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The influence of perceptual stabilisation on perceptual grouping of temporally asynchronous stimuli

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ABSTRACT

Even during fixation, our eyes constantly make small, involuntary eye movements that cause the retinal image to be swept across our retinae. Despite this, our world appears completely stable, due to powerful perceptual stabilisation mechanisms. Whether these mechanisms are of functional consequence for visual performance remains largely unexplored, however. We directly tested this by using a perceptual grouping task, where physically aligned alternate grid elements were presented with an imperceptible temporal offset. Observers' abilities to reliably group the grid into rows (or columns) is posited to arise from the failure in compensation of retinal slip arising from the small eye movements that occur during the temporal offset, effectively introducing a spatial shift in the arrangement of grid elements. We incorporated this perceptual grouping task within the *on-line jitter* illusion, which temporarily disables perceptual stabilisation mechanisms through a 10 Hz flickering annulus of random noise (Vision Res 43 (2003) 957–969). Observers' abilities to correctly group the grid stimulus were measured with and without perceptual stabilisation mechanisms engaged (i.e. non-flickering vs. flickering annulus). Grouping performance was better when eye movements were perceived, suggesting that the influence of retinal slip is increased when perceptual stabilisation mechanisms are disabled. We therefore find that perceptual stabilisation can measurably influence visual function, in addition to its perceptual effects.

1. Introduction

The on-line jitter illusion demonstrates how jittery our visual perception would be if we were aware of the incessant eye movements that occur during fixation (Murakami, 2003). In this illusion, a central static region is seen to jitter coherently when concentrically surrounded by a flickering region. Perceptual stabilisation mechanisms are temporarily disabled by the flicker to reveal the retinal motion arising from small, fixational eye movements. The on-line jitter illusion has previously been used to examine the correlation between fixation stability and motion sensitivity (Murakami, 2004), thereby demonstrating that a functional consequence of perceptual stabilisation mechanisms could be measured. The theory of retinal based stabilisation of small eye movements suggest that the visual system dismisses common image motions (as they are likely to originate from small eye movements) while interpreting differential motion as arising from external objects (Murakami & Cavanagh, 1998). As such, Murakami (2004) posited that sensitivity for detecting external motion would likely be poorer in the absence of a differential motion signal, or when this differential signal was unreliable. The on-line jitter stimulus was used to test this, where detection thresholds for linear motion of the random dot texture in the central disk region were measured under conditions where there was (1) no surround, (2) static surround, or (3) flickering surround. The results showed that motion detection thresholds were the lowest with a static surround, and were elevated either without a surround or when the surround flickered. Murakami (2004) suggested that the elevated thresholds with a flickering surround was due to the perceived relative motion between the centre and surround, preventing there being a stable reference frame for judging motion in the centre region (Murakami, 2004). However, the presence of a flickering surround would have temporarily disabled perceptual stabilisation mechanisms, where the physically moving central region would also be subject to perceived retinal motion arising from small eye movements in the absence of perceptual stability. It is therefore unclear whether the lack of perceptual stabilisation impairs the detection of local motion signals directly, or only indirectly through the lack of a stable reference frame to which to compare local motion signals to. Finding evidence that perceptual stabilisation mechanisms directly influence function is important as in the natural world, fixational eye movements shift all objects (e.g. targets and reference surrounds) equally and perceptual stabilisation mechanisms act on all objects in the field equally.

We have shown that the on-line jitter illusion is largely unaffected

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