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The aperture problem in egocentric motion

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When only a featureless straight contour of a moving object is visible, one cannot tell its true velocity and the object seems to be moving perpendicularly to its orientation. Using psychophysics and brain imaging, Goltz *et al.* have now demonstrated that this aperture problem also occurs in visual representations in egocentric coordinates. An afterimage of inclined lines that is perceived to move with smooth-pursuit eye movements appears to move perpendicularly to the lines rather than in the tracking direction.

Our visual perception surely depends on light projected on the retina. In lower levels of visual processing, each neuron is sensitive only to visual signals within a tiny patch on the retina, or the receptive field. Because our eyes are constantly moving, however, any single neuron can only 'see' a sequence of visual signals from different objects projected in turn onto one retinal location. To construct a meaningful visual world out of these early representations, the visual system has to monitor eye movements so as to transform images from retinal coordinates to 'egocentric' ones (i.e. relative to the center of oneself). However, coordinate transformation does not mean the end of processing for object motion. In a recent study [1], objects coded in egocentric coordinates were shown to suffer from the same problem that had been believed to emerge only in retinotopic stages – that complicates interpretation of object motion.

The aperture problem
This problem normally arises from a moving object viewed through a small window, and so is referred to as the 'aperture problem' [2]. Through the window, only a small part of a contour of the object is visible at one time. If only a straight contour is viewed, it is impossible to tell how the object is actually moving because an infinite number of object velocities are consistent with the observed image motion (Figure 1a).

Several schemes for solving this problem have been proposed. First, two linearly independent measurements can uniquely determine the true motion at the 'intersection of constraints' [2] (Figure 1b,c). Second, multiple measurements can also be averaged to yield a useful estimation [3] (Figure 1b,c). Third, the true motion can be inferred from unambiguous motion measurements at the ends (terminators) of the contour nearby [4] (Figure 1d). Perhaps all of these schemes would work in concert in a normal environment. However, they all fail if a moving contour is presented alone; in such cases, the contour normally appears to move perpendicularly to its orientation [4–6]. Perhaps this is the most conservative

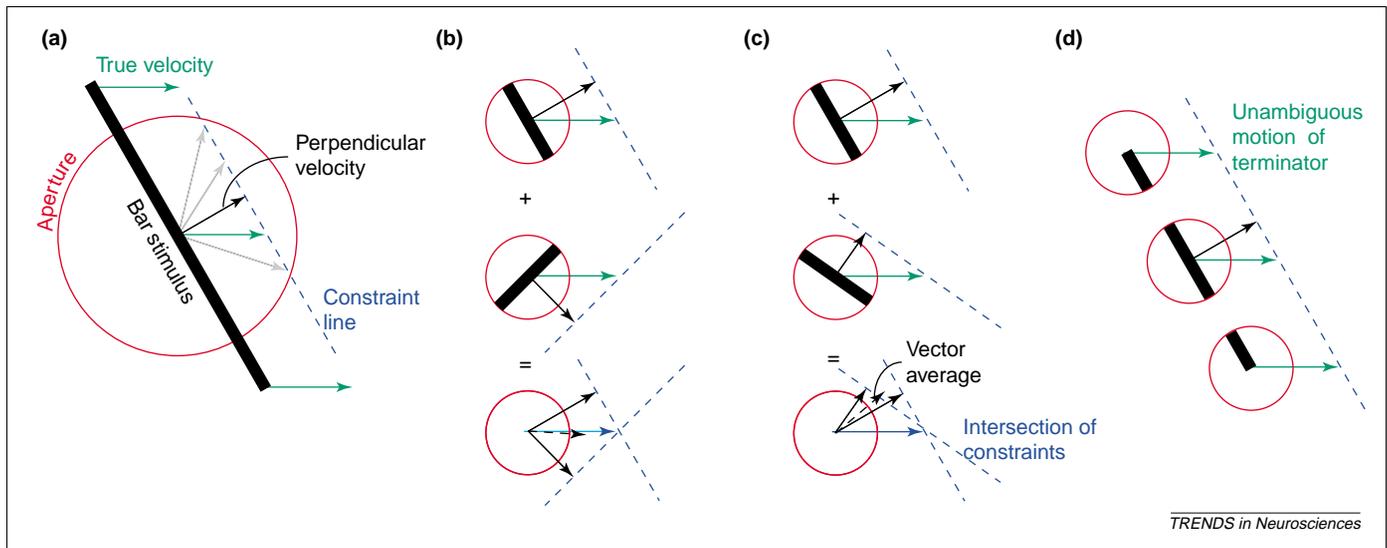*Corresponding author:* Ikuya Murakami (ikuya@apollo3.brl.ntt.co.jp).

