

# Unpredictability does not hamper nonretinotopic motion perception

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**The motion of parts of an object is usually perceived relative to the object, i.e., nonretinotopically, rather than in retinal coordinates. For example, we perceive a reflector to rotate on the wheel of a moving bicycle even though its trajectory is cycloidal on the retina. The rotation is perceived because the motion of the object (bicycle) is discounted from the motion of its parts (reflector). It seems that the visual system can easily compute the object motion and subtract it from the part motion. Bikes move usually rather predictably. Given the complexity of real-world motion computations, including many ill-posed problems such as the motion correspondence problem, predictability of an object's motion may be essential for nonretinotopic perception. Here, we used the Ternus–Pikler display to investigate this question. Performance was not impaired when contrast polarity, shape, and motion trajectories changed unpredictably. Our findings suggest that predictability is not crucial for nonretinotopic motion processing.**

## Introduction

Early visual processing is *retinotopic*: Neighboring points in the visual field map onto neighboring photoreceptors in the retina and this principle is preserved in the early visual areas (e.g., Sereno et al., 1995). However, perception is usually *nonretinotopic*. This is evident in the everyday recognition of moving objects, which are usually perceived relative to other objects (Agaoglu, Clarke, Herzog, & Ögmen, 2016; Duncker, 1929; Johansson, 1950, 1974, 1976). In

particular, parts of an object are perceived relative to the object. For example, when viewing a moving bicycle without moving the eyes, the reflector on its wheel appears to circle, although in retinotopic and Euclidian coordinates it follows the path of a curtate cycloid (cf. Figure 1). The reflector motion appears circular because the bicycle serves as a reference–frame, and the horizontal motion of the bike is subtracted from the cycloidal motion of the reflector. The retinotopic, cycloidal trajectory cannot be perceived because the nonretinotopic motion dominates.

Predictability plays an important role in visual perception in general. Predictable stimuli are processed more efficiently and are more readily detectable (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Posner, 1980; Vetter, Grosbras, & Muckli, 2015). In particular, predictability plays an important role in the non-retinotopic perception related to eye movements. We perceive a stable visual world across eye movements because the brain can compensate the shift of the retinal image since the shifts are predictable (Duhamel, Colby, & Goldberg, 1992; von Holst & Mittelstädt, 1950; Wurtz, 2008). The motion of a bicycle is usually fairly predictable and thus it is easy to subtract the predictable bike motion from the reflector motion in an online fashion. Hence, the question arises to what extent predictability is crucial for nonretinotopic motion perception.

Here, we investigate this question by using the Ternus–Pikler display (Boi, Ögmen, Krummenacher, Otto, & Herzog, 2009; Pikler, 1917; Ternus, 1926). In the retinotopic conditions, two black disks with white dots are briefly presented and reappear in the same

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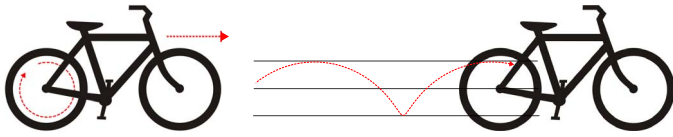


Figure 1. Moving parts of an object are perceived relative to the object. The reflector of a moving bicycle is perceived as circling (left) even though the motion is cycloidal in retinotopic coordinates (right). The motion of the bicycle is subtracted from the cycloidal motion yielding circular motion.

position after a brief interstimulus interval (ISI). The white dots change position with every stimulus presentation and appear to move up and down in one disk and left and right in the other disk (Figure 2a). In the nonretinotopic conditions, a third disk with a white dot is added alternately to the left or to the right from frame to frame, which changes the percept profoundly: The three disks now form a perceptual *group* that appears to move left and right in concert (*group motion*, Figure 2b). The dot in the middle disk of the group appears to move circularly (nonretinotopic motion), because the group serves as reference-frame and is discounted from the up-down and left-right dot motion. The task of the observer is to indicate whether the dot rotates clockwise or counterclockwise.

