Non-retinotopic Adaptive Center-Surround Modulation in Motion Processing

Boris Peñaloza[1], Michael H. Herzog[2], Haluk Öğmen[1,*]

[1] *Perceptual and Cognitive Dynamics Laboratory, Department of Electrical & Computer Engineering, University of Denver, Denver, CO 80208, USA.*

[2] *Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland.*

[*] *Corresponding author. Email: ogmen@du.edu*

Abstract

The early visual system is organized retinotopically. However, under ecological viewing conditions, motion perception occurs in non-retinotopic coordinates. Even though many studies revealed the central role of non-retinotopic processes, very little is known about their mechanisms and neural correlates. Tadin and colleagues found that increasing the spatial size of a high-contrast drifting-Gabor deteriorates motion-direction discrimination, whereas the opposite occurs with a low-contrast stimulus. The results were proposed to reflect an adaptive center-surround antagonism, whereby at low-contrast the excitatory center dominates whereas at high-contrast suppressive-surround mechanisms become more effective. Because ecological vision is non-retinotopic, we tested the hypothesis that the non-retinotopic system also processes motion information by means of an adaptive center-surround mechanism. We used the Ternus-Pikler display designed to provide either a retinotopic or a non-retinotopic reference-frame. Our results suggest that the non-retinotopic processes underlying motion perception are also mediated by an adaptive center-surround mechanism.

Keywords: Motion perception, motion detection, reference-frames, non-retinotopic processes, adaptive center-surround mechanisms, ecological vision

1. Introduction

The early visual system is organized retinotopically i.e., neighboring points in the visual field are mapped onto neighboring photoreceptors in the retina. This *retinotopic* encoding principle is maintained in the early visual areas. However, motion perception occurs usually in *non-retinotopic coordinates*. For example, consider the perceived trajectory of a reflector located on the wheel of a moving bicycle. With eyes fixed, the reflector's motion on the retina is a curtate cycloid (Fig. 1A). However, perceptually, the reflector appears to move on a circular orbit (Fig. 1B) because the horizontal motion of the bicycle is subtracted from the curtate motion. The curtate cycloid is invisible (but can still influence decisions, Lauffs et al., 2018). Likewise, Öğmen et. al. (2006), Otto et. al. (2006) and Boi et. al. (2009) showed that perception of *form* and *motion* is influenced not only by retinotopic stimulation but also by the establishment of perceptual groups. Perceptual groups as well as perceptually organized form (Tadin, Lappin, Blake, & Grossman, 2002) establish reference-frames in which motion is computed. Even though the importance of non-retinotopic processes in motion perception has been established (e.g., Johansson, 1973, 1974; Pikler, 1917; Ternus, 1926), very little is known about the neural mechanisms that mediate them.

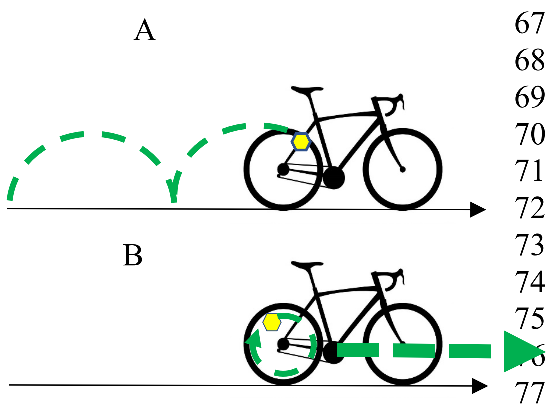

Figure 1. When the eyes are fixed, the yellow reflector on the rear wheel of the bicycle traverses a curtate cycloid trajectory as shown in (A). Hence, the perceived trajectory of the reflector should be a curtate cycloid if perception were to follow retinotopic coordinates. However, as shown in (B), the perceived trajectory of the reflector is circular. Thus, we perceive the reflector relative to the horizontal motion of the bicycle, i.e., according to a non-retinotopic reference-frame set by the horizontal motion of the bicycle.

Using a drifting Gabor, Tadin and colleagues (Tadin, Lappin, Gilroy, & Blake, 2003) demonstrated that increasing the spatial size of a high-contrast stimulus renders the discrimination of motion-direction more difficult. The opposite effect occurs with a low-contrast stimulus. The authors proposed that this is a perceptual correlate of a center-surround antagonism, whereby highly visible objects are processed by a *spatial suppressive mechanism* and weak low-contrast sensory inputs are processed by a *spatial summation mechanism*. In other words, the interaction between size and contrast may be explained by an *adaptive center-surround mechanism*. Tadin et. al.'s (2003) experimental design did not distinguish between retinotopic and non-retinotopic processes. The goal of this study was to use the Ternus-Pikler display to test the hypothesis that similar adaptive center-surround mechanisms operate in non-retinotopic coordinates. This generalization is of interest because, as mentioned above, motion perception in natural environments is essentially non-retinotopic.

The Ternus-Pikler display (Pikler, 1917; Ternus, 1926)[1] is an experimental paradigm that offers the possibility to pit against each other retinotopic and non-retinotopic reference frames. A

[1] There are extensive studies examining how various stimulus parameters affect the perceived motion in Ternus-Pikler displays (e.g., Pantle & Picciano, 1976; Pantle & Petersik, 1980; Breitmeyer & Ritter, 1986; Dawson & Wright, 1994; He & Ooi, 1999; Kramer & Rudd, 1999; Scott-Samuel & Hess, 2001; Alais & Lorenceau, 2002; Hein & Moore, 2012; review: Petersik & Rice, 2006).

conventional Ternus-Pikler display consists of three elements that are spatially shifted by one inter-element distance from frame to frame (Fig. 2). Depending on the Inter-Stimulus Interval (ISI) between frames, two different percepts occur (Pantle & Picciano, 1976): Element motion for short ISIs (0 ms in this experiment) or group motion for long ISIs (266 ms in this experiment).

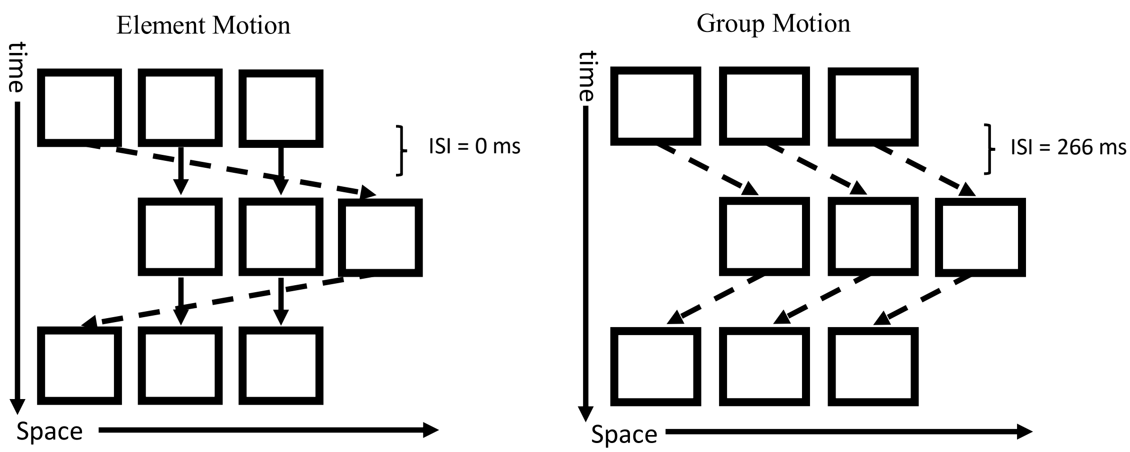

Figure 2. The Ternus-Pikler display. The conventional Ternus-Pikler display consists of three elements that are spatially shifted by one inter-element distance from frame to frame. Depending on the time interval between frames (ISIs), two different percepts are obtained: Element motion (left panel) and Group motion (right panel). In the ***Element Motion (0ms ISI):*** *the two central elements are perceived as stationary (indicated by the solid lines) while the outermost squares are perceived to alternate from left to right (dashed line).* ***Group*** Motion *(266ms): all three squares appear to move in tandem as a group from left to right (dashed lines).*

When *element motion* prevails, the two central elements are perceived as stationary (indicated by the solid lines in Fig. 2), while the outermost elements are perceived to move back and forth from left to right (dashed line in Fig. 2). In the *group motion* percept, the elements appear to move in tandem from left to right in a trajectory indicated by the dashed lines in Fig. 2.

To test the hypothesis of this study, we used a modified version of the Ternus-Pikler display. We embedded Gabor patches inside the squares that make up the Ternus-Pikler display and varied the spatial size and the contrast of the Gabor patches. We measured phase-shift thresholds for discrimination of motion-direction in retinotopic and non-retinotopic tasks.

2. General Methods

2.1 Participants

Six observers (6 males) including one of the authors participated in this study. The same observers participated in all experiments. Participant's age ranged from 23 to 35 years and all participants had normal or corrected-to-normal vision. Experiments followed a protocol approved by the University of Denver Institutional Review Board for the Protection of Human Subjects. Each observer gave written consent before the experiments.

2.2 Apparatus

Observers viewed the stimulus on a NANAO F2-21 monitor driven by a ViSaGe card (Cambridge Research Systems). The stimulus was displayed at a resolution of 1280 x 960 with a refresh rate of 60 Hz. The background luminance was set to 30.5 cd/m^2 as measured with a Minolta (LS-110) luminance meter. The room was dimly illuminated. A head/chin rest was used. Observers reported their responses by pressing the arrow keys of a keyboard. The viewing distance was set to 1.07 m.

2.3 Stimuli

Our version of the Ternus-Pikler display consisted of three drifting Gabor patches embedded in black square frames. The square width and length was set to 4.5 degrees of visual angle (deg). The square lines had a thickness of 0.15 deg. The horizontal center-to-center separation of the Ternus-Pikler squares was 5 deg. The spatial frequency of the Gabor elements was fixed to 1 cpd. In all experimental conditions, the size of the Gabor patch was 2σ, where σ is the standard deviation of the stationary Gaussian envelope that windowed a vertical sine grating. The contrast varied from 2.8% to 90% Michelson contrast.

