



'But still, it moves'

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A striking example of our sensitivity to dynamic information is our ability to infer motion from still images depicted in paintings, photographs or cartoons. What are the neural mechanisms that mediate this implied motion perception? In a recent paper, Krekelberg *et al.* demonstrate that form cues that imply motion are integrated with real motion information, and influence perception in both humans and monkeys and the neural processing in prototypical motion areas of the monkey brain.

Perception and successful interaction with moving objects entail that the visual system integrates information from form and motion cues into unified dynamic perceptual events. However, traditionally, shape and motion processing have been attributed to anatomically and functionally separable neural pathways in the primate brain [1]. An extrastriate visual area in the medial temporal monkey brain (MT/V5) and its human analogue in the ascending limb of the inferior temporal sulcus (hMT + /V5) have been identified as one of the main regions involved in the analysis of visual motion [2,3]. By contrast, regions in the occipitotemporal cortex (V4, IT) have been implicated in the analysis of shape properties and object recognition in the monkey and the human brain [4,5].

Although significant progress has been made in uncovering the neural mechanisms that mediate motion and form perception, surprisingly little is known about possible interactions of these mechanisms that may underlie the unified perception of moving objects in our dynamic visual environments. Krekelberg *et al.* [6] provide evidence for such interactions by showing similar responses in monkey MT and MST cells to real motion and static form patterns that have no coherent physical motion but imply motion. These physiological findings are consistent with the perception of their human and monkey subjects.

Dynamic object representations: observations and psychophysics

The title of this article, a quote from Galileo Galilei (1632) referring to the motion of the earth around the sun (rather than the other way around), makes the point that we can infer motion when it is not actually present. The perception of implied motion in still images is compelling in paintings and photographs. Edgerton's 'Bullet and Apple' (1964) vividly depicts a bullet shot through an apple and generates spontaneously the strong impression of high-speed movement, enhanced by the motion energy streaks

illustrated in the path of the bullet (Figure 1). Similarly, cartoonists use 'speedlines' in the path of motion to generate a strong impression of motion in still images. Many different visual illusions, such as Enigma (Figure 2a), have been used to demonstrate the perception of implied motion.

To study the neural correlates of motion perception in still images, Krekelberg *et al.* used 'Glass patterns' (Figure 2b) [7]; that is, random dot patterns in which global structure is defined by the spatio-temporal orientation of correlated pairs of dots. Observers perceive these patterns as dynamic forms that move in an ambiguous direction but coherently, in accordance with the global form structure (e.g. translational, radial, concentric). These stimuli are ideal for the study of implied motion perception: physically they lack motion coherence as the local motion vectors are random in each frame of the motion sequence. However, their global form structure guides the integration of the oriented dot pairs over space and time, and results in the perception of coherent motion. Psychophysical studies have shown that perception of coherent motion in dynamic Glass patterns depends on the separation between the dots of the oriented pairs that form the global structure, suggesting that form information determines the perception of motion [8].

Evidence for interactions between form and motion perception comes from psychophysical studies showing effects of (i) motion on form perception and (ii) form cues on the perception of motion paths. In particular, forms

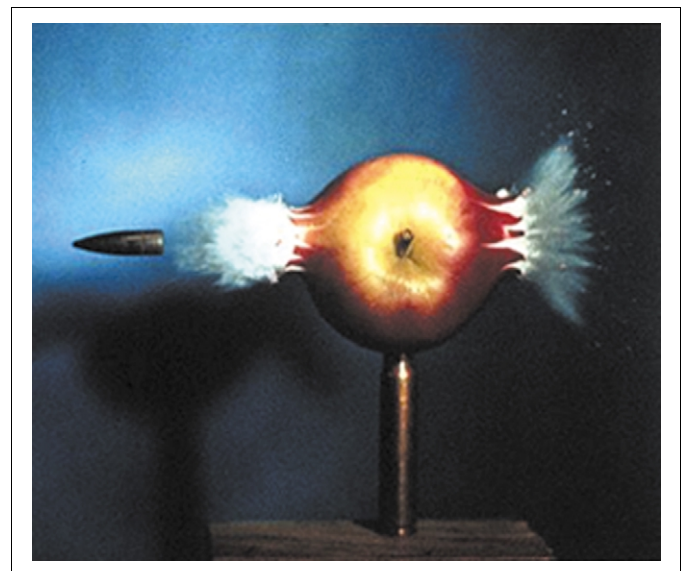


Figure 1. 'Bullet and Apple' (Edgerton, 1964): an example of a still image that implies motion.