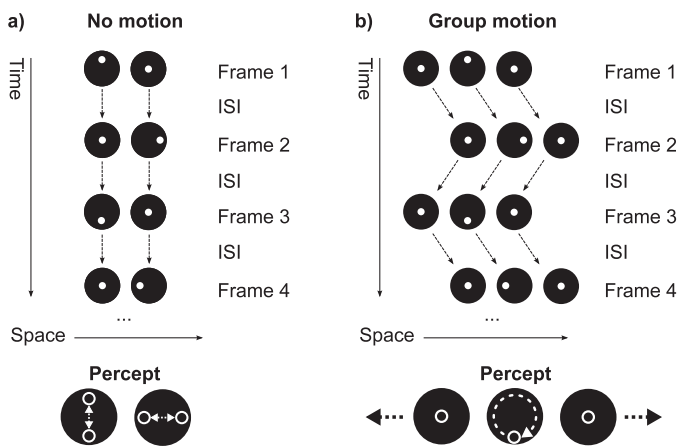


Figure 2. Ternus–Pikler display. (a) Two black disks with white dots are presented centrally above a fixation point (not shown here) and reappear in the same position after an ISI. The dots change position in every frame, giving rise to the percept of apparent up-down motion in the left and left-right motion in the right disk. (b) When a third disk is added alternately to the left and right, the three disks in each frame form a perceptual group that appears to be moving left-right in concert across frames. The left-right motion of the disks is discounted from the dot motions, and thus the dot in the middle disk is perceived to rotate. Arrows indicate the perceived object correspondence and were not shown in the experiment.

## Experiment 1

In Experiment 1, we investigated whether predictability of the group motion is essential to perceive the nonretinotopic motion of the dot. The group of the three disks changed the position randomly from frame to frame. In addition, we investigated whether unpredictable changes in contrast–polarity and shape of the stimuli perturbs perception and performance. Schematics of the stimuli are shown in Figure 3 and movie demonstrations are provided in the online supplementary materials.

## Methods

### Participants

Fourteen participants took part in the experiment after signing informed consent forms (12 naïve, two collaborators, nine female, three left-handed, age  $M = 20.4$  years,  $SD = 1.30$ , range: 18–22 years). The participants were recruited from the École Polytechnique Fédérale de Lausanne student population and were paid 20 CHF (Swiss franc) per hour. All participants had normal or corrected-to-normal vision, and had to reach a value of 1.0 or more in the Freiburg visual acuity test in at least one eye (Bach, 1996). The experiment was approved by the local ethics committee and performed in accordance with the declaration of Helsinki (World Medical Association, 2013).

### Stimulus and task

Participants were seated in a dimly lit room with their chin and forehead resting in an eyetracker. Stimuli were presented at a distance of 1 m on a 21-in. Philips 201B4 CRT monitor (1,280 × 1,024 pixels, 75 Hz; Philips Eindhoven, Amsterdam, The Netherlands) using MATLAB with Psychtoolbox (Brainard, 1997; Pelli, 1997).

Participants were instructed to fixate on a fixation point in the middle of the screen. In the control conditions, two horizontally aligned black disks with white dots were presented centrally above the fixation point for 120 ms (Figure 2). After an ISI of 213 ms, in which only the fixation point was shown, the disks reappeared in the same position and so on. With every appearance of the disks the white dots were repositioned to create apparent motion percepts of up-and-down motion in one, and left-and-right motion in the other disk (Figure 2a). In the experimental conditions, we used exactly the same stimulus, but added a third disk with central dot alternately to the left and right (Figure 2b). The

