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Illusory contours: a window onto the neurophysiology of constructing perception

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Abstract:	Seeing seems effortless, despite needing to segregate and integrate visual information that varies in its 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 spatio-temporal brain dynamics in generating models of brain function and perception.

Highlights

- Illusory contours exemplify core challenges for perception and binding
- Competing models stem from diverse neurophysiologic metrics in animals and humans
- Consideration of spatio-temporal brain dynamics reconciles these differences

Illusory contours: a window onto the neurophysiology of constructing perception

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Abstract

Seeing seems effortless, despite needing to segregate and integrate visual information that varies in its 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 spatio-temporal brain dynamics in generating models of brain function and perception.

Keywords

Visual perception; perceptual completion; binding; object recognition; illusory contour; neuroimaging

Models of Illusory Contour Processing

Illusory contours (ICs) constitute 'simple' stimuli for the investigation of vision (**Figure I in Box 1**). They have received 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 as 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 vs. feedback activity, as well as the locus of neural sensitivity 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) [2](**Box 3**). 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 illusory contours such contextual modulations in V1/V2 extend only out by ~3° 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 illusory contour sensitivity if the gap distance between inducers is too large [4]. Additionally and as evident from the examples shown in Box 1, illusory contours 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 across the neural population are extensively overlapping [5,6]. Such properties, particularly when considered alongside the rapidity of signal propagation through visual cortices (see **Box 3**), in principle would allow for a predominant role of higher-level cortices, such as infero-temporal cortices in macaque monkeys and lateral-occipital cortices 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 lateral occipital cortices (LOC), that are not themselves sensitive to ICs [7]. A third model localizes IC sensitivity first in LOC as well as 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] as well as plays a role in visuo-spatial attention and state-dependent phase-resetting of ongoing oscillatory activity in visual cortices [9].

Figure 1 about here

The progressive development of these models and the data supporting them in many regards highlights what may be considered a general tendency in neuroscience research over the past 30 or so years; namely, a progression from an interest in characterizing individual neurons’ responses 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 for improving 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 already noted by William James [10] when 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.” (Volume II, page 103). 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 were assumed to be responsible for perception [12].

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

Figure2 about here

However, an unequivocal interpretation from these and other single-unit studies is not forthcoming for several reasons. First and despite the technique's exquisite spatial resolution, the timing and laminar distribution of effects has typically not been reported or quantified. Second, the 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 vs. a form (**Box 4**).

One notable exception is found in 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 ~70ms post-stimulus onset, followed by effects at ~100ms within deep layers in V2 as well as superficial layers in V1. The latest effect was observed at 120-190ms post-stimulus onset in deep layers of V1. In addition to these data concerning illusory contour processing as a result of modal completion, Lee and Nguyen likewise measured responses to amodally completed illusory contours as well as luminance-defined contours. Responses in all measured areas and layers were stronger to modally versus amodally completed illusory contours. 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 illusory contour) than to amodally completed illusory contours. Likewise, responses were weaker and delayed by ~55ms for illusory contours (both modally and amodally 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 (see also [17]).

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

The above notwithstanding, data in 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. [13] collected optical imaging and single-unit electrophysiological recordings in areas V2 and V1 of anesthetized cats (see also [15]). Responses to ICs induced by misaligned line gratings were observed in both regions (though 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 due to the use of misaligned, abutting gratings that themselves included luminance differences at the location of the presumed illusory contour [2]. Ramsden et al. [17] combined optical imaging and single-unit electrophysiology in anesthetized monkeys. In V1 they observed an inverse relationship between orientation coding of real vs. illusory lines, while such coding corresponded in V2. The implication is that V1 and V2 (and likely other areas) operate in concert to generate IC sensitivity (cf. their Figure 13) **(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 & Magnetoencephalography

While 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 magneto-encephalographic 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 spatio-temporal brain mechanisms ([20–23]) (**Figure 1b**). ERPs can likewise be acquired simultaneously with TMS [24] or fMRI [25], allowing for inferences to be drawn on the correspondence between ERP modulations and hemodynamic signals [26]. Decomposition of EEG/MEG into time-frequency representations allows for the 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 first manifested (**Figure 3**). Murray et al. [25] found that sensitivity to Kanizsa-type ICs onsets at ~90ms post-stimulus onset (see also [33] for initial evidence for such timing and [34] for an alternative paradigm yielding similar results), lagged ERP onset by ~40ms, and is localized first to the LOC (**Figure 2**). This *"IC effect"* has been shown to be an amplitude rather than a topographic modulation of the ERP that is superimposed upon the so-called N170 component [28]([8,35–38]), which is a peak of the visual evoked potential at ~150-200ms with a negative distribution of 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] (see also [39]), ruling out an explanation in terms of perceived brightness enhancement (see also [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 illusory contour, the number of inducers generating the illusory shape, and the surface area of the illusory shape [8,42]. The *IC effect* is indistinguishable both when the illusory shape is completed modally as well as amodally [36]. This latter finding provides another argument against a mechanism mediated solely by feed-forward activity in V2/V1, as single-unit recordings either failed to observe sensitivity in V2 to amodal completion [16,43] or observed significantly smaller responses to amodal vs. modal completion of illusory contours [16]. Another study reported amodal completion in a small number of simple (9 of 73) and complex (13 of 113) V1 neurons [14]. Sugita likewise argued from his data for a critical role of feedback and lateral connections from areas “very close to V1” (page 271 of [14]). However, “close” could presumably refer either to spatial or temporal proximity (see 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 ~100ms later (i.e. to onset at ~200ms) when inducers are positioned within a single visual hemifield (though 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 about here