Motion correspondences in the Ternus-Pikler display establish a reference frame underlying computations of form, motion, etc. (Öğmen & Herzog, 2010). In the element motion condition (Fig. 2 left), the central elements are perceived at their retinotopic positions (depicted by solid arrows) and hence any stimulus positioned in these elements is processed following a *retinotopic* reference frame. In group motion, all three elements are perceived to move left-and-right in tandem, thereby establishing a *non-retinotopic* reference frame depicted by dashed arrows in Fig. 2 right. In sum, the Ternus-Pikler display generates retinotopic (element motion, solid arrows in Fig. 2 left) and non-retinotopic (group motion, dashed arrows in Fig. 2 right) reference frames. We embedded Gabor patches in the Ternus-Pikler display elements (Fig. 3) and the observers' task was to report the drift direction (up or down) of Gabor patches. The drift of the Gabor was implemented by adding a coherent spatial phase-shift from frame to frame (integer multiples of δ; see Fig. 3).

This phase-shift can be added according to retinotopic or non-retinotopic coordinates. Adding a spatial phase-shift according to retinotopic coordinates means that the phase-shift is added to a Gabor that remained in the same spatial (retinotopic) position from frame-to-frame (Fig. 3A and 3B). As shown by solid arrows in Fig. 2A, there are two such possible cases. Here we used the case that starts with the *central* element of the first frame (see the yellow arrows in Fig. 3A). A spatial phase-shift according to non-retinotopic coordinates means that the phase-shift was added from frame-to-frame to Gabors at different spatial (retinotopic) positions following the non-retinotopic reference frame shown by dashed arrows in Fig. 2B. Among the three possible choices, we used the case that starts with the *central* element of the first frame (see the yellow arrows in Fig. 3D).

Hence, we obtained a 2x2 design, with reference frame as one factor with two levels (retinotopic, non-retinotopic) and Gabor drift as the other factor with two levels (retinotopic, non-retinotopic) as shown in Figure 3. The arrows in the display indicate the *perceived* motion correspondences of the Ternus-Pikler elements (the squares) from frame to frame. The rest of the pathways in the displays were filled with mainly ambiguous motion, i.e. whenever possible we added 180° phase-shifts from frame to frame (shown in red). The purpose of this was to eliminate the possibility of participants picking up motion signals from pathways other than the one containing the coherent drift information. This was empirically verified through a control experiment.

2.4 General Procedures

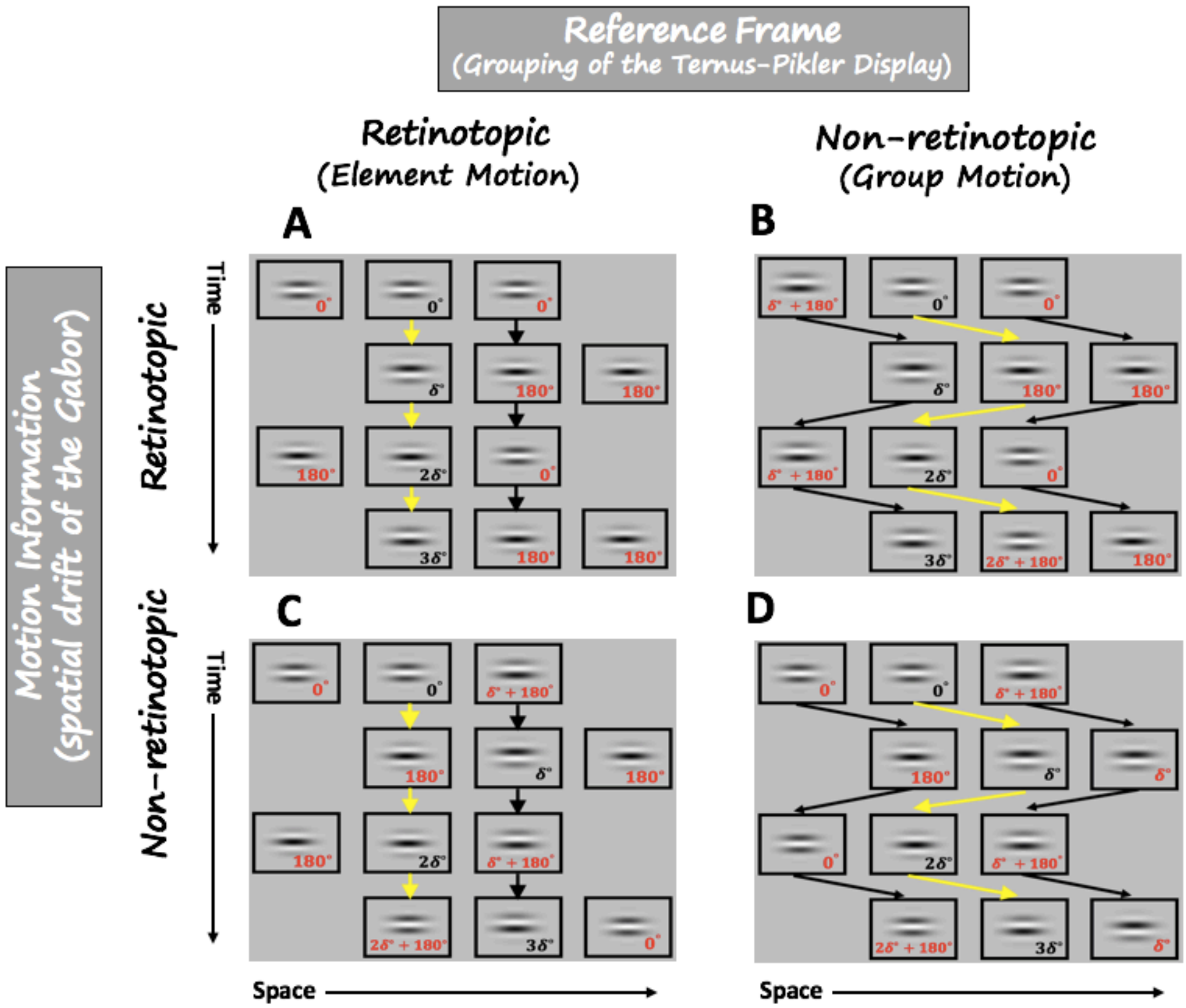

Figure 3. Schematic of the 2x2 factorial design. The left column (panels A and C) shows the Element-motion condition (i.e., retinotopic reference-frame, ISI = 0 ms) with retinotopic (panel A) and non-retinotopic (panel C) drift-information, respectively. In these two conditions, the central elements of the display appear to be stationary indicated by the yellow and black arrows. Note that in the retinotopic reference-frame and retinotopic drift condition (panel A), coherent phase-drift (represented by integer multiples of δ) is placed in the same retinotopic location whereas for the retinotopic reference-frame and non-retinotopic drift condition (C), coherent phase-shift is in non-retinotopic coordinates (the integer multiples of δ shown in black bold font). The right column (panels B and D) represents the Group-motion condition (i.e., non-retinotopic reference-frame, ISI = 266.67 ms) with retinotopic (panel B) and non-retinotopic (panel D) drift. In these two conditions, the Ternus-Pikler elements(rectangular frames) appear to move in tandem in a trajectory indicated by the black and yellow arrows. As before, coherent phase-shift δ is placed in either retinotopic (B) or non-retinotopic coordinates (D).

At the beginning of each session, participants were adapted for 4 minutes to the background luminance of the display. Each trial started with a fixation cross in the middle of the screen presented for 1000-ms. After that, the stimulus sequence was presented. The stimulus sequence consisted of 4 Ternus-Pikler frames (Fig. 3) each displayed for 133.33-ms. Between these frames, a blank screen was shown for an Inter Stimulus Interval (ISI) duration of either 266.67 (group motion) or 0 ms (element motion). After stimulus presentation, a blank screen appeared until observer's response. Throughout the experiment observers were instructed to attend to one of the Gabor elements of the display (indicated by the yellow arrows in Fig. 3) while maintaining fixation on the center of the screen. The *task* was to report the perceived direction of drift (upward/downward) of the attended Gabor element as accurately as possible by pressing the up or down arrows of the keyboard. The next trial started 1000 ms after the observer gave a response.

We measured the *threshold phase-shift* δ, required for the observers to accurately identify the motion direction of the drifting Gabor stimulus. The threshold was set to 80% correct performance. We used the Quest+ adaptive method (Watson, 2017) to obtain the thresholds. Data was fitted with a Weibull function. The lapse level was fixed to 0.01. In some experimental conditions, observers were at chance and never reached 80% accuracy. In those cases, we report % correct performance. As the focus of our study was primarily on measuring performance *changes* as a function of contrast and size rather than identifying optimal performance, we did not provide feedback to the participants.

One important observation is the potential interference of eye movements with non-retinotopic processing. For example, if subjects follow the non-retinotopic stimulus with eye movements by foveating it, the non-retinotopic stimuli will be projected at a retinotopically fixed position (fovea) even though it occupies different spatial positions in the external world. In several previous studies (Boi, Ogmen, & Herzog, 2011; Boi, Ogmen, Krummenacher, Otto, & Herzog, 2009; Lauffs, Choung, Öğmen, & Herzog, 2018; Lauffs, Choung, Öğmen, Herzog, & Kerzel, 2019; Lauffs, Öğmen, & Herzog, 2017; Thunell, van der Zwaag, Ögmen, Plomp, & Herzog, 2016) we addressed this point in detail by measuring directly eye movements during experiments using the Ternus-Pikler display. The results showed that observers can and indeed do maintain a steady fixation with negligible eye movements. Thus, we have strong experimental evidence that eye movements do not play a role in perceptual effects associated with the Ternus-Pikler displays.

An experimental block consisted of 51 trials. The direction of drift was randomized across trials. During a given session, the order of experimental condition and the combination of Gabor patch-width and contrast level were randomized. Each observer ran a total of 165 blocks. Typically, a block was completed in about 1.5 minutes, which resulted in approximately 6 sessions of 40 minutes each.

3. Experiments, Their Rationales and Predictions

As discussed above and as depicted in Fig. 3, depending on the match between the reference frame (retinotopic/element-motion or non-retinotopic/group-motion) and the placement of the coherent drift information δ (placed in either retinotopic or non-retinotopic coordinates), four main experimental conditions are generated.

Condition 1: Retinotopic reference-frame and retinotopic drift-information (Fig. 3A): In this condition, the element-motion percept establishes a retinotopic reference-frame and the coherent drift-information (represented by integer multiples of δ) is added in retinotopic coordinates. Thus, there is a *match between the reference-frame and the drift information*, both in retinotopic coordinates similar to the design of Tadin et al. (2003). Therefore, for high-contrast Gabors we expect a decrease in performance as a function of size whereas for a low-contrast stimulus we expect an improvement in performance.

