Trends in Neurosciences

When the eyes act on
what they do not see

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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Keywords: awareness; eye movements; perception-action dissociation; visual pathways; visual perception.

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

Table 1. Behavioral studies revealing perception–eye movements differences, grouped by type of difference

Study	Procedure (visibility manipulation)	Perceptual task	Eye movement	Evidence of perception–eye movements difference
Variability differences				
Gegenfurtner et al. [41]	Subthreshold	2AFC speed change discrimination; small dot	Pursuit	Perceptual and pursuit errors uncorrelated on a trial-by-trial basis; similar sensitivity in both responses
Blum and Price [42]	Subthreshold	Continuous direction estimation; large random-dot pattern	OFR	Perceptual and OFR errors uncorrelated on a trial-by-trial basis; similar sensitivity in both responses
Price and Blum [43]	Subthreshold	Continuous direction estimation; OFR: large random-dot pattern; pursuit: small spot	OFR and pursuit	Perceptual and OFR errors uncorrelated across observers; perceptual and pursuit errors correlated across observers
Quantitative differences				
Tavassoli and Ringach [44]	Subthreshold	2AFC speed discrimination of small spots	Pursuit	Pursuit more sensitive than perception; perceptual and pursuit errors uncorrelated
Boström and Warzecha [45]	Subthreshold	2IFC speed discrimination; whole-screen random-dot pattern	OFR	Perception more sensitive than OFR; perceptual and OFR errors uncorrelated
Naber et al. [32]	Binocular rivalry	2AFC dominance judgment; two colored sinusoidal gratings with opposite direction and orientation	OKN	Faster direction change in OKN than in perception
Masson et al. [48]	Brief dichoptic presentation, anticorrelated stimulus	2AFC depth discrimination of large, dense random-dot patterns	Vergence	Patterns cannot be perceptually discriminated (humans), but elicit short-latency reflexive vergence eye movements (humans, monkeys)
Van Zoest and Donk [49]	Saccade-contingent masking of search display	2AFC judgment of saccade correctness	Saccades	No perceptual awareness of saccade goal despite correct saccadic selection
Eggert et al. [50]	Briefly flashed distractor	2AFC target localization	Saccades	Saccades land in between target and distractor (global effect); distractor does not affect perception
Van der Stigchel et al. [51]	Onset masking of distractor	4AFC location of distractor	Saccades	Vertical saccade trajectories deviate away from unperceived distractor
Zhaoping [52]	Saccade-contingent masking of search display	2AFC detection of orientation singleton in visual search	Saccades	Saccades to orientation singleton even though it was unperceived
Rothkirch et al. [53]	CFS	Localization and 2AFC orientation discrimination of a Gabor patch	Saccades and fixations (dwell time)	Saccades to unperceived (suppressed) Gabor patches
Qualitative differences				
Glasser and Tadin [46]	Surround suppression	2AFC direction discrimination; small and large sinusoidal gratings	OFR	Opposite spatial tuning in perception and OFR; small stimuli: perception > OFR; large stimuli: OFR > perception; perceptual and OFR errors uncorrelated