Situating the role of V2/V1

Identification of IC sensitivity within V1/V2 has been notoriously evasive with ERPs/ERFs. This null result could prompt some advocates of feed-forward models in V1/V2 to dismiss EEG/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 dispelled with two sets of findings (**Figure 1b**). First, some ERP/ERF studies have reported effects in V2/V1, though 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] or inducer eccentricity [8,46]. These effects were independent of IC presence vs. 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, we would like to mention that clever stimulus presentation as well as 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 likewise unaffected by participants' accuracy in discriminating the curvature of the induced contours and also occurs prior to modulations of the concavity/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* [7] (**Figure 1**). This claim was based on fMRI results showing equivalent depth of modulation within the LOC to Kanizsa-type ICs as well as 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 for such nor any V1/V2 responses were shown.

An ERP study [35] using rounded stimuli from [7] directly assessed this model and its inherent temporal predictions (see also [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 (reviewed in [23]). Source estimations indicated that that while 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. Fig. 5 of [35]; **Figure 3**). Thus, initial responsiveness within the LOC cannot simply reflect the discrimination of salient regions within the visual scene.

Other evidence speaks against models that prioritize salient region detection over IC sensitivity. Sugawara and Morotomi [39] not only presented Kanisza-type stimuli but also Ehrenstein-type stimuli (while also varying contrast polarity). Both types of stimuli led to similarly robust ERP modulations highly similar to the above-described *IC effect*. The Ehrenstein-type stimuli lack salient regions (see also [44]). In agreement are data concerning the relative insensitivity of IC processes to the spatial frequency of the misaligned gratings used as inducers (cf. Figure 6 in [40] as well as [55] for corresponding single-unit data).

Binding and gamma activity

To perceive ICs the brain likely binds together the edges of the inducing elements. Binding is hypothesized to manifest as synchronized neuronal firing in the gamma band frequency range (i.e. typically considered to be frequencies above 30Hz) [56]. In human EEG, this might manifest as enhanced amplitude or power in this frequency range. As expected, evoked and induced 40Hz oscillations were stronger in response to Kanizsa figures as compared to non-Kanizsa figures ([57][27][28][29], though see [58]). The evoked responses peaked at ~90ms ([28][29]; reviewed in [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 [60][29]. 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 vs. 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, e.g. if the two figures attract different amounts of attention from the participants, gamma-band responses may instead reflect attention processes rather than binding (see also [61] for arguments based on neural modeling).

Hemodynamic Imaging

Positron emission tomography (PET) and functional magnetic resonance imaging (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 vs. feedback mechanisms contributing to the same effect. In a first blocked-design fMRI study of 4 healthy subjects, regions in extra-striate 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” (p. 6472 of [62]; see also [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 of the effect relying on feedback modulations. Similarly, Larsson et al. [65] observed response modulations in both V1 and V2, as well as regions within the fusiform gyrus. Inter-regional coupling (quantified with functional connectivity analyses) was reduced between V2 and V1 when viewing ICs but not real contours (see also [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. [40] conducted arguably the most comprehensive fMRI study to date in terms of range of stimulus parameters combined with retinotopic mapping and cortical surface reconstructions. Activations were stronger within LOC for Kanizsa-type ICs vs. control stimuli and luminance-defined contours, with no reliable modulations in lower-tier regions (cf. their Figure 2; 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 now also within 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. Plus, the effects within V1 and V2 (when observed) were limited to retinoptic representations where the illusory contour 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 grosser 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, where the task was oftentimes 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 [55] collected both behavioral and single-unit electrophysiological data from owls (**Figure 2**). Owls that were trained to discriminate luminance-defined squares and triangles could transfer this ability at above 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 (see also [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 derives from lesion studies in both humans and more recently in animal models. Generally-speaking, these studies provide evidence for 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 visuo-spatial neglect made no explicit report of the 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 therefore are 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 illusory contour sensitivity. However, ERP studies in such patients remain to be conducted in order to detail any alterations in the spatio-temporal brain dynamics of IC sensitivity. In addition, cortical cooling of higher cortical areas [78] as well as disruption of processing by transcranial magnetic stimulation [79] support the important role of feedback for processing in early visual areas. This has led to the formulation of the *reverse hierarchy of the visual system* stating that sensation follows a feed-forward path through this hierarchy from lower to higher visual cortices, but that perception proceeds from higher to lower levels of the anatomical hierarchy [80]. However, the necessity of higher-level cortices does not forcibly exclude a causal role for low-level cortices. Directly testing this hypothesis is not straightforward, of course, because of the critical role played by V1/V2 in seeing (though see reports on aperceptive agnosia [68,81] and hemianopic patients [82]). Another approach that as yet has not been rigorously applied to IC processing is non-invasive neurostimulation in healthy subjects.

