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Unconscious retinotopic motion processing affects non-retinotopic motion perception

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ABSTRACT

Unconscious visual stimuli can affect conscious perception: For example, an invisible prime can affect responses to a subsequent target. The invisible interpretation of an ambiguous figure can have similar effects. Invisibility in these situations is typically explained by stimulus-suppression in early, retinotopic brain areas. We have previously argued that invisibility is closely linked to Gestalt ("object") organization principles. For example, motion is typically perceived in non-retinotopic, object-centered, and not in retinotopic coordinates. Such is the case for a bicycle-reflector that is perceived as circling, although its retinotopic trajectory is cycloidal. Here, we used a modified Ternus-Pikler display in which, just as in everyday vision, the retinotopic motion is invisible and the non-retinotopic motion is perceived. Nevertheless, the invisible retinotopic motion, can strongly degrade the conscious non-retinotopic motion percept. This effect cannot be explained by inhibition at a retinotopic processing stage.

1. Introduction

Conscious and unconscious perception are usually investigated with experimental techniques such as backward masking (Bachmann, Breitmeyer, & Öğmen, 2007; Bachmann & Francis, 2013; Breitmeyer & Öğmen, 2006), binocular rivalry (Wheatstone, 1838; Blake, 2001), or (continuous) flash suppression (Wolfe, 1984; Tsuchiya & Koch, 2004). Interestingly, even when an element is invisible, it can influence the processing of visible elements. For example, an invisible prime can speed up the responses to an element presented later (Klotz & Wolff, 1995; Klotz & Neumann, 1999; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). Invisibility of the stimulus is usually explained by inhibition between neurons sensitive to the target and neurons sensitive to the mask or the stimuli in the other eye. In line with the organization of the early visual areas in cortex (Wandell, Dumoulin, & Brewer, 2007; Engel, Glover, & Wandell, 1997), inhibition is either explicitly or implicitly assumed to be *retinotopically* organized. For example, in binocular rivalry, neurons processing information originating from the left and right eye mutually suppress each other, by each inhibiting the neuron of the other eye coding for the same position in the visual field (Blake, 1989; however, see Leopold & Logothetis, 1996, Kovacs, Papathomas, Yang, & Fehér, 1996).

In ambiguous figures, one of two rivaling interpretations is perceived. For example, in Rubin's vase, the silhouette of either a goblet or two faces is perceived, depending on which one is interpreted as figure and which one as ground. Unlike in masking and

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rivalry, all elements of the display are fully visible, but one *interpretation* is suppressed. As in masking, the suppressed interpretation of the image can influence stimuli presented later (e.g., Peterson & Kim, 2001; Peterson & Skow, 2008). Also for ambiguous figures, retinotopic inhibition may explain why stimuli or interpretations are invisible, for example, by mutual inhibition of boundary-ownership neurons in V2 (Zhou, Friedman, & von der Heydt, 2000; Zhaoping, 2005).

Perception is usually *non-retinotopic* (Öğmen & Herzog, 2010). The parts of a moving object are perceived relative to the object, rather than in retinal coordinates (Duncker, 1929; Johansson, 1950, 1974, 1976; Clarke, Öğmen, & Herzog, 2016; Ağaoğlu, Clarke, Herzog, & Öğmen, 2016). For example, the reflector on the wheel of a bicycle is perceived to rotate, although its motion is cycloidal in retinotopic coordinates. The horizontal bicycle motion is discounted from the cycloidal retinotopic motion of the reflector, leading to a circular motion percept. Only the circular non-retinotopic reflector motion is perceived consciously, whereas the cycloidal retinotopic motion is invisible. Similar to ambiguous figures, all elements are visible, only one interpretation is suppressed (Herzog, Hermens, & Öğmen, 2014). Obviously, the percept cannot be explained exclusively by retinotopic inhibition because it depends on non-retinotopic information. Almost nothing is known about the unconscious processing of invisible retinotopic motion and its influences on the consciously perceived non-retinotopic motion. Here, we used an adapted version of the Ternus-Pikler display (Ternus, 1926; Pikler, 1917). In the Ternus-Pikler display, two disks are briefly presented on a computer screen and reappear after an inter-stimulus interval (ISI). The disks are perceived to flicker on and off in the same positions (*no motion*). Next, a third disk is added alternately to the left or right. When the ISI is very brief (e.g., 0 ms) the third disk appears to jump from the left to right of the two stationary disks and so on (*element motion*). However, when the ISI is long (e.g., 200 ms), the three disks form a perceptual group and all three disks appear to shift left and right in concert (*group motion*).