Simoncini et al. [57]	Subthreshold	2IFC speed discrimination of textured patches	OFR	Opposite sensitivity in perception and OFR in response to increasing spatial frequency; OFR pool across a wider range of frequency channels
Spering and Gegenfurtner [58]	Motion illusion	2AFC speed discrimination of small dot surrounded by dynamic sinusoidal context	Pursuit	Perception follows relative motion of target and context; pursuit follows vector average of target and context
Spering et al. [59]	Monocular adaptation, binocular rivalry flash suppression	Continuous motion direction estimation of two dichoptically presented sinusoidal gratings	Pursuit	Perception follows component motion (horizontal/vertical), pursuit follows pattern motion (diagonal)
Spering and Carrasco [60]	Adaptation, binocular rivalry flash suppression	Continuous motion direction estimation of two dichoptically presented sinusoidal gratings	Pursuit	Perception follows component, pursuit follows pattern motion; both responses follow attended direction
Badler et al. [47]	Ambiguity in causal motion direction	2AFC causality judgments of two colliding small spots	Pursuit	Opposite causal judgments in perception and pursuit; errors uncorrelated across and within observers
Van der Steen and Dits [61]	Dichoptic presentation creating different depth planes	Continuous motion direction estimation of dichoptically presented random dot patterns	Vergence	Perception follows pattern motion; vergence is disjunctive and follows component motion with one eye tracking horizontal, the other eye vertical motion direction
Kuhn and Land [62]	Vanishing ball illusion	Qualitative verbal assessment of perceived illusion	Saccades and fixations	Perception follows illusion; eye movements do not track illusory ball trajectory, but remain fixated
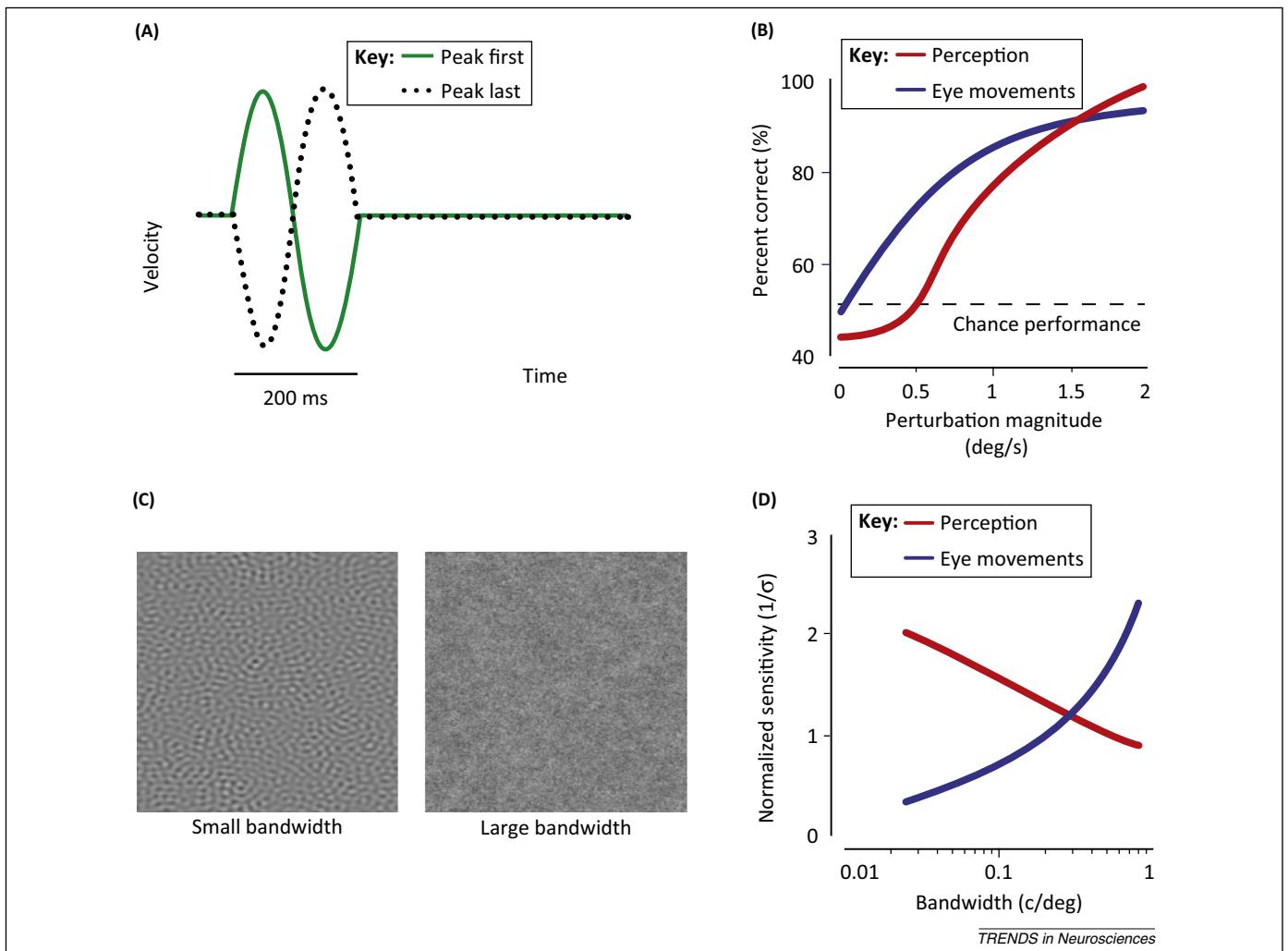
Figure 1. When eye movements and perception yield different results. **(A)** Observers discriminated speed changes (perturbation magnitude between 0 and 2.5 deg/s). Stimulus speed either increased first and then decreased (peak first), or decreased first and then increased (peak last); five speed perturbation magnitudes (in degrees per second) were tested. **(B)** Schematic of results from one observer. Pursuit eye movements were more sensitive to speed changes and discriminated between peak-first and peak-last changes reliably even when perception was at chance; data points were below chance performance for perception, but above chance performance for pursuit. **(C)** Ocular following responses (OFR) were elicited by large motion texture stimuli with varying spread of the spatial frequency distribution (bandwidth in cycles per degree) across trials. Eye movement velocity was compared with perceptual sensitivity in a speed discrimination task, in which mean spatial frequency and bandwidth were constant in a given trial but varied across trials. **(D)** Mean sensitivity results from three observers showing an opposite trend in OFR and perception. Eye movement sensitivity (inverse standard deviation of OFR velocity) increased, whereas perceptual sensitivity (inverse discrimination threshold) decreased with increasing bandwidth. Adapted, with permission, from [44] (A,B) and [57] (C,D). See also Table 1.

