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# Spatial properties of non-retinotopic reference frames in human vision

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ABSTRACT

Many visual attributes of a target stimulus are computed according to dynamic, non-retinotopic reference frames. For example, the motion trajectory of a reflector on a bicycle wheel is perceived as orbital, even though it is in fact cycloidal in retinal, as well as spatial coordinates. We cannot perceive the cycloidal motion because the linear motion of the bike is discounted for. In other words, the linear motion common to all bicycle components serves as a non-retinotopic reference frame, with respect to which the residual (orbital) motion of the reflector is computed. Very little is known about the underlying mechanisms involved in formation and operation of non-retinotopic reference frames. Here, we investigate spatial properties of non-retinotopic reference frames. We show that reference frames are not restricted within the boundaries of moving stimuli but extend over space. By using a variation of the Ternus–Pikler paradigm, we show that the spatial extent of a non-retinotopic reference frame is independent of the size of the inducing elements and the target position near the object boundary. While dynamic reference-frames interact with each other significantly, a static reference-frame has no effect on a dynamic one. The magnitude of interactions between two neighboring dynamic reference-frames increases as the distance between them reduces. Finally, our results indicate that the reference-frame strength is significantly attenuated if the locus of attention is shifted to the elements of the neighboring reference instead of the main reference. We suggest that these results can be conceptualized as reference frames that act and interact as fields.

## 1. Introduction

### 1.1. Retinotopic organization and non-retinotopic processes

The optics of the eye map neighboring points in the environment to neighboring retinal photoreceptors, and these neighborhood relations, known as retinotopic organization, are preserved in early visual cortical areas. Under normal viewing conditions, due to object and observer movements, the stimuli impinging on the retinotopic representations are highly dynamic and unstable. Thus, understanding ecological vision requires an understanding of how visual processes operate under dynamic conditions. Retinotopic theories are not sufficient to explain how clarity of form is achieved in a dynamic environment (Ogmen & Herzog, 2010). Non-retinotopic theories provide an alternative view. Indeed, under dynamic conditions, visual attributes such as form (Ogmen, Otto, & Herzog, 2006), luminance (Shimozaki, Eckstein, & Thomas, 1999), color (Cavanagh, Holcombe, & Chou, 2008; Nishida et al., 2007), size (Kawabe, 2008), and motion (Boi et al., 2009; Cavanagh, Holcombe, & Chou, 2008) are computed according to non-retinotopic reference frames. In the present study, we examine the nature and spatial extent of these non-retinotopic reference frames.

### 1.2. Experimental paradigms for exploring retinotopic vs. non-retinotopic processing

Saccadic Stimulus Presentation Paradigm (SSPP) has been the classical experimental technique to pit retinotopic against non-retinotopic processes (Davidson, Fox, & Dick, 1973; Irwin, 1991; Knapen, Rolfs, & Cavanagh, 2009; McRae, Butler, & Popiel, 1987; Melcher & Colby, 2008; Melcher & Morrone, 2003). In a typical SSPP experiment, two spatially overlapping but temporally separated stimuli are presented to the observers immediately before and after a saccade. Since the respective stimulated retinal regions for the two stimuli are distinct due to the saccadic eye movement, retinotopic processing theories predict no interaction between the respective percepts. Spatiotopic processing theories,

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on the other hand, predict significant interactions as both stimuli share the same region in space. SSPP provides a powerful method for exploring non-retinotopic processing across saccades. However, this paradigm involves eye-movement related processes, such as saccadic suppression and efference copy, and cannot be employed to study non-retinotopic reference frames independent of eye movements.

The Reviewing Paradigm (Kahneman, Treisman, & Gibbs, 1992) is also used to study non-retinotopic processes. This paradigm consists of three successive displays, namely preview field, linking display, and target field. The preview field contains two stationary shapes (a square and a triangle) and two letters displayed within those shapes. During the linking display, the letters disappear while the square and the triangle smoothly move to a different retinotopic location. The target field contains those two shapes, stationary at their final positions, and only one letter displayed within one of the two shapes. The task of the observer is to name the letter shown in the target field as quickly as possible. With this paradigm, one can examine, for example, whether the letters shown in the preview field can modulate responses to letters shown in other retinotopic locations. Kahneman, Treisman, and Gibbs (1992) reported a preview advantage and interpreted this finding as an object-specific integration of information across different retinotopic locations.

An alternative method for exploring non-retinotopic processing is the Ternus–Pikler paradigm, a bistable apparent motion display introduced by Gestalt psychologists about a century ago (Petersik & Rice, 2006; Pikler, 1917; Ternus, 1926). As we discuss in the next section, this paradigm has the advantage of pitting retinotopic and non-retinotopic processes against each other directly. It also provides strong control conditions that can be used to rule out any potential retinotopic artefacts.