Conclusions

Visual scenes contain a mishmash of information, requiring the 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/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/perceptual sensitivity manifests, 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 to clinical settings and industry (Box 4).

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Figure Captions

Figure 1. Brain areas involved in IC sensitivity. (a) Putative models of illusory contour sensitivity – numbers indicate sequence, diamond indicates 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/V1 at a later stage that is mediated by a temporally preceding sensitivity to salient regions in LOC, which itself is not sensitive to illusory contours (at least during initial stages of processing). Model 3 localizes IC sensitivity first in LOC as well as later in V1/V2, both of which are mediated by temporally preceding sensitivity to salient regions in parietal cortices (Initial responses to stimulus presence, irrespective of IC presence, of course precede IC sensitivity; see Box 3.) (b) Schematized localization of IC sensitivity in human studies. The colored symbols indicate the approximate locations of IC sensitivity for human studies using EEG/MEG source estimations (left), PET/fMRI (middle), and lesion studies / TMS (right). The stars in the left panel indicate secondary and subsequent effects.

Figure 2. Examples of single-unit IC sensitivity across species. (a) Individual V2 neurons in awake, fixating monkeys exhibit sensitivity to real (top) as well as illusory (bottom) contours, even though the latter consisted entirely of stimuli outside of the neuron’s classical receptive field (oval). White dots in the raster plots represent action potentials during the movement of the stimuli (forward and reverse sweep each lasting 500ms). (b) Individual V1 and V2 neurons in anesthetized cats exhibit sensitivity beyond baseline levels (left) to illusory contours induced by misaligned gratings (right). Peri-stimulus time histograms display neural firing rate. (c)

Individual neurons recorded from the awake barn owls' visual Wulst (analogous to V2) 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 [83] (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 by permission from Macmillan Publishers Ltd: *Nature Neuroscience* [55], copyright 1999.

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

Box 1. Figure I. Examples of illusory contours. In (a) and (b) illusory contours are composed of lines. In (c) the IC is composed of geometric figures. In (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 un-occluded 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 by [84], [85], [86], and [87], respectively.

Box 2. Figure I. Architectures for computational modelling. (a) Illustration of feed-forward connections (blue) in a network of artificial neurons (black circles). (b) Illustration of feedback (red) and lateral connections (green).

Box 3. 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 schematization 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 as well as from center to periphery (reproduced with permission from [88]). (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 [89]).

Glossary

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

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

Event-related oscillation: the phase-resetting of ongoing EEG activity within a given frequency band/bin (0-4Hz: delta, 4-8Hz: theta, 8-12Hz: alpha, 12-30Hz: beta, 30-80Hz low gamma, 80-200Hz: 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): the EEG activity that is time-locked and phase-locked to a stimulus [90]. 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 vs. 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 [91].

Illusory Contours (ICs): The perception of lines, forms, volumes, etc. in the absence of physical support (e.g. luminance gradients). The first human experiments describing the conscious perception of illusory contours (ICs) date back to the early 20th century with variations continually created [84–86,92].

Modal completion vs. amodal completion: Modally completed ICs typically comprise at least three aspects: i) perception of the figure's borders, ii) brightness enhancement of the illusory figure vs. 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, a neuron's receptive field typically refers to that region of space from which a firing rate can be elicited beyond spontaneous activity levels. This space can alter dynamically [93], and influences on neural activity can extend spatially beyond the classical receptive field borders [94].

Salient Region: a term borrowed from computer vision to refer to pixels likely belonging to the same surface or form without forcibly delineating their borders.

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 would induce such illusions, typically instructing observers to indicate whether or not they perceived illusory contours 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 [95]. Shipley and Kellmann [96] independently varied inducer size, inducer spacing, and overall stimulus size of Kanizsa figures. They found that only the inducer size and the inducer spacing had an effect on the perceived intensity of the ICs. From such, they proposed integrating these two variables into a single metric that they called ‘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 the illusion (though see [8,42]). Temporal factors also influence IC perception. Kojo et al. [97] 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. There is therefore a degree of spatio-temporal coupling in IC perception. Nonetheless, psychophysical data also support IC sensitivity occurring pre-attentively [73] and directing the allocation of spatial attention [74].

Figure I about here

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 (e.g. [15]; though see [19] wherein IC sensitivity originated in area V4 despite anesthesia). Causal data linking neural activity and perceptual abilities in animals is 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 vs. learned capacity. EEG/ERP recordings from babies demonstrated that infants younger than three months of age do not show enhanced gamma-band oscillations when viewing Kanizsa figures while older ones do [98]. This supports the notion that IC perception is an acquired ability of our brains which in turn speaks in favor of the involvement of higher cognitive functions.