fluctuations in stimulus speed, even when observers were unaware of the perturbation (Figure 1B).

OKN. Many binocular rivalry studies have used reflexive OKN as a sensitive indicator of perceptual awareness, based on the assumption that eye movements reflect the dominant percept. However, two recent studies support quantitative differences between perception and action in rivalry by using OKN [32] and pupil dilation [32,33]. Whereas perceptual responses are typically 'all-or-none' (observers see one stimulus or the other, except for occasional trials with 'piecemeal' rivalry, where parts of both images are perceived), eye movement responses can reflect gradual differences in space and time. These studies found that transitions between perceptual states were reflected faster in eye movement responses than in perception. Pupil dilation and direction changes in slow-phase OKN velocity preceded perceptual reports (awareness) by

about half a second [33] and a second [32], respectively. Control experiments ruled out that this temporal lead was due to a faster response time of the eye versus manual response. In consonance, frontal brain activity underlying binocular rivalry correlated better with eye movements than with perception [55].

Vergence. A study comparing humans and monkeys reported a quantitative difference between perception and vergence [48]. Random-dot patterns were shown separately to each eye through orthogonal polarizing filters. The patterns were anticorrelated (each black dot in one eye corresponded to a white dot in the other eye) and did not produce a consistent depth percept in humans. However, when small disparity steps (binocular misalignments) were induced, these stimuli reliably elicited reflex-like vergence at ultra-short latencies, even though observers were unaware of these changes.

Saccades. Notwithstanding similarities between perceptual and oculomotor target selection in paradigms such as visual search or under natural viewing conditions [17,21–24], some studies have revealed saccadic target selection in the absence of visual awareness [49–53]. For instance, in a visual search task [49] in which observers had to saccade to a salient object and ignore a distractor, correct saccades were made in about two-thirds of the trials and saccadic latencies were shorter in response to the target than to the distractor. However, observers were not perceptually aware of their saccadic choice, suggesting that low-level visual information can guide saccade target selection without awareness. These findings were confirmed by a subsequent study using continuous flash suppression, in which gaze was directed at a suppressed stimulus even though observers were not able to correctly locate it or discriminate its orientation, (i.e., they were not aware of it) [53]. Furthermore, saccades landed in between a target and distractor (global effect), even when the distractor did not affect localization judgments [50], and they deviated away from unperceived distractors presented in the periphery [51]. Similar deviations in saccade trajectories were observed in patients with blindsight when distractors were shown in the blind hemifield and, thus, did not reach awareness [12].

To conclude, quantitative differences between perception and eye movements reflect that, with one exception [45], voluntary and reflexive eye movements are more sensitive compared with perception. Eye movements may even respond to visual stimuli that are rendered perceptually invisible (i.e., observers are not aware of them) through rivalry or flash suppression, akin to blindsight [8,9]. These results are complemented by a clinical study of one-eyed (enucleated) observers showing that eye movements can be more resilient compared with perception: whereas motion perception was severely impaired in these observers, the accuracy of their pursuit did not differ from that of two-eyed observers tested either monocularly or binocularly [56]. The studies reported here favor a model incorporating the idea that visual information for perception and eye movements is processed in different populations of neurons within the same area(s) or in different pathways (see final section).

Qualitative differences (dissociations)

Cases in which eye movements and perception follow different response directions, rather than just a weaker or absent response, have been reported for OFR [46,57], pursuit [47,58–60], vergence [61], and saccades [62].

OFR/pursuit. Reflexive OFR and perception seem to integrate motion information across different spatial frequency ranges. Simoncini *et al.* [57] elicited reflexive OFR using large motion texture patches of constant speed but variable spatial frequency distribution (Figure 1C). Larger bandwidth ('richer' stimuli, similar to natural scenes) resulted in stronger, less variable OFR and higher OFR sensitivity (Figure 1D). By contrast, when discriminating the speed of a test stimulus that moved either slower or faster than a reference, observers' perceptual sensitivity decreased with increasing spatial-frequency bandwidth (Figure 1D).

Eye movement responses integrate motion information across a wider range of spatiotemporal frequencies compared with perceptual responses.

The oculomotor system also seems to integrate motion information across a larger spatial range compared with the perceptual system. Glasser and Tadin [46] asked observers to discriminate the motion direction of small (1° radius) and large (8° radius) sinusoidal luminance gratings. For small stimuli, perceptual discrimination was more reliable than discrimination by the elicited OFR. By contrast, for large stimuli, perceptual performance deteriorated, due to spatial suppression, while oculomotor performance improved, indicating spatial summation.

A qualitative difference between perception and pursuit was first reported when observers were asked to track a small, central moving target and ignore the motion of a peripheral context. Spering and Gegenfurtner [58] showed that context motion in the periphery affected perception and pursuit differently: while perception followed the relative motion of target and context, eye movements followed the vector average.

In a novel procedure developed by Spering and Carrasco [59,60], observers viewed a pattern that comprised two superimposed gratings moving in two different directions, one horizontal and one vertical. The two gratings were shown separately to each eye, creating a dichoptic plaid (Figure 2A). The strength of each grating was manipulated through monocular adaptation, similar to binocular rivalry flash suppression. Perceptual reports of the motion direction of the plaid followed the unadapted grating exclusively (e.g., vertical downward motion in Figure 2B,C), indicating that observers were aware of such stimulus. However, the eyes did not follow the perceived direction but tracked the vector average of both gratings (pattern motion), disregarding the perceived strength of each individual component (Figure 2C,D).