## 2. Exploring non-retinotopic processing using the Ternus–Pikler paradigm

### 2.1. Non-retinotopic feature processing

We have modified the Ternus–Pikler paradigm to study non-retinotopic bases of various visual processes (Aydin, Herzog, & Ogmen, 2011a; Boi, Ogmen, & Herzog, 2011a, 2011b; Boi et al., 2009; Noory, Herzog, & Ogmen, 2015; Ogmen, Otto, & Herzog, 2006; Otto, Ogmen, & Herzog, 2008; Scharnowski et al., 2007). Fig. 1 shows the application of the Ternus–Pikler paradigm to study motion processing (Boi et al., 2009). This Ternus–Pikler display includes four frames, each of which contains three disks, separated by ISIs.

Depending upon the ISI, two types of motion are perceived between the Ternus–Pikler disks (Pantle & Picciano, 1976). For long ISIs (e.g., 210 ms) observers perceive the disks to be moving as a group (Fig. 1A: group motion). For short ISIs (e.g., 0 ms) observers perceive the leftmost disk in the first/third frame to be moving to the position of the rightmost disk in the second/fourth frame and vice versa (Fig. 1B: element motion). In the case of element motion, no motion is perceived for the other two disks. Finally, in the no-motion control condition (Fig. 1C: no motion condition), removing the leftmost and the rightmost reference disks in the Ternus–Pikler display frames eliminates perception of both group and element motion, regardless of the ISI. The percept in this case is that of two static or flickering disks. The black dots, depicted inside the Ternus–Pikler disks in Fig. 1, are the probe stimuli for exploring motion perception. A retinotopic hypothesis predicts that the retinotopic proximity will dictate the perceived motion of the dots. Since the retinotopic proximity of subsequently presented dots in the middle disks follows the pattern shown by the arrows in Fig. 1B and C, a purely retinotopic hypothesis predicts perception of up-down and left-right dot motion, regardless of the ISI value. Non-retinotopic hypotheses, however, predict that the perceived dot-motion depends on the perceived motion of the Ternus–Pikler disks. More specifically, the motion of the dots should be computed according to their proximity in a reference frame that moves according to the perceived motion of the Ternus–Pikler disks. In other words, the reference frame should move according to the dashed arrows in Fig. 1A and B. When the Ternus–Pikler disks are perceived to be in element motion (Fig. 1B), the non-retinotopic prediction is the same as the retinotopic prediction (perception of up-down and left-right dot motion). However, when group motion is established between the Ternus–Pikler disks (Fig. 1A), the non-retinotopic prediction for dot motion will be that of a rotation. In other words, non-retinotopic motion grouping based hypothesis predicts that group motion of Ternus–Pikler disks will serve as a non-retinotopic reference leading to the perception of dot rotation in group motion condition. Boi et al.'s results supported the predictions of non-retinotopic reference frame hypothesis.

As another example of how Ternus–Pikler display can be used to probe visual processes, let us consider visual search, in which a target is to be searched among several distractors. Employing the Ternus–Pikler paradigm, Boi et al. (2009) instructed their subjects to visually search for a horizontal green bar among red and green vertical bars (Boi et al., 2009). Orientation and color maps are generally assumed to be retinotopic (e.g., Huang & Pashler, 2007; Treisman & Gelade, 1980; Palmer, 1999, p. 532). The conjunction search task defined by both orientation and color, however, was shown to operate in non-retinotopic reference frames, as subject performance modulated with perceived motion (element or group) of the Ternus–Pikler disks (Fig. 2).

## 3. Rationale of the study

To the best of our knowledge, in all prior studies exploring non-retinotopic visual processing, the targets appeared inside the boundaries of the elements generating their respective non-retinotopic reference frames. However, under normal ecological vision, conditions such as occlusions, similarities between foreground and background luminance and texture dictate that not all targets are seen within the boundaries of a given object. In fact, spatio-temporal grouping, i.e., Gestalt formation, can occur without connectedness and enclosure. Hence, visual attributes such as enclosure and connectedness seem to be insufficient for defining the spatial extent of non-retinotopic reference frames in human vision. In physics, the concept of *field* is used to characterize non-local interactions without direct physical contact. Gestalt psychologists adopted the same concept to explain non-local interactions in perception.

A powerful demonstration of this concept is the biological motion paradigm introduced by Johansson (Johansson, 1973). The light points placed on an invisible walker appear all disconnected, but their perceived motion is organized according to a reference frame that tracks the global motion of the walker. We can also easily demonstrate this effect by modifying the visual search paradigm discussed in Section 2.1. As shown by demos (Video-1, Video-2, and Video-3), the non-retinotopic reference frame induced by the moving disks can influence the perception of targets outside their luminance-defined boundaries.

The goal of this study was to test whether the reference frame is "object-based", i.e., limited within the confines of a reference object, or it extends over space outside the "object". Our results