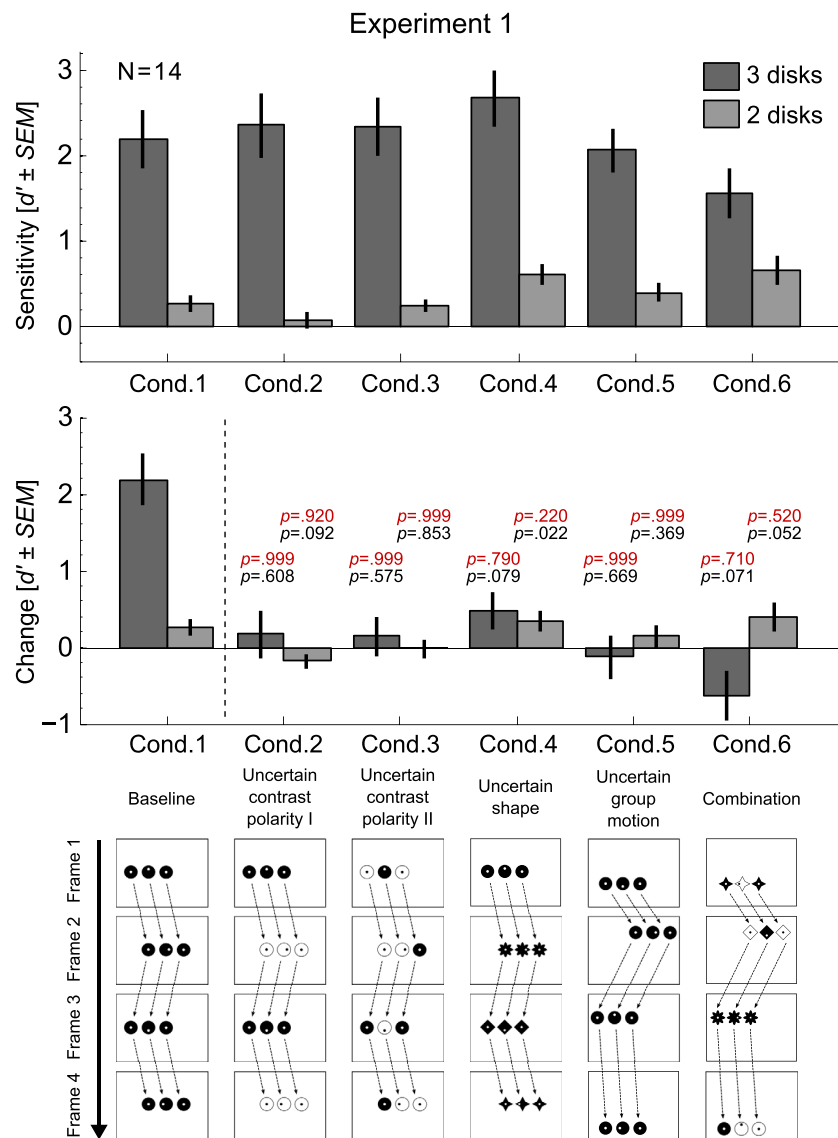


Figure 3. Experiment 1 stimuli and results. Top: Absolute performance in terms of sensitivity  $d'$ . Bottom: Mean change in sensitivity  $d'$  compared with performance in Condition 1. Note, that in the bottom plot for Condition 1, the actual  $d'$  values (as opposed to change in  $d'$ ) are plotted for comparison.  $P$  values were computed in one-sample  $t$  tests against 0 and are reported Bonferroni corrected in red and uncorrected in black. In Condition 1 three black disks moved predictably left and right. The displacement was exactly one interstimulus distance, so that the position of the middle disk in frame 1 spatially overlapped the position of the left-most disk in frame 2, and so forth. In Condition 2, the contrast polarity of the disks reversed from frame to frame but was the same for all three disks. In condition 3, the contrast polarity was randomly chosen for each individual disk from frame to frame. In Condition 4, the shape changed from frame to frame. Shapes were identical in each frame. In Condition 5, the three disks were as in Condition 1, but the position of the three disks changed randomly from frame to frame. In Condition 6, the disks moved as in Condition 5 and changed contrast polarity and shape as in Conditions 3 and 4. We did not find significant differences between the baseline and the less predictable conditions. Performance was insignificantly lower in Condition 6. In the control conditions with two disks, where no nonretinotopic dot motion is perceived, performance is near chance level in all conditions, indicating that the dot rotation direction cannot be cognitively inferred from the retinotopic percepts.

addition of the third disk changes the perceptual organization: Not two stationary plus one alternating disks were perceived, but a group of three disks moving left and right in concert. The retinotopic up-down and left-right dot motions were invisible and a nonretinotopic rotation of the dot in the middle disk

of the group was perceived. The task was to indicate via push button presses if this rotation was clockwise or counterclockwise (counterbalanced within blocks). This nonretinotopic motion discrimination task is challenging to impossible in the two-disk control conditions, because no rotation is perceived.

### Stimulus specifics

A red fixation point (square,  $0.07^\circ$  side-length) was displayed in the middle of the screen throughout the trial. The disks had a diameter of  $1.35^\circ$  and were presented  $1.6^\circ$  above the fixation point (center-to-center). The interdisk distance was  $1.6^\circ$  (center-to-center). The default displacement to the left and right was  $1.6^\circ$  (one inter-disk distance), i.e., in the two central stimulus positions the two disks are presented in every frame. The white dots had a diameter of  $0.21^\circ$  and were placed halfway between the disk's center and the rim. The stimuli were presented on a midlevel gray background. In each block we counterbalanced the rotation direction of the dot in the middle disk (clockwise, counterclockwise), start-side of the third disk (left, right), and the start orientation of the dot ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ ,  $270^\circ$ ). Each trial started with two frames in which the disks were presented without dots, followed by four frames with dots and ending with another frame without dots. When no response was registered within 3 s after the last stimulus disappeared, a beep indicated the omission and the trial was repeated at a random moment during the block. No other feedback was provided. Trials were separated by a blank screen intertrial interval of 1.6 s.

### Conditions

Movie demonstrations of all conditions are provided in the online supplementary materials.