Figure 1. The aperture problem and its possible solutions. **(a)** Through a small window ('aperture'), only a straight contour of the horizontally moving bar is visible. A family of possible velocity vectors (including the true velocity) that are consistent with the observed image motion are illustrated by multiple arrows stretching from the center. The arrowheads are constrained along a straight 'constraint line' that is parallel to the bar. With no other information, the bar is normally interpreted to move in the 'perpendicular direction'. **(b)** If the same object has contours of two different orientations, two different constraint lines are obtained, and their intersection specifies the true velocity (blue arrow). Also in this example, the vector average of the two perpendicular velocities roughly points at the true velocity (dotted arrow). **(c)** When two contours are both inclined towards the same side of the true velocity, the intersection of constraints still coincides with the true velocity but the vector average of the two perpendicular directions points away. Surprisingly, in some cases the object appears to move in the vector-average direction rather than the direction correctly specified by the intersection. **(d)** Terminators (ends) of the contour viewed through the apertures move unambiguously, essentially escaping the aperture problem.

assumption the visual system makes by default when there is no evidence of other solutions.

Retinotopic and egocentric motions

This perceptual bias is not limited to the case of moving bars viewed with fixation (Figure 2a); it is also seen when stationary bars are viewed with moving eyes [7,8] (Figure 2b). Thus, the aperture problem occurs whenever there is a motion ambiguity of oriented contours in retinotopic coordinates. This is explained by the fact that motion-sensitive neurons in early levels have receptive fields delineated in retinal terms.
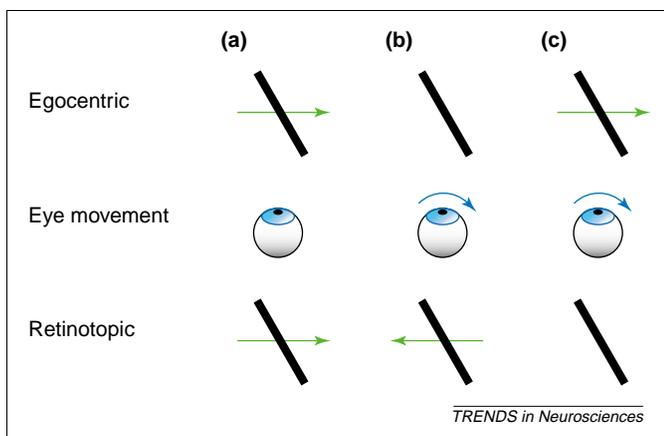

Figure 2. Motions in the egocentric and retinotopic coordinates. The row designated 'egocentric' illustrates the object motion in front of the head of the observer. 'Eye movement' indicates whether the eye is stationary or moving. 'Retinotopic' illustrates the retinal image motion of the object. **(a)** When the eye is stationary, an egocentrically moving object is also moving on the retina. **(b)** When the eye is moving, a stationary object is projected onto the moving retina and therefore the image moves relative to the retina in the direction opposite to the eye movement. **(c)** When an object is actually moving but the eye is perfectly tracking it, its image on the retina stays still at the center of the retina, the fovea.

