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Using Illusions to Track the Emergence of Visual Perception

Patrick Cavanagh

Department of Psychology, Glendon College; and Center for Vision Research, York University, Toronto, Ontario, Canada; email: patcav1@yorku.ca

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Abstract

Everybody loves illusions. At times, the content on the internet seems to be mostly about illusions—shoes, dresses, straight lines looking bent. This attraction has a long history. Almost 2,000 years ago, Ptolemy marveled at how the sail of a distant boat could appear convex or concave. This sense of marvel continues to drive our fascination with illusions; indeed, few other corners of science can boast of such a large reach. However, illusions not only draw in the crowds; they also offer insights into visual processes. This review starts with a simple definition of illusions as conflicts between perception and cognition, where what we see does not agree with what we believe we should see. This mismatch can be either because cognition has misunderstood how perception works or because perception has misjudged the visual input. It is the perceptual errors that offer the chance to track the development of perception across visual regions. Unfortunately, the effects of illusions in different brain regions cannot be isolated in any simple way: Top-down projections from attention broadcast the expected perceptual properties everywhere, obscuring the critical evidence of where the illusion and perception emerge. The second part of this review then highlights the roadblocks to research raised by attention and describes current solutions for accessing what illusions can offer.

INTRODUCTION

In the scientific literature, there is no real consensus on a definition of illusions—some say that everything is an illusion (e.g., Cutter 2021), and others claim that there is no such thing as an illusion (e.g., Rogers 2022). Thankfully, this debate has not held back the spread of interest in illusions or the science that has emerged from studying them. In any case, the goal of this review is not to catalog illusions in any way (many papers have done that already; see the sidebar titled Illusion Reviews and Opinion Pieces), but instead to examine how we can use illusions to reveal the mechanisms and anatomy of perceptual processing. For simplicity, I use a very open definition of illusions—they are conflicts between perception and cognition, i.e., differences between what we see and what we believe we should see. This definition risks overgeneralizing illusions, but there is no obvious harm in that. Instead, it should encourage continued explorations by the general public, who have been the source of many recently discovered illusions. For example, Cecilia Bleasdale took a picture of a dress she wanted to wear to her daughter's wedding, and her daughter posted the photo to Facebook (**Figure 1**, right), while the curved lines illusion was created by American graphics illustrator Lesha Porche (Denega) in 2021. We should do what we can to strengthen this broad buzz of discovery or, at the least, not dampen the fun. As a small piece of evidence for the scope of the public's interest, there were 6 million Google search hits for "illusions" in 2006 (Bruno 2012) but 635 million in 2023. What other field can boast of such legions of highly engaged explorers? To start this overview, I briefly cover different types of illusions (for comprehensive reviews and opinion pieces, see the sidebar titled Illusion Reviews and Opinion Pieces; for websites providing demonstrations, see the sidebar titled Illusion Resources). The study of illusions is often justified by the promise that illusions can reveal how perception works and where in the brain it happens; however, as the second part of this review shows, this does not turn out to be the case. Once the illusory percept has emerged, attention will broadcast its location and features throughout the visual system. This is what attention is supposed to do to favor the processing of selected input, but its effect is to hide where perception has emerged by copying its outcome everywhere. However, all is not lost. The second part of the article also reviews techniques that can overcome attention's interference to recover where perception emerges. Remarkably, the evidence

ILLUSION REVIEWS AND OPINION PIECES

There have been many articles and books on illusions. Not only do they cover a wide range of examples, but they also have extensive references to earlier work. As always, a good place to start is with Richard Gregory, a champion of illusions and their value to vision science (e.g., Gregory 1997a,b). Gillam (1998) and Wade (2005) summarized the work on illusions of the twentieth century. Morgan (1996) described a range of explanations for several illusions and pointed out that many of the more celebrated illusions remain mysteries because they likely have multiple causes. Bruno (2012), Calabi (2012a), Ninio (2014), Eagleman (2001), Robinson (2013), Coren & Girgus (2020), and Purves et al. (2008) all give extensive reviews of illusions and discuss their nature and causes. More recently, Todorović (2020) and Tyler (2022) have offered sweeping discussions of illusions and ways to categorize them. On the other side, there are contrarians who argue that our focus on illusions is misguided. Rogers (2022) takes the view that, for the most part, there are no illusions, only perceptual facsimiles and effects. Schwartz (2012) added to these doubts, and Braddick (2018) suggested that there is no purpose in considering illusions as a special class of stimuli. All of these discussions are laid out in great detail in the weighty *The Oxford Compendium of Visual Illusions* (Shapiro & Todorović 2016). This is the ultimate reference tome for illusions, comprising several chapters discussing definitions and foundational principles of vision and 105 chapters presenting individual illusions. Rose (2018) published a review of this book that gives a helpful analysis of the contributions.

Figure 1

Illusions come in many varieties. (*Left*) The upper diamonds appear darker than the lower ones even though they are all identical (reproduced with permission from Cavanagh & Anstis 2018). (*Middle*) The boy appears to be picking up his own head (reproduced with permission from Casati & Cavanagh 2019), and the horse appears to be much longer than is possible. (*Right*) Some see the dress as blue and black, while others see it as white and gold (Iyengar 2015) (reproduced from Wikimedia, CC BY 4.0). These and many other examples fill textbooks on perception and posts on social media. Can they really help us understand how perception works?

ILLUSION RESOURCES

Scientific articles on illusions abound in several journals, and since 2020, there has even been a *Journal of Illusion* (**https://journalofillusion.net/index.php/joi/index**). There are also several excellent web resources giving demonstrations and explanations for many illusions, including Michael Bach's Visual Phenomena & Optical Illusions (**https://michaelbach.de/ot/**), the NTT Illusion Forum (**https://illusion-forum.ilab.ntt.co.jp/index.html**; in Japanese), *The Oxford Compendium of Visual Illusions* website (**https://fdslive.oup.com/www.oup.com/booksites/uk/booksites/content/9780199794607/l0k-illusions/toc.html**; requires a password), the Best Illusion of the Year Contest (**http://illusionoftheyear.com/**), the Illusions Index (**https://www.illusionsindex.org/**), the Illusion Science blog from Art Shapiro (**https://illusionscience.com/**), Real Artifacts (**https://www.realtimerendering.com/realartifacts/**), Akiyoshi Kitaoka's lab website (**http://www.ritsumei.ac.jp/~akitaoka/index-e.html**), George Mather's Motion Demos (**http://www.georgemather.com/MotionMP4.html**), Patrick Cavanagh's Demonstrations (**https://cavlab.net/Demos/**), and Stuart Anstis' Illusions (**http://anstislab.ucsd.edu/illusions/**).

covered suggests that perception, at least of location, may emerge outside of the visual system, in the frontal lobes (Liu et al. 2019).

