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Phantom perception: voluntary and involuntary nonretinal vision

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Hallucinations, mental imagery, synesthesia, perceptual filling-in, and many illusions are conscious visual experiences without a corresponding retinal stimulus: what we call 'phantom perception'. Such percepts show that our experience of the world is not solely determined by direct sensory input. Some phantom percepts are voluntary, whereas others are involuntarily, occurring automatically. Here, by way of review, we compare and contrast these two types of phantom perception and their neural representations. We propose a dichotomous framework for phantom vision, analogous to the subtypes of attention: endogenous and exogenous. This framework unifies findings from different fields and species, providing a guide to study the constructive nature of conscious sensory perception.

Nonretinal phantom vision

One commonly held notion is that the way we see the world is much like a high-definition digital camera: what we see is a simple, but accurate replication of the outside world. However, years of research have taught us that this intuitive idea is far from the truth. The visual world that we experience is a collaborative project between memories of the past, current stimulation, and predictions about the future. In other words, much of what we experience does not come directly from retinal stimulation, but originates from inside the brain: a phantom experience. Such internally triggered vision is not only under our control (we can imagine scenarios or objects at will), but also seemingly outside voluntary control. Visual illusions provide many striking examples of how the brain produces involuntary phantom visual experiences. In this review, we describe phantom visual perception and how research observations fit two categories of phenomena: voluntary and involuntary.

Although there has been much research in each of these fields, little work bridges the voluntary–involuntary gap. Accordingly, many exciting questions remain. How similar are voluntary and involuntary phantom visual representations? Can historically separate literatures (e.g., from animal work and human neuroimaging) co-inform each other? How does this dichotomy map on to mental disorders in which patients report involuntary images?

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The product of voluntarily generating a sensory experience from information stored in memory is typically referred to as 'mental imagery' [1,2]. Mental imagery is involved in a range of processes, from those underlying spatial navigation, visual memory, language comprehension, and even creativity [3–7] to those involved in vision [8] and audition [9]. Imagery is even thought to have a role in solving moral dilemmas [10]. Uncontrollable vivid mental imagery is also a characteristic symptom of many psychopathologies [11] and voluntary imagery is now utilized during some behavioral therapies [12].

Given its subjective nature, mental imagery has been difficult to study. However, recent behavioral and neuroimaging studies have provided a large body of empirical evidence that imagery can be studied objectively [8,13–16]. For example, behavioral studies have shown that single episodes of imagery, generated for at least 5 s, can bias subsequent perception in a manner specific to early visual cortex [8]. Furthermore, these studies have used indirect techniques; participants are not required to self-report anything about their imagery, thus avoiding some of the methodological limitations of self-report techniques. Neuroimaging studies have shown that it is possible to determine, from activity in the visual cortex, which of two visual patterns a person is imagining or retaining in visual working memory [14,15,17,18] or even the content of dream imagery [19]. More recent work has demonstrated that the content of a mental image can be decoded using fMRI voxel-wise models of visual features, such a retinotopic location, orientation, and spatial frequency [16]. Together, recent behavioral and brain-imaging work has

Glossary

Binocular rivalry: a visual phenomenon in which two different patterns are presented on to each eye; the patterns compete for perceptual dominance, such that awareness alternates between the two patterns.
Bistable sensory perception: a general class of perceptual stimuli whose interpretation has two primary forms; binocular rivalry is included.
Epiphenomenal: a secondary effect or byproduct of something.
Gabor pattern: a sine wave grating seen through a Gaussian window.
Kaniza shapes: a class of illusion that induces the perceptual experience of an edge or shape, where there is no luminance- or color-defined edge or shape.
McCollough effect: a phenomenon in which nonchromatic patterns appear colored after a specific set of color-pattern exposure.
Metacognition: awareness and understanding about one's own thoughts.
Neon color spreading: a colored transparent disk is experienced even though no transparent surface is physically present. This is a type of color filling-in, in which co-aligned perceptual colored lines or shapes themselves define an overall shape that is experienced as the transparent colored disk.
Phantom motion: a type of illusory motion induced by surrounding co-aligned moving patterns.