1. Baseline condition: Three black disks with white dots moved left and right in concert.
2. Unpredictable contrast polarity I: The three disks inverted contrast polarity alternately from frame to frame, that is, black disks switched to white and white dots to black, or vice versa. Per frame, all three disks had the same contrast polarity.
3. Unpredictable contrast polarity II: Per frame, the contrast polarity of each disk was chosen randomly. For example, in one frame the left and middle disk are black with white dots and the right disk is white with black dot; in the next frame the middle disk is white with a black dot and the left and right disks are black with white dots, etc. The dot had always the opposite contrast of "its" disk.
4. Unpredictable shape: The shape of the disks changed with every frame. Disks, stars, diamonds, and "flowers" were presented in random order, and squares without dots were presented in the preceding two and the last frame. Per frame, the three shapes were the same.
5. Unpredictable group motion: The group of three disks did not move predictably left and right, but moved randomly across the screen. The horizontal

alignment of the disks and interstimulus distances were maintained. All disks stayed within a distance of  $3.7^\circ$  from the fixation point and displaced by at least  $1.1^\circ$  between one frame and the next.

6. Combination: The group moved randomly across the screen as in Condition 5 and their contrast polarity and shape changed from frame to frame as in Conditions 3 and 4, respectively. All disks stayed within  $4.5^\circ$  from the fixation point and displaced by at least  $1.1^\circ$  between one frame and the next.

All distances are edge-to-edge unless noted otherwise. In the random-motion conditions the stimulus could overlap with the fixation point, in which case the fixation point was drawn on top of the stimulus. The conditions were presented in random order. For each condition, we presented one block of 96 trials (128 trials for the first two participants). Each block was followed by a control condition that was *identical* to the experimental block, except that the third alternating disk was omitted. Therefore, the rotation was not perceived and the dots appeared to move up-and-down in one and left-and-right in the other disk (cf. Figure 2). The task was the same as in the three-disk conditions, but it was very difficult because the rotation was not perceived. Each block took about 7 min to complete.

### Fixation control

If stable gaze is maintained, the retinotopic dot motion percept is linear while the nonretinotopic percept is rotating. If the Ternus–Pikler display is tracked with the eyes, the dot rotates in both retinotopic and nonretinotopic coordinates and one cannot disentangle their respective contributions. In addition, tracking eye movements would create efference copies that could be used for discounting common motion, thereby invalidating our method. To control that participants did not track the stimulus, we recorded their gaze position binocularly at 500 Hz using a SMI iViewX HiSpeed 1250 eyetracker (SensoMotoric Instruments, Berlin, Germany). The eyetracker was calibrated for each participant before the start of the experiment using the manufacturer's calibration routine.

### Statistical analysis

We analyzed performance in terms of sensitivity  $d'$ , which we corrected for extreme values using the log-linear correction proposed by Hautus (1995). Analyses in terms of percent correct led to the same conclusions in all cases. We used the individual performance level in Condition 1 as a baseline value and subtracted it from the performance level in the other conditions. All

differences were tested against 0.0 with two-sided one-sample  $t$  tests. All statistical tests were performed in the free and open-source JASP software (JASP Team, 2016).

## Results

Participants indicated whether they perceived clockwise or counterclockwise dot rotation in the Ternus–Pikler display. In the baseline condition (Condition 1), performance was high when the three disks were presented, and low when only two disks were presented, replicating previous findings (Boi et al., 2009). A similar pattern of results was observed in all other “unpredictable” conditions (Figure 3, top). We subtracted the individual performance levels in Condition 1 from the performance levels in the other conditions (Figure 3, bottom). Most differences were close to zero in both the three and two disk conditions, indicating that, despite unpredictability of the motion paths and changes in shape and contrast polarity, performance was effectively the same as in the baseline condition. One-sample  $t$  tests of the differences against zero were all nonsignificant (cf. Figure 3, bottom). Only in Condition 6 there was a trend toward lower performance,  $t(13) = -1.968$ ,  $p = 0.071$ , which did not survive Bonferroni correction ( $p = 0.710$ ).

### Fixation control

Observers did not track the disks (see Supplementary Figure 1). We plot the grand average of the horizontal eye positions for each condition. Tracking of the stimulus with the eyes had manifested in an alternation of positive amplitudes when the stimulus is presented to the left and negative amplitudes when the stimulus is presented to the right. In the random motion conditions, tracking of the stimulus had manifested in an increased variance compared with the reliable conditions. We found no such patterns at a scale of  $\pm 0.2^\circ$  (the stimulus was presented at  $1.6^\circ$ ), indicating that on average the participants maintained stable fixation. Data and details of the analysis can be found in the supplementary materials online.