The dissociation between perception and pursuit, which indicates that pursuit can track motion signals that do not reach awareness, was replicated under feature-based attention [60]. Observers were asked to attend to the motion direction of either the unadapted or the adapted grating (the former reaches awareness, the latter does not). Perception and pursuit were both shifted towards the attended motion direction regardless of whether the observers had adapted to the attended stimulus. Hence, feature-based attention affected perception and pursuit similarly, even though the former reflects awareness, whereas the latter does not.

Perceptual judgments of causality and predictive pursuit responses [47] illustrate another qualitative difference. When observers judged the motion direction of a target (the 'reaction' target) as either caused or not caused by a colliding first stimulus (the 'launcher' target), perception and predictive pursuit showed a similar preference for the 'causal' motion direction (i.e., the motion angle that follows the physical laws of a collision event). When a time delay between collision and target motion was introduced, experienced observers based their judgments on direction information, whereas naïve observers classified trials based on time information (as 'non-causal'). Critically, whereas perception was strongly influenced
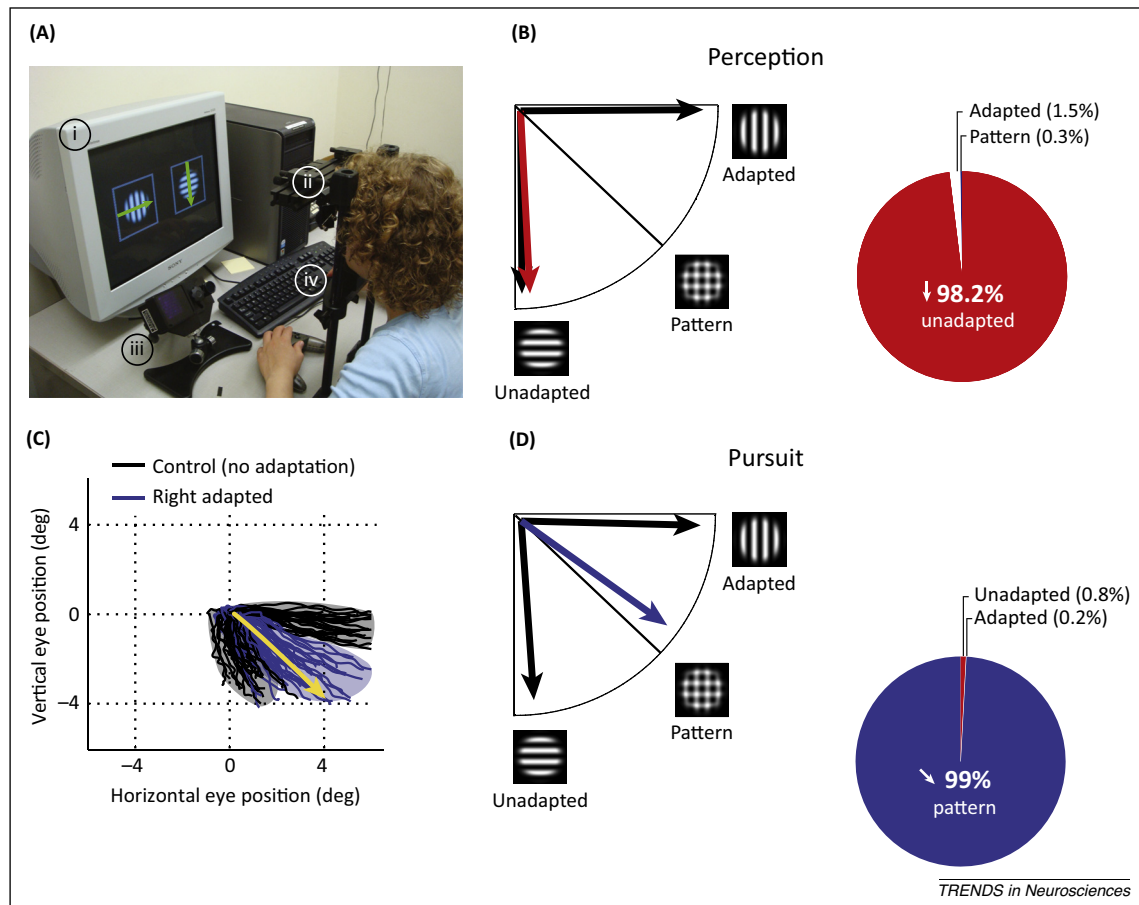
Figure 2. When eye movements track unperceived motion. **(A)** Set-up (i) Display monitor; left stimulus shows adapted motion direction, right stimulus shows unadapted motion direction; green arrows for illustration purposes only. (ii) A four-mirror stereoscope to present separate images to the two eyes. (iii) Eye tracker recording binocular eye movements. (iv) Track-ball mouse used to indicate perceived motion direction (right hand partially blocked by stereoscope). **(B)** Perceived motion direction when rightward motion is adapted and downward motion is unadapted (red) or when both stimuli move rightward or downward as shown in control conditions (black). Pie chart indicates percent of total responses (pattern response and adapted response only occurred in <1% of trials each). **(C)** Individual eye position traces for one representative observer; blue traces are for rightward motion adapted and downward motion unadapted, black traces are for control conditions (both stimuli to right or down, respectively). **(D)** Pursuit direction when rightward motion is adapted and downward motion is unadapted (blue) or in control conditions (black). Pie chart indicates percent of total responses (adapted responses and unadapted responses only occurred in <1% of trials each). Eye movements were recorded binocularly and both eyes showed the same vector-averaging response. Adapted from [59]. See also Table 1.

by individual differences and seemed to rely on heuristic shortcuts, predictive pursuit consistently tracked causal motion, illustrating that pursuit can respond to aspects of stimulus motion that do not reach awareness.

