. **(A)** Putative models of IC sensitivity; numbers indicate sequence, diamonds indicate IC sensitivity, and circles indicate sensitivity to salient regions or similar visual features. Model 1 claims that IC sensitivity is mediated by low-level visual areas V1 and V2 via an exclusively feed-forward mechanism. Model 2 assumes IC sensitivity in V2 and V1 at a later stage that is mediated by a temporally preceding sensitivity to salient regions in lateral occipital cortices (LOC), which itself is not sensitive to ICs (at least during the initial stages of processing). Model 3 localizes IC sensitivity first in LOC and later in V1 and V2, both of which are influenced by temporally preceding sensitivity to salient regions in parietal cortices. (Initial responses to stimulus presence, irrespective of IC presence, of course precede IC sensitivity; Box 3.) **(B)** Schematic localization of IC sensitivity in human studies. The colored symbols indicate the approximate locations of IC sensitivity for human studies using electroencephalography (EEG)/magnetoencephalography (MEG) source estimations (left), positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (middle), and lesion studies or transcranial magnetic stimulation (TMS) (right). The stars in the left panel indicate secondary and subsequent effects.

completed) versus luminance-defined contours. This combination of timing and laminar profile led Lee and Nguyen to support models whereby effects in V2 and V1 may be driven by feedback inputs from other cortical regions [17].

Another exceptional study is that of Sáry *et al.*, who recorded single units within the anterior inferior temporal cortex (aIT) of awake monkeys and observed differential responses to Kanizsa-type ICs at 148 ms [18]. Although this latency is substantially later than the ~70-ms effect in superficial layers of V2 described in [16], it should be noted that the size of the stimuli used by Sary *et al.* was substantially larger (~18°) than the <2.25° used by Lee and Nguyen. Consequently, their effect may be relatively delayed and is difficult to directly juxtapose with that of Lee and Nguyen [16].

The above notwithstanding, data from anesthetized animals represent a particular challenge to models favoring the interpretation of effects within V2/V1 as emanating from feedback from other, higher-level cortices. For example, Sheth *et al.* collected optical imaging and single-unit electrophysiological recordings in areas V2 and V1 of anesthetized cats [13] (see also [15]). Responses to ICs induced by misaligned line gratings were observed in both regions (although with higher frequency in V2 than V1). The latency of these effects relative to stimulus onset was not quantified. Reports of similar effects in anesthetized monkeys are problematic owing to the use of misaligned, abutting gratings that themselves included luminance differences at the location of the presumed IC [2]. Ramsden *et al.* combined optical imaging and single-unit electrophysiology in anesthetized monkeys [17]. For V1 they observed an inverse relationship between orientation coding of real versus illusory lines, whereas such coding corresponded in V2. The implication is that V1 and V2 (and likely other areas) operate in concert to generate IC sensitivity (cf. Figure 13 in [17]) (Box 2). The fact that IC sensitivity of one form or another is observable in anesthetized preparations argues for some contribution of (largely) feed-forward inputs to effects in V1/V2. Recent optical imaging data collected across V1, V2, and V4 of anesthetized macaques would nonetheless suggest that population-level IC sensitivity in V1/V2 in anesthetized preparations may reflect a largely hard-wired feedback mechanism from V4 or other higher-level cortices [19].

Electroencephalography (EEG) and magnetoencephalography (MEG)

Although animal experiments allow for precise localization of the electrodes intracranially, it is not always clear whether the animals share the same perceptions as humans when viewing experimental stimuli (see Lesion and neurostimulation studies below). Therefore, it is also desirable to perform electrophysiology on awake behaving humans who can report their perceptions. Event-related potentials (ERPs) and their MEG counterpart (event-related fields, ERFs) are frequently used to assess the temporal dynamics of brain processes in response to sensory stimuli. Advances in signal analysis and source reconstruction have allowed these methods to provide not only correlates of sensory–perceptual phenomena but also information regarding putative spatiotemporal brain mechanisms (Figure 1B) [20–23]. ERPs can likewise be acquired simultaneously with transcranial magnetic stimulation (TMS) [24] or functional magnetic resonance imaging (fMRI) [25], allowing inferences to be drawn on the correspondence between ERP modulations and hemodynamic signals [26]. Decomposition of EEG or MEG into time–frequency representations allows assessment of the contribution of frequency and phase information to IC processing specifically and the binding problem more generally [27–32].