Box2. 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 a neuron’s classical receptive field. 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 comprised of mixtures of feed-forward, feedback, and lateral interactions (**Figure I**) [99,100].

Figure I about here

Some of the original propositions based on neurophysiological observations already included such interactions [101]. 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. Those neurons that do receive stimulation with real contours in their receptive fields respond with an increase of their firing rate that would “spread” in the case of lateral connections to excite those neurons that do not “see” real contours. However, this mechanism alone would result in illusory contours 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 [102]. 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. Incorporating both, spiking neurons as well as lateral connections and bipolar cells, results in a realistic model for the processing of illusory contours [103]. 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 comprised of 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 spatio-temporal interplay of neural populations [99][100]. Key features of this variety 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 that in turn are only effective over time [99]. These features parallel the neurophysiological properties of IT neurons.

IC sensitivity is but one of myriad examples when 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 illusory contours as well as occluded objects [104]. A recent modeling study was able to achieve both perceptual tasks in one biologically plausible network architecture [105]. 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.

Box 3. Hierarchies in the Visual System

The primate visual system consists of multiple, inter-dependent varieties of essentially hierarchical representations. First, anatomical 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 [91]. Situating regions is based on the density and laminar profile of its axonal projections and terminations relative to those of other regions. Anatomical connectivity likewise supports parietal and infero-temporal pathways that originate in magnocellular and parvocellular retinal ganglion cells. Functional data generally-speaking graft onto this subdivision, yielding “where” and “what” pathways for spatial/action and object recognition functions, respectively [106]. The infero-temporal “what” pathway includes the parvocellular layers of the lateral geniculate nucleus (LGN), the primary visual cortex (V1), as well as areas V2, V4, and IT (**Figure Ia**).

Second, receptive field mapping supports another type of hierarchy centered on retinotopic vs. non-retinotopic representations [107]. Higher-order functions such as object recognition that is size-, position-, and cue- invariant are likely more suited to non-retinotopically organized regions [108]. 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 a neuron’s receptive field and ii) the dynamics of and contextual influences upon a neuron’s receptive field. Across regions, receptive fields are consistently larger for neurons sensitive to more eccentric visual field locations (**Figure Ib**, also [88,109]). Likewise, receptive fields are not static constructs, but rather are dynamic and change in their shape and response selectivity [93,94]. Such considerations likely play a crucial role in mechanisms of IC sensitivity where 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 [89,110,111]. Neural activity propagates (almost) simultaneously across multiple brain regions (**Figure Ic**) and there is a latency advantage for “where” vs. “what” pathway structures. This latency difference can result in the co-occurrence of feed-forward inputs and (dorsal pathway mediated) feedback/lateral inputs within regions of the “what” pathway that promote interactive modes of stimulus processing [89].

Figure I about here

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 transcranial magnetic stimulation (TMS) and transcranial electric stimulation (TES) can provide causal inference[112]. Similar inferences can be made by acquiring brain imaging/mapping data from anesthetised individuals or patients with disorders of consciousness or impairments in perception/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 [98,113,114].
- Are the spatio-temporal brain mechanisms of IC sensitivity for induced lines and forms equivalent?
- Do mechanisms of IC sensitivity generalize 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 [46,115,116]. Patients exhibit intact IC sensitivity but impaired perceptual filling-in of fragmented drawings of common objects [116]. In both cases, though, early-latency visual processing was severely diminished within parieto-occipital cortices [46,115]. 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 [117].

- 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 the recognition of known objects and attention, influence seemingly low-level vision [118]?
- 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's threshold for blindness [119].
- What is the requisite architecture for a computational model to achieve IC sensitivity with similar temporal dynamics as observed in humans and animal models?