Condition 2: Non-retinotopic reference-frame and retinotopic drift-information (Fig. 3B): Here, group-motion establishes a non-retinotopic reference-frame (depicted by the black and yellow arrows in Fig. 3B), whereas the drift direction is perceived retinotopically. Hence, in this case, there is a *mismatch between the reference frame and the drift information*. Because of this mismatch, we predict that observers will not reach the threshold level set at 80% correct. In fact, their performance should be about chance level (50% correct).

Condition 3: Retinotopic reference-frame and non-retinotopic drift-information (Fig. 3C): The outermost elements are perceived to move on the trajectory shown by the black dashed lines in Fig 3C, whereas the central elements are perceived as stationary. Drift information is added in non-retinotopic coordinates. Based on the *mismatch* between the reference frame and the drift information, as in the previous case, we predict that observers will be at chance.

Condition 4: Non-retinotopic reference-frame and non-retinotopic drift-information (Fig. 4): In this condition, the reference-frame is non-retinotopic and the drift information is added in non-retinotopic coordinates. Hence, there is a *match* between the reference-frame and the drift information. Here we will test the main hypothesis of the study: If indeed, adaptive center-surround mechanisms, as observed by Tadin et al. (2003) is general, we expect to replicate their results not only when there is a match in retinotopic coordinates (Condition 1), but also when there is a match in non-retinotopic coordinates. Accordingly, similar to Condition 1, we expect to observe a decrease in performance with size for high-contrast stimuli and an increase in performance for low-contrast stimuli. Preliminary pilot data showed that the lowest contrast value to perform the non-retinotopic task of Condition 4 above chance level was 5.5%. Therefore, in order to keep consistency in the stimulus parameters, we used this minimum value for *all experiments* except for Condition 1, where we set the low-contrast value to 2.8% in order to match closely the parameters used by Tadin et. al. (2003) in his experiment.

In all these experiments, in order to measure how observers perceive stimuli according to different reference-frames, observers were asked to attend to an element according to the reference-frame prevailing for that condition. Hence, in Conditions 1 and 3 observers attended to a retinotopic location (see the yellow arrows in Figures 4 and 7), whereas in Conditions 2 and 4 they attended along the non-retinotopic pathway (see the yellow arrows in Figures 6 and 8). It may be also of interest to ask what happens if the observers' attention is directed to an element outside the reference frame. We studied the dissociation between attention and the reference frame in Lauffs, Choung, Öğmen, Herzog, & Kerzel (2019). That study showed that, whereas tracking by focal attention can generate an attention-based reference-frame, the effect is rather small compared with reference-frames generated by motion-based grouping, as in Ternus-Pikler displays. Hence, in the experiments reported in this paper, attention and reference-frame were congruent in order to generate strong effects upon which we could investigate center-surround modulation effects.

Control Condition: No Ternus-Pikler motion (Fig. 11): Across all experiments, the path along which the drift information is introduced has only integer multiples of δ from frame to frame. Other task-irrelevant paths contain mainly ambiguous motion (180^o phase shift), but there are still some frames containing multiples of δ. For example, consider the phase shifts added to the Gabors placed in the left-square of the display in Fig. 11A. The phase shift from the first frame to the second frame (from 0^o to 180^o) is ambiguous, since it is equally likely to result from an upward or downward drift. Similarly, the transition from the third to the fourth frame is ambiguous (from 2δ to $2\delta + 180^o$). However, the transition from the second to the third frame (from 180^o to 2δ) is not ambiguous and observers may be able to use the transition in this frame alone to determine the direction of drift. To test the possibility that this "artefactual drift information" can be used effectively, we ran a control condition in which we removed the leftmost and rightmost elements of the Ternus-Pikler display as depicted in Figure 11A. If observers are at chance in this experiment, it indicates that the artefactual drift information (e.g., in the transition from the second to the third frame) is not sufficient to accomplish the task. This could be simply due to the fact that this transition is temporally preceded and succeeded by ambiguous counter-phase (180^o) frames. On the other hand, if observers' performance turns out to be above chance in this experiment, this would necessitate a redesign of how phase-shift information is placed in the Ternus-Pikler display so that sufficient drift information exists *only* in the paths tested in specific experiments. Since the interpretation of Conditions 1 to 4 assume that observers will be at chance in this control condition, we ran this condition first to test this fundamental hypothesis.

The demos included with this manuscript illustrate each of these stimuli.

4. Results

4.1 Experiment 1. *Condition 1:* Retinotopic reference-frame and retinotopic drift-information:

4.1.1 Procedure

In this condition we evaluated two contrast values (2.8% and 90%) for each Gabor patch size (0.6, 1.4, and 2.7 deg) matching the values in Tadin et. al. (2003). Observers were instructed to fixate on a fixation cross placed in the middle of the screen for 1000 ms and to *attend* to the element marked with the yellow arrow in Figure 4A.

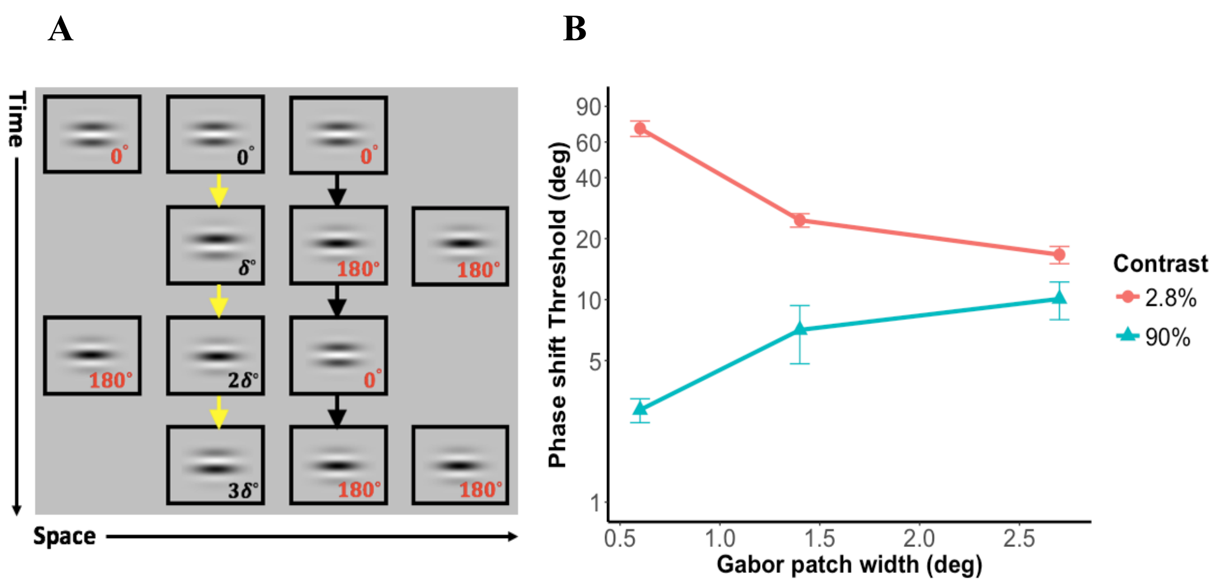

Figure 4: (A) Stimulus for the retinotopic reference-frame and retinotopic drift information condition. The arrows represent the perceived trajectory of the Ternus-Pikler elements (squares) across frames. In this case the two central elements are perceived as stationary. The yellow arrow highlights the element to be attended in the display (the yellow arrows were not displayed in the actual stimulus; see demos). Coherent phase-shift is represented by successive integer multiples of **δ** *across frames. The rest of the pathways contained mainly ambiguous motion. (B) Results: Effect of contrast on phase-shift threshold as a function of Gabor patch size. The data represent the average phase-shift threshold across observers (N=6) for low and a high-contrast Gabors. Error bars are ± S.E.M.*

4.1.2 Results and discussion

A two-way repeated-measures ANOVA (Greenhouse-Geisser corrected where appropriate) showed a statistically significant main effect of size (F(1.1, 5.5), $p = 0.001$, $\eta_p = 0.89$) and contrast ((F(1, 5), $p < 0.001$, $\eta_p = 0.93$)). Likewise, there was a statistically significant interaction between size and contrast ((F(2, 10), $p < 0.001$, $\eta_p = 0.97$)). For the low-contrast stimulus, thresholds decreased with increasing patch size suggesting that a *spatial summation mechanism is at work* known to occur for low contrast stimuli (Anderson & Burr, 1991; Kapadia, Westheimer, & Gilbert, 1999; Watson & Turano, 1995). To the contrary, for the high-contrast stimulus, thresholds increased as stimulus size increased. This effect is consistent with a *spatial suppression mechanism* (Tadin et al., 2006, 2003; Tadin & Lappin, 2005, 2012).

For comparison purposes, in Fig. 5 we plot the average data from Tadin's study (dashed lines) alongside our results (solid lines) for the three stimulus sizes. The data from the two studies are similar, even though there were differences in the stimuli. For instance, in Tadin's experiment, observers identified the motion direction of a Gabor patch that abruptly shifted in phase in the middle of a 100 ms presentation interval. Whereas in our study, the stimulus was more complex, containing multiple squares and Gabors, of which observers had to attend to one. The Ternus-Pikler display introduces additional motion compared to Tadin et al's stimulus. The squares used as part of the Ternus-Pikler display provide a strong horizontal motion signal thereby making the resulting reference-frame salient. To test that our results hold even in the absence of these squares, we ran a control experiment on one subject and obtained similar results (see Appendix A). Overall this experiment replicated Tadin et. al.'s (2003; Fig. 3a) results in the Ternus-Pikler stimulus.