ILLUSIONS AS CONFLICTS BETWEEN PERCEPTION AND COGNITION

Shapiro (2021) suggests that illusions are conflicts between alternative constructions of reality; in this review, following van Buren & Scholl's (2018) suggestion, I take perception and cognition to be the sources of these two constructs. Illusions arise when perception and cognition are in conflict, i.e., when there is a difference between what we see and what we believe we should see. This is not a mismatch between perception and what is physically out there; it is a mismatch between perception and what we think should be out there. However, not all conflicts between cognition and perception are illusions. I may have ordered a hamburger at the restaurant, but my vision says I received a hot dog; I saw my chosen card go back in the deck, but the magician just pulled it out of my pocket. In these cases, the conflict arises due to some external agent—human error or human sleight of hand. For an illusion, the trickster must be internal, our own brain, so that we cannot attribute the mismatch to anyone else and, more importantly, so we can use the mismatch

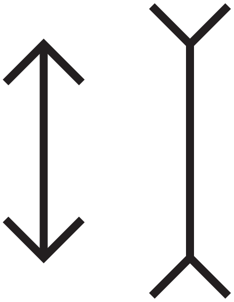

Figure 2

The Muller-Lyer illusion.

to better understand the brain or teach about its principles. The illusion also has stability over time, ruling out other, less reliable tricksters such as hallucinations and delusions.

Why would perception and cognition ever disagree? Perception and cognition are two separate agents inhabiting the same brain, and they can have differences of opinion, i.e., in-house conflicts or spats that we call illusions. Why do they disagree? The visual brain is quite smart, taking up to 30–40% of our prime cortical real estate, and it can independently generate high-level interpretations of visual input (Cavanagh 2011, 2021). These descriptions of the external world rely on early measurements, sophisticated inference processes, and a vast storehouse of knowledge about scenes, objects, and actions. Even with all of this computing power and knowledge, vision still must take some shortcuts, some of which lead to misinterpretations that cognition can catch. Cognition can reason about virtually anything, using its own knowledge base and sources, and in this case, it reasons that perception is reporting something that it does not agree with. We can call these instances perceptually based illusions—we see something that we know must be wrong. One consequence of this definition is that an illusion is only present if the viewer is aware of the mismatch; if not, perception has simply misjudged the image. In **Figure 2**, a viewer may see the right-hand vertical line as longer than the one on the left, but that is the end of it. There is no illusion until they are informed that this is not true. This personal aspect, which is clearly open to boundless debate, is similar to the claim that sounds only become music when someone listens to them. Whatever the case, our cognitive knowledge never appears to sway our perception (e.g., Firestone & Scholl 2016, Pylyshyn 1999). Knowing, for example, that the two lines in the Muller-Lyer illusion are identical in length does not make them look any more equal.

Our cognitive predictions are equally open to missteps and false assumptions leading to mismatches between what we expect and what we see. Cognition can take a second look at what is seen, but it accesses a very different database of world knowledge and information sources than perception (e.g., verbal descriptions, external measuring devices, social media), and it does not have direct access to the raw sensory input that perception does. When cognition stumbles and differs from the visual system, that, too, counts as an illusion. For example, if cognition misunderstands size or lightness constancy (see **Figure 3**), then it may consider an object's perceived size or reflectance to be implausible. However, in these cases, perception is working as it should, and the conflict arises from cognition's mistake. Many argue that these instances are not illusions at all (e.g., Rogers 2022), and this discussion is taken up in the section titled Mismatch Due More to Cognitive than Perceptual Factors. Whatever the case, we can uncover the faulty or inappropriate assumptions that lead to the cognitive errors, which tell us more about our culture and education than about brain function. Of course, in some cases, both perception and cognition may be in error.

Figure 3

Illusions that are conflicts between scene properties and image properties. Cues to depth and lighting lead reflexively to 3D interpretations. The underlying 2D image properties differ radically from the 3D shapes and lighting that they create. Some of these differences have become celebrated as illusions. In the Shepard Tables (reproduced from Shepard 1990; CC BY-SA 4.0) on the left, the depth cues indicate two quite different tabletop shapes, but their 2D shapes in the image are exactly matched. In the center panel, the depth cues indicate that the top van is much farther away than the bottom van, and even though the two vans have identical size in the image, their perceived sizes are scaled to compensate for the apparent distances (size constancy). As a result, the top, farther van looks much larger (Akiyoshi Kitaoka, reproduced with permission). In the Checker Shadow Illusion (from Adelson 1995; CC BY-SA 4.0) on the right, tiles A and B have the same luminance in the image but very different reflectances in the scene. Their match in luminance is due to the impression of a shadow falling on tile B and the compensation from lightness constancy.

Several other authors have presented elaborate taxonomies of illusions. For example, Gregory (1997b) offered 16 categories resulting from the combination of four kinds of illusions at four levels of processing. Tyler (2022) described an expanded set of 20 categories, adding one extra kind. In this review, I only describe two: cognitive errors and perceptual errors. Braddick (2018) argued that there is no real category of illusions that should be studied as a class of perceptual phenomena: All illusions are different in their own way, just like there is no real class of broken furniture because each piece of furniture breaks in its own way, revealing insights about that particular piece of furniture rather than about generalized breaking. For that matter, different diseases arise from dysfunctions of different organs or systems, revealing to some extent how that organ or system ought to work when healthy. However, few have argued that there is no real category of diseases that should be studied as a class, and Braddick's (2018) broadside against the study of illusions earned several opposing commentaries (Shapiro 2018, Todorović 2018, van Buren & Scholl 2018). Nonetheless, illusions definitely form a heterogeneous class of phenomena, as errors can arise in any stage or process in vision, they do not have to share anything in common, and each tells us about the particular process that it affects. This suggests that Gregory's (1997b) and Tyler's (2022) proposals, for example, are taxonomies of perception, rather than of illusions, and as such, they do help us understand the architecture of perception. Whatever the case, the grouping in this review into just two types simplifies the illusion landscape and is sufficient for the purpose of finding out how to use illusions to track the emergence of perception, the goal of the second half of the review.

The following brief overview of illusions starts with situations in which cognition is more in error than perception and ends with dominant perceptual errors. In truth, neither source for illusions needs to be seen as an error; this is just how cognition and perception work, doing their best based on the assumptions in play and the predictions that are generated.

MISMATCH DUE MORE TO COGNITIVE THAN PERCEPTUAL FACTORS

Typically, cognitive missteps arise from a misunderstanding of the pervasive and reflexive extraction of 3D interpretations by vision, a process that cannot be turned off. In general, the source of these cognitive errors is understood by vision scientists but not by many nonspecialists. We could argue, as some do, that, once the source of the mismatch is understood by even a few people, there is no illusion at all. However, this argument misses the point. For those not familiar with size or lightness constancy or pictorial cues, these remain puzzling illusions, making them, if nothing else, excellent teaching tools for these principles of perception. In addition, some do reveal new properties of the processes that extract 3D interpretations.

