

Acting without seeing: eye movements reveal visual processing without awareness

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Visual perception and eye movements are considered to be tightly linked. Diverse fields, ranging from developmental psychology to computer science, utilize eye tracking to measure visual perception. However, this prevailing view has been challenged by recent behavioral studies. Here, we review converging evidence revealing dissociations between the contents of perceptual awareness and different types of eye movement. Such dissociations reveal situations in which eye movements are sensitive to particular visual features that fail to modulate perceptual reports. We also discuss neurophysiological, neuroimaging, and clinical studies supporting the role of subcortical pathways for visual processing without awareness. Our review links awareness to perceptual-eye movement dissociations and furthers our understanding of the brain pathways underlying vision and movement with and without awareness.

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Using our eyes to actively explore the world and to gather information is a central part of human visual experience. The link between eye movements and visual perception is so tight that perception is facilitated even during the preparation of eye movements [1–5]. Recently, however, behavioral studies have revealed dissociations between perceptual reports, that is, the contents of visual awareness, and different types of voluntary (e.g., saccades, smooth pursuit, and vergence; see [Glossary](#)) and involuntary (e.g., microsaccades, ocular following, and optokinetic nystagmus) eye movement. Here, we review these perception–action dissociations, in which eye movements are sensitive to particular visual features, even though observers show no awareness of those features, as assessed by explicit perceptual reports. Some authors refer to ‘awareness’ and ‘consciousness’ interchangeably; we use the term

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Glossary

Procedures to manipulate stimulus visibility

Adaptation: prolonged viewing of an image resulting in decreased sensitivity to the adapted stimulus during subsequent viewing.

Binocular rivalry: when two different images are projected to corresponding retinal areas of the two eyes, observers report that the images alternate at a random rate, with one image dominant and the other suppressed, rather than fused into a coherent percept. Some of the physical visual information does not reach awareness, while the rest does, dissociating physical stimulation and awareness.

Binocular rivalry flash suppression: variation of binocular rivalry; one image is shown to one eye for a prolonged period of time (monocular adaptation), followed by a test period, during which the adapted eye sees the same stimulus as during adaptation and the unadapted eye sees a novel stimulus. The timing of awareness periods is under the experimenter’s control.

Continuous flash suppression (CFS): procedure in which one eye is presented with a static stimulus, while the other eye sees a series of distinct images flashing successively at ~10 Hz. The dynamic stimuli suppress the perception of the static stimulus longer and deeper compared with binocular rivalry.

Spatial suppression: reduction in the activity of a neuron in response to a stimulus outside its classical receptive field.

Eye movements

Microsaccades: largest (<1°) and fastest fixational eye movement, occurring a couple of times per second. They are involuntary and humans are generally unaware of their existence; however, they are thought to have a functional role in visual perception and cognition.

Ocular following response (OFR): reflexive, smooth tracking movement in response to sudden-onset, large-field, rapid stimulus motion; characteristic short latency (humans: ~85 ms).

Optokinetic nystagmus (OKN): involuntary tracking movement evoked by large-field visual motion. Smooth tracking in the direction of stimulus motion (slow phase) alternates with fast backward saccades (quick phases) to reset the eye.

Saccades: discrete, ballistic movements that direct the eyes quickly toward a visual target.

Smooth pursuit eye movements: continuous, slow movements that keep the eyes close to a moving visual target.

Vergence: movements that rotate the eyes simultaneously in opposite directions to direct the fovea of both eyes at objects of interest located at different distances relative to the observer.

Vestibuloocular reflex (VOR): compensates for head motion and is evoked by signals arising in the semicircular canals in the inner ear.

Brain structures for unaware processing of visual information

Dorsal lateral geniculate nucleus (dLGN): thalamic nucleus that transmits visual signals from the retina to V1 along the retinogeniculate pathway, as well as directly to extrastriate areas, bypassing V1 through SC and pulvinar. Feedback connections from V1 and brainstem modulate information processing in the dLGN.

Pulvinar nucleus: largest nucleus of the human thalamus, processes visual information and lies posterior, medial, and dorsal to the LGN; strongly connected to visual cortex.

Superior colliculus (SC): multilayered brainstem structure on the roof of the midbrain; has a major role in the control of eye movements. It receives direct projections from retinal ganglion cells and conveys information to V1 through dLGN and to extrastriate visual areas through pulvinar.

‘awareness’ throughout and operationally define it as an explicit perceptual report. A further distinction can be made between situations in which visual processing could potentially lead to awareness (i.e., may or may not produce a perceptual report) and those in which visual processing is inaccessible to awareness (i.e., could not result in a perceptual report). Both situations may produce an eye movement in the absence of awareness, and our review focuses on these perception–action dissociations.