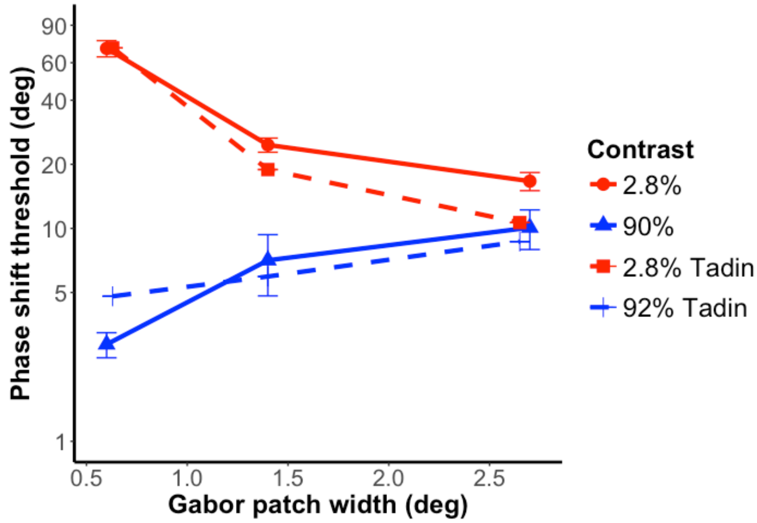

Figure 5: Comparison of Tadin's data (Tadin et al, 2003; Fig. 3a) with the results of our Experiment 1. Solid lines represent the results of Experiment 1 while dashed lines show Tadin's data. Red lines correspond to the low-contrast stimulus and blue lines represent high-contrast stimulus. Error bars are ± S.E.M.

4.2 Experiment 2. *Condition 2:* Non-retinotopic reference-frame and retinotopic drift-information:

4.2.1 Procedure

Observers were instructed to fixate on a fixation cross placed in the middle of the screen for 1000-ms at the beginning of each trial and to attend to the central element of the display (yellow arrow in Fig. 6A). In this condition two contrast values (5.5% and 90%) and three Gabor patch sizes were tested.

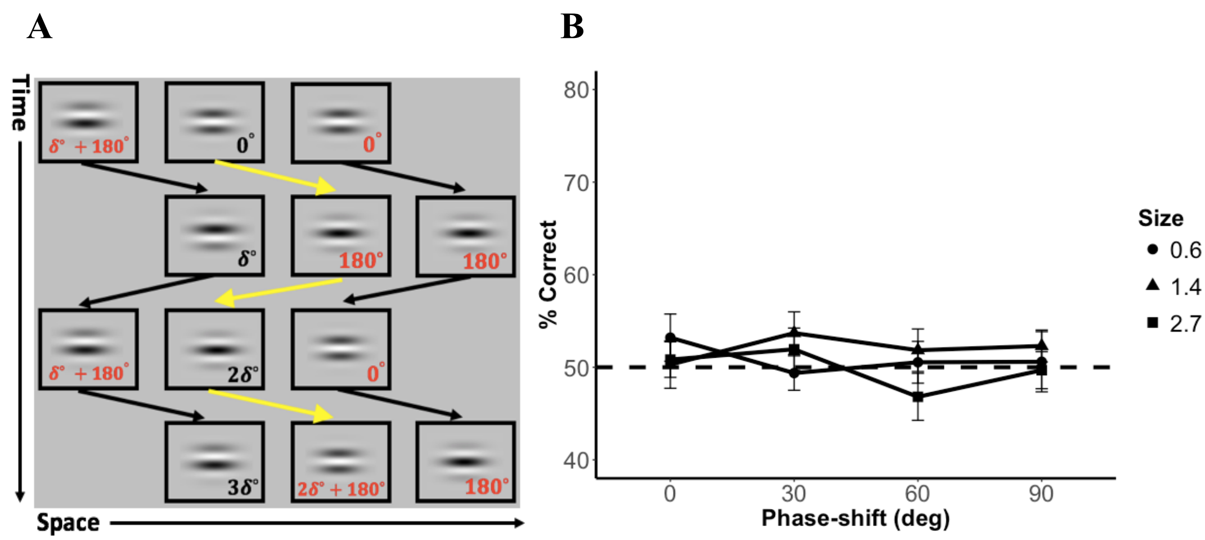

Figure 6: (A) In the group motion percept the three elements appear to move from left to right in a trajectory marked by the black and yellow arrows . The yellow arrows highlight the element to be attended in the display. Coherent phase-shift is inserted in retinotopic coordinates (follow the successive integer multiple values of **δ** *across frames). The rest of the motion pathways contained mainly ambiguous motion. (B) Results: Observers were at chance level regardless of stimulus contrast and size. Panel B shows the psychometric functions averaged across observers (N=6) for a stimulus set to 90% contrast (see Appendix for the low-contrast results). Error bars are ± S.E.M.*

4.2.2 Results and discussion

It could be argued that, even though the Ternus-Pikler display establishes a non-retinotopic reference-frame, the drift information could be read out from retinotopic coordinates. For instance, by inspecting Fig. 6A, it can be noted that drift information in retinotopic coordinates may be used by the participants to make a decision on the task. Nevertheless, the results in Fig. 6B show that regardless of phase-shift magnitude (δ) the observers were at chance performance. Participants' anecdotal reports after the experiment stated that the task was impossible to perform. This was the case *regardless* of contrast or size. The data in Fig. 6B show the high contrast data. The plot for the low-contrast case can be found in the Appendix. The reason for the poor performance is that in the group motion percept the feature attributes of the elements in one frame of the display are perceptually linked with the elements of subsequent frames in a manner highlighted by the arrows in Fig. 6A. Thus, if the trajectory of the yellow arrow in Fig. 6A is followed, it can be seen that it possesses mostly ambiguous motion which then explains the performance. In total, this result shows that information put in retinotopic coordinates does not inform motion direction when the reference system is non-retinotopic.

4.3 Experiment 3. *Condition 3:* Retinotopic reference-frame and non-retinotopic drift-information

4.3.1 Procedure

Fig. 7A shows the stimuli for Experiment 3. In this case, multiples of are added in non-retinotopic locations whereas the element-motion percept establishes a retinotopic reference-frame. Observers were asked to attend to the central element in the display marked by the yellow arrow in Fig. 7A while maintaining fixation in the center of the display on a fixation cross that appeared for 1000-ms at the beginning of each trial. Once again, we evaluated two contrast values (5.5% and 90%) for each of the three Gabor patch sizes.

4.3.2 Results and discussion

From Fig. 7B it is clear that observers in the high contrast conditions are at chance level in this experiment. The results for the low-contrast conditions also show chance performance (Appendix B).

This result and the result of the previous experiment indicate that a match between the reference frame and the motion information is essential for detecting the direction of motion. In addition, comparing this stimulus to that in Experiment 5 (cf. Figs 7A and 11A), one can see that adding or removing the outermost Ternus-Pikler elements (squares) do not influence how motion is perceived since the same retinotopic reference-frame is maintained in both stimuli.

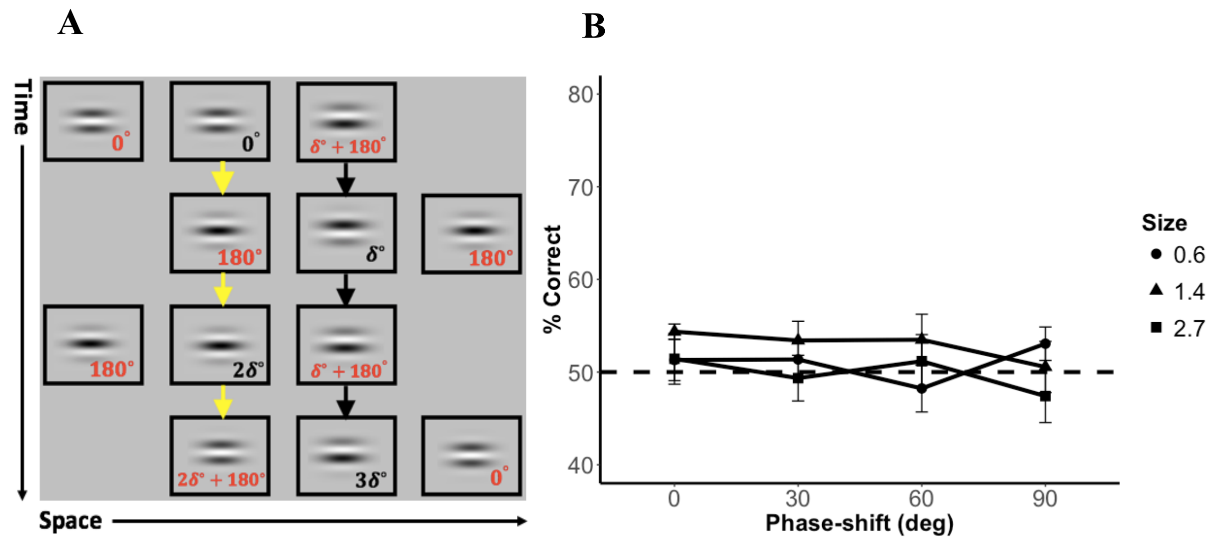

*Figure 7: (A) Stimulus for the retinotopic reference-frame and non-retinotopic drift information condition. The display configuration is similar to the control condition, but this time the outermost element of the Ternus-Pikler display were included. This configuration of the Ternus-Pikler display only allows the formation of retinotopic representations (regardless of ISI). Motion information is inserted in non-retinotopic coordinates while perception is established in a retinotopic reference system. Observers were instructed to attend to the element highlighted with the yellow arrow and to report the perceived direction of drift. (B) Results: Average percent correct across observers (N=6) is shown as a function of phase-shift **δ** value. The data come from the 90% contrast stimulus evaluated at all sizes. As predicted, the result shows that observers were at chance performance. Error bars are ±S.E.M.*

4.4 Experiment 4: *Condition 4:* Non-retinotopic reference-frame and non-retinotopic drift information

4.4.1 Procedure

A schematic of the stimulus is depicted in Fig. 8A. This time both the reference frame and the coherent phase-shift for motion drift are in non-retinotopic coordinates. That is, the motion correspondences of the elements in the display coincide with the placement of integer multiples of δ values, that together create a coherent drift along non-retinotopic coordinates. Based on previous studies (Agaoglu et. al., 2017; Boi et. al., 2009; Clarke & Herzog, 2013; Clarke et. al., 2015; Grossberg et. al., 2011) and based on the theoretical concept of reference-frame match, we expected that observers will be able to extract this non-retinotopic drift information and perform at a higher than chance level on the experiment.

As in the other conditions, observers were instructed to fixate on a fixation cross located in the center of the screen for 1000-ms at the beginning of each trial and to attend to the central element in the Ternus-Pikler display (yellow arrows in Fig. 8A). In order to capture a transition from spatial suppression to spatial summation, if it exists, five contrast values ranging from low to high were tested (5.5%, 9.16%, 15%, 55%, and 90%).