Three of the most celebrated examples of cognitive-error illusions are the Shepard Tables, the size constancy illusion (often presented with two identical images of a person at different locations in a corridor), and Adelson's Checker Shadow Illusion (**Figure 3**). In these, cognition misinterprets what should be seen. Vision, as always, automatically builds a 3D representation of space and light from whatever is present. This is its role in helping us to navigate and act on the 3D world around us—a process that cannot be switched off (Perdreau & Cavanagh 2011). In the illusions in **Figure 3**, we are surprised that these reflexive 3D interpretations lead to impressions of shape and light that are strikingly different from the 2D layout on the page. Yes, the tabletops (**Figure 3**, left) look different, as they would in the world, where their surfaces would be slanted in three dimensions, as indicated by the receding table legs and their occlusions by the tabletops. Nevertheless, in the image, the surfaces have identical 2D shapes. This appears puzzling to us even though it is exactly as it should and must be. Similarly, in the road version of the corridor illusion shown in **Figure 3** (center), two copies of the same van are placed at different points on the road. They have identical size in the image, but the perspective of the 3D scene layout indicates that the farther van must be much larger than the closer one. We may be puzzled because the two vans are the same size in the image, but vision scales up the apparent size of the farthest one. In **Figure 3** (right), the light tile in the cylinder's shadow and the dark tile in the direct illumination have the same luminance (they reflect the same amount of light). In this case, visual processes have corrected the apparent lightness of the two surfaces to compensate for the different amounts of light landing on them. This compensation, or lightness constancy, is why we see a white sheet of paper as white whether we are holding it in direct sunlight or in deep shadow. The cues to lighting in **Figure 3** (right) trigger these processes and, again, cannot be undone (Perdreau & Cavanagh 2011).

These are cognitive errors: We are confused that the 3D scene has different apparent shapes and light than the 2D image that generated it—sometimes referred to as a proximal-distal confusion (Todorović 2002). To be fair, perception does have it wrong—these images are on flat surfaces, and yet we see them with depth and lighting. To avoid this error, we could create 3D scenes that match those depicted in **Figure 3**. This would make the layout and lighting more obvious; in this case, in **Figure 3** (center), for example, we would need a gargantuan van at the far end of the road and a small one nearby—the fact that the enormous van and the small van cover equal amounts of the retina might be an interesting coincidence, but not the most startling aspect of the scene. Overall, the 2D versions of these images are the more useful choice for engaging students while teaching about pictorial cues.

Of course, all flat art also relies on exactly these principles for constructing our experience of depth and surface properties. Just as we are surprised that the two tabletops have the same 2D shape in **Figure 3** (left), we might look at a scene in any photograph or painting and marvel that we see different depths and lighting when it is all just pigments on a flat surface. There is really no difference between this 2D versus 3D conflict and the examples in **Figure 3**, although those examples make the conflict more palpable. In general, the recovery of 3D layout from the 2D pictorial cues is underdetermined, but instead of seeing a mishmash of all possible interpretations, perception settles on the one that is considered the most likely, even if it is not physically possible [e.g., the Penrose staircase (**Figure 4**)]. We often use regular paintings and photographs to teach

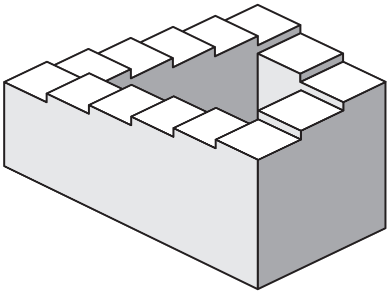

Figure 4

An impossible shape: the Penrose staircase. Image credit: Mabit1 (Wikimedia Commons; CC BY-SA 4.0).

about these pictorial cues to depth and lighting, but the more intriguing versions, like those in **Figure 3**, have greater puzzle appeal.

Other illusions have been described as simply better-camouflaged versions of 3D depth cues interfering with our 2D image judgments. The arrowheads of the Muller-Lyer illusion are possible sources of an implicit depth cue of a convex and concave corner (Gregory 1997a). Although this has been debated, the converging lines of the Ponzo illusion (**Figure 5**) are clearly a reduced cue to linear perspective (as in **Figure 3**, center).

It is true that most of these cognitive-error illusions reveal no more than common misunderstandings of how perception recovers 3D layout and lighting from 2D cues. This might relegate them to the rank of good teaching opportunities, but some have opened up new insights into the processing of pictorial cues and lighting. For example, the dress illusion (**Figure 1**, right) appears to rely on subtle cues to the light source in the photograph, cues that are biased in one direction for many but in a different direction for others (Wallisch 2017). Moreover, it is wrong to claim that the principles of pictorial cues are already explained. Yes, the informative cues in the image have been named (perspective, occlusion, etc.) but there is as yet no research on the physiology of these pictorial cues—how they actually work and what mechanisms identify them, collate them, and generate a 3D representation. The lateral occipital complex (LOC) appears to register the depth derived from monocular cues (e.g., Kourtzi & Kanwisher 2001), but we have no understanding of how the cues are processed. It may be that illusions of this type are the most promising tools for exploring the actual mechanisms of cue processing. In contrast, it may be that regular scenes will be more productive; this remains to be explored.

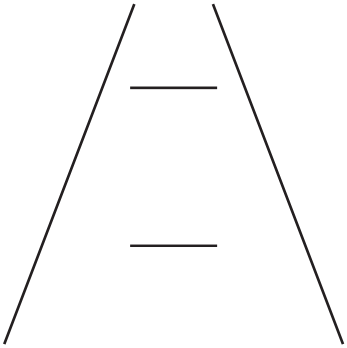

Figure 5

The Ponzo illusion.

Figure 6

Alternative 3D interpretations from the alignment of shapes and shadows. These accidental arrangements in natural scenes give rise to alternative 3D configurations, captured in this case in 2D images. Vision constructs a 3D interpretation from a small set of cues; when cues conflict, and the wrong one prevails, there are discrepancies between the actual scene and our perception. On the top left, the shadows of the fire escape are continuous with the stairs themselves, creating an illusory looping staircase (reproduced with permission from u/hey_baberuba, Reddit). On the top right, the attached shadow appears to be the cast shadow of the reef knot, creating the illusion that it is floating (image courtesy of Rick Bowmer, used with permission). On the bottom left, the corners of the Ames room appear to be right-angled corners from one viewpoint, creating the illusion that the back corner of the room on the left is as close as the back corner on the right (CC BY-SA 2.0). On the bottom right, the matching ground textures make the cyclist and the pedestrians appear to be at the same distance on the same ground plane—the cyclist appears to be tiny as a result (image courtesy of Stan De Zoysa, used with permission).

MORE PERCEPTUAL THAN COGNITIVE

In some cases, perception does make the error; in this section, I mention only a few of the vast number of these cases. This overview is only meant to give a flavor of the illusions that have been studied as an opening to the following sections on what illusions can and cannot do for us. The sidebar titled Illusion Resources provides various, extensive online demonstrations of these and other illusions.