## Experiment 2

In Experiment 1, shape, contrast, and the location of the group changed unpredictably. Here, we further decreased motion predictability by randomly choosing the location of the group and jittering the positions of the disks *within* the group. To perceive the nonretinotopic motion of the dot, it is necessary that the

disks move as a group, providing the reference frame for the dot motion (Boi et al., 2009). Jittering the positions of the single disks may impair group motion perception, which is crucial for the nonretinotopic perception of the dot (Boi et al., 2009). We determined to which extent observers perceived group motion using subjective measures, to separate performance changes caused by either diminished group–motion perception or decreased predictability.

## Methods

The methods for Experiment 2 were identical to Experiment 1 unless noted otherwise as follows.

In Conditions 1–3, the group moved left-right. Condition 1 is the standard condition, identical to Condition 1 of Experiment 1. In Condition 2, the individual disk positions were jittered horizontally with respect to the group center. In Condition 3, the individual disk positions were jittered both horizontally and vertically. In Conditions 4–6, the group moved randomly as in Condition 5 of Experiment 1. Condition 4 was very similar to Condition 5 of Experiment 1. In Condition 5, the individual disk positions were jittered horizontally, relative to the randomly moving group center. In Condition 6 the disk positions were jittered horizontally and vertically. In Condition 7, the disk positions were no longer anchored to the group center before being jittered. Instead, for each individual disk random positions were chosen that were independent of the other disks. All conditions were run in random order and were followed by a block of control trials, in which only two disks were presented (one disk in Condition 7, see the following material). The control conditions are identical to the experimental conditions, except that only the two disks with up-down and left-right moving dots are presented (cf. Figure 2). In the control condition for Condition 7, only a single disk with rotating dot was presented.

### Participants

Ten new, naïve participants participated in the experiment (five female, all right-handed, age  $M = 23.0$  years,  $SD = 3.0$ , range: 20–30 years).

### Stimulus and task

Each block comprised 40 trials and took about 3.5 min. Black disks with white dots were used in all conditions. The task was again to indicate whether clockwise or counterclockwise rotation was perceived. Stimuli were presented at a distance of 0.66 m on a 24-in. Asus VG248QE LCD monitor ( $1,920 \times 1,080$  pixels, 60 Hz; Asus, Taipei, Taiwan).

### Stimulus specifics

Stimulus duration was 133 ms and ISI duration was 200 ms. Each trial was followed by an intertrial interval of 1 s and the next trial started only after a central fixation was detected. The disks were  $1.92^\circ$  and the dots  $0.24^\circ$  in diameter. A red fixation point (round,  $0.05^\circ$  diameter) was presented in the middle of the screen throughout the trial. Unless noted otherwise as follows, the disks were presented  $3.8^\circ$  (two disk diameters, center-to-center) above the fixation point and were separated by  $0.5^\circ$  (edge-to-edge).

### Conditions

Movie demonstrations of all conditions are provided in the online supplementary materials.

1. Baseline condition: Three black disks with white dots moved left and right in concert.
2. Horizontal position jitter: The three disks moved left and right in concert. The disks were in the same vertical position, but the horizontal interdisk distances were jittered randomly by  $\pm 0.0$ – $1.0$  disk diameter. Importantly, the order of the disks was maintained across frames (i.e., left-most disk is the left-most disk in all frames, etc.)
3. Horizontal and vertical position jitter: The three disks moved left and right in concert. Both their vertical and horizontal positions within the group were jittered randomly by  $\pm 0.0$ – $1.0$  disk diameter in each frame. The order of the disks was maintained across frames.
4. Uncertain group motion: The three disks did not move predictably left-right, but moved randomly across the screen. From one frame to the next, the group displaced by at least one disk diameter in a random direction, while staying vertically and horizontally aligned and within  $7.5^\circ$  (four disk diameters) from the fixation point. The order of the disks was maintained across frames.
5. Uncertain group motion with horizontal jitter: The three disks moved randomly across the screen as in Condition 4. The disks were in the same vertical position, but their horizontal interstimulus distances were jittered randomly by  $\pm 0.0$ – $0.5$  disk diameter in each frame. The order of the disks was maintained across frames.
6. Uncertain group motion with horizontal and vertical jitter: The three disks moved randomly as in Condition 4. From frame to frame, the disks' positions within the group were jittered randomly by  $\pm 0.0$ – $0.5$  disk diameter in the vertical and by  $\pm 0.0$ – $1.0$  disk diameter in the horizontal direction. The order of the disks was maintained across frames.
7. Uncertain individual motion: Each individual disk moved randomly across the screen, independent of the other disks. Consequently, the order of the disks could change from frame to frame (e.g., the left-most disk in one frame could be the right-most disk in the next frame, etc.) All disks stayed within  $3.8^\circ$  (two disk diameters) from the fixation point. Contrary to the other conditions, only a single rotating disk was presented in the control condition, and performance was expected to be high.