Vergence. An opposite dissociation to those reported in Spering and Carrasco's studies [59,60] (Figure 2) occurs between vergence and motion perception when stimulus components are shown dichoptically in different depth planes [61]. When presenting two orthogonally oscillating random-dot patterns (horizontal and vertical motion directions) separately to the two eyes using red and green filters, observers perceived diagonal motion direction (i.e., the vector sum of the two images), as indicated in a continuous motion estimation task. However, each eye followed the direction of the stimulus motion presented to that eye; one eye tracked horizontal motion, the other eye tracked vertical motion. The finding of independent left and right eye movements violates the assumption that movements between the two eyes should be coupled and aimed at the same point in space, creating binocular retinal correspondence. These results may emerge because dichoptic presentation with red and green filters yields a stimulus with

different depth planes, in which both components are equal in perceptual strength. Similar stimuli reliably elicit vergence even in the absence of a corresponding depth percept [48].

Saccades. Kuhn and Land [62] discovered an impressive qualitative difference between perception and saccades by showing observers a magician's trick: the vanishing ball illusion. In this trick, the magician pretends to throw a ball up in the air and uses social cues (following the imagined ball trajectory with his head and eyes) while the ball remains in his hand. Observers' perception was driven by social cues (they reported seeing the ball flying through the air) but their fixations were mostly on the magician's face. Interestingly, observers reported that their eyes were always on the ball. By contrast, when the ball was actually thrown, observers' fixations were on the ball at the peak of its trajectory. These results indicate that cognitive expectations alter perception, whereas eye movements are not deceived; instead, they more accurately reflect low-level visual information.

In sum, in studies reporting dissociations, perception and eye movements follow opposite motion directions or

response patterns. These studies support the hypothesis of partly separate pathways for conscious perceptual reports and eye movements to visual stimuli of which the observers are not aware (see last section).

When do differences and dissociations emerge?
To conclude, the three groups of perception–eye movement differences discussed (Table 1) are not uniquely driven by the type of eye movement, task, or stimulus used. However, certain configurations enable the emergence of differences and dissociations: (i) eye movements: reflexive OFR, predictive or short-scale pursuit eye movements are more prone to variability differences [41–47] compared with longer-scale pursuit in direction discrimination tasks [43,63]; (ii) task: most studies reporting similarities in sensitivity between perception and pursuit used 2AFC methods for perceptual judgments [27,41,63]. Interestingly, all studies reporting quantitative differences [32,44,45,48–53] also used alternative forced-choice methods (2AFC, 4AFC, or 2IFC). By contrast, several studies with dissociations used continuous estimation tasks in perception [59–62]; and (iii) stimulus: ambiguity in visual information, either through the use of dichoptically presented plaids, random-dot patterns [59–61], or illusory motion [47,58,62], as well as large stimulus size [46] and bandwidth [57], can give rise to qualitative dissociations.

Structural and physiological bases underlying perception–eye movement differences
What brain machinery could underlie both similarities and differences between perception and eye movements? Whereas variability differences between perception and eye movements can be reconciled with a model of similar processing mechanisms along shared brain pathways, quantitative and qualitative differences indicate separate pathways, neuronal populations, or mechanisms.

Same brain pathway
There is strong evidence for shared brain pathways for pursuit and motion perception [14,16]. The classical assumption is that the separation of pathways for perception and pursuit occurs downstream from visual areas, closer to the motor output stage. Studies reporting differences in variability (Table 1) are consistent with the idea of processing along the same pathway and postulate the existence of different sources of sensory and motor noise within this pathway, motion processing in different subpopulations of neurons, or different thresholds or decision criteria in perception and eye movements.

Different sources of noise. Variability similarities between the precision of sensory coding and the precision of pursuit and OFR have been taken to indicate that both systems rely on similar visual signals and are limited by the same neuronal noise. However, there is a debate over whether perception and eye movements rely on shared or separate sources of noise. Some authors suggest that perception and the earliest, visually driven phase of pursuit depend almost exclusively on noise in the sensory representation of motion signals in area MT [14,64]. Others affirm that motor noise can account for

up to 50% of pursuit variability, even during pursuit initiation [65].

Studies reporting differences in variability [41–47] (Table 1) indicate that perception and eye movements likely rely on at least partly separate sources of noise. Given that these studies focus on later time intervals of the eye movement response and/or transient changes in ongoing pursuit velocity, they are not necessarily in conflict with the idea that visually driven eye movements may be guided by some amount of shared sensory noise. Common sensory noise may affect both perception and pursuit, but additional motor noise may be added to oculomotor areas downstream from visual areas (e.g., frontal eye field or cerebellum [14]). This explanation could account for results in studies finding differences in variability despite similar sensitivity [41–43].