Independent series of studies by a number of laboratories have focused on the question of when and where IC sensitivity is first manifest (Figure 3). Murray *et al.* found that sensitivity to Kanizsa-type ICs first occurs at ~90 ms after stimulus onset (see also [33] for initial evidence of such timing and [34] for an alternative paradigm yielding

Box 3. Hierarchies in the visual system

The primate visual system consists of multiple interdependent varieties of essentially hierarchical representations. First, anatomic connectivity patterns support the distinction between low-level (e.g., V1 and V2) and high-level (e.g., V4, IT, MT, IP, and STS) cortices [92]. Situation of regions is based on the density and laminar profile of its axonal projections and terminations relative to those of other regions. Anatomic connectivity likewise supports parietal and inferotemporal pathways that originate in magnocellular and parvocellular retinal ganglion cells. In general, functional data graft onto this subdivision, yielding 'where' and 'what' pathways for spatial/action and object recognition functions, respectively [102]. The inferotemporal 'what' pathway includes parvocellular layers of the lateral geniculate nucleus (LGN), the primary visual cortex (V1), and areas V2, V4, and IT (Figure IA).

Second, receptive field mapping supports another type of hierarchy centered on retinotopic versus non-retinotopic representations [103]. Higher-order functions such as object recognition that is size-, position-, and cue- invariant are probably more suited to non-retinotopically organized regions [104]. Individual neurons within low-level cortices contain relatively small receptive fields, and populations of neurons are arranged retinotopically within a given region. Neurons within high-level cortices contain relatively large receptive fields that are not forcibly arranged in a strictly retinotopic manner within a given region. Two additional considerations to this organization are (i) the interplay between eccentricity and the size of the receptive field for a neuron and (ii) the dynamics of and contextual influences on the receptive field of a neuron. Across regions, receptive fields are consistently larger for neurons sensitive to more eccentric visual field locations (Figure IB) [105,106]. Likewise, receptive fields are not static constructs, but rather are dynamic and change in their shape and response selectivity [94,95]. Such considerations likely play a crucial role in mechanisms of IC sensitivity in which individual neurons in low-level cortices receive (feed-forward) information only about a subset of an illusory figure but never about the whole figure if the size of the figure exceeds the size of the receptive field.

Third, response dynamics support a final type of hierarchy that focuses on information flow [107–109]. Neural activity propagates (almost) simultaneously across multiple brain regions (Figure IC) and there is a latency advantage for 'where' versus 'what' pathway structures. This latency difference can result in the co-occurrence of feed-forward inputs and (dorsal-pathway-mediated) feedback or lateral inputs within regions of the 'what' pathway that promote interactive modes of stimulus processing [107].