Perception constructs the 3D layout from a sparse set of cues. When a critical cue is lost or weak, or when a spurious cue is created accidently, an erroneous 3D interpretation may emerge. **Figure 6** presents several of these accidental alignments of shapes and shadows in natural scenes that create a second 3D interpretation (Shapiro 2021). Perception makes the wrong choice in these cases but for understandable reasons. Sometimes both interpretations can be seen, but sometimes

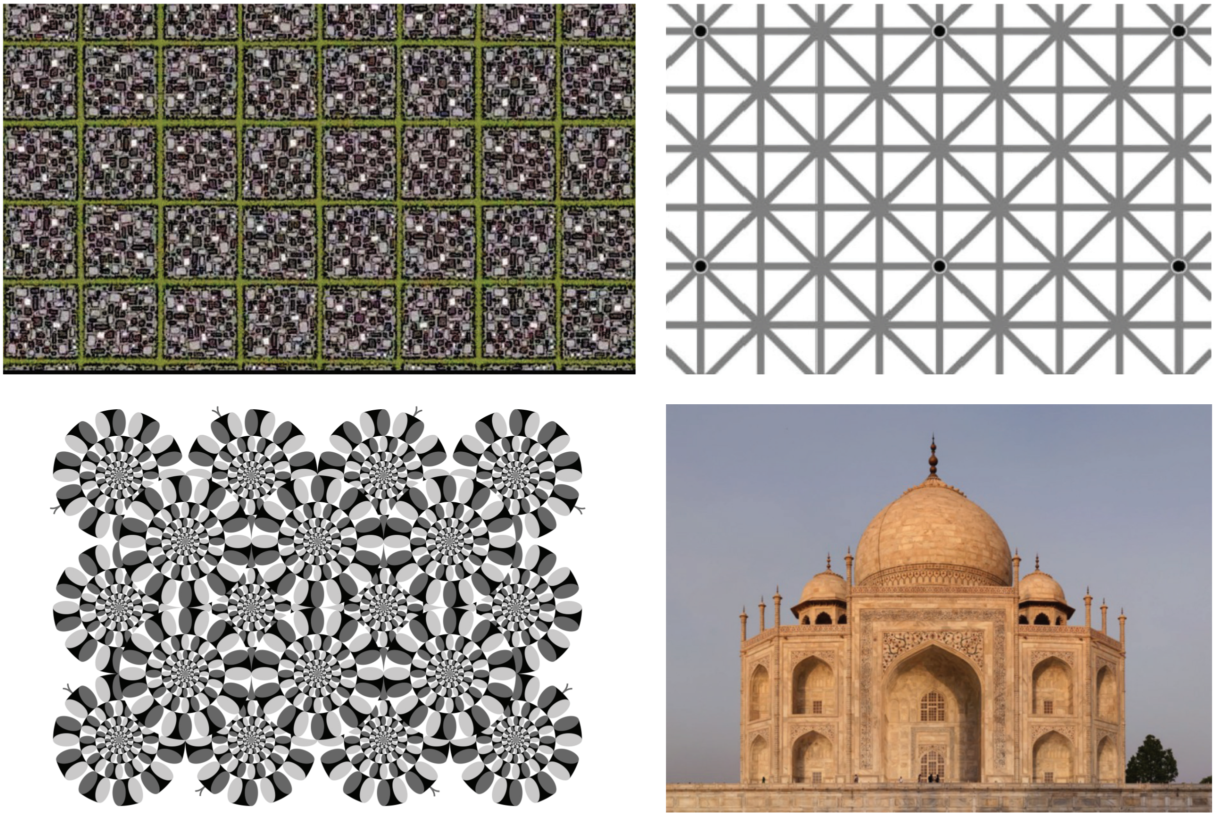

Figure 7

Perception gets it wrong. On the top left, we see illusory curved green lines when random paths in the noise are attributed to the green contours [image courtesy of Lesha Proche (Denega), used with permission]. On the top right, there are six dark spots at the intersections of the grid (reproduced with permission from Ninio & Stevens 2000), but we see only the one we fixate. The others would be visible at these spacings if the grid were not present. On the bottom left, ramp stimuli give an illusion of motion on each eye movement if the image is big enough (image courtesy of Akiyoshi Kitaoka, used with permission). On the bottom right, the error is in the image (inconsistent shadows under the arches), but perception fails to detect it. Neither does cognition until alerted by this caption, so there is no conflict, i.e., no illusion (reproduced with permission from Casati & Cavanagh 2019).

not, as in the Ames room (**Figure 6**, bottom left). The examples shown in **Figure 6** can be seen in the actual 3D settings but typically only when viewed monocularly and without head movements, as these often reinstate the correct interpretation.

In addition to errors of cue choice, there are also errors of processing that lead to effects like the illusory motion seen in the many versions of the Kitaoka's Snakes illusion (for one example, see **Figure 7**, bottom left) or illusory curved lines (**Figure 7**, top left). Memory color is an interesting case where, for example, a gray banana may appear to have a slightly yellow hue (its expected color) that can be nulled by adding a bit of blue (e.g., Olkkonen et al. 2008). These results have been controversial (Cutler et al. 2024, Valenti & Firestone 2019), but the expected hues of grayscale objects can be decoded from functional magnetic resonance imaging (fMRI) signals in V1 (Bannert & Bartels 2013, Vandenbroucke et al. 2016). Each of these cases informs us of some perceptual process that does not get the interpretation quite right. Many of them have provided insights into early visual processes, although some depend on missteps of mid-level processes (e.g., the stretched horse in **Figure 1**, where continuity overrules a familiar shape) or at higher levels (e.g., the boy who lost his head in **Figure 1**, where body schemas group the head with the body despite the lack of connection). We can examine properties of perceptual processing in much the same way in which we do when studying visual aftereffects or afterimages or simultaneous contrast effects. Visual aftereffects or afterimages and simultaneous contrast effects are illusions in their own right, according to the definition used in this review, but they have been studied for many decades under their own names, so nothing much is gained by relabeling them.

There are also numerous motion-based illusions, such as reverse apparent motion (Anstis & Rogers 1975), where the perceived direction is opposite to the physical displacement, and stopped motion, where a slowly moving stimulus stops when viewed in the periphery (Campbell & Maffei 1979) or at equiluminance (Cavanagh et al. 1984). At one level, these examples show, unsurprisingly, that motion energy determines the perceived direction and that the directions of motion energy are not always obvious in the image (to cognition). Indeed, many of the illusory motion effects can be explained by a simple motion energy analysis of the stimulus (Battaje et al. 2023). In the case of stopped motion (**https://cavlab.net/Demos/SlowColor/**), however, this analysis is only half of the story. Yes, the motion energy has dropped below its threshold even though the pattern is still above its threshold. However, an intriguing puzzle remains: How can the still-moving stimulus be seen at a fixed position even though it is actually not there anymore? Motion-induced blindness produces the fading in and out of steady dots when they are presented on a moving background (Bonneh et al. 2001), while motion silencing suppresses the color cycling of dots when they are in motion (Suchow & Alvarez 2011). There are also many examples of motion-induced position shifts (e.g., Cavanagh & Anstis 2013, Eagleman & Sejnowski 2007, Nijhawan 1994, Whitney & Cavanagh 2000), where a moving stimulus or a nearby flash is displaced ahead in the direction of motion. There are several competing explanations for these displacement effects, but none of them is completely successful (Takao et al. 2022).

What can these illusions tell us about the brain? Illusions can often inform us about the computational principles involved in perceptual processes. Each illusion is an error that reveals a rule or process or an effect of context that has been overgeneralized or simplified for expediency. We can learn the rules of language by studying grammatical errors even when we are not aware that there are rules. No one says, “Look at the red big house.” It sounds like an error, but we cannot quite say why (e.g., Kemmerer 2000). The sense that there is an error reveals the rule that operates unconsciously. Similarly, illusions can expose which rules or processes could possibly have led to the error. This is very good for revealing computational processes, but, to date, illusions have told us much less about the physiological stages underlying perception—where in the brain perception emerges. Surprisingly, the reason for this is interference from attention, as it broadcasts the final perceptual representation throughout the cortex. We can chip away at various levels of visual processing using illusions, as I describe below, but tests using ordinary stimuli may be equally productive. Only when attention is controlled can we begin to trace the stages in the emergence of perception across the visual system, and illusions offer significant advantages for this process.