In all conditions, the disks respected a distance of at least  $0.5^\circ$  to each other and the fixation point. All distances are edge-to-edge unless noted otherwise.

### Fixation control

The eyetracker was recalibrated before each block with in-house software using a dice-like five calibration point pattern (dots in the center and corners of an imaginary  $10^\circ \times 10^\circ$  square).

### Subjective ratings

After each condition of Experiment 2, we asked the participants to rate the predictability and grouping strength of the stimulus they had just seen. We used 5-point Likert scales with the endpoints labeled, respectively, “unpredictable–predictable” and “weak–strong.” Before the experiment, participants were shown a demonstration of Condition 1 with three disks as an example for strong grouping and of Condition 7 with three disks for weak grouping.

### Results

In the baseline condition (Condition 1), performance was high when the three disks were presented and low when only two disks were presented (Figure 4, top). We again subtracted the individual performance levels in Condition 1 from the performance in the other conditions (Figure 4, bottom). In the three-disks conditions, performance decreased significantly in all conditions and performance tended to decrease as a function of the amount of unpredictability in the stimulus—the more unpredictable the stimulus was, the lower was the performance.

Specifically, performance was lower when the stimulus moved randomly over the screen, instead of reliably left-right (Condition 4). Uncertainty of the disks' positions *within* the group further decreased performance, both when the group moved left-right (Conditions 2 and 3) and when the group moved randomly (Conditions 5 and 6). The differences did not