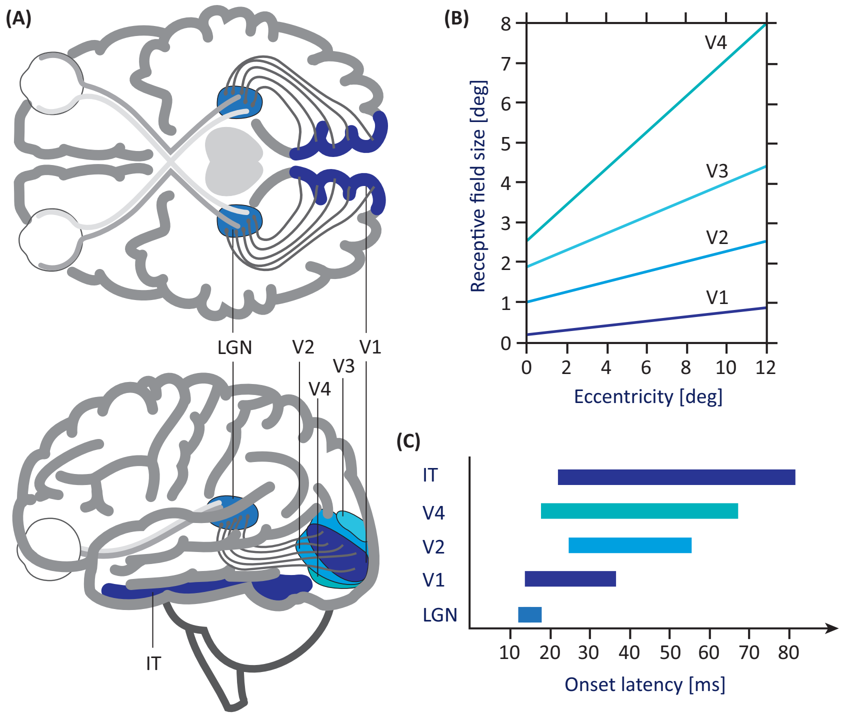

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Figure I. Organization within the primate visual system. **(A)** The human visual system includes several anatomically and functionally dissociable regions, a sample of which is illustrated along with a schematic of the major retino–thalamo–cortical pathway. **(B)** The size of receptive fields across a sample of regions in the monkey visual system generally increases from lower-tier to higher-tier areas and from the center to the periphery (reproduced, with permission, from [105]). **(C)** The range of onset latencies across a sample of regions in the monkey visual system illustrates rapid and parallel signal propagation (reproduced, with permission, from [107]).

similar results), lagging ERP onset by ~40 ms, and is localized first to the LOC (Figure 2) [25]. It has been shown that this IC effect is an amplitude rather than a topographic modulation of the ERP that is superimposed on the so-called N170 component [8,28,35–38], which is a peak of the visual evoked potential at ~150–200 ms with a negative distribution over the parieto-occipital scalp with predominant sources within ventral and lateral occipital cortices. In addition, the IC effect is insensitive to variations in the contrast polarity (i.e., whether inducers are black on a gray background or *vice versa*) [8,39], ruling out an explanation in terms of perceived brightness enhancement [40]. The IC effect is mediated by the presence of the illusory figure but not collinear lines [41]. The IC effect is likewise robust to variation in the support ratio of the IC, the number of inducers generating the illusory shape, and the surface area of the illusory shape [8,42]. The IC effect is indistinguishable when the illusory shape is completed both modally and amodally [36]. This latter finding provides another argument against a mechanism mediated solely by