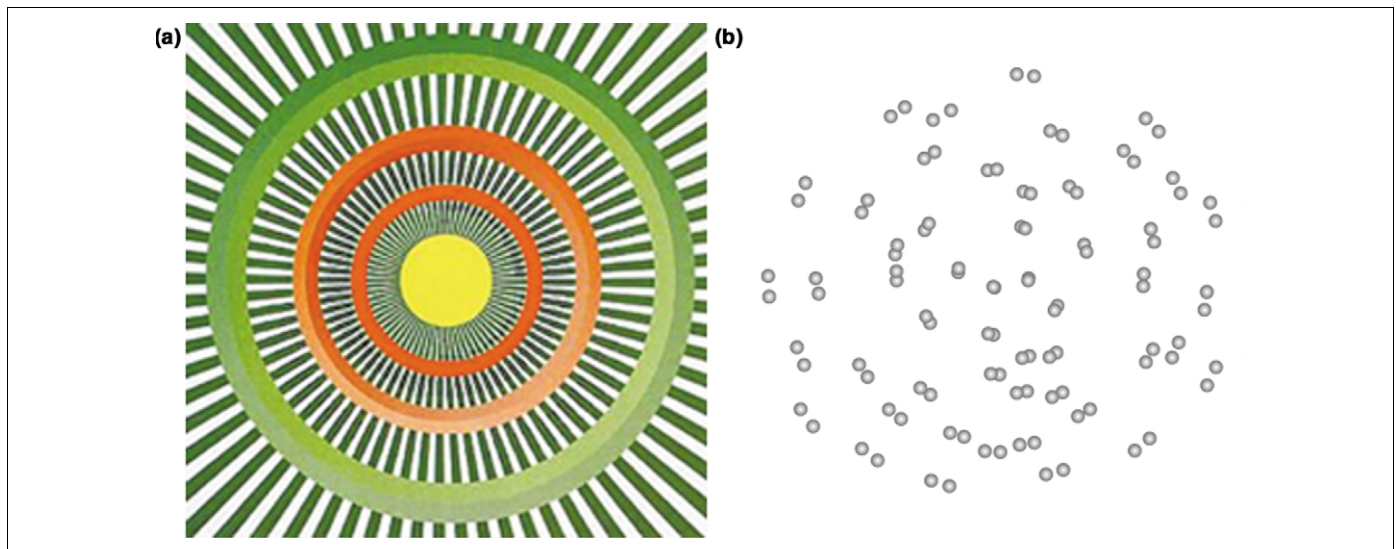


Figure 2. (a) the 'Enigma' illusion, in which motion can be perceived in the concentric circles when focussing at the yellow centre. (b) a Rotational Glass pattern, a stimulus used to study implied motion, which contains local random-dot motion but any globally coherent movement is implied by its form structure.

embedded in cluttered backgrounds that cannot be detected when static, 'pop out' from the background when in motion [9]. Recent studies have shown that motion facilitates invariant representations of object views that fall within the path of the object motion [10] and the discrimination and identification of faces [11]. Furthermore, it has been shown that observers wrongly categorize two different still photographs that imply motion (e.g. images of an object falling) as identical when they depict the same event at different moments in time, suggesting dynamic representations of objects in the direction of implied motion [12].

On the other hand, several recent studies provide evidence for the effect of global form structure on the perception of motion paths. For example, lines trailing behind a moving object that are oriented in the direction of the object's motion (e.g. motion streaks or oriented dot pairs in Glass patterns) have been shown to influence the perception of motion direction [13,14] and resolve motion direction ambiguity [15]. Similarly, biomechanical constraints of the human body's motion have been shown to influence the perception of motion paths [16].

Neural correlates of dynamic object perception

In contrast to the proposed functional dissociation between shape and motion-related areas in the ventral and dorsal neural pathways respectively, there is accumulating evidence for interactions between these areas. A recent functional imaging study [17] showed that coherent motion and form patterns activate distinct but neighboring regions in both the ventral and dorsal streams. MT/V5 has been suggested to be involved in the perception of object structure from motion [18], and the 3-D structure of static objects [19]. Interestingly, recent human imaging studies have shown responses in MT/V5 for still images with implied motion, as in the Enigma visual illusion [20], or a snapshot of an athlete running [21] or a cup falling off a shelf [22]. Consistent with these studies, Krekelberg *et al.* provide novel evidence that cells in the monkey STS show similar tuning to real motion and implied motion in Glass

patterns. More importantly, the direction selectivity of these neurons appears to reflect the combination of form and motion information. That is, when real motion (e.g. a translating flow field) and implied motion (a translational Glass pattern) were presented transparently but in conflict (i.e. signals of different motion directions) humans and monkeys perceived motion in a compromised direction, and cells in monkey STS altered their direction preference to that of the perceived motion. Previous physiological studies have suggested that orientation-tuned V1 cells complete the first stage of the spatiotemporal integration of the oriented dot pairs in Glass patterns, which mediates the perception of the global structure [23]. It is possible that further analysis of these signals by motion and orientation selective neurons in MT/MST mediates the combination of real motion signals and form cues that imply motion (e.g. motion streaks, oriented dot pairs in Glass patterns).

Conclusions

The integration of form and motion information is crucial for the unified perception of moving objects and for our successful interactions in complex and dynamic environments. Krekelberg *et al.* demonstrate that the direction preference of cells in prototypical motion areas in the monkey brain is (i) influenced by static form cues that imply motion and (ii) reflects the perceived combined motion direction. These results suggest that the unified perception of moving objects is computed during the analysis of their motion in MT/MST. Further questions remain open: Do neurons in MT/MST show similar selectivity to motion-from-form patterns as do ventral areas involved in the analysis of global shape structure? What is the role of feedback from higher areas in the integration of form and motion information in MT/MST? For example, cells in the anterior superior temporal sulcus have been shown to respond more strongly to implied actions than to static postures [24] and parietal regions have been suggested to encode the subjective perception of motion direction in cases of ambiguous motion [25]. The

study of these questions will enhance our understanding of the mechanisms for form and motion coupling at different stages of visual analysis that underlie our perception, decisions and actions.

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