In past experiments (e.g., Boi, Öğmen, Krummenacher, Otto, & Herzog, 2009), we used this effect to study non-retinotopic motion perception. We added a white dot to each disk, that we repositioned from frame to frame (Fig. 1a). The observer's gaze was focused on a central fixation point and an eye tracker controlled that no eye movements were made. Hence, the stimulus positions were the same in screen based and retinotopic coordinates. We chose the dot positions, so that when no motion or element motion was perceived, the dots in the two stationary disks appeared to move up-down and left-right, respectively (*retinotopic dot motion percept;* Fig. 1a left and Movie 1). However, when group motion was perceived, the dot in the middle disk was perceived to rotate (*non-retinotopic dot motion percept;* Fig. 1a right and Movie 2). This dot rotation percept is *non-retinotopic*, because it can only be perceived in disk-centered coordinates; in retinotopic coordinates, the dots still move linearly up-down and left-right.

Interestingly, the perceptions of retinotopic and non-retinotopic dot motion are mutually exclusive: When two stationary disks are presented, the retinotopic dot motion is perceived, and the non-retinotopic dot motion is invisible. When the three disks in group motion are presented, the non-retinotopic dot motion is perceived, and the retinotopic dot motion is invisible. In both cases, the stimulus is identical on the screen and in retinotopic coordinates, except for the third disk. In both cases, the disks and dots are fully visible. Hence, the retinotopic dot motion does not become invisible because retinotopic information is suppressed, but because the addition of the third disk changes how the stimulus is grouped and interpreted. Here, we show that unconscious processing of the retinotopic motion strongly affects the conscious perception of non-retinotopic motion.

2. Experiment 1a: Interactions between retinotopic and non-retinotopic motions

In Experiment 1a, we chose the positions of the white dots so that a dot rotation was perceived in both the retinotopic and non-retinotopic interpretations of the display (cf. Fig. 1b). When two disks were presented, retinotopic dot rotation was perceived in the left disk, while the dot in the right disk jumped left-and-right or up-and-down every second frame (Fig. 1b left and Movie 3). When the third disk was added, non-retinotopic dot rotation was perceived in the middle disk, and the dots in the outer disks jumped left-and-right or up-and-down every second frame (Fig. 1b right and Movie 4). The dot positions were identical in both cases, except that a third disk and dot were added. The retinotopic and non-retinotopic dot rotations could either be in the same direction (*congruent* rotation, e.g., both clockwise; Movie 5) or in opposite directions (*incongruent* rotation; e.g., retinotopic clockwise and non-retinotopic counter-clockwise; Movie 6). The observers were asked to report either the retinotopic or non-retinotopic rotation direction (clockwise/counter-clockwise).

To test the influence of the retinotopic rotation on the non-retinotopic percept we presented three disks and had observers report the non-retinotopic rotation direction. We then compared performance between trials in which the retinotopic rotation was in the same (Movie 5) versus the opposite direction of the non-retinotopic rotation (Movie 6). We hypothesized that incongruent retinotopic rotation might impair the non-retinotopic rotation percept, whereas congruent retinotopic rotation might facilitate it. As a baseline condition, we first presented a Ternus-Pikler display with only a non-retinotopic dot-rotation in the middle disk, but no dots in the flanking disks (Movie 7). To determine whether the influences on non-retinotopic motion are specific to the motion type, i.e., to determine whether the non-retinotopic rotation percept is modulated by retinotopic *rotation* rather than the mere presence of retinotopic dot motions per se, we included control conditions in which the retinotopic dot motions were linear (up-down or left-right; Fig. 1a and Movies 1–2) or random (Movie 8).

2.1. Methods

2.1.1. Observers

Sixteen naïve observers took part in the experiment, but three observers were excluded from the analysis due to inferior performance in the baseline condition (60% correct responses or less). Three other observers were excluded because they were unable to maintain stable central fixation. Hence, 10 observers were available for analysis (mean age = 23.3 years, *SD* = 2.3 years, 5 female, 1