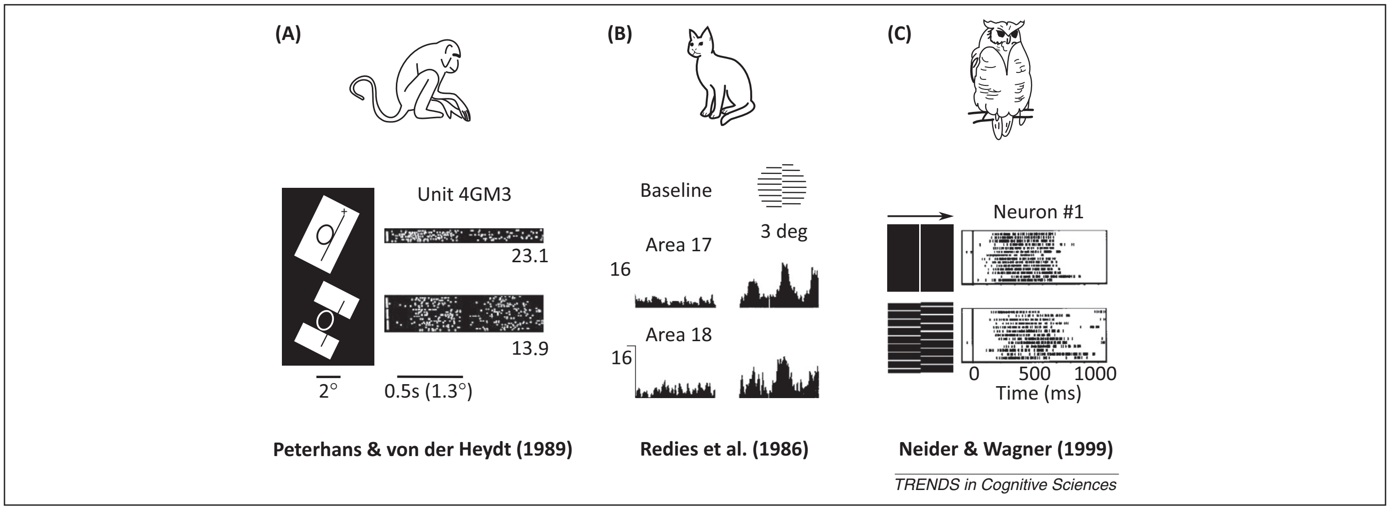

Figure 2. Examples of single-unit illusory contour (IC) sensitivity across species. **(A)** Individual V2 neurons in awake, fixating monkeys exhibit sensitivity to real (top) and illusory (bottom) contours, even though the latter consisted entirely of stimuli outside of the classical receptive field of a neuron (oval). White dots in the raster plots represent action potentials during movement of the stimuli (forward and reverse sweep each lasting 500 ms). **(B)** Individual V1 and V2 neurons in anesthetized cats exhibit sensitivity beyond baseline levels (left) to ICs induced by misaligned gratings (right). Peri-stimulus time histograms show the neural firing rate. **(C)** Individual neurons recorded from the visual Wulst (analogous to V2) in awake barn owls show similar responses to real and illusory contours (top and bottom row, respectively). Stimuli moved across the receptive field and generated action potentials shown in the raster plots (right column). Drawings of animals are adapted from the Snodgrass and Vanderwart database [110] (image numbers 49, 145, and 160). Neurophysiologic data are reproduced and adapted, with permission, from [43] and [15]. Neurophysiologic data in panel (C) were adapted, with permission, from Macmillan Publishers Ltd.: *Nature Neuroscience* [55], copyright 1999.

feed-forward activity in V2/V1, because single-unit recordings either failed to reveal sensitivity in V2 to amodal completion [16,43] or revealed significantly smaller responses to amodal verses modal completion of ICs [16]. Another study reported amodal completion in a small number of simple (9 of 73) and complex (13 of 113) V1 neurons [14]. Likewise, Sugita argued that his data point to a critical role of feedback and lateral connections from areas 'very close to V1' [14]. However, 'close' could presumably refer either to spatial or temporal proximity (Box 3), allowing for IC sensitivity to be initially mediated in regions such as LOC. The IC effect is likewise observed when using misaligned gratings instead of Kanizsa-type stimuli [38,39,44]. The timing of the IC effect shifts to ~100 ms later (i.e., to onset at ~200 ms) when inducers are positioned within a single visual hemifield (although still within the central 8°) [8,33]. This shift in the timing of the IC effect is counter to what would be predicted by a strictly feed-forward V2/V1 mechanism, because placement of all of the inducers within a single visual field should obfuscate the need for inter-hemispheric transfer and by extension perceptual completion across the representation of the vertical meridian.