Different subpopulations of neurons. Alternatively, different subpopulations of MT neurons may carry motion signals with different signal-to-noise ratios. Neurophysiological studies in monkeys have described MT neurons with different receptive field properties [66,67]. One type of neuron responds to wide-field motion stimuli that extend beyond the area of the classical receptive field, indicating an excitatory surround. Another type does not respond to these stimuli, indicating an inhibitory surround. Excitatory and inhibitory center-surround interactions may be related to the processing of global and local motion, respectively [68]; surround-suppressed MT neurons also integrate motion signals faster and respond better to briefly shown visual stimuli compared with nonsurround suppressed neurons [69].

Such differences in receptive field properties in MT neurons could also underlie some of the quantitative and qualitative differences between perception and pursuit and between perception and OFR (Table 1). For instance, studies reporting opposite spatial or spatial frequency tuning in perception and OFR find superior sensitivity (lower threshold) in eye movements in response to larger stimuli [46] and stimuli with larger spatial frequency bandwidth [57]. Different subpopulations of MT neurons (surround-suppressed for perception and non-surround suppressed for OFR [58,70]) could explain these effects. According to this model, motion perception and eye movements rely on the same source of visual information, but may integrate it differently through an adjustable, task-dependent tuning [57] in different subpopulations of neurons, potentially with different signal-to-noise ratios [44]. Such a model would reconcile similarities in perception and eye movements in behavior and neurophysiology with the differences and dissociations discussed here.

Different response thresholds or decision signals. Accumulate-to-threshold models have provided explanations based on differences in decision signal or response threshold (lower for eye movements than for perception [16]); these models could potentially explain quantitative differences in response sensitivity. However, this view is too simplistic and cannot explain the diverse differences discussed here, particularly those qualitative differences in which effects go in different directions. Underlying mechanisms likely include
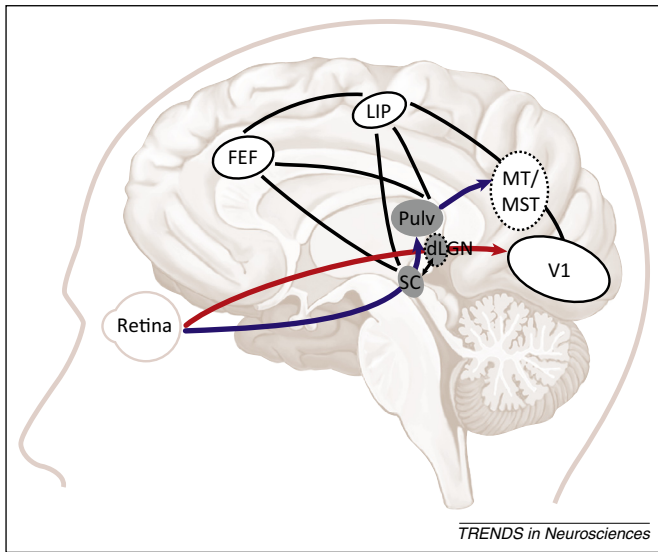
Figure 3. Brain pathways for eye movements to unaware visual information. Two separate but interconnected pathways may mediate visual information for perception (retinogeniculate pathway, red) and eye movements in the absence of awareness (retinocollicular pathway, blue). In the retinogeniculate pathway, the dorsal lateral geniculate nucleus (dLGN) transmits visual information from retina to primary visual cortex (V1); V1 then projects to higher-order visual and visual-motor areas in occipital, parietal, and frontal cortex, as well as to subcortical areas in midbrain and brainstem. The retinocollicular pathway directly connects the retina to the superior colliculus (SC) and pulvinar (Pulv), and thence to middle-temporal area (MT) and medial-superior temporal area (MST), forming a subcortical route that can bypass the dLGN and V1. The dorsal Pulv connects directly to cortical areas involved in eye movement control, such as frontal eye field (FEF) and lateral intraparietal sulcus (LIP). Structures that are not in the midsagittal plane are indicated by dotted outlines; area illustration does not correspond to exact anatomical size and location; only feedforward connections are shown and not all areas implicated in oculomotor control are shown.

differences in neuronal decoding efficiency, firing rate, and/or in the way information is integrated or normalized [57].

Different brain pathways
The main brain pathway for visual information processing, the retinogeniculate pathway (red arrow, Figure 3), has been well characterized: the dorsal lateral geniculate nucleus (dLGN) of the thalamus receives information from retinal ganglion cells and projects mostly to primary visual cortex (V1). V1 sends feedback projections to the thalamus [6,7] and feedforward projections to higher-level visual areas, such as MT/MST, feeding into the dorsal or posterior parietal processing streams, and key frontoparietal areas for oculomotor control [71]. Visual information for perception and eye movements could be processed largely in parallel, with separation into perceptual awareness and motor output control happening downstream from visual areas. However, quantitative and qualitative differences (Table 1) suggest that visual information is processed more readily for eye movements than for explicit perception and, thus, that pathways may separate at an earlier stage of visual processing.