PAYOFF

In this section, I describe three ways in which illusions contribute to identifying where and how perceptual processes happen. The first two are standard approaches that have been developed and used extensively for ordinary, nonillusory stimuli. The addition of illusory stimuli in these cases adds to the array of available test stimuli but does not offer much information that is not already available using standard stimuli. It is the third approach that offers real promise: using illusions to map the development of the perceptual representation across areas of the brain.

The first contribution from illusions is simply the opportunity that they offer for the instruction of visual principles. When observers are not yet aware of the principles of constructing 3D representations from 2D cues, for example, illusions like those in **Figure 3** offer good examples for teaching these principles. This does not tell us anything particularly interesting about the brain, but there are some instances where new illusions do inform us about the processing of pictorial cues, for example, the assumptions of lighting behind the dress illusion (Wallisch 2017).

Second, we can recover information about the sequence of visual processes by finding out whether particular illusions act before or after specific stages of processing. This technique has been used extensively with visual aftereffects to determine if the site of, say, motion aftereffect is before or after the site of combination of the information from the two eyes (e.g., Anstis & Duncan 1983). This sequence test can be applied to illusions as well. For example, a motion-induced position shift, the flash-grab effect (Cavanagh & Anstis 2013), produces strong distortions of shapes flashed on a moving border as it reverses direction (Adamian et al. 2023; **https://cavlab.net/Demos/ShapeDistortion/Movie1**). This implies that the nonuniform shifting that distorts the visual features happens before the shape is identified and established, i.e., prior to object-specific areas such as the LOC (Kourtzi & Kanwisher 2001). This inference is strengthened by the opposite result that is found for saccadic compression (Ross et al. 1997), where tests flashed around the time of a saccade are compressed toward the saccade target. In this case, if multiple shapes are flashed, then the spacing between the shapes is compressed, but the shapes themselves are not distorted (Matsumiya & Uchikawa 2001). Position shifts triggered by the saccade must affect the visual representation after the shapes have been established, perhaps after area LOC. This approach offers insights into the sequences of processing, adding to similar insights taken from standard stimuli (Frisby 1979).

The third, and most promising, payoff from illusions comes from finding where the illusory percept emerges, i.e., where its representation differs from that specified by the bottom-up input. To see how this works, let us look at how most ordinary research proceeds. The information from the retina goes through several stages of processing to reach some high level of representation, say, face-specific activity. The emergence of this face representation can be found by presenting face and nonface stimuli and finding which areas of the brain respond better to the faces (Gross et al. 1972, Kanwisher et al. 1997, Sergent et al. 1992). However, with a standard stimulus like a face, we cannot be sure that the level at which the stimulus-specific representation emerges is also the level at which the perception emerges. In fact, for faces, there is evidence, for example, that activity in the face areas is not sufficient for face perception (Schubert et al. 2020).

In comparison, using illusory stimuli offers some important advantages. Depending on the illusion, the illusory percept will differ from the stimulus properties in color, motion direction, size, or position. **Figure 8** presents a hypothetical case where position already deviates from the bottom-up input in V4, where it matches instead the perceived illusory position. Indeed, in some studies, detectors already signal the illusory features at an early level. For example, the position advance of the moving stimulus in the flash-lag illusion can be detected already in V1 units (Subramaniyan et al. 2018); and in the Kitaoka's Snakes stimulus, the illusory response is seen already in the motion center, the human MT+ (Kuriki et al. 2008). However, in other illusions, it may be present at a very late stage, as is the case for the double-drift illusion (Liu et al. 2019), which I describe below. In this case, the illusion can identify the site at which perception itself emerges. Unfortunately, efforts to achieve this goal are almost always foiled by the effects of an interloper—attention.

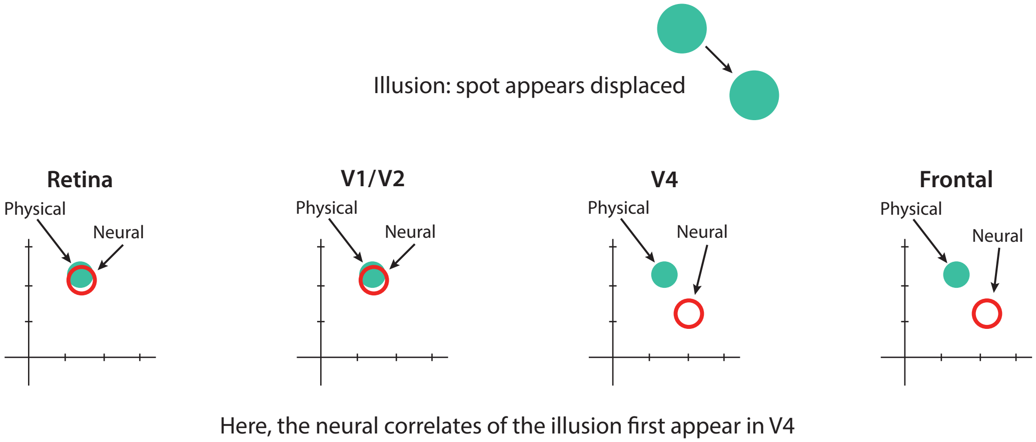

Figure 8

Using physiological activity or functional magnetic resonance imaging activation to track the emergence of the illusory location. In this example, some process, such as a motion-induced position shift, has displaced the perceived location of a test spot away from its physical location. On the retina, the neural activity matches the physical stimulation landing on the retina. Progressing further up the visual hierarchy, the locus of neural activity may shift to match the illusory perceived location.

ATTENTIONAL SPOOFING

There is an overwhelming confound in using illusions to search for the emergence of perception. Specifically, attention will act to mask the stages at which bottom-up processing still dominates: Once a conscious percept has emerged, attention's role is to broadcast that representation to lower levels to support processing of the features that should be there (but are not). We can already see this attentional feedback to the expected location of a stimulus in fMRI activation in V1, even when the stimulus is not present (e.g., Silver et al. 2007). This feedback means that even early cortex will show evidence of the high-level percept, and it will not be easy to determine what activity is an early emergence of the percept and what is only attentional feedback (**Figure 9**). This section provides several examples showing that illusory effects can be found in early cortex, but that all of these effects can be attributed to attention's downward projections from the higher-level percept to early cortex.