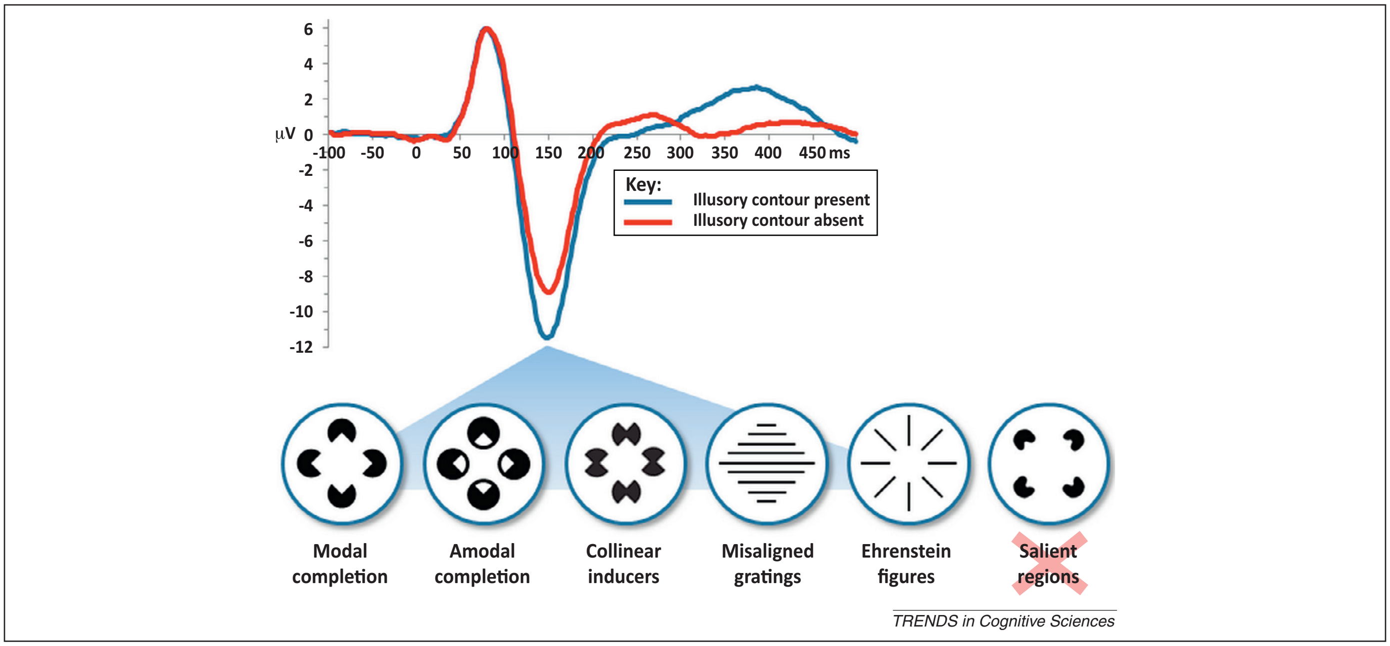

Figure 3. Illusory contour (IC) sensitivity via event-related potentials (ERPs). Top: Exemplar ERP from a lateral occipital scalp site in response to the presence and absence of an IC form (red and blue traces, respectively). Differential responses (i.e., the IC effect) typically peak at ~150–170 ms after stimulus onset. Bottom: The IC could be any of the ones shown except the salient region stimulus.

Box 4. Outstanding questions

- What is the exact relation between the physiological measures that are associated with IC processing and conscious perceptions? Transcranial stimulation methods such as TMS and transcranial electric stimulation (TES) can reveal causal inference [111]. Similar inferences can be made by acquiring brain imaging or mapping data from anesthetized individuals or patients with disorders of consciousness or impairments in perception or attention (e.g., neglect and extinction).
- How do IC perception and its brain mechanisms develop and/or depend on visual experience? Data would suggest that perceptual abilities and brain correlates only appear at approximately 6 months of age [86,112,113].
- Are the spatiotemporal brain mechanisms of IC sensitivity equivalent for induced lines and forms?
- Can mechanisms of IC sensitivity be generalized to other forms of visual completion? The integrity of early-latency visual processing, IC sensitivity, and perceptual completion of fragmented objects are dissociable in patients with schizophrenia [46,114,115]. Patients exhibit intact IC sensitivity but impaired perceptual filling in of fragmented drawings of common objects [115]. In both cases, however, early-latency visual processing was severely diminished within parieto-occipital cortices [46,114]. Different varieties of perceptual completion may thus have distinct temporal (and network) dynamics, and IC sensitivity may not critically rely on the integrity of early-latency and low-level visual processing. In parallel, it will be important to ascertain the relative contributions of specific retino–cortical pathways to IC sensitivity [116].
- What is the mechanistic interplay between IC sensitivity (and perception), depth stratification, perceived brightness enhancement, and salient region processing? What are the mechanisms whereby higher cognitive functions, including recognition of known objects and attention, influence seemingly low-level vision [117]?
- Can ICs be induced via sensory substitution? Sensory substitution converts information conveyed to one (impaired) sensory modality (e.g., vision) into signals of another, intact sensory modality (e.g., audition). Blind and sighted individuals have been successfully trained to discriminate visual-to-auditory substitution stimuli at levels above the World Health Organization threshold for blindness [118].
- What is the requisite architecture for a computational model to achieve IC sensitivity with similar temporal dynamics to that observed in humans and animal models?

Situating the role of V2/V1

Identification of IC sensitivity within V1/V2 has been notoriously evasive using ERPs and ERFs. This null result could prompt some advocates of feed-forward models in V1/V2 to dismiss EEG and MEG as simply insensitive to modulations within V2/V1 and by extension to the presumed true neurophysiology of IC processing. This criticism can be largely refuted with two sets of findings (Figure 1B). First, some ERP/ERF studies have reported effects in V2/V1, although temporally subsequent to those in LOC [45]. Second, early-latency effects within V2/V1 have been observed in response to variations in low-level stimulus features such as grating orientation [38] and inducer eccentricity [8,46]. These effects were independent of IC presence versus absence and demonstrate that ERPs/ERFs possess adequate sensitivity to detect the activity of small (sub)populations of (synchronously active) neurons in V1/V2. In addition to these effects, clever stimulus presentation and improvements in ERP/ERF signal analysis are allowing for retinotopic mapping and the distinction of activity arising from V1, V2, and V3 [47–52].