At some stage, however, visual representations must be coded in egocentric coordinates, because retinotopic coding is subject to eye movements, which have nothing to do with ongoing events in the environment (compare Figure 2a and 2b). Therefore, it is generally assumed that the perceived motion of any object is given by subtracting the estimated eye movement from the retinal image motion [9–12]. If the subtraction is perfect, a stationary object would appear egocentrically stationary no matter how the eyes might move. Conversely, a retinally stationary object can move perceptually with eye movements (Figure 2c). For example, while the eyes are pursuing a flying bird, it appears to move even though its retinal projection remains almost stationary. Likewise, an afterimage appears to move together with eye movements [13–15]. The last example is especially interesting because clear motion is perceived in the egocentric frame, although the afterimage, of course, never moves on the retina.

Perceived motion of an oriented afterimage

The question arises, then, as to whether the aperture problem occurs in the perceived motion of the afterimage that is shaped like an oriented bar. If the motion processing system 'knows' that the afterimage is retinotopically stabilized, subtraction will take place between this retinally zero velocity and the eye velocity, and the same direction and speed as eye movements will be perceived irrespective of orientation. If, alternatively, retinotopic velocity estimation is not completed before subtraction, subsequent egocentric velocity estimation will depend on image orientation, and the afterimage after subtraction will still suffer from the aperture problem.

Goltz *et al.* demonstrated that the second idea is correct [1]. In their psychophysical experiments, a negative

afterimage of parallel lines was first created by prolonged observation and then was viewed in total darkness. The observer was requested to estimate the speed and direction of the afterimage while making smooth pursuit. First, the perceived speed was found to be maximal when the line orientation was orthogonal to the pursuit direction and was minimal when they were parallel. Indeed, the perceived speed changed as a sine function of angular difference. Second, there was a strong correlation between the perceived direction and the line orientation, such that the direction perpendicular to the orientation was always reported. These results are highly consistent with the idea that retinotopically stabilized but egocentrically moving lines are still ambiguous with respect to velocity; the visual system makes the most conservative assumption of perpendicular motion out of a family of possible velocities.

Brain activity during the afterimage motion

What part of the brain is activated when one perceives the motion of the afterimage? Functional magnetic resonance imaging (fMRI) revealed increased signal in area MT + (the putative homologue of the monkey MT and MST; see next section) while the observer saw the afterimage motion, compared with the signal in this area when the same eye movements were made without perception of afterimages [1]. However, this differential activity might have reflected the presence of an afterimage *per se*, rather than its motion. So, in the next experiment, the afterimage of oriented lines was always produced, and smooth pursuit was made in the direction orthogonal or parallel to the lines – a situation more similar to the psychophysical experiments. The activation was greater when the line orientation was orthogonal to the pursuit direction than when they were parallel, in accord with the psychophysical data on perceived speed. Such a differential activation pattern was not observed in V1, an antecedent level of processing. These fMRI data nicely demonstrate that MT + is presumably the place where egocentric motion is represented explicitly. I would note, however, a potential effect of the tracking target. Whenever tracking is imperfect, the retinal image of the tracking target and the orthogonal lines of the afterimage always create relative motion on the retina for which MT + , the presumed neural basis of motion perception [16], is highly sensitive. To clarify this difficulty, correlations between pursuit accuracy and brain activation could be checked, and also the fMRI experiment could be repeated without a visual target stimulus but with an auditory or afterimage target instead, as in the psychophysical experiments. In addition, it would be interesting to see an activation pattern when the same afterimage is observed in steady fixation, so ideally one could isolate activity related to the afterimage *per se*, activity related to its motion, and pursuit-specific activity.