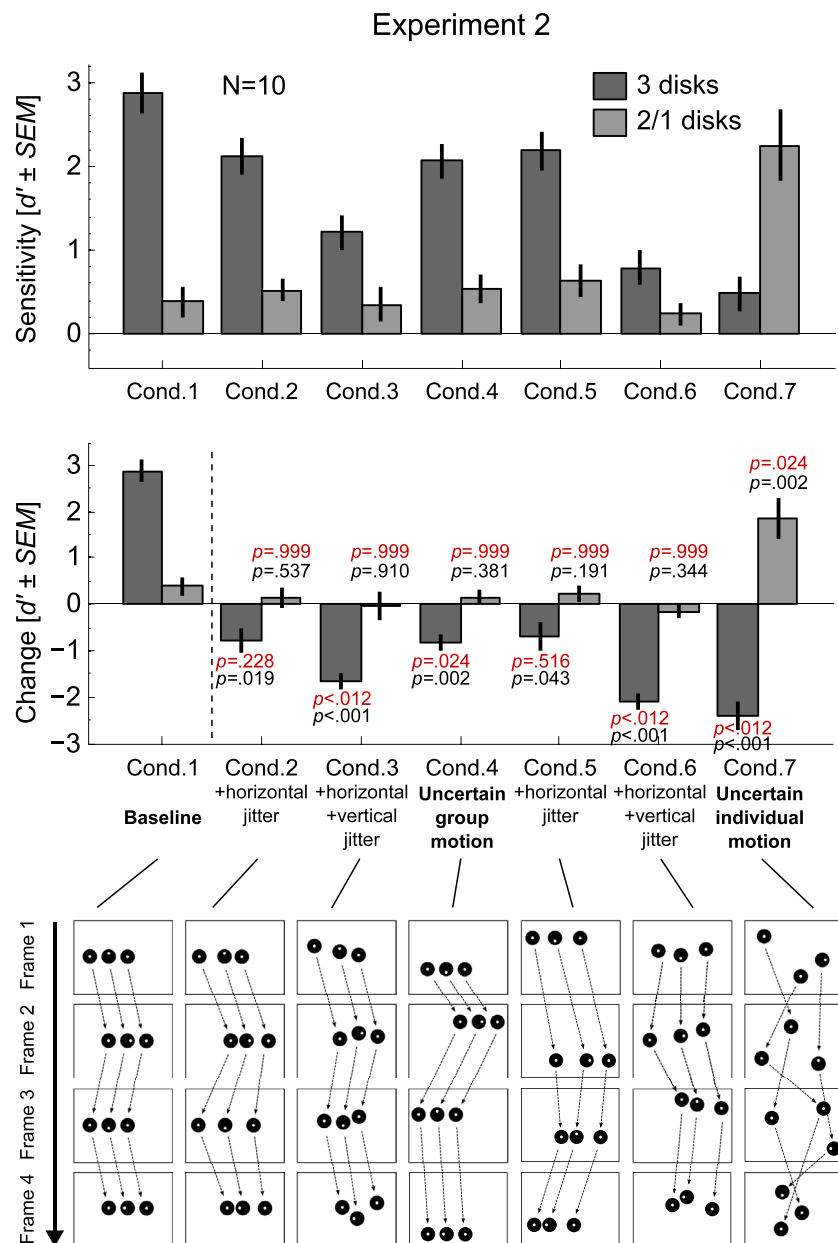


Figure 4. Experiment 2 stimuli and results. Top: Performance in terms of sensitivity  $d'$ . Bottom: Mean change in sensitivity  $d'$  compared with performance in Condition 1. Note that in the bottom plot for Condition 1, the actual  $d'$  values (as opposed to Change in  $d'$ ) are plotted for comparison.  $P$  values were computed in one-sample  $t$  tests against 0 and are reported Bonferroni corrected in red and uncorrected in black. In Conditions 1–3, three black disks moved predictably left and right and in Conditions 4–6, the three disks moved randomly across the screen as a group. In Conditions 2 and 5, we randomly jittered the interstimulus distance of the disks. In Conditions 3 and 6, we additionally jittered each disk's vertical position. Performance in all conditions was lower than in Condition 1 (all  $p$ s  $\leq 0.043$ ; see main text). Performance in the control conditions with two disks did not differ significantly from Condition 1. In Condition 7, the disks did not move as a group, but each disk followed an individual, randomly determined motion trajectory. Performance was near chance level. Unlike in the other control conditions, only a single disk was presented in the control condition of Condition 7, to show that observers can track the disk well.

survive Bonferroni correction in the conditions with only horizontally jittered positions (Conditions 2 and 5). Importantly, performance was equally low in all conditions when only two disks were presented (all  $p$ s  $> 0.191$ ). This shows that the invariably higher

performance in the three disks conditions was not due to cognitive inference, but indeed due to nonretinotopic perception.

In Conditions 1–6, the order of the disks was maintained across frames, that is, the left-most disk in

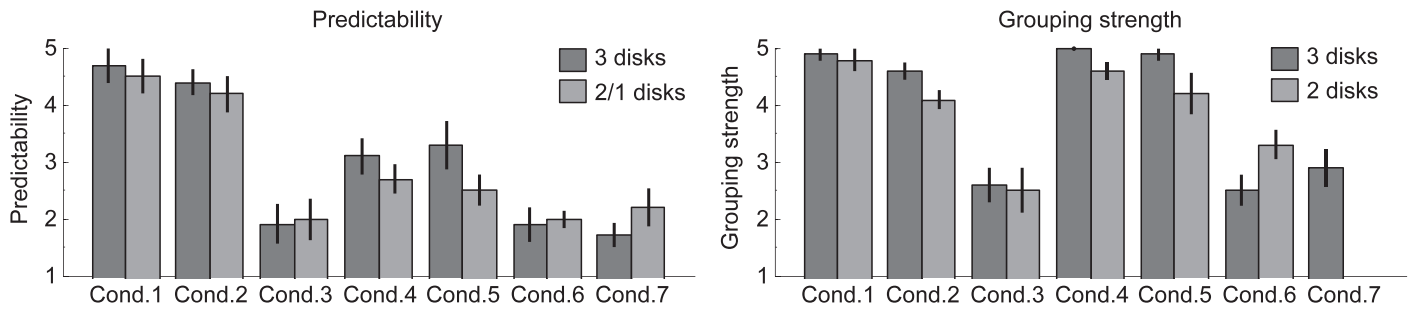


Figure 5. Mean subjective ratings of predictability (left) and grouping strength (right) of the different stimuli. Error bars depict the standard error of the mean. No grouping strength ratings were obtained for the control condition of Condition 7, because only a single disk was presented.

frame  $N$  corresponded with the left-most disk in frame  $N+1$ , and so forth. In Condition 7 we dropped this constraint and each disk moved randomly across the screen, independently from the other disks. As a control condition, we only presented one disk that moved randomly across the screen, instead of two disks as in the other conditions. When three disks were presented, performance was strongly reduced compared to the baseline condition and was lowest overall. However, when only one disk was presented, performance was high and comparable with Condition 4, where three aligned disks moved randomly over the screen (cf. Figure 4, top).

### Fixation control

We performed the same analyses as for Experiment 1. Compliance with the central fixation instruction was again good, except for one subject who tracked the stimulus in a small proportion of trials, primarily in Conditions 1–3. The remaining subjects fixated well, except for very rare exceptions on single trials. Data plots and details of the analysis can again be found in the supplementary materials.