Murray et al. (2006) used a size constancy (corridor) illusion (see **Figure 3**, center) to increase the apparent size of a stimulus. They found that the blood oxygen level–dependent (BOLD) signal in V1 reflected the perceived stimulus size, rather than the retinal input. Muckli et al. (2005) found BOLD activation in V1 along an apparent motion trajectory where there was no direct stimulation. Again in V1, Chong et al. (2016) were able to recover the intermediate horizontal or vertical orientation of a stimulus in apparent motion that switched from right oblique to left oblique at the end points of the motion. Meng et al. (2005) found neural filling in over the missing portion of the phantom grating illusion in areas V1 and V2. The Muller-Lyer illusion produced a change in BOLD activity in V1 that mirrored the perceived lengths (Ho & Schwarzkopf 2022). Two articles have reported that the memory color of a familiar object presented in neutral gray could be decoded from activity in V1 (Bannert & Bartels 2013, Vandenbroucke et al. 2016). For the flash-drag illusion (Whitney & Cavanagh 2000), activity in MT+ shows strong correlation between perceived and matched physical positions (Maus et al. 2013). In one case, we know that the illusion's effect on fMRI activation must be due to top-down projections to the expected location. Kohler et al. (2017) and Ge et al. (2020) reported that the spatial displacement produced by the flash-grab effect was present already at the illusory location in area V1. However, in a separate experiment,

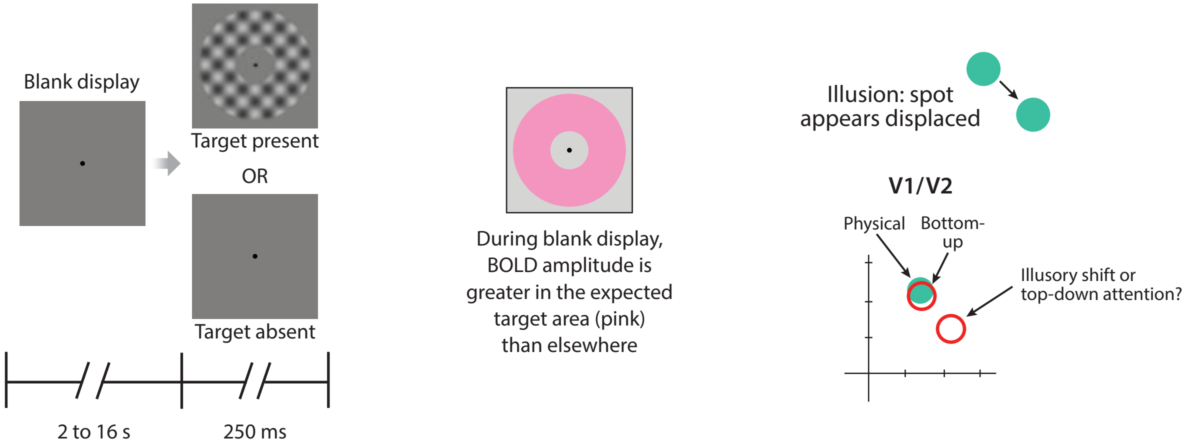

Figure 9

Effect of attention on activity in early areas. (*Left*) Participants had to report whether the near-threshold, textured annulus was present. (*Center*) Blood oxygen level–dependent (BOLD) activation during the pretest interval when the display was blank was higher within the expected location than elsewhere, suggesting that attention was projecting to the target's location even when it was not there (adapted with permission from Silver et al. 2007). (*Right*) In the example of the displaced spot from **Figure 8**, the activity in area V1 may be displaced to the illusory position, but this may be the effect of attention projecting to the expected location.

Kosovicheva et al. (2012) showed behaviorally that the effective displacement of activity in V1 was at most 10% of the perceptual effect. The activation at the illusory location must have been due to attentional projections to the expected location.

Unfortunately, it is very difficult to escape this pervasive interference, as attention will broadcast activity to the expected features and locations throughout the cortex. Although some studies have attempted to control attention (Chong et al. 2016, Meng et al. 2005), it is never possible to completely block attention from a stimulus while it remains visible. In the sections below, I review two approaches to solving this problem: One uses electroencephalogram (EEG), single-cell recording, or layer imaging in the early cortex to separate top-down and bottom-up activity, and the other uses unique illusions that have no effect on attention, so that the feedback arrives at the physical location of the stimulus, not the perceived location. These approaches have already made important advances in identifying the locus of the emergence of perception and, in one case, point remarkably to areas outside of the classic visual system: the frontal lobes.

SOLUTION 1: DISTINGUISHING TOP-DOWN ATTENTION FROM FEEDFORWARD REPRESENTATIONS

There are several measurement techniques that can distinguish feedforward from feedback activity, although each has its drawbacks. Methods like electroencephalogram (EEG) and single-cell recordings have the temporal resolution to separate the earlier bottom-up activity from the attentional influence that arrives later. For example, Hogendoorn et al. (2015) used EEG decoding techniques with the flash-grab illusion to determine when the representation of the stimulus began deviating from its physical location toward the illusory location. A significant deviation was found as early as 81 ms, suggesting a contribution from early processing before attention could play a role. However, the technique could not reveal what portion of the final illusion was available in the early response, nor where in the visual system these early signals arose. Ge et al. (2020) also analyzed EEG responses to the flash-grab illusion, but in contrast to Hogendoorn et al., they were unable to isolate any illusory response in early visual cortices prior to the arrival of attentional projections (at 118 to 161 ms). This timing analysis, although promising, would be less informative at higher levels of cortex, not only because the EEG signal is not optimal for recovering the cortical location, but also because the bottom-up and feedback signals may be closer together in time at that point.

With single-cell recordings, cortical locations and timing are directly accessible (e.g., Cox et al. 2013, Ni et al. 2014, Nieder 2002, Subramaniyan et al. 2018, Sundberg et al. 2006). For example, Sundberg et al. (2006) recorded responses to a flashed test in a moving stimulus in V4 and found that the locus of activity was shifted forward along the motion path. The magnitude of the shift was consistent with the illusory perceptual shift reported by humans viewing the same stimulus. The timing of the responses was early, in the range of feedforward responses for these cells, rather than later top-down activity. These results indicate that the influence of motion on the representation of location for this particular illusion (called the flash jump) occurs either in V4 or before, with little or no influence from attention. However, the shift in neural responses was also found for a flash-terminated condition where the motion sequence stopped when the flash occurred. Under these conditions, human observers report no illusion. This indicates that the activity in V4 is not the final signal underlying perception because, for this flash-terminated case, the location information coming from V4 must be edited out at a later stage, where the continuing evidence for no further position shift influences the percept (Hogendoorn 2022). Thus, while single-cell recordings can separate out the later top-down influence of attention at any given recording site, the drawback is that many sites throughout the brain would need to be probed to track down the evolution of the illusion.

fMRI techniques have the advantage of allowing an evaluation of response throughout the brain but lack the temporal resolution to distinguish early from late activity. Nevertheless, the different layers of cortex can distinguish bottom-up from top-down activity. Specifically, activity in the middle cortical layers of V1 is dominated by bottom-up retinal input, whereas the upper and lower layers register the top-down feedback to retinotopic cortex (Kok et al. 2016, Muckli et al. 2015). Ge et al. (2020) used this approach with the flash-grab illusion, where a moving background shifts the apparent location of a flashed test. They showed that the upper layers of V1, V2, and V3 showed a significant shift in the location of the peak activity in response to the flash, consistent with the illusion, whereas the middle layers did not. These results support the claim that attentional feedback is the source for the shift seen in the early visual cortex (Kohler et al. 2017). Although this layer analysis can help isolate the attentional projections from bottom-up signals, it becomes less effective in higher areas of the cortex, like the parietal and frontal regions, where important processing stages for perception may be occurring. There is, however, an easier way to avoid the interference of attentional spoofing.