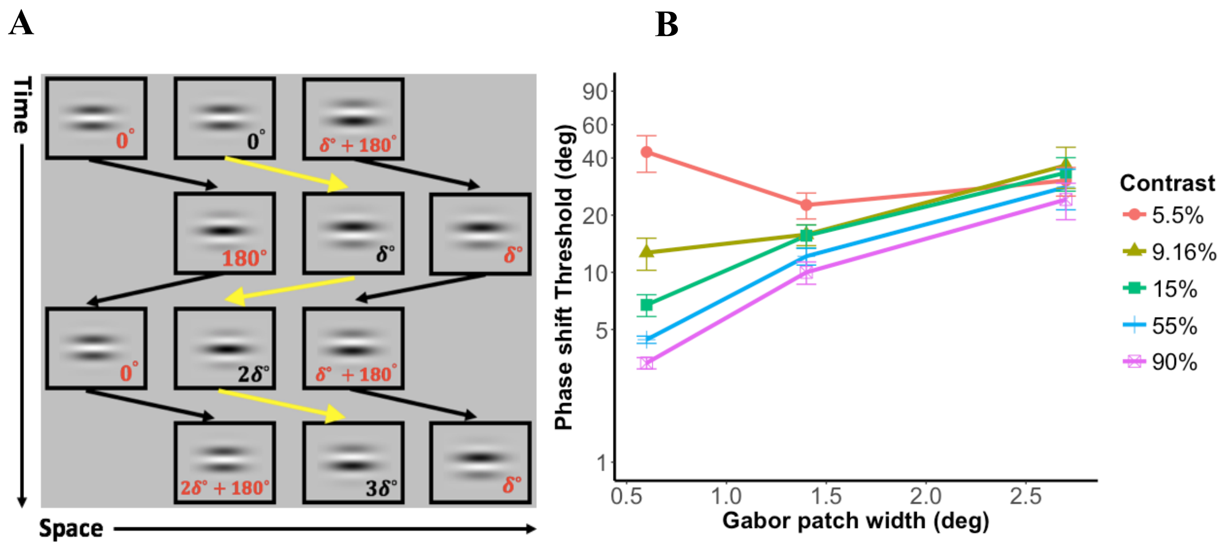

Figure 8: (A) Stimulus for the non-retinotopic reference-frame and non-retinotopic drift information condition. There is agreement between the reference frame and the location of coherent phase-shifts, as both are in non-retinotopic coordinates. The yellow arrow highlights the element to be attended in the display. Observers were instructed to attend this element and report its perceived direction of drift. The rest of the motion pathways contained mainly ambiguous motion. (B) Results. A statistically significant interaction of size and contrast was found. We observe a decrease in performance as a function of size for contrast values up to 15% Michelson contrast. For the low-contrast stimulus, there is an improvement in performance with size. These results suggest that the non-retinotopic processes may be mediated by a similar adaptive center-surround mechanism as the one found in retinotopic representations. Error bars are ±S.E.M.

4.4.2 Results and discussion

The results are presented in Fig. 8B. A statistically significant interaction between size and contrast (($F(2.55, 12.78)$, $p = 0.006$, $\eta_p = 0.59$)) was found. The main effects of contrast (($F(1.38, 6.88)$, $p = 0.002$, $\eta_p = 0.81$)) and size (($F(1.08, 5.38)$, $p = 0.04$, $\eta_p = 0.58$)) were also statistically significant. It is observed that thresholds increase as a function of stimulus size for high-contrast stimuli. This suggest the presence of a spatial suppression mechanism. Also, note that threshold curves for contrast values between from 90% to 15% run parallel with relatively small improvement in performance as contrast is increased. For low contrast stimulus (5.5%), the threshold decreases as a function of size. This result in turn, signals the transition from spatial suppression to a spatial summation mechanism.

Fig. 9 presents the results of Experiment 4 replotted next to Tadin et al's data (Tadin et al., 2003; Fig. 3a). One major quantitative difference is the range of threshold values: Quantitatively, Tadin et al's results are more "compressed" on the threshold axis compared to ours. On the other hand, qualitatively, the general profile of both results is similar. For example, for the lowest- and highest-contrast stimuli, there is improvement of performance as a function of size and deterioration of performance with size, respectively. Also, in both results there is a progressive transition from *spatial summation* to *spatial suppression* for contrast values between 5.5% to 15%, which is within the range of contrast values where spatial grouping transitions to spatial segregation (Takeuchi, 1998). Finally, for contrast values higher than 46%, we observe a plateauing in performance.

On possible reason for the better performance in Tadin et al's results is that our study contains a long ISI between frames while their study did not. Another reason may be the higher complexity of our stimulus in comparison to Tadin et al's. Finally, the threshold differences in this experiment may be also due to differences in the reference-frames: Let us recall that Experiment 4 is a non-retinotopic motion-direction task whereas Tadin's data come from a retinotopic motion-direction task. In other words, the reference-frame in our study was non-retinotopic whereas it was retinotopic in Tadin et al's study.

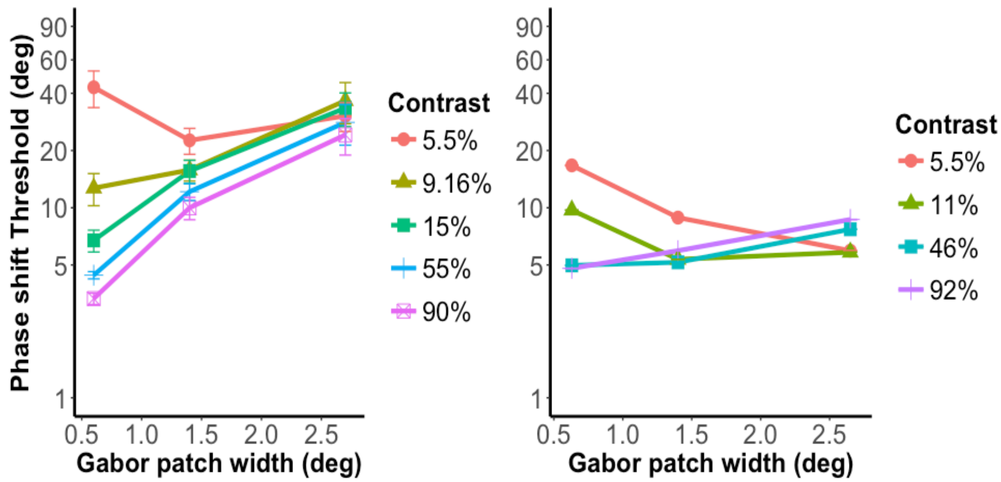

Figure 9: (A) Replot of the results for Experiment 4. (B) Data obtained from Tadin et. al. (2003), Fig. 3a. We extracted the data points for the three stimulus sizes evaluated in our study and for the contrast values examined in that experiment. Error bars are ±S.E.M.

In order to compare more directly the effects of retinotopic vs non-retinotopic reference-frames, we can compare the results of Experiment 1 (retinotopic task) to those of Experiment 4 (non-retinotopic task) in the present study. In this way, we compare the performances of retinotopic and non-retinotopic reference-frames using the same stimulus paradigm and the same group of observers and hence, eliminating the differences between our and Tadin et al's studies. In Fig. 10, we replot the data from Experiment 1 (dashed lines) together with the results from the lowest and highest contrast values from Experiment 4 (solid lines). Data look similar. Notice that for low-contrast stimuli (red lines) there is a decrease in threshold with size. The opposite effect is observed for the high-contrast stimuli (blue lines). Also observe that in some conditions the performance for Experiment 1 is slightly better than the performance for Experiment 4. This may be due to the long ISI included in Experiment 4. In other words, the experiments had different temporal conditions. These results suggest that the nature of the reference-frame, whether it is retinotopic or non-retinotopic, does not affect strongly the computation of motion information. In Appendix A, we also show that similar results are obtained in the absence of the squares that are part of the Ternus-Pikler display.

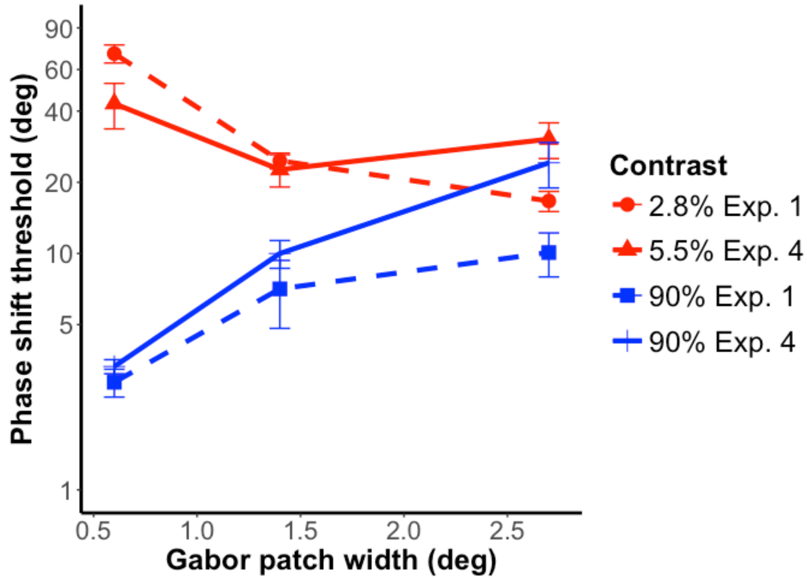

Figure 10: Comparison of results from Experiment 1 and Experiment 4. Dashed lines and solid lines correspond to Experiment 1 and Experiment 4, respectively. The low-contrast stimuli are shown in red while the high-contrast stimuli are shown in blue. Error bars are ±S.E.M.

Taken together, these findings provide support for the main hypothesis of this study, viz., non-retinotopic computation of motion is mediated by an adaptive center-surround mechanism similar to that found in retinotopic coordinates.

4.5 Experiment 5. *Control condition:* No Ternus-Pikler motion (Fig. 11):

4.5.1 Procedure

Participants were instructed to attend to either the left element or the right element (Fig. 11) and report the direction of drift. The Gabor patch size and the contrast were 2.65° and 90%, respectively. The critical point was to assess whether the non-ambiguous phase shifts (i.e., phase shifts other than integer multiples of 180°) were used by the subjects to produce above chance performance. These non-ambiguous phase-transitions occur in the transition from frame two (180°) to frame three (2δ) in the left side of the display, as well as in the transition from frame three to frame four in the right side of the display (from δ + 180° to 3δ).