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Figure 1

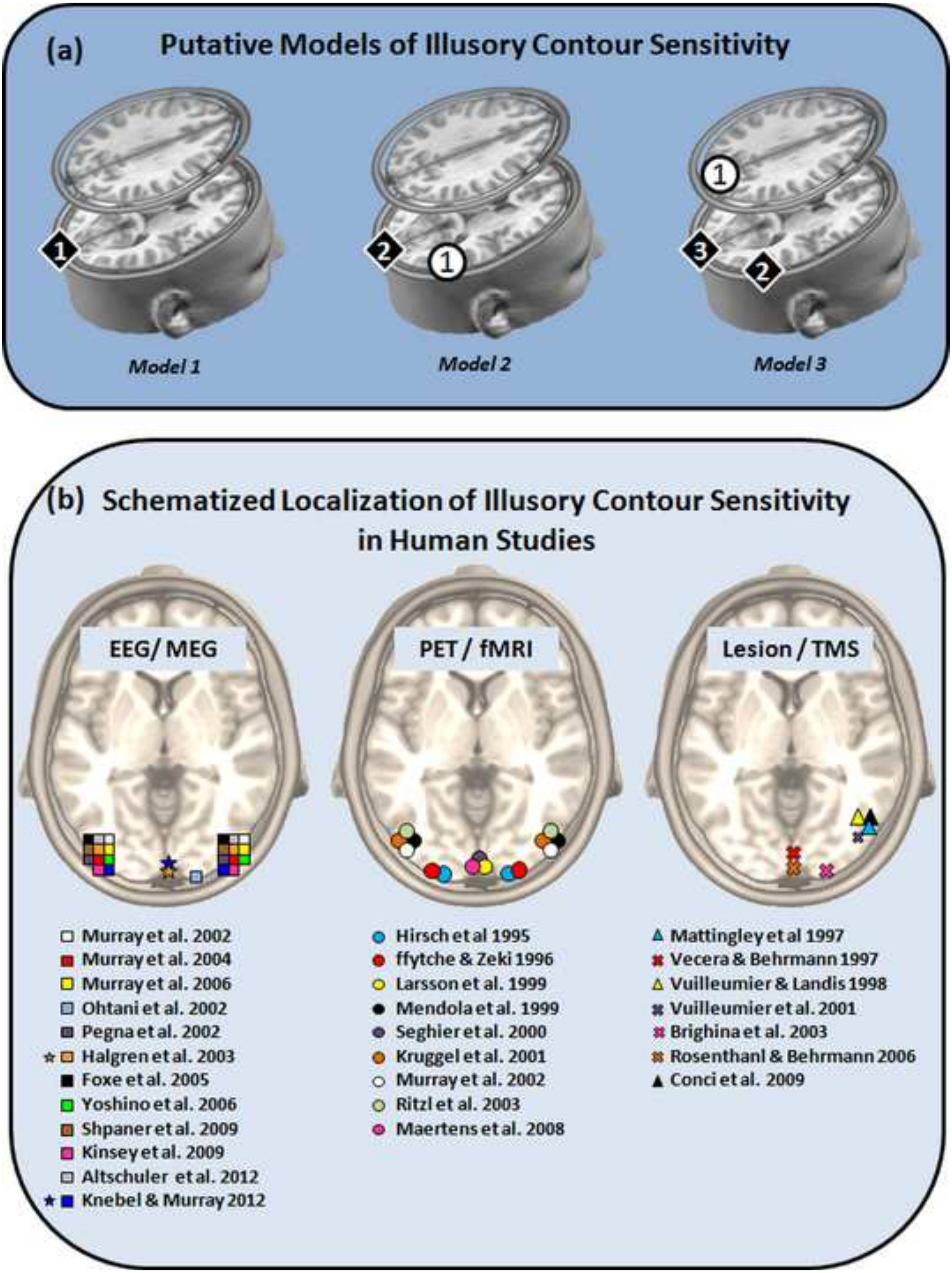

(a) Putative Models of Illusory Contour Sensitivity
1
2
1
1
3
2
Model 1
Model 2
Model 3
(b) Schematized Localization of Illusory Contour Sensitivity in Human Studies
EEG/ MEG
PET / fMRI
Lesion / TMS
□ Murray et al. 2002
■ Murray et al. 2004
■ Murray et al. 2006
■ Ohtani et al. 2002
■ Pegna et al. 2002
☆ ■ Halgren et al. 2003
■ Foxe et al. 2005
■ Yoshino et al. 2006
■ Shpaner et al. 2009
■ Kinsey et al. 2009
■ Altschuler et al. 2012
★ ■ Knebel & Murray 2012
● Hirsch et al 1995
● ffytche & Zeki 1996
● Larsson et al. 1999
● Mendola et al. 1999
● Seghier et al. 2000
● Kruggel et al. 2001
○ Murray et al. 2002
● Ritzl et al. 2003
● Maertens et al. 2008
▲ Mattingley et al 1997
✖ Vecera & Behrmann 1997
△ Vuilleumier & Landis 1998
✖ Vuilleumier et al. 2001
✖ Brighina et al. 2003
✖ Rosenthanl & Behrmann 2006
▲ Conci et al. 2009