SOLUTION 2: ILLUSIONS THAT DO NOT AFFECT ATTENTION

Supplemental Material >

There is one illusion, the double drift (**Figure 10**, left; **Supplemental Movie 1**), that appears to affect perception but not attention. It causes a dramatic mismatch between retinal and perceived location, producing a perceived motion path that can differ from its physical path by 45° or more. It is also known as the Infinite Regress (Tse & Hsieh 2006) or curveball illusion (Shapiro et al. 2010). A stationary Gabor with internal drift is also seen to be displaced (De Valois & De Valois 1991), although the displacement is smaller and saturates quickly (e.g., 100 ms) (Jeon et al. 2020). The double-drift stimulus has two motion vectors, one in the direction of the Gabor and the other in the orthogonal direction of the internal texture. These combine to form a new vector, and the Gabor is seen to move in this illusory direction (Cavanagh & Tse 2019, Heller et al. 2021), accumulating larger and larger illusory offsets in position over a second or more ('t Hart et al. 2022). The illusory drift may continue so long because the moving Gabor lacks the stationarity signal present in the De Valois & De Valois (1991) stimulus. Importantly, the illusion seems unaffected by attention, having the same magnitude regardless of whether the target is attended (Haladjian et al. 2018). Moreover, saccades directed to the double-drift stimulus land near its physical location, rather than its perceived location (Lisi & Cavanagh 2015). Given the close link between saccades and attention (e.g., Awh et al. 2006), these results support the claim that attention is unaffected by this illusion. Importantly, in this case, any downward projections from attention should target the physical, rather than the perceived, location.

In the case of other motion-induced position shifts that displace the target along the direction of motion, such as the flash-lag and flash-drag, saccades are directed to the perceived, rather than physical, locations (de'Sperati & Baud-Bovy 2008, Schafer & Moore 2007, van Heusden et al. 2018, Zimmermann et al. 2012). The double-drift stimulus is therefore unique in its potential to remove the confound of attention projections to the perceived path throughout the visual system, as the illusion does not seem to affect attention. As a result, it should allow the perceptual coordinates of object position to be tracked through the processing hierarchy without attentional interference.

Indeed, Liu et al. (2019), using fMRI and multivariate pattern analysis (**Figure 10**, right; **Figure 11**), found that the illusory path did not share activity patterns with a matched physical path in any visual areas. This finding has been replicated for V1 by Ho & Schwarzkopf (2022). In contrast, a whole-brain searchlight analysis revealed a shared representation in anterior regions of the brain, indicating that these are the first regions that could represent perceptual experience, where the illusory and matched physical paths would appear quite similar. These higher-order

Supplemental Material >

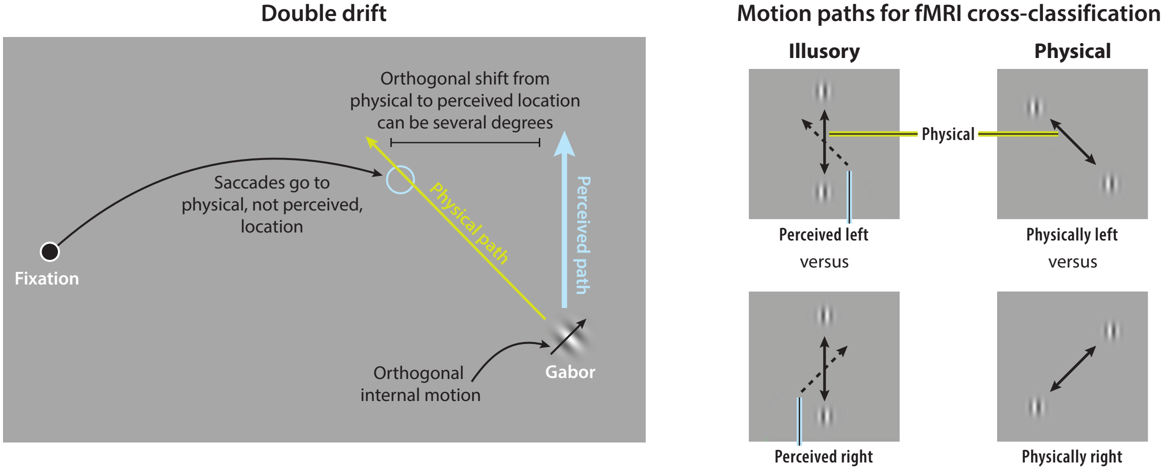

Figure 10

(*Left*) The double-drift illusion. The perceived position and direction of a translating and internally drifting Gabor patch deviate radically from its bottom-up, physical position and motion (see **Supplemental Movie 1**). The illusion is not influenced by attentional load (Haladjian et al. 2018), and saccades also show little or no effect on the illusion (Lisi & Cavanagh 2015). Both of these results suggest that attention is not affected by the illusion and that it would be directed to the physical location, not the perceived location, of the stimulus. This provides the first opportunity to track the emergence of the perceived motion path without the confounding influence of attention. (*Right*) Stimulus conditions for functional magnetic resonance imaging (fMRI) in a study by Liu et al. (2019). In the left two panels, the Gabors move vertically up and down but are perceived to have left or right oblique tilt due to their internal motion directions. The control Gabors on the right move on a physical path matched to the perceived orientations seen in the illusion conditions but have no internal motion, so the perceived and physical directions are the same. A searchlight classifier was trained with the data corresponding to the control stimuli with matched oblique physical motion paths and tested with the data for the double-drift stimuli with a physically vertical but perceived oblique motion path (and vice versa). The results are shown in **Figure 11**.

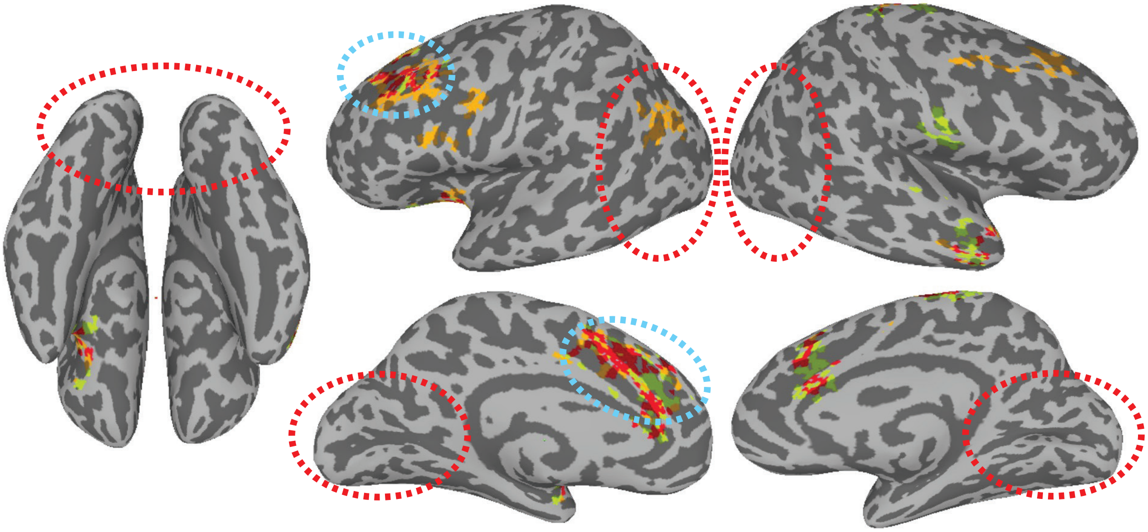

Figure 11

Where is the neural response to the illusory paths similar to the response to physical motion paths that match the illusion directions? Statistical significance maps for whole-brain cross-classification searchlight analysis are shown. Early visual areas showed no cross-classification accuracies that were significantly above chance. However, in several regions in the prefrontal cortex (outlined in *blue*), the activity for the illusory path could be predicted from the activity for the orientation-matched physical path (and vice versa). This result suggests that the percept was represented in these areas, as the perceived directions match for these stimuli even though the physical directions do not. Figure adapted with permission from Liu et al. (2019).

areas also have the longer time constants that match the long duration of accumulation of the illusion.