4.5.2 Results and discussion

For each of the four phase-shifts, participants were at chance level (Fig 11B). The presence of multiples of δ, i.e., non-ambiguous phase shifts, in some frames did not allow observers to successfully report the direction of drift. Hence, even though our stimulus is not perfectly ambiguous with respect to the direction of drift (shifts of 180° are ambiguous whereas shifts by δ degrees are not), this control experiment shows that the “artefactual drift information” is unnoticed.

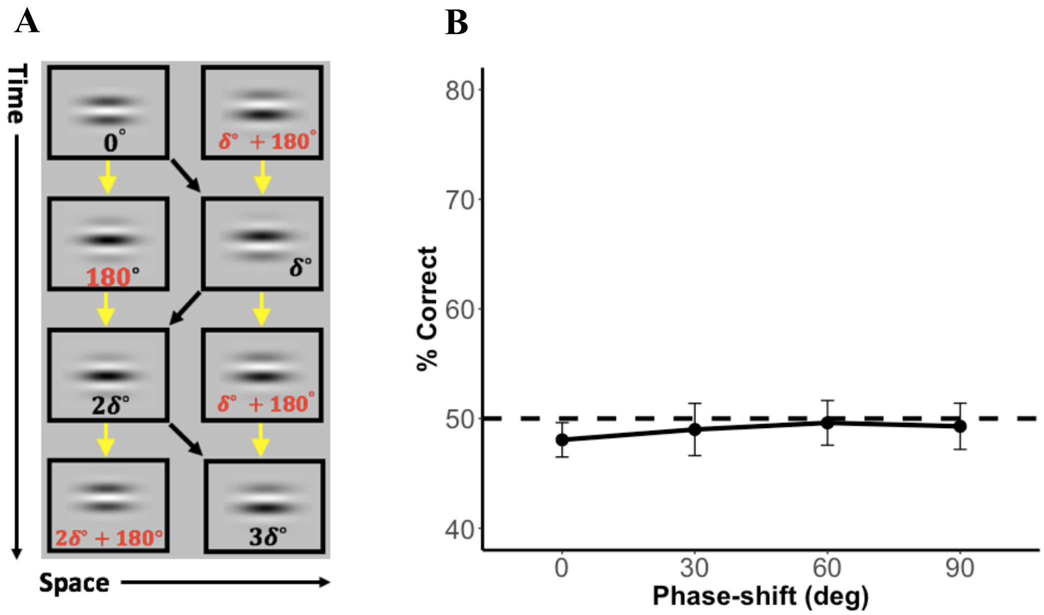

Figure 11: (A) Control condition. The outermost elements of the Ternus-Pikler display were removed. The black arrows indicate the non-retinotopic trajectory of the coherent motion. The yellow arrows show the retinotopic trajectories. Observers were instructed to attend to one of the elements in the display and to report the perceived direction of drift. (B) Results of the control condition. Average percent correct across observers (N=6) as a function of phase-shift $\boldsymbol{\delta}$*. Observers are at chance level. Error bars are ±S.E.M.*

5. General discussion

Motion perception occurs usually in non-retinotopic coordinates. However, the neural correlates underlying non-retinotopic motion processing are still elusive. The major goal of the study was to investigate whether the adaptive center-surround mechanisms reported in Tadin et al. (2003) generalize to non-retinotopic reference-frames. Our results support the hypothesis that adaptive center-surround mechanisms are used in the computation of non-retinotopic motion.

Spatial suppression is thought to be the psychophysical correlate of neurophysiological surround suppression processes (e.g., Tadin, 2015) Moreover, correlational and causal evidence suggest that spatial suppression of background motion signals is critical for the rapid segregation of moving objects (Tadin et al., 2019). More generally, surround-inhibition may be a solution to the noise-saturation problem (Grossberg, 1988): The system needs to amplify weak signals to improve the signal-to-noise ratio. However, when signals become strong, the same amplification may lead to saturation. How can a system be sensitive to weak inputs while avoiding saturation for strong inputs? In other words, how can an adaptive gain-control mechanism be used to match the dynamic range of the processing units (neurons) to that of input signals, given that the latter tends to be much larger than the former. At high input levels, the surround suppression can reduce the net signal thereby preventing saturation. On the other hand, for weak input signals, the surround suppression would be detrimental since it will weaken further the signal burying it in noise. The adaptive strategy reduces the effectiveness of the surround for weak signals (low contrast) thereby leading to summation by the center of the receptive field. The summation in turn amplifies weak signals so that they can be reliably detected in the presence of noise. Given this adaptive dynamic-range property, it is not surprising to find antagonistic center-surround (or similar) receptive-field profiles throughout the visual system, starting from the retina. However, it remains to be seen at which stage(s) this mechanism operates when it comes to motion detection. In the primate visual processing, visual motion detection starts in the cortex and involves center-surround receptive fields found in V1 (Cavanaugh, Bair, & Anthony Movshon, 2002), MST (Eifuku & Wurtz, 1998) and in V5/MT (Pack, Hunter, & Born, 2005). Correspondences between the characteristics of psychophysical spatial-suppression and the properties of suppressive center-surround receptive fields in area MT suggest this area as the main locus of these adaptive mechanisms (Liu, Haefner, & Pack, 2016; Schallmo et al., 2018; Tadin & Lappin, 2005, 2012; Tadin et al., 2003; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011). For instance, the dependency of spatial suppression on contrast accords with contrast dependency of a population of MT neurons (Pack et al., 2005); MAE which is linked to MT mechanisms, is reduced with large high-contrast stimulus (Tadin et al., 2003); isoluminant moving stimuli are unable to produce spatial suppression effects, a result consistent with weak MT responses to isoluminant gratings (Gegenfurtner et al., 1994; Tadin et al., 2003). Therefore, it is proposed that spatial suppression is, at least in part, a behavioral correlate of surround suppression in cortical area MT (Tadin, 2015). The above arguments apply to spatial suppression generated with stimuli encoded in retinotopic coordinates. The results of Experiment 5 support the involvement of similar mechanisms in non-retinotopic motion computation. In an fMRI study, also using the Ternus-Pikler display, Thunell et. al. (2016) found that the average blood-oxygen-level (BOLD) activation in areas V1, V2 and V3 correlated with retinotopic percepts but not with non-retinotopic percepts. On the other hand, the human motion processing complex (hMT+) was active with both retinotopic and non-retinotopic encoding which suggested the hMT+ as the first visual area encoding non-retinotopic percepts. Thus, the available evidence about the location of non-retinotopic encoding in the brain also suggests area MT as a potential candidate. Given the similarities in the use of adaptive center-surround mechanisms in retinotopic as well as non-retinotopic processing, both in terms of behavioral performance and potential neural correlates, it remains to determine whether adaptive center-surround mechanisms are "inherited" from one computation to another (e.g., from retinotopic motion computation to non-retinotopic motion computation) or they are independently implemented at each stage.

To our knowledge, this is the first study to provide evidence for the existence of adaptive center-surround mechanisms in non-retinotopic encoding. The flexible spatial integration mechanisms described in this work might be a way in which vision deals with the wide variability of motion signals found in the natural environment. Even though the early visual system is organized retinotopically (Tootell et. al. ,1998), this retinotopic organization is insufficient to support perception under natural viewing conditions (Boi et al., 2009). Additionally, our results add further evidence that most visual features are processed in non-retinotopic coordinates, including motion (Boi et al., 2009, Thunell, Plomp, Öğmen & Herzog, 2016), attention (Boi et al., 2009; Boi et al., 2011), fine spatial detail such as vernier offsets and feature fusion (Ogmen et al., 2006; Scharnowski et al., 2007), backward masking (Noory et al., 2015), but not adaptation in the tilt aftereffect (Boi et al., 2011).

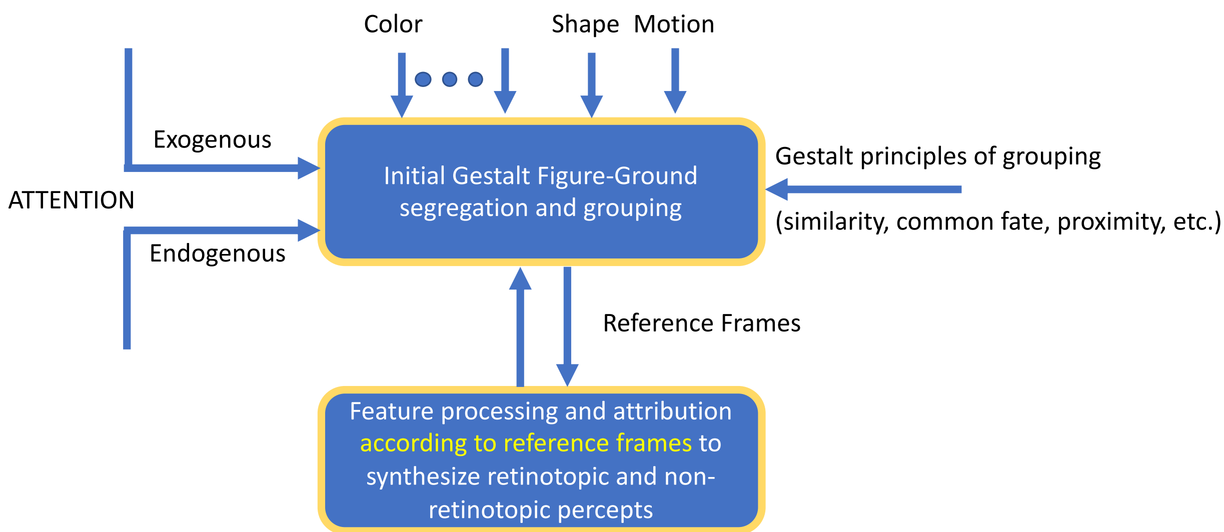

Figure 12: The "two-stage" model for non-retinotopic processing. The model assumes that the primitive building blocks of perceptual processing are groups, as proposed by Gestalt psychologist. Hence, the first stage of visual processing consists of separating figure from ground and grouping stimuli according to Gestalt principles of grouping. These groups, in turn, provide reference-frames that are used to synthesize retinotopic and non-retinotopic percepts.