Figure 2

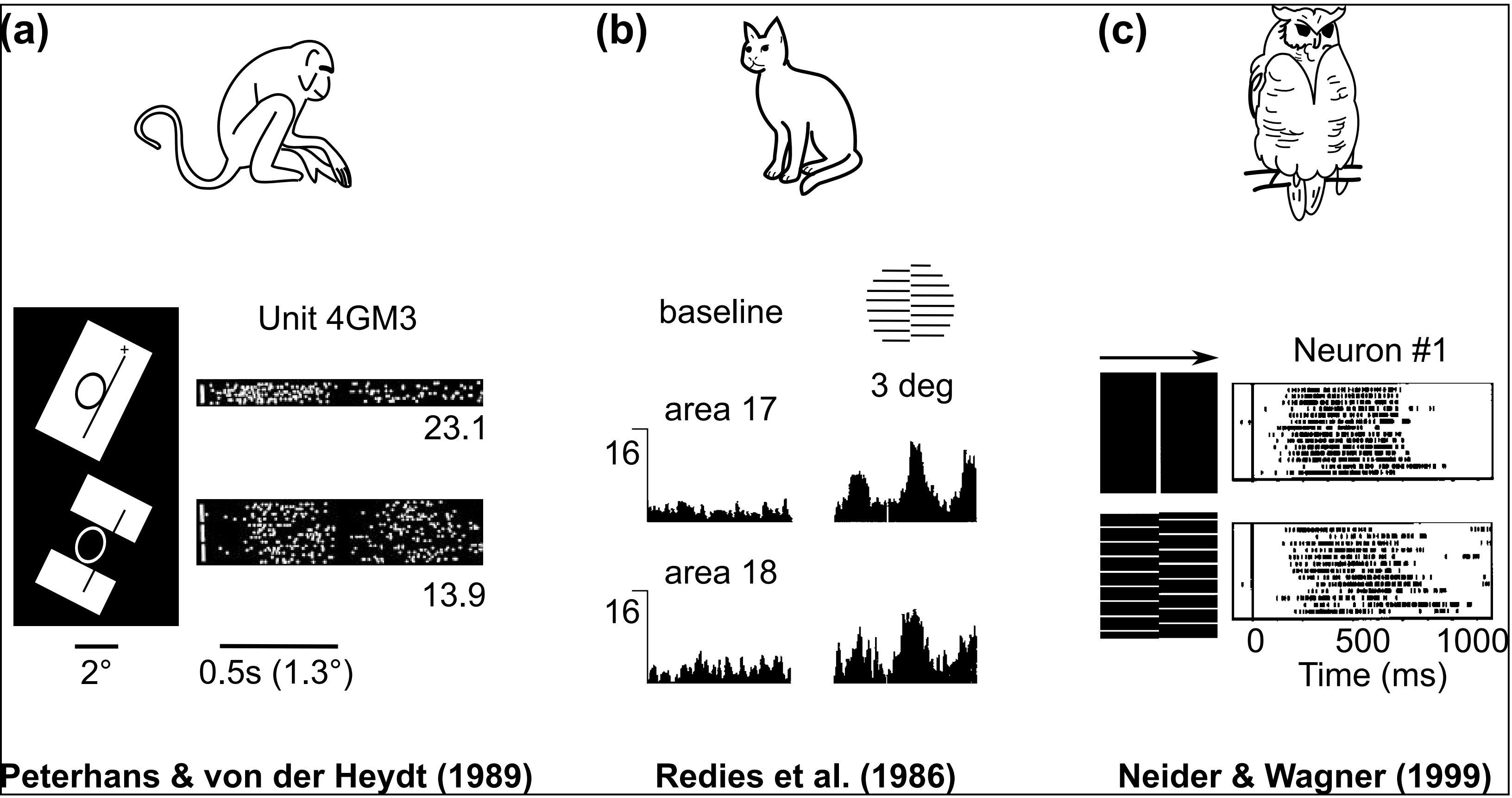