Dorsal versus ventral visual processing streams. Some of the studies finding saccade–perception differences [49,53] refer to the dual-pathway model [38,39] as an explanation. This model proposes largely independent neuronal processing for perception and motor action in a ventral processing stream projecting to the inferior temporal cortex and a

dorsal stream, projecting to the posterior parietal cortex, respectively. A separation between the two streams, where 'vision-for-perception' information is more accessible to awareness compared with 'vision-for-action' information [72], could underlie perception–eye movement differences. However, there are known interconnections between some areas in the two streams [38–40]. Moreover, given the involvement of MT (located in the dorsal processing stream) for both perception and pursuit, these processing streams are unlikely to be the neural correlate for differences between perception and pursuit and between perception and OFR.

Subcortical pathways. Involvement of the retinocollicular pathway (blue arrows, Figure 3) is a more likely explanation for why eye movements reveal a more sensitive processing of information, even when observers are unaware of it. This pathway directly connects the retina to superficial layers of the superior colliculus (SC); projections also go to the brainstem through the nucleus of the optic tract (NOT) and to the inferior (ventral) part of the pulvinar nucleus of the thalamus.

Given that regions in this pathway (SC, NOT, and pulvinar) have direct connections with area MT [7,71], providing fast transmission of retinal input to dorsal visual cortex [7,73] and mediating pursuit control and target selection [74], Spering and Carrasco [59,60] proposed that this pathway may also underlie the responses of pursuit eye movements to visual information of which the observers are not aware. Subsequent studies on perception–eye movement differences agree with this view [46,53]. Indeed, the fast transmission time from SC through pulvinar to MT via this pathway (∼5 ms [73]) may mediate fast visual processing for the control of eye movements, whereas readout for perception may take longer, or may occur at higher decision areas, enabling the differences and dissociations described in Table 1.

Psychophysical and neuroimaging studies in humans, neurophysiological studies in monkeys, and clinical studies in patients with deficits related to awareness have provided evidence for an involvement of this pathway in visual processing without awareness; however, there is ongoing debate regarding the exact role of areas such as the pulvinar and dLGN [75]. We cannot provide an in-depth review of this literature here; instead, we focus on representative studies illustrating recent progress in this topic.

The retinocollicular pathway is associated with residual visual abilities in blindsight [8–11] and with the translation of unperceived visual signals into oculomotor outputs in these patients. In these studies, patients with blindsight can be prompted with a visual cue presented in an area of normal vision or by a sound to shift their gaze to unperceived but salient stimuli in the blind hemifield. (A recent study in monkeys also revealed involuntary gaze shifts to objects in the blind hemifield during free viewing [76].) Patients with blindsight, occipital cortex lesions, and relative sparing of retinocollicular function exhibit saccade trajectories that deviate away from blindfield distractors [12]. Together with a parallel study in healthy observers [51], this suggests an involvement of the retinocollicular pathway in the processing of unperceived

visual information for eye movements. This pathway is also implicated in blindsight studies assessing hand movements (reaching [77] and pointing [78]).

The involvement of the SC in blindsight was confirmed by a study reporting that an unperceived stimulus, presented to the blind hemifield of a patient with unilateral blindsight, quickened reaction times and enhanced pupillary constriction when a perceived stimulus was presented simultaneously to the intact hemifield [13]. Critically, this effect was found for gray stimuli, which elicit SC activation, but not for purple stimuli, which are invisible to the SC due to its insensitivity to S-cone input (although the lack of S-cone input to the SC has been questioned, see [79]). The authors suggested that unperceived, gray stimuli mediate perceptual and motor responses through direct projections via the SC.

Damage to the pulvinar has also been implicated in visual-spatial neglect [80], a frequent and disabling deficit of awareness. In visual-spatial neglect, objects and events in the contralesional visual hemifield are ignored or even unperceived and patients exhibit biased eye and head orientation towards the ipsilesional hemisphere [81]. There is debate over whether these patients show similar 'blindsight'-like effects in perception or eye movements: on the one hand, distractors presented in the contralesional (neglected) hemifield do not affect saccade latencies to targets in the ipsilesional field [81–83], in contrast to what has been reported for blindsight [12]. On the other hand, saccades to targets in the neglected hemifield may be preserved even in the absence of awareness (as assessed in a verbal detection task) [83]. Selective inactivation of the pulvinar in monkeys also caused neglect symptoms

[84]. Moreover, when monkeys were trained to report the visibility of a small, high-contrast target (by releasing a lever), changes in the spiking rate of pulvinar neurons reflected their perceptual awareness of the stimulus. By contrast, spiking activity of the LGN is solely driven by the physical presence or absence of the stimulus [85].

However, human neuroimaging during a binocular rivalry task suggests involvement of the dLGN in the processing of visual information of which observers are not aware [86,87]. Although these neuroimaging results could be caused by cortical feedback, the idea that dLGN is a critical relay in visual processing without awareness is supported by a study in monkeys with chronic V1 lesions resulting in blindsight: residual visual functions in their blind hemifield and neuronal activity in extrastriate areas, assessed by functional MRI, were both eliminated by temporary dLGN inactivation in the V1-lesioned hemisphere [88]. These results agree with studies proposing that visual information is also transmitted to extrastriate areas directly from the dLGN, bypassing V1 [89].