Fig. 12 shows the "two-stage" model that we proposed for non-retinotopic processing (Ogmen & Herzog, 2010). According to this model, the first stage of processing consists of grouping stimuli using Gestalt principles of grouping. This grouping process generates reference-frames, which in turn are used in a second stage where non-retinotopic processes are carried out according to these reference-frames. For example, different motion signals on the bicycle of the example in Fig. 1 are grouped together (e.g., by the principle of "common fate") and a "common motion vector" is selected as reference-frame (e.g., Johansson, 1973, 1974; Agaoglu et al., 2015, 2017). This reference-frame is passed on to the following stage where it provides coordinates to judge relative motion according to an exocentric (non-retinotopic) reference-frame. In this study, we used the Ternus-Pikler display to generate retinotopic and non-retinotopic reference frames that are pitted against each other due to overlapping elements between different frames. Changing the geometry and/or timing of Ternus-Pikler elements allows the generation of experimentally-controlled reference frames. The key however is not the specifics of the stimulus that generates the reference frame. It could be the bicycle in a natural environment as in Fig. 1. Regardless how it is generated, the resulting reference-frame is passed on to the second stage where it controls how stimuli are processed and integrated (Fig. 12). Future work will determine where in this model the adaptive center-surround organization may be operating.

Acknowledgements

We thank Mehmet Ağaoğlu for his input, in particular for suggesting the Quest+ method. We also thank the reviewers for helpful comments and suggestions. Michael Herzog was supported by the Swiss National Science Foundation grant 'Basics of visual processing: from elements to figures' (176153).

Appendix A

Our stimulus consisted of Gabor patches embedded in squares elements. The purpose of the square elements was to strengthen the formation of group motion and thereby strengthen the underlying non-retinotopic reference-frame. To show that the results of Experiments 1 and 4 are independent of the presence of these square elements, we ran on one subject (BP) a control condition where we removed them from the stimulus. In Fig. A1, we show the results of the control condition for Experiment 1. The control data (dashed lines) are similar to the data from the same subject in Experiment 1 (solid lines). For the high contrast stimulus there is a small increase in threshold for the control condition; however, the general interaction between size and contrast remains.

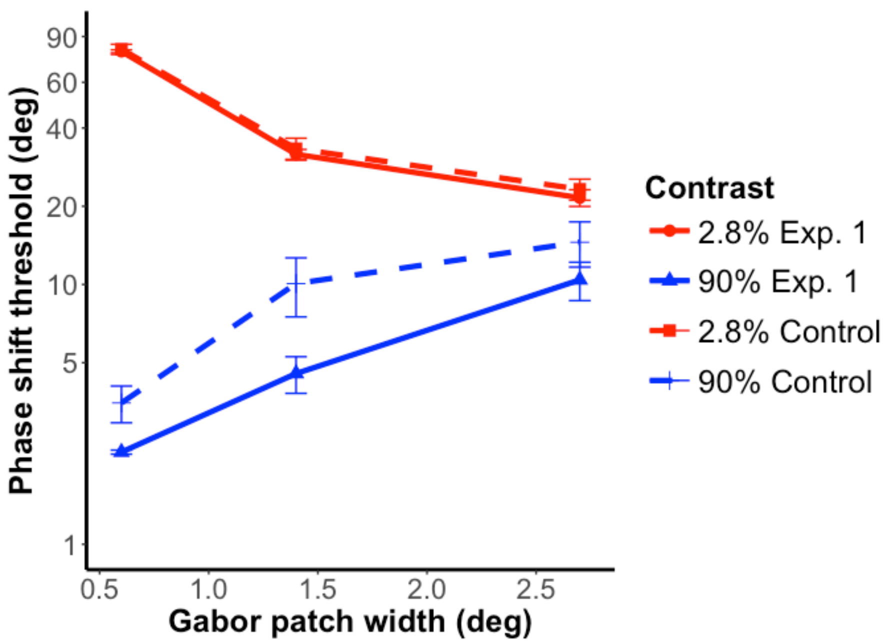

Figure A1: Results of the no-square control condition for Experiment 1. Solid lines represent the results from Experiment 1 for subject BP whereas dashed lines show the results from the control for the same subject. Error bars are ± S.E.M.

Fig. A2 shows the results of the same control condition (i.e., stimuli without the squares) for Experiment 4 obtained from subject BP and compared to the data of subject BP in Experiment 4. The only major difference is that the minimum contrast required for the no-squares control condition was higher (8% vs 5.5%).

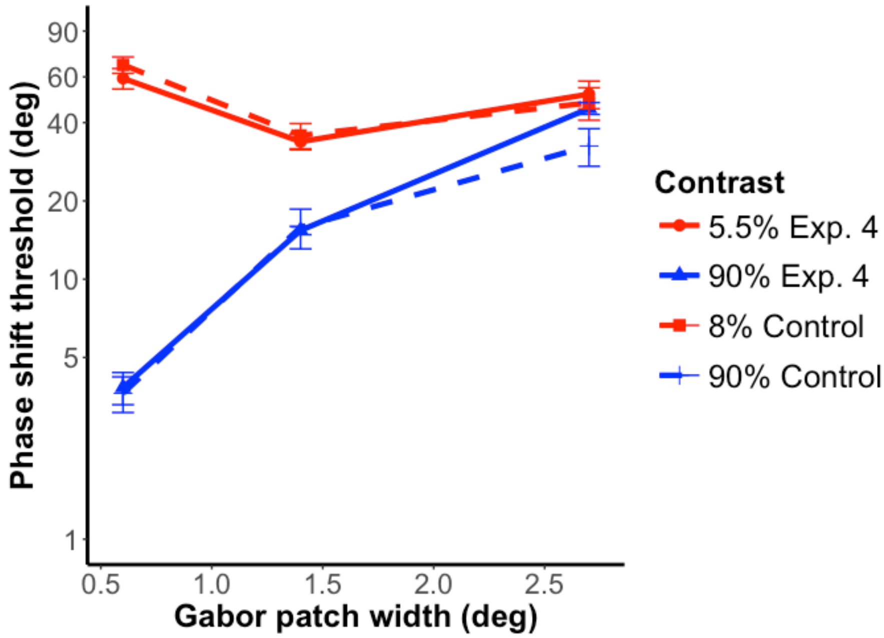

Figure A2: Results of the no-square control condition for Experiment 4. Solid lines represent the results from Experiment 4 whereas dashed lines show the results from the control. The data come from one subject. Error bars are ±S.E.M.

Appendix B

The *retinotopic reference-frame and non-retinotopic drift information condition* and the *non-retinotopic reference-frame and retinotopic drift-information condition* showed chance performance due to the mismatch between the reference-frame system and the motion information. Fig. B1 illustrates the average percent correct across observers (N=6) as a function of phase-shift value for a low-contrast stimulus (5.5%).

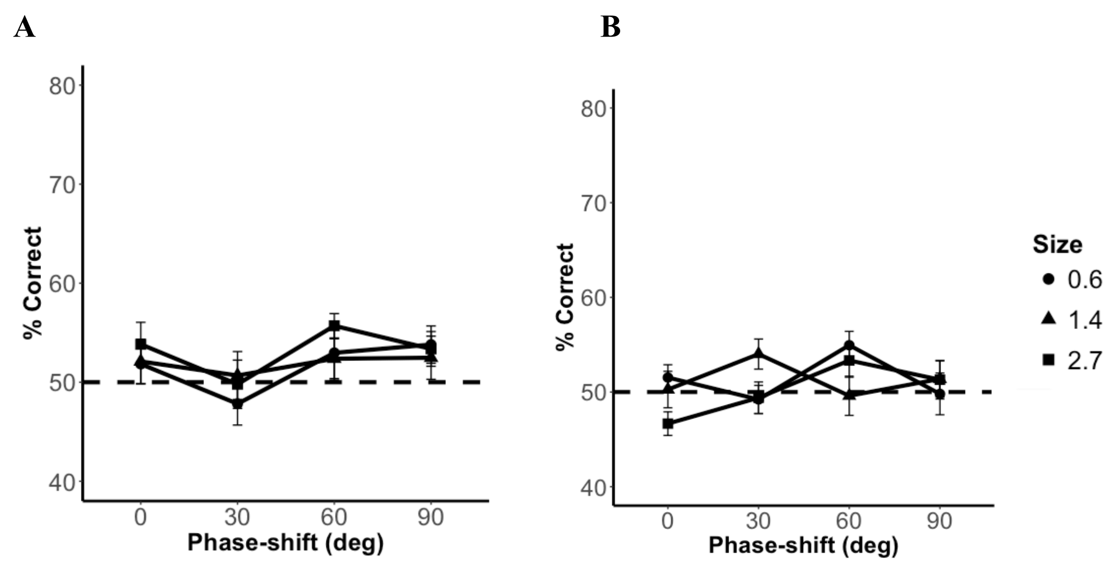

Figure B1: (A) Average percent correct across observers (N=6) is shown as a function of phase-shift $\boldsymbol{\delta}$ value for the low-contrast stimulus in the retinotopic reference-frame and non-retinotopic drift information condition. (B) Average percent correct across observers (N=6) is shown as a function of phase-shift $\boldsymbol{\delta}$ value for the low-contrast stimulus in the non-retinotopic reference-frame and retinotopic drift-information condition. Error bars are $\pm$S.E.M.

References

Agaoglu, M. N., Clarke, A. M., & Herzog, M. H. (2017). Motion-based nearest vector metric for reference frame selection in the perception of motion, *16*(2016), 1–16. https://doi.org/10.1167/16.7.14.doi

Alais, D., & Lorenceau, J. (2002). Perceptual grouping in the Ternus display: evidence for an 'association field' in apparent motion. Vision Research, 42, 1005–1016.

Anderson, S. J., & Burr, D. C. (1991). Spatial summation properties of directionally selective mechanisms in human vision. *Journal of the Optical Society of America. A, Optics and Image Science*, *8*(8), 1330–1339. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1919836

Boi M, Vergeer M, Öğmen H, Herzog M.H. (2011) Nonretinotopic Exogenous Attention. Current Biology, 21(20), p1732-1737.

Boi, M., Ogmen, H., & Herzog, M. H. (2011). Motion and tilt aftereffects occur largely in retinal, not in object, coordinates in the Ternus-Pikler display. *Journal of Vision*, *11*(3), 7–7. https://doi.org/10.1167/11.3.7

Boi, Marco, Oğmen, H., Krummenacher, J., Otto, T. U., & Herzog, M. H. (2009). A (fascinating) litmus test for human retino- vs. non-retinotopic processing. *Journal of Vision*, *9*(13), 5.1-511. https://doi.org/10.1167/9.13.5

Breitmeyer, B. G., & Ritter, A. (1986). Visual persistence and the eVect of eccentric viewing, element size, and frame duration on bistable strobo- scopic motion percepts. Perception & Psychophysics, 39, 275–280.