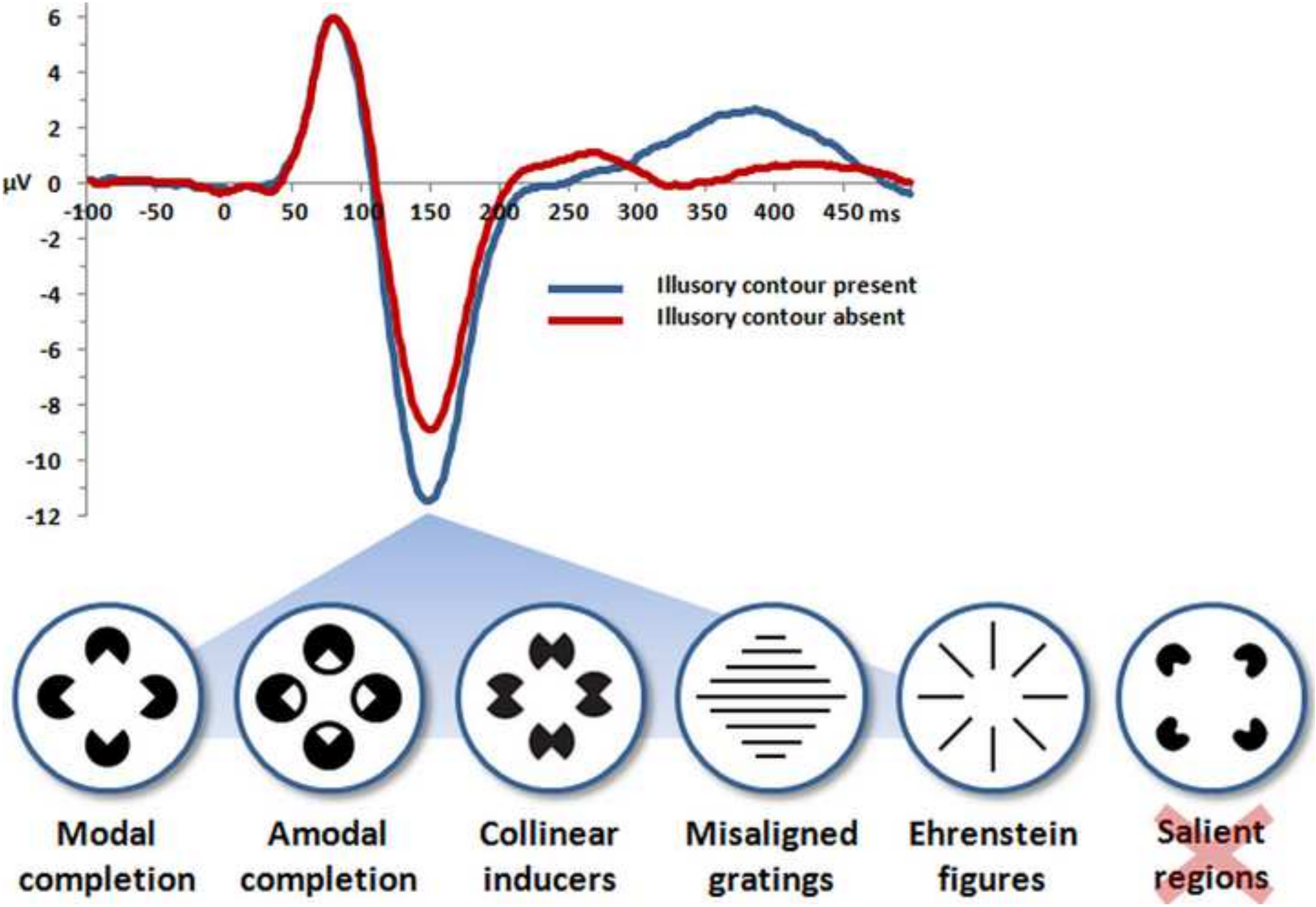
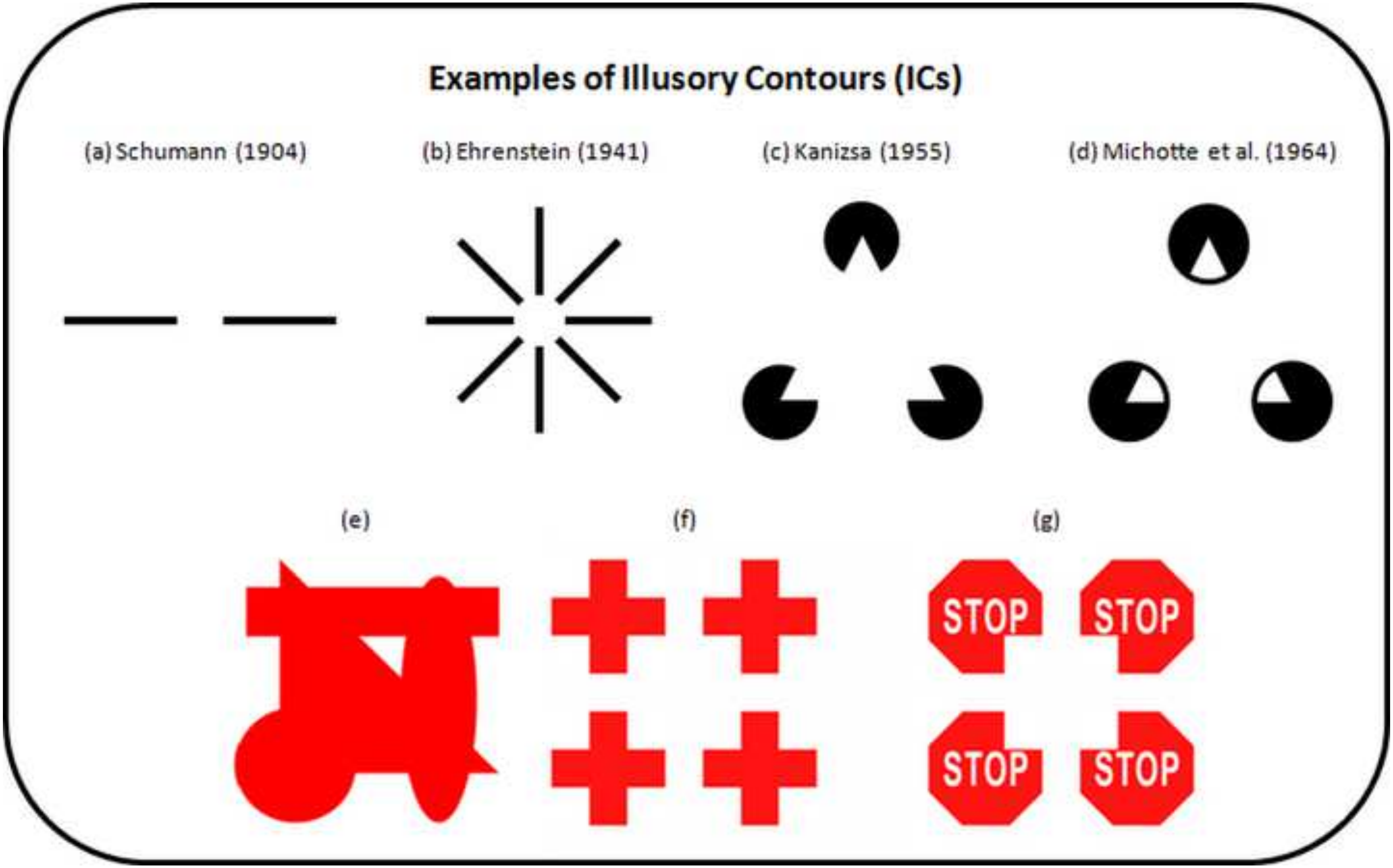