Although Liu et al. (2019) did not address where in the cortex other perceived features emerge, their results do place clear constraints on the neural correlates of perceived position. Surprisingly, the construction of perceived location appears to emerge in areas beyond the visual cortex.

Supplemental Material >

Are there other illusions that do not influence attention and allow unfettered tracking of the emergence of perception? There may be at least one other, the frame effect, where probes flashed within a moving frame are dramatically displaced (Cavanagh et al. 2022, Özkan et al. 2021, Wong & Mack 1981). These flashed probes are often perceived with the separation that they have in frame coordinates—a 100% effect (**Supplemental Movie 2**). Interestingly, one study of this frame effect (Wong & Mack 1981) tested whether saccades were directed to the physical or perceived location of the flashed target. This study reported that saccades were unaffected by the moving frame, opening the possibility of a second illusion that can track the emergence of perceived location without interference from attention. It would be promising if these two illusions, the double drift and the frame effect, could be generalized to other features, say, color or orientation, also without affecting attention, which would allow us to explore the emergence of perception of these features.

CONCLUSIONS

In this review, I give a broad overview of illusions—privileged conflicts between perception and cognition—and find that many of the popular examples are simply confusions of image properties and scene properties (e.g., **Figure 3**). Vision's goal is to find 3D interpretations of the visual input, and anything with some pictorial cues to depth and light is seen in 3D. This cannot be turned off. Thus, the perplexing match of sizes or luminance in the illusion images of **Figure 3** reveals only that image properties often differ greatly from the scene properties that are derived from them. It is a cognitive error to expect that they should match, not a perceptual error. Most of these illusions provide excellent teaching opportunities, but only a few actually tell us anything new about these pictorial cues (Wallisch 2017).

In contrast, illusions based on perceptual errors provide opportunities to study early processes in much the same way that visual aftereffects do. Some illusions go further, offering the potential to track the emergence of perception, and in these cases, illusions offer more exploratory power than ordinary stimuli. However, to access this power, we need to overcome the interference from attention, which diligently broadcasts activity to the expected locations and features of the illusory percept. This makes it difficult to discriminate the emergence of the percept from the downward attentional projections. As a result, many articles that have reported illusory processing in the early cortex have actually found only the attentional projections from some unknown site of origin in higher cortices.

Fortunately, there is at least one illusion, the double drift (Lisi & Cavanagh 2015), that has little or no impact on attention, such that we can follow the processing of the stimulus until the illusory percept emerges. Normally, of course, attention and perception work together to bring resources to the locations at which we perceive targets. Interestingly, the results for this one exception, the double-drift illusion, suggest that, in some cases, attention may have different spatial coordinates than perception, and this provides a unique opportunity to track where the illusion and perception emerge. Unexpectedly, experiments (Liu et al. 2019) showed that the perception of location emerged in cortical areas outside the visual system, where spatial location may not be coded in map coordinates but instead in some other manner, possibly as features. For example, an object may be red and long and at position 5, 10 in the upper right quadrant. These are provocative and compelling new directions for understanding perception.

The involvement of frontal areas in the coding of perception is not entirely unexpected. Binocular rivalry studies have shown that both the perceived and suppressed images are represented throughout the visual system, and only frontal areas show complete switching from one to the other in step with the perceived patterns (e.g., Dwarakanath et al. 2023). In addition, Weilnhammer et al. (2021) used computational modeling, fMRI, and transcranial magnetic stimulation to show that the inferior frontal cortex detects and resolves perceptual conflicts during bistable perception of structure from motion. These studies raise the possibility that the entire visual system may be engaged only in data collection, while the perceived scene layout is constructed at least in part in the frontal cortex. This possibility is challenging because the areas identified by Liu et al. (2019) are not known to have any spatial maps; thus, spatial layout may need to be coded in some other format.

This possibility is promising, but we must ask why we should bother with illusions when we could explore the emergence of perception with nonillusory stimuli. In this case, we again run into the pervasive interference of projections from attention, activating the features and locations of the perceived stimulus in early areas. Can we avoid attention with an ordinary, nonillusory stimulus, as we did with the double-drift illusion? This would limit us to unconscious stimuli and, more specifically, unattended, unconscious stimuli, as attention can be directed to unconscious stimuli and, indeed, must be to bring them into awareness (Cavanagh et al. 2023, Cohen et al. 2012). Tracking the processing of these unseen stimuli through the visual system can tell us about the nature of unconscious processing, but this entirely misses the essential step of tracking the emergence of perception because these stimuli are not perceived. They cannot tell us about the emergence of perception.

In conclusion, illusions may not be able to tell us much about the emergence of perceptual representations that we cannot derive from ordinary stimuli—with, to date, one exception. However, this one exception has opened a completely new outlook on where perception emerges—that it happens not in the visual areas, but in frontal and other anterior areas. Moreover, it points to a coding format for perceived location that may not be map based. These insights point the way for novel investigations of perception based on attention-free illusions.

SUMMARY POINTS

1. Illusions are conflicts between perception and cognition, i.e., differences between what we see and what we believe that we should see.
2. Illusions may be due to cognitive errors when perception is correct. These typically involve misunderstandings of how perception works.
3. Illusions can also arise from perceptual errors detected by cognition, and these can inform us about the computational principles involved in perception.
4. Illusions can be used to track the evolution of the perceptual representation as it moves up the hierarchy of visual areas. Starting in early areas, the representation will encode the bottom-up, physical values but will shift to match the illusory values at higher levels.
5. Tracking this evolution using illusions is confounded by attention, which broadcasts activity to the expected locations and features based on the final, illusory percept.
6. One illusion, the double drift, affects perception but not attention. This and similar illusions provide the opportunity to track where perception emerges without interference from attention.
7. Functional magnetic resonance imaging studies of responses to the double-drift illusion indicate that the perception of location may not emerge until the frontal areas, in regions that do not have spatial maps.
8. One other attention-free illusion is known to date, and others may be discovered that will allow us to explore the emergence of perception of a wider range of features.

FUTURE ISSUES

1. Attention-free illusions offer powerful opportunities for tracking the evolution of perception. What properties do the double drift and frame effects have that make them attention free, and how can other illusions be modified so that they too become attention free?
2. If the frontal areas are where the perception of location emerges, then what is the format of space in this area, and how could we discover it?
3. Illusions are errors that the visual system has not yet been able to correct. Some illusions do go away with repeated presentation, while others do not. What determines which errors can be corrected?

4. Many classic illusions remain mysteries because they are based on several different errors. Like cases of double diseases, the presence of multiple causes makes explanation or diagnosis very challenging. How can this be dealt with?

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