Dissociations provide important insights into the neural underpinnings of vision and movement with or without awareness; they may also further our understanding of diseases involving awareness deficits. We bring together these recent behavioral studies with neurophysiological, neuroimaging, and clinical evidence supporting the role of the subcortical retinocollicular pathway [6,7] for visual processing without awareness. This fast-transmission pathway is associated with residual visual abilities in patients with blindsight [8–11] and with the translation of unperceived visual signals into oculomotor outputs in such patients [12,13].

When eye movements reflect awareness

The visual content in our environment drives visually guided eye movements, which in turn serve perceptual judgments (reviewed in [14–20]). Accurate eye movements improve different aspects of vision, such as spatial acuity and the ability to discriminate motion direction or color [17,18]. Close links between perception and saccades as well as between perception and microsaccades have been consistently demonstrated in visual illusions, fading paradigms, rivalry, and visual search [17,19–26].

Probably the tightest perception–action link is between the perception of visual motion and the control of smooth tracking movements [i.e., voluntary pursuit and reflexive ocular following responses (OFR)]. Motion perception and pursuit as well as motion perception and OFR share anatomical substrates, namely the middle-temporal (MT) area and medial-superior temporal area (MST) [14]. Behavioral studies report similarities in perceptual and pursuit sensitivity in response to motion direction, speed, acceleration, biological motion, and illusory motion (literature until 2011 reviewed in [16–18]; for more recent studies see [27,28]).

Consistent with early studies (e.g., [29,30]), recent studies of binocular rivalry [31–34], which is widely used to manipulate awareness [35], report similar perceptual alternations in rivalry with alternations in reflexive optokinetic nystagmus (OKN); i.e., both eyes track the perceived motion direction of the dominant percept. These studies advocate the use of eye movements and changes in pupil size as objective indicators of awareness, complementing subjective indicators [36,37].

When eye movements reflect processing of unaware information

Despite tight perception–action links, dissociations have also been reported. The prominent model of ‘vision-for-perception’ and ‘vision-for-action’ pathways [38,39] regards neuronal processing for perception and action to be largely separate in ventral and dorsal visual-processing streams,

respectively, although interactions between the two streams exist [38–40]. This model is based on decades of behavioral, neurophysiological, imaging, and patient data comparing visual perception and goal-directed hand movements (i.e., reaching and grasping). Eye movements have classically been viewed as ‘information-seeking adjunct to visual perception’ ([39] pp. 1567–1568). If perceptual reports and eye movements rely on the same processing mechanism and brain pathway, the two responses should be equally sensitive (same threshold) and highly correlated (same variability). However, recent research questions the tight coupling between perception and eye movements, with three main differences or dissociations emerging in studies simultaneously measuring perception (as explicit perceptual reports, indicating awareness) and eye movements (Table 1).

Differences in variability

This section includes studies revealing differences in response variability between perception and the reflexive OFR or pursuit, despite similarities in sensitivity [41–43]. Blum and Price [42] used a continuous motion estimation task in which observers aligned an arrow shown on the screen with the motion direction of a large pattern of coherently moving random dots. This type of stimulus is known to produce a perceptual bias away from the reference (e.g., horizontal motion direction). The study revealed a similar bias in OFR; however, biases in perception and OFR were uncorrelated on a trial-by-trial basis, indicating a variability difference. By contrast, biases in perception and voluntary pursuit are correlated [43]. These results [42,43] indicate differences in motion processing between voluntary pursuit and reflexive OFR.

Variability differences also emerge when comparing perception and pursuit in response to brief speed changes [41] as well as in studies discussed below reporting quantitative differences [44,45] (Table 1) and qualitative differences [46,47] (Table 1). Variability differences are seemingly common in studies comparing perception and eye movements on a short timescale, either by examining reflexive OFR or by studying responses to brief speed perturbations in pursuit. These differences may rely on different sources of sensory and motor noise originating at different points along the sensorimotor processing hierarchy (see final section).

Quantitative differences

This section contains studies in which smooth tracking eye movements (smooth pursuit [44], OFR [45], OKN [32]), vergence [48], and saccades [49–53] are either more or less sensitive (including no response) compared with perceptual reports. Comparisons are mostly based on the analysis of detection or discrimination thresholds derived from psychometric and oculometric functions.

Pursuit. Consistent with an early report of superior sensitivity in pursuit [54], a recent study revealed more sensitive pursuit compared with perception when observers simultaneously tracked moving targets and discriminated changes in stimulus speed in a two-alternative forced choice (2AFC) task [44] (Figure 1A). Eye velocity reflected

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