In sum, retinocollicular and/or geniculo-extrastriate projections could provide rapid processing of visual information for motor actions in the absence of perceptual awareness. Furthermore, the retinocollicular pathway and its amygdala connection are associated with the rapid processing of emotional information and with the heightened visual sensitivity of primates to evolutionarily salient stimuli, such as faces and snakes [90]. Thus, a subcortical route could provide a short-cut to drive motor actions, such as fast orienting eye movements to targets of interest, before visual information reaches awareness.

Box 1. Outstanding questions and future research directions

Our understanding of perception–action will be further advanced by the integration of different levels of analysis and methodologies in both healthy and clinical populations. Ideally, future studies will shed light on these issues by combining knowledge gathered from psychophysics, single-unit neurophysiology, neuroimaging, and computational techniques.

Here, we present some possible future directions in, and approaches to, the investigation of eye movements as an objective indicator of unperceived information that does not reach awareness.

- Systematic investigations of which tasks, procedures, and stimulus properties yield dissociations between perception and eye movements. Patterns may be identified by holding one property constant (e.g., same task) while systematically varying the other (e.g., different types of eye movement).
- Preliminary evidence indicates that quantitative differences between perception and eye movements may also extend to nonvisually triggered, reflexive eye movements, such as the vestibulo-ocular reflex (VOR) [93]. Conclusive interpretation of these findings awaits studies comparing perception and VOR in the same experiment and the same species.
- Neurophysiological studies have identified MT neurons with different center-surround properties [66–69]. Several paradigms presented in our review lend themselves to the examination of perception–action differences using motion stimuli that are known to modulate MT neurons with excitatory and inhibitory receptive field properties (akin to studies identifying MT pattern versus component cells [31,94]). For instance, Glasser and Tadin [46] and Spering and Gegenfurtner [58] used stimuli that could differentially activate either type of neuron.
- There are still many unanswered questions regarding our understanding of the neuronal mechanisms underlying blindsight [75].

A novel combination of blindsight with suppression procedures (rivalry or adaptation), in which either the dominant (unadapted) or suppressed (adapted) stimulus is presented in the blind field, could provide insight into the processing mechanisms in blindsight. Effects on perception and eye movements could be compared.

- Assessments of behavioral effects on eye movements and perception while characterizing single-unit activity. Basic electrophysiology studies are needed that link mechanistic properties of neurons along the retinocollicular pathway (i.e., to identify activity in different subpopulations of neurons) to perceptual and oculomotor processing. This research could be complemented by neuroimaging studies in humans to reveal activity in these pathways [95].
- The pulvinar, which lies along the retinocollicular pathway associated with the processing of unaware visual information, also seems to have a critical role in visual attention [96,97]. Thalamic nuclei, such as pulvinar and dLGN, could be areas of interest in future behavioral and neuroimaging studies in healthy populations, to assess the interplay between attention and awareness [60]. Targeting the pulvinar and dLGN through a combination of psychophysics, neuroimaging, and electrophysiology may also shed light on their connection to cortex (bottom-up projections and top-down inputs) and their role in blindsight.
- A recent study showed that feature-based attention affects both perceptual reports and eye movements similarly, even when qualitatively dissociated [60]. Further investigating whether and how spatial and feature-based attention [98–100] affect perceptual reports, assessed by different tasks, and different eye movements, would help probe situations in which visual processing could potentially lead to awareness.

Concluding remarks

This review emphasizes that differences and dissociations between perception and eye movements are not the exception, especially when visual information is ambiguous, and when reflexive or short-scale eye movements are assessed with continuous estimation tasks. In these situations, observers' eye movements demonstrate that they are processing visual information even when they are not aware of it.

Perception–eye movement dissociations may be adaptive responses to different task requirements and to diverse ecological demands. The access of the motor system to visual information that does not reach awareness may help manage limited bioenergetic resources [91]; it may also enables humans to act fast in fight or flight situations. On the one hand, eye movements rely mainly on estimation and are updated continuously. They provide a fast orienting response to information of which observers may be perceptually unaware; they may also respond faster than perception. They integrate information across space [46,50], a large range of spatial frequencies [57], and local motion directions (i.e., vector averaging [14,27,58–60]). On the other hand, the perceptual system needs to reliably discriminate or categorize visual information. Perceptual decisions are discrete; they may be based on visual signals at a specific moment in time or averaged across the whole presentation time and beyond. They are more prone to spatial suppression [46] and are constrained to a smaller spatial [50] and spatial-frequency range [57]. These differences in how information is processed across space, spatial frequencies, and time are crucial methodological factors to consider when directly comparing perception and eye movements [16,92].

Although there are still many unanswered questions about the origin, nature, and functional significance of differences and dissociations between perception and eye movements (Box 1), converging evidence suggests that the classical view of a tight link between perception and eye movements should be revised. Eye movements are often more sensitive compared with perception and may serve as an indicator of visual processing without awareness. Both reflexive and voluntary oculomotor responses can be earlier, faster, and more accurate predictors of the way we locate and track events in the visual world compared with perceptual reports. Such differences can provide important insights into brain function and merit further investigation.

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