(a)
Unit 4GM3
23.1
13.9
2°
0.5s (1.3°)
Peterhans & von der Heydt (1989)
(b)
baseline
3 deg
area 17
16
area 18
16
Redies et al. (1986)
(c)
Neuron #1
0
500
1000
Time (ms)
Neider & Wagner (1999)

Figure 3

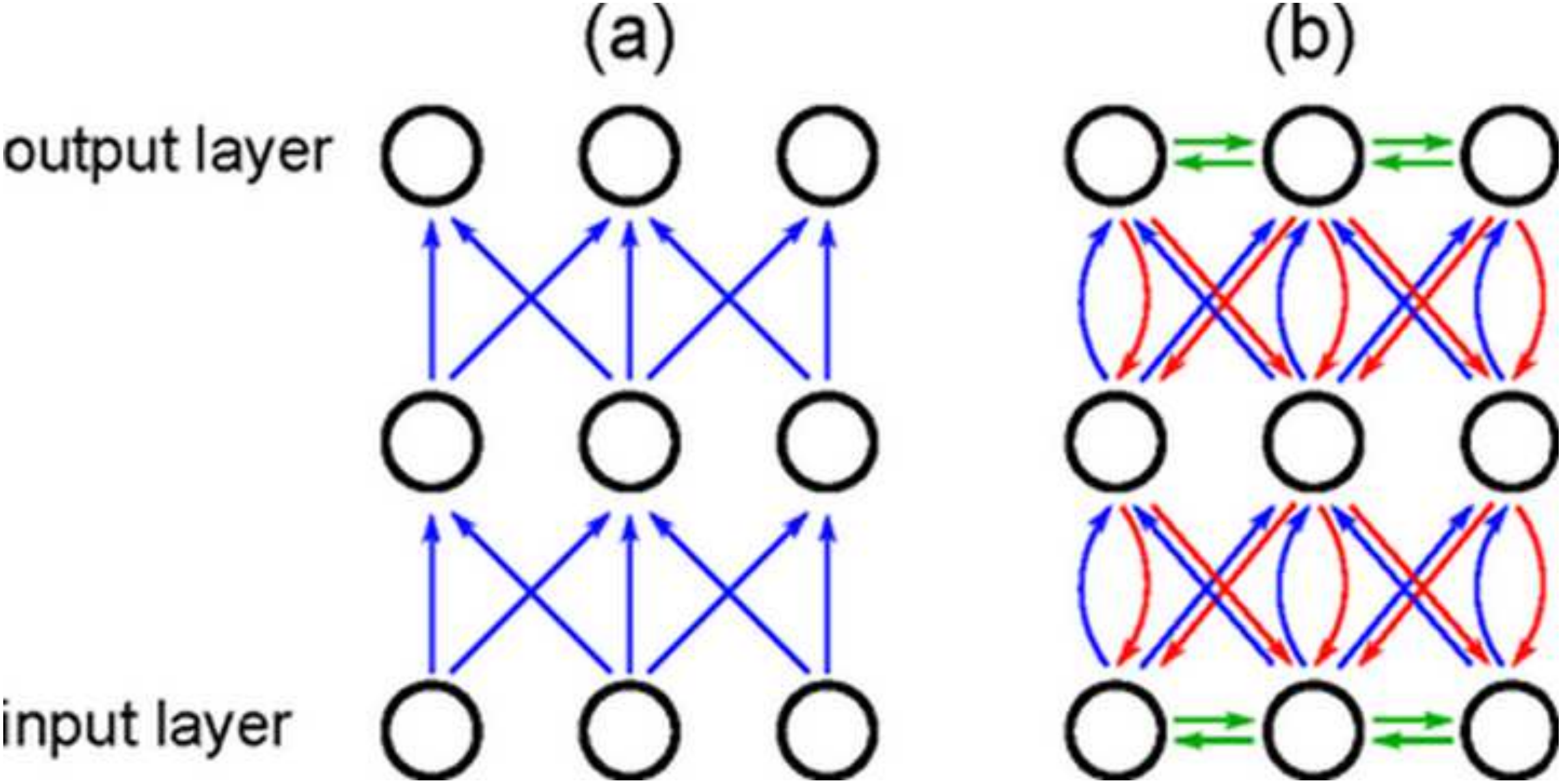


6
4
2
μV 0
-2
-4
-6
-8
-10
-12
-100
-50
0
50
100
150
200
250
300
350
400
450 ms
Illusory contour present
Illusory contour absent
Modal completion
Amodal completion
Collinear inducers
Misaligned gratings
Ehrenstein figures
Salient regions

Box 1, Figure I



Box 2, Figure I



Box 3, Figure I