Hierarchical motion processing

In the primate visual system, motion signals are processed in a hierarchical order, through area V1, the middle temporal area (MT), the medial superior temporal area (MST) and so on, and each stage seems to be trying to solve the aperture problem. Many V1 neurons prefer a stimulus moving in a specific direction within their small receptive fields. Hence, they suffer from the aperture problem when a moving bar extends beyond their receptive-field borders [17]. However, their 'end-stopped' response characteristics make it possible to fire unambiguously to a terminator of the same bar moving in the preferred direction [18]. In a higher stage, MT neurons have larger receptive fields that would support information averaging [19]. In addition, if two gratings in different orientations are superimposed, many neurons fire maximally when the overall pattern moved in their preferred direction [20,21], as if they could code the intersection of constraints [22]. At one stage higher, in the MST, many cells exhibit directionally specific activation with smooth pursuit (even without visual stimulation) [23,24]. Moreover, many cells can distinguish real motions from spurious retinal motions of stationary stimuli produced by pursuit [25]. Thus, the observed human MT + activity could correspond to this stage. Alternatively, the directional misperception of the afterimage might result from interactions among MT + and other shape-processing areas where precise orientation information is preserved. Future fMRI investigations with higher resolutions will clarify this issue. To sum up, the findings of Goltz *et al.* tell us that the aperture problem (Figure 1a) occurs not only within retinotopically confined receptive fields but also in egocentric coordinates, where we perceive oriented lines as if moving perpendicularly, with consistent brain activity in MT + . Thus, the next step is to understand how the aperture problem in egocentric motion is solved in more naturalistic situations. Because classical studies outlined in Figure 1b–1d have concentrated on retinotopic coordinates, it is totally unknown whether specific mechanisms are at work in egocentric representations to support the proposed processing schemes. Making the afterimages of lines of more than one orientation, or of shorter lines with enhanced terminator visibility, would be a good parametric approach to resolving these challenging issues.

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ET – phone the pain clinic

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Recent findings by Khodorova *et al.* demonstrate that the vasoconstrictor endothelin-1 plays an important role in certain nociceptive behaviors in an animal model of pain, through activation of sensory neurons. Endothelin-1 might also have the unexpected capacity to release an opioid from surrounding keratinocytes and thereby inhibit the pain response. Such results suggest that, in the periphery, there are important interactions between sensory nerve terminals and surrounding cells, and that glia and keratinocytes could modulate the perception of environmental stimuli to a greater extent than previously considered.

Localized tissue trauma leads to the release of a multitude of chemical mediators that have well-established roles enhancing sensitivity to various non-painful or painful stimuli. For example, the release of prostaglandins and their causal role in producing hypersensitivity, and the ability of non-steroidal anti-inflammatory drugs (NSAIDs) to reverse these effects, are well understood. However, we are continuing to learn about new and novel mediators from other, presumably unrelated, areas of investigation that could play key roles in altering the sensitivity of sensory neurons. Furthermore, many of these compounds have unique actions in that they modulate the activity of other cell types, such as keratinocytes, in addition to altering neuronal excitability. Recent work by Davar's group at Harvard [1] has shown that endothelin-1 (ET-1), a very potent vasoconstrictor [2,3], is not only a crucial mediator in initiation of the nociceptive or pain response from primary sensory neurons but also might be involved in the simultaneous suppression of this pain signal through the release of an opioid from skin cells.

ET-1 signaling is mediated by G-protein-coupled receptors

The precursor of ET-1 is preproendothelin-1 (212 amino acids), which is broken down by a protease into big ET-1 (38 amino acids) and consequently by endothelial converting enzyme into ET-1 (21 amino acids) [4,5]. ET-1 is synthesized and released by a variety of cell types. It acts through two distinct receptors, ET_A and ET_B (sharing $\sim 63\%$ homology), which are coupled to the G proteins G_i and G_q and activate multiple cell-type-dependent signaling pathways, with phospholipase C (PLC) being the most predominant effector pathway [6–8]. PLC liberates inositol (1,4,5)-trisphosphate and diacylglycerol, which cause the release of intracellular Ca^{2+} and activation of protein kinase C (PKC). The physiological actions of ET-1 in cardiac myocytes appear to be mediated through PKC [5,7,9], particularly the non-classical isoform ε [9]. PKC subsequently activates downstream effectors such as the extracellular-signal-regulated kinases ERK1 (p42) and ERK2 (p44) and the p38 subtypes of mitogen-activated protein (MAP) kinase [5,7,8].

ET-1 and nociception

The notion that ET-1 might be involved in nociception arises from its vasoconstrictor properties, in that significant ischemia can produce pain. Early reports demonstrated that injection of ET-1 into the plantar surface of a rat hindpaw produced hyperalgesia to mechanical stimulation [10], that intraperitoneal injection triggered abdominal constrictions [11,12], and that injection into the brachial artery of humans initiated a deep muscular pain

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