Cavanaugh, J. R., Bair, W., & Anthony Movshon, J. (2002). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *Journal of Neurophysiology*, *88*(5), 2530–2546. https://doi.org/10.1152/jn.00692.2001

Clarke, A. M., & Herzog, M. H. (2013). Does spatio-temporal filtering account for nonretinotopic motion perception ? Comment on Pooresmaeili , Cicchini ,. *Journal of Vision*, *13*(2013), 1–14. https://doi.org/10.1167/13.10.19.doi

Clarke, A. M., Öğmen, H., & Herzog, M. H. (2015). A computational model for reference-frame synthesis with applications to motion perception. *Vision Research*, *126*, 242–253. https://doi.org/10.1016/j.visres.2015.08.018

Dawson, M. R., & Wright, R. D. (1994). Simultaneity in the Ternus configuration: psychophysical data and a computational model. Vision Research, 34, 397–407.

Eifuku, S., & Wurtz, R. H. (1998). Response to motion in extrastriate area MSTl: Center-surround interactions. *Journal of Neurophysiology*, *80*(1), 282–296. https://doi.org/10.1152/jn.1998.80.1.282

Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M. H., Carandini, M., Movshon, J. A., & Zaidi, Q. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience*, *11*(3), 455–466. https://doi.org/10.1017/S095252380000239X

Grossberg, S., Léveillé, J., & Versace, M. (2011). How do object reference frames and motion vector decomposition emerge in laminar cortical circuits? https://doi.org/10.3758/s13414-011-0095-9

He, Z. J., & Ooi, T. L. (1999). Perceptual organization of apparent motion in the Ternus display. Perception, 28, 877–892.

Hein, E., & Moore, C. M. (2012). Spatio-Temporal Priority Revisited: The Role of Feature Identity and Similarity for Object Correspondence in Apparent Motion. J Exp Psychol Hum

Percept Perform. 38, 975–988. doi:10.1037/a0028197.
Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*(2), 201–211. https://doi.org/10.3758/BF03212378
Johansson, G. (1974). Vector analysis in visual perception of rolling motion - A quantitative approach. *Psychologische Forschung*, *36*(4), 311–319. https://doi.org/10.1007/BF00424568
Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1999). Dynamics of spatial summation in primary visual cortex of alert monkeys. *Proceedings of the National Academy of Sciences*, *96*(21), 12073–12078. https://doi.org/10.1073/pnas.96.21.12073
Kramer, P., & Rudd, M. (1999). Visible persistence and form correspondence in Ternus apparent motion. Perception & Psychophysics, 61, 952–962.
Kramer, P., & Yantis, S. (1997). Perceptual grouping in space and time: evi- dence from the Ternus display. Perception & Psychophysics, 59, 87–99.
Lauffs, M. M., Choung, O. H., Öğmen, H., & Herzog, M. H. (2018). Unconscious retinotopic motion processing affects non-retinotopic motion perception. *Consciousness and Cognition*, *62*, 135–147. https://doi.org/10.1016/j.concog.2018.03.007
Lauffs, M. M., Choung, O. H., Öğmen, H., Herzog, M. H., & Kerzel, D. (2019). Reference-frames in vision: Contributions of attentional tracking to nonretinotopic perception in the Ternus-Pikler display. *Journal of Vision*, *19*(12), 1–15. https://doi.org/10.1167/19.12.7
Lauffs, M. M., Öğmen, H., & Herzog, M. H. (2017). Unpredictability does not hamper nonretinotopic motion perception. *Journal of Vision*, *17*(9), 1–10. https://doi.org/10.1167/17.9.6
Liu, L. D., Haefner, R. M., & Pack, C. C. (2016). A neural basis for the spatial suppression of visual motion perception. *ELife*, *5*. https://doi.org/10.7554/elife.16167
Noory B., Herzog M.H., Ogmen H. (2015). Retinotopy of visual masking and non-retinotopic perception during masking. Attention, Perception & Psychophysics, 77, 1263-1284.
Öğmen, H., & Herzog, M. H. (2010). The geometry of visual perception: Retinotopic and nonretinotopic representations in the human visual system. *Proceedings of the IEEE*, *98*(3), 479–492. https://doi.org/10.1109/JPROC.2009.2039028
Öğmen, H., Otto, T. U., & Herzog, M. H. (2006). Perceptual grouping induces non-retinotopic feature attribution in human vision. *Vision Research*, *46*(19), 3234–3242. https://doi.org/10.1016/j.visres.2006.04.007
Otto, T. U., Ogmen, H., & Herzog, M. H. (2006). The flight path of the phoenix V The visible trace of invisible elements in human vision. *Journal of Vision*, *6*, 1079–1086.
Pack, C. C., Hunter, J. N., & Born, R. T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *Journal of Neurophysiology*, *93*(3), 1809–1815. https://doi.org/10.1152/jn.00629.2004
Pantle, A., & Picciano, L. (1976). A multistable movement display: evidence for two separate motion systems in human vision. *Science (New York, N.Y.)*, *193*(4252), 500–502. https://doi.org/10.1126/science.941023
Pantle, A. J., & Petersik, J. T. (1980). Effects of spatial parameters on the perceptual organization of a bistable motion display. Perception & Psychophysics, 27, 307–312.
Petersik, J. T., & Rice, C. M. (2006). The evolution of explanations of a perceptual phenomenon: A case history using the Ternus effect. Perception, 35, 807-821.
Pikler, J. (1917). Sinnesphysiologische Untersuchungen. *Leipzig, Germany: Barth*.
Pollen, D. A., Nagler, M., Daugman, J., Kronauer, R., & Cavanagh, P. (1984). Use of gabor elementary functions to probe receptive field substructure of posterior inferotemporal

neurons in the owl monkey. *Vision Research*, *24*(3), 233–241. https://doi.org/10.1016/0042-6989(84)90125-1
Schallmo, M.-P., Kale, A. M., Millin, R., Flevaris, A. V, Brkanac, Z., Edden, R. A., … Murray, S. O. (2018). Suppression and facilitation of human neural responses. *ELife*, *7*. https://doi.org/10.7554/elife.30334
Scharnowski F., Hermens F., Kammer T., Ogmen H., Herzog, M.H. (2007). Feature fusion reveals slow and fast visual memories. Journal of Cognitive Neuroscience, 19(4), 632-641.
Scott-Samuel, N. E., & Hess, R. F. (2001). What does the Ternus display tell us about motion processing in human vision? Perception, 30, 1179–1188.
Tadin, D. (2015). Suppressive mechanisms in visual motion processing: From perception to intelligence. *Vision Research*, *115*, 58–70. https://doi.org/10.1016/j.visres.2015.08.005
Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., & Park, S. (2006). Weakened center-surround interactions in visual motion processing in schizophrenia. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(44), 11403–11412. https://doi.org/10.1523/JNEUROSCI.2592-06.2006
Tadin, D., & Lappin, J. S. (2005). Optimal size for perceiving motion decreases with contrast. *Vision Research*, *45*(16), 2059–2064. https://doi.org/10.1016/j.visres.2005.01.029
Tadin, D., & Lappin, J. S. (2012). *Linking Psychophysics and Physiology of Center-Surround Interactions in Visual Motion Processing*. https://doi.org/10.1093/acprof
Tadin, D., Lappin, J. S., Blake, R., & Grossman, E. D. (2002). What constitutes an efficient reference frame for vision? *Nature Neuroscience*, *5*(10), 1010–1015. https://doi.org/10.1038/nn914
Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre–surround antagonism in visual motion processing. *Nature*, *424*(6946), 312–315. https://doi.org/10.1038/nature01812
Tadin, D., Park, W. J., Dieter, K. C., Melnick, M. D., Lappin, J. S., & Blake, R. (2019). Spatial suppression promotes rapid figure-ground segmentation of moving objects. *Nature Communications*, *10*(1), 2732. https://doi.org/10.1038/s41467-019-10653-8
Tadin, D., Silvanto, J., Pascual-Leone, A., & Battelli, L. (2011). Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. *Journal of Neuroscience*, *31*(4), 1279–1283. https://doi.org/10.1523/JNEUROSCI.4121-10.2011
Takeuchi, T. (1998). Effect of contrast on the perception of moving multiple Gabor patterns. *Vision Research*, *38*(20), 3069–3082. https://doi.org/10.1016/S0042-6989(98)00019-4
Ternus, J. (1926). Experimentelle Untersuchungen über phänomenale Identität. *Psychological Research*, *7*, 81–136.
Thunell, E., van der Zwaag, W., Ögmen, H., Plomp, G., & Herzog, M. H. (2016). Retinotopic encoding of the Ternus-Pikler display reflected in the early visual areas. *Journal of Vision*, *16*(3), 26. https://doi.org/10.1167/16.3.26
Thunell E, Plomp G, Öğmen H, Herzog M.H. (2016). EEG Correlates of Relative Motion Encoding. Brain Topography, 29(2), p273-282.
Tootell, R. B. ., Hadjikhani, N. K., Mendola, J. D., Marrett, S., & Dale, A. M. (1998). From retinotopy to recognition: fMRI in human visual cortex. *Trends in Cognitive Sciences*, *2*(5), 174–183. https://doi.org/10.1016/S1364-6613(98)01171-1
Watson, A. B. (2017). QUEST+: A general multidimensional Bayesian adaptive psychometric method. *Journal of Vision*, *17*(3), 10. https://doi.org/10.1167/17.3.10
Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision Research*, *35*(3), 325–

336. https://doi.org/10.1016/0042-6989(94)00182-L

Demo - control condition

Click here to download Supplementary Material: Control.mp4

Demo - Condition 1

Click here to download Supplementary Material: Condition1.mp4

Demo - Condition 2

Click here to download Supplementary Material: Condition2.mp4

Demo - Condition 3

Click here to download Supplementary Material: Condition3.mp4

Demo - Condition 4

Click here to download Supplementary Material: Condition4.mp4

Credit Author Statement

Boris Penaloza: Conceptualization, methodology, software, formal analysis, investigation, writing – original draft.

Michael H. Herzog: Conceptualization, methodology, formal analysis, writing – review & editing, funding acquisition.

Haluk Ogmen: Conceptualization, methodology, formal analysis, writing – review & editing, supervision, project administration.