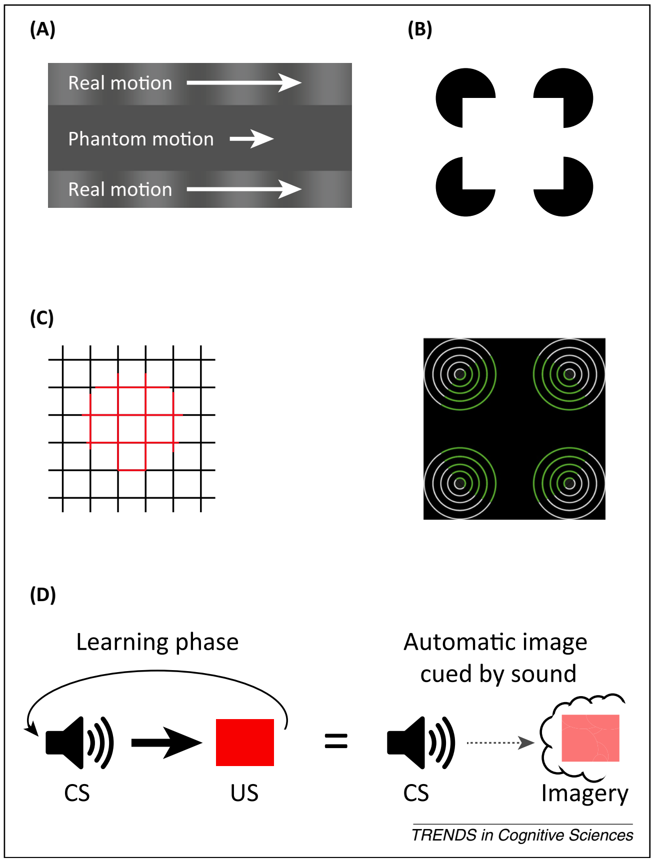

Figure 1. Examples of automatic visual imagery. **(A)** Phantom motion perception. Rightward physical visual motion at the top and bottom induces an illusory experience of motion in the central strip, where there are no incoming motion signals. **(B)** An illusory square. The surrounding Pac-men stimuli induce an illusory experience of a white square sitting over four black circles. **(C)** Neon color spreading. Viewed from the right distance, you might have the experience of seeing a red shaded circle on the left or green shaded circle on the right, between the lines in the center: the color experience is spreading the pigment in the lines. **(D)** After a period of associative learning, in which a sound and a visual stimulus are paired together multiple times, the sound when presented subsequently alone induces an automatic mental image of the visual stimulus. Abbreviations: CS, conditioned stimulus; US, unconditioned stimulus.

demonstrated how voluntary imagery can be assessed objectively.

There are many visual illusions that induce a visual experience that does not directly originate from retinal stimulation. Phantom motion ([20]; see Glossary, Figure 1A), Kaniza shapes, neon color spreading ([21], see Figure 1C), the McCollough effect [22], and simply flickering your computer monitor between black and white can produce various shape and color hallucinations [23]. Although there is no general name for this class of visual illusion, these examples, plus many more, all involve nonretinal (i.e., not originating from the retina) visual experience of color, form, or motion. In other words, they are phantom percepts.

Examples of nonretinal vision have been utilized to study the constructive nature of visual perception [20], and many are thought to occur within the visual cortex as a product of the probabilities of co-occurrence of particular objects in the environment. For example, one can explain the neon color-spreading illusion by proposing that the brain knows that there is a higher probability that a transparent color surface lies over the top of the black lines than a color that belongs to the lines and abruptly stops in a co-aligned manner [24]. Many of these involuntary illusions have been understood and modeled in a Bayesian inference framework [25].

The above examples of involuntary nonretinal vision are thought to be largely dependent on learnt associations based on probabilities within the visual domain (e.g., visual–visual associations) [26]. However, learning can extend beyond spatial and temporal probabilities between visual stimuli.

Associative learning is one of the means by which organisms represent the temporal, spatial, and predictive relations among events: the ‘causal texture’ of their worlds [27]. These representations enable the organism to predict or respond to absent (but important) events, such as the likelihood of food or the presence of a predator. A basic question in learning theory and of interest here is: ‘How much of this texture is represented by the organism?’ According to traditional theoretical accounts of Pavlovian conditioning, the outcome of learning between events can be described as the substitution of an event with a neural representation of that event in its absence [28,29]. Within this substitution view, the stimulus (i.e., CS) stands in for and, thus, activates a subset of neural activity previously only activated by the otherwise absent event (i.e., the unconditioned stimulus; US). One extreme view posits that, after an animal has learned that a tone CS is associated with a food US, the tone will not only elicit salivation and other consummatory responses, but also excite a representation of the sensory properties of the food (e.g., its flavor, smell, and so on), as if the food itself were present. In fact, one common proposition in the literature is that the animal salivates because of this activated ‘sensory’ representation of the absent food. In short, the animal involuntarily hallucinates the food (Figure 1D).

Here, we compare and contrast data on the sensory representations involuntarily triggered by various cues with those activated by voluntary control. Both result in nonretinal sensory representations, but do the different causal routes lead to the same or different sensory representations? The following sections describe evidence for two different but related types of phantom perception, one voluntary and the other automatic. Our discussion of this subject is by no means exhaustive and many of the crucial experiments are yet to be done (see Outstanding questions and future experiments). We propose a dichotomous framework for the study of phantom perception: voluntary and involuntary. We view this proposition in the light of historical developments in research on visual attention. Endogenous voluntary attention requires an individual to direct his or her attention to a particular item, whereas exogenous attention, considered a ‘bottom-up’ sensory process, does not require voluntary action because the item automatically commands that attention. Although these two types of attention involve distinct mechanisms [30,31], research and theory have benefited from grouping them under the general category of visual attention.

The role of sensory brain areas in voluntary phantom perception

There is considerable evidence that voluntary mental imagery involves neural activity in early sensory areas, such