The salient region hypothesis

The IC effect is unaffected by participant accuracy in discriminating the curvature of induced contours and occurs prior to modulations of the concavity or convexity of the perceived contour [37], prompting at least two conceivable interpretations. First, IC sensitivity may dissociate from and precede shape discrimination. Second, the IC effect may not index IC sensitivity, but instead sensitivity to a different and perception-independent feature [53]. This counter-claim was formalized to suggest that the IC effect reflects sensitivity to the detection of salient regions bound by the inducers rather than to IC processes *per se* (Figure 1) [7]. This claim was based on fMRI results showing equivalent depth of modulation within the LOC to Kanizsa-type ICs and rounded versions of these stimuli that lack a perception of bound contours, but nonetheless demarcate a territory at which a shape could appear [39]. However, whereas this model proposes a differential response within V1/V2 to ICs versus these rounded versions, no direct evidence of such nor any V1/V2 responses was shown.

An ERP study [35] using rounded stimuli [7] directly assessed this model and its inherent temporal predictions [54]. Initial responses within the LOC were significantly stronger for IC stimuli than for rounded versions of the stimuli [35]. The ERP also differed topographically across stimulus types, indicative of different configurations of intracranial generators and distinct brain networks [23]. Source estimations indicated that whereas IC stimuli resulted in significant modulations (relative to the no-contour control condition) in LOC, this was not the case at this latency in response to salient-region stimuli (cf. Figure 5 in [35]; Figure 3). Thus, initial responsiveness within the LOC cannot simply reflect the discrimination of salient regions within the visual scene.

Other evidence contradicts models that prioritize salient region detection over IC sensitivity. Sugawara and Morotomi presented both Kanizsa-type and Ehrenstein-type stimuli (while also varying contrast polarity) [39]. Both stimulus types led to similarly robust ERP modulations highly similar to the above-described IC effect. The Ehrenstein-type stimuli lack salient regions [44]. In agreement are data on the relative insensitivity of IC processes to the spatial frequency of misaligned gratings used as inducers (cf. Figure 6 in [40] and [55] for corresponding single-unit data).

Binding and gamma activity

To perceive ICs the brain probably binds together the edges of the inducing elements. It is hypothesized that binding is manifest as synchronized neuronal firing in the gamma-band frequency range (typically considered to be frequencies > 30 Hz) [56]. In human EEG, this might manifest as enhanced amplitude or power in this frequency range. As expected, evoked and induced 40-Hz oscillations were stronger in response to Kanizsa compared to non-Kanizsa figures [27–29,57] (but see [58]). The evoked responses peaked at ~90 ms [28,29,59]. However, binding is not the only cognitive process that modulates gamma-band oscillations; the same also holds for processes of attention, object recognition, and language perception

[29,60]. Thus, just like the ERP effects described above, gamma-band oscillations are sensitive to IC presence but are in no way specific to binding mechanisms. In other words, if the only difference between two conditions is the presence of a bound versus an unbound figure, the bound figure will result in stronger gamma-band responses. If, however, two conditions differ in more than whether a perceived figure can be bound to a coherent object, for example, if the two figures attract different amounts of attention from the participants, gamma-band responses may instead reflect attention processes rather than binding (see [61] for arguments based on neural modeling).

Hemodynamic imaging

Positron emission tomography (PET) and fMRI provide direct visualization of brain areas that contribute to IC sensitivity, complementing the inferences drawn from ERP/ERF source estimations (Figure 1B). However, the poor temporal resolution of these methods cannot differentiate feed-forward versus feedback mechanisms that contribute to the same effect. In a first blocked-design fMRI study of four healthy subjects, regions in extrastriate visual cortex – most likely area V2 – responded preferentially to IC presence [62]. These results were considered as ‘consistent with a data-driven, bottom-up approach to illusory-contour perception’ [62] (see [63] for nearly contemporaneous PET results). Another blocked-design fMRI study [64] observed robust modulations within V1 in response to apparent vertical motion of IC stimuli, but left open the possibility that the effect relies on feedback modulations. Similarly, Larsson *et al.* observed response modulations in both V1 and V2, as well as in regions within the fusiform gyrus [65]. Inter-regional coupling (quantified with functional connectivity analyses) was reduced between V2 and V1 when viewing ICs but not real contours (see [17] for qualitatively similar findings in monkeys), which was taken as consistent with the role of feedback signals, potentially originating from the fusiform gyrus [65].