### Subjective ratings

After each condition of Experiment 2, our participants rated how predictable and how strongly grouped the disks were perceived (Figure 5). We correlated the mean subjective ratings of predictability and grouping strength with performance, i.e., mean sensitivity  $d'$ . In the conditions with three disks we found strong correlations between performance and both predictability ( $r = 0.925$ ,  $p = 0.003$ ) and grouping strength ( $r = 0.897$ ,  $p = 0.006$ ). In the control conditions, performance did not correlate significantly with predictability ( $r = -0.237$ ,  $p = 0.608$ ) or grouping strength ( $r = 0.541$ ,  $p = 0.268$ ), because performance was invariably low.

## Discussion

The parts of a moving object are perceived relative to the object rather than in retinal coordinates. For example, we perceive a reflector to rotate on the wheel of a moving bicycle, even though its trajectory is cycloidal on the retina (Figure 1). This nonretinotopic percept occurs because the motion of the object (bicycle) is discounted from the motion of its parts (reflector).

Using the Ternus–Pikler display, we found that unpredictability of the stimulus generally does not hamper nonretinotopic motion perception, at least not within the range of manipulations we tested. In Experiment 1, the stimulus unpredictably changed contrast polarity, shape (i.e., contours), its motion trajectory, or even all three combined. In all conditions, nonretinotopic motion–direction discrimination did not significantly decrease compared to the predictable baseline condition. Hence, the brain is capable of computing the nonretinotopic motion of objects even when their appearance changes and they move unpredictably. The current experiments used apparent motion with rather discrete steps, but we believe that the results can be generalized to “normal,” ecological viewing conditions. If this is the case, the results suggest that nonretinotopic motion can be computed online, for each stimulus anew, because predictability is not necessary.

This computation is contrast–polarity invariant. We tested contrast polarity, because contrast-reversal in apparent motion stimuli can lead to the reversal of the perceived direction of phi motion, a phenomenon known as reverse–phi (Anstis, 1970). The spatiotemporal properties of phi motion with the same contrast polarity (phi) and with the opposite contrast polarity (reverse–phi) are similar; however, the perceived directions are opposite (Bours, Kroes, & Lankheet, 2009). Hence, our finding that the perception of the direction of motion remains invariant with respect to contrast polarity in nonretinotopic motion is in sharp



contrast with the perception of phi motion. This finding has important implications for the computational modelling of nonretinotopic motion perception. There are two types of edge-detectors in primary visual cortex, simple and complex cells (De Valois, Albrecht, & Thorell, 1982). Only the responses of complex cells are contrast-polarity invariant. Because our observers were able to perceive nonretinotopic motion in spite of contrast polarity reversals, the brain seems to be capable of using the complex cell responses to guide nonretinotopic motion perception. This finding confirms the implementation of edge detection in computational models of nonretinotopic motion perception (Agaoglu et al., 2016; Clarke, Ögmen, & Herzog, 2016). The perception of “classic apparent motion”, which Wertheimer (1912) called beta motion, is relatively robust to featural changes such as shape, dimension, and color (Kolers & Pomerantz, 1971; Kolers & von Grünau, 1976). Here, we found that nonretinotopic processing is largely independent of the shape of elements, too. Most importantly, we were interested in how changes in the location of the stimulus influence nonretinotopic processing. Performance was almost unchanged in Conditions 5 and 6 of Experiment 1 compared with the standard condition, when the group changed location randomly from frame to frame. It seems that nonretinotopic perception does not crucially depend on the predictability of the reference frame motion.

In Experiment 2, we further perturbed the group structure by also jittering the positions of the individual disks relative to the group center. Performance decreased with increased uncertainty. Performance was close to chance-level in the most uncertain condition, where all elements moved independently (Condition 7). These results are likely explained by a decrease in the perception of group motion, as evident in the subjective ratings. Since, however, subjective ratings of predictability and grouping strength both strongly correlated with performance, we cannot disentangle to what extent unpredictability *per se*, i.e., independent of the deteriorated group motion percept, caused the decrease in performance. However, in most other conditions, nonretinotopic perception was largely robust to strong positional changes. For example, performance decreased only slightly and nonsignificantly in Conditions 2 and 5 with horizontal jitter. In Conditions 3 and 6 with horizontal and vertical jitter, performance decreased significantly but was still good and significantly above chance level.

Predictability plays an important role in many fields of vision and usually leads to better performance (Alink et al., 2010; Posner, 1980; Vetter et al., 2015). We found that nonretinotopic processing seems to be robust to unpredictable positional, contrast, and shape changes, even though many complex computations,

such as the ill-posed problem of motion correspondence, needs to be solved for both the reference frame and the part motion. Nonretinotopic processing plays an important role in ecological situations, and this may be the reason for the efficient computation of nonretinotopic information.

*Keywords:* nonretinotopic processing, uncertainty, predictability, grouping

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