Mendola *et al.* conducted arguably the most comprehensive fMRI study to date in terms of the range of stimulus parameters combined with retinotopic mapping and cortical surface reconstructions [40]. Activations were stronger within LOC for Kanizsa-type ICs compared to control stimuli and luminance-defined contours, with no reliable modulations in lower-tier regions (cf. Figure 2 in [40]; see also [53]). IC sensitivity in LOC was size-invariant and no effects were observed in lower-tier regions, despite using stimuli with inter-inducer spans of less than 2°. Both Kanizsa-type ICs and stereopsis-defined shapes modulated activity within a similar network of higher-tier cortices. Finally, ICs induced by misaligned line gratings resulted in activation in both LOC and lower-tier regions. However, these LOC responses were stronger with decreased spatial frequency, suggesting that they are not driven by the physical features of the stimuli, but instead by the IC itself. In addition, the effects within V1 and V2 (when observed) were limited to retinotopic representations in which the IC would have been perceived, indicating that hemodynamic imaging has the requisite sensitivity to measure subtle effects in lower-tier visual cortices; something already apparent at a broader scale in the earlier hemodynamic studies cited above.

Lesion and neurostimulation studies

It is difficult to draw causal inferences between neural activity and perception from either electrophysiology or neuroimaging. Anesthetized preparations exclude perceptual reports, and studies conducted in awake animals typically only required fixation. Similar critiques are often applicable to EEG/MEG and PET/fMRI studies in humans, in which the task was often so trivial that it was only seldom (if at all) that ICs were not perceived when presented.

In a rather elegant study, Nieder and Wagner collected both behavioral and single-unit electrophysiological data from owls (Figure 2) [55]. Owls that were trained to discriminate luminance-defined squares and triangles could transfer this ability at greater than chance performance levels to the discrimination of IC squares and triangles. Neurons within a region homologous with area V2 were sensitive to IC presence in an orientation-specific manner and responded invariantly across spatial frequencies of the misaligned gratings [4]. However, causal inference is limited by separate psychophysical and neurophysiological experiments. Other shortcomings are that response latency was not assessed and neural responses were limited to a single functional region.

Causal inference regarding the role of specific brain regions, but not their dynamics, in IC sensitivity is derived from lesion studies in both humans and more recently in animal models. In general, these studies provide evidence of the critical role of higher-level visual cortices in generating the benefits of ICs for attention and perception (Figure 1). In support of pre-attentive mechanisms of IC sensitivity, patients with visuospatial neglect made no explicit report of IC shapes despite benefiting from their presence to complete orthogonal visual tasks [66–72] (see also [73,74]). Lesion analysis revealed the necessity of lateral occipital cortices (cf. Figure 5 in [70]; see also [75–77] for comparable studies in monkeys). Such data are therefore consistent with model 3 in Figure 1A, but also indicate that modulatory inputs from parietal cortices (at least those affected in the patients in the above studies) are not necessary for intact IC sensitivity. However, ERP studies in such patients remain to be conducted to detail any alterations in the spatiotemporal brain dynamics of IC sensitivity. In addition, cortical cooling of higher cortical areas [78] and disruption of processing by TMS [79] support the important role of feedback for processing in early visual areas. This has led to the formulation of a reverse hierarchy for the visual system, according to which sensation follows a feed-forward path through the hierarchy from lower to higher visual cortices, but perception proceeds from higher to lower levels of the anatomical hierarchy [80]. However, the necessity of higher-level cortices does not necessarily exclude a causal role for low-level cortices. Direct testing of this hypothesis is not straightforward because of the critical role played by V1/V2 in seeing (but see reports on aperceptive agnosia [68,81] and hemianopic patients [82]). Another approach that has not yet been rigorously applied to IC processing is non-invasive neurostimulation in healthy subjects.

Conclusions

Visual scenes contain a mishmash of information, requiring discernment of which elements belong to the same objects and which should remain perceptually distinct. The brain is organized to make the transition from sensation to perception as efficiently and reliably as possible. The neurophysiological and brain mapping and imaging data reviewed here suggest that the constructivist nature of visual perception, exemplified in the case of IC sensitivity, engenders this efficiency and reliability through rapid and distributed responses combining feed-forward, feedback, and lateral architectures. This forces us to reconsider the importance not only of where neural or perceptual sensitivity is manifest but also when and how it relates to similar processes elsewhere in the brain. Further research is clearly required to resolve some of the many open issues and to effectuate applications in clinical settings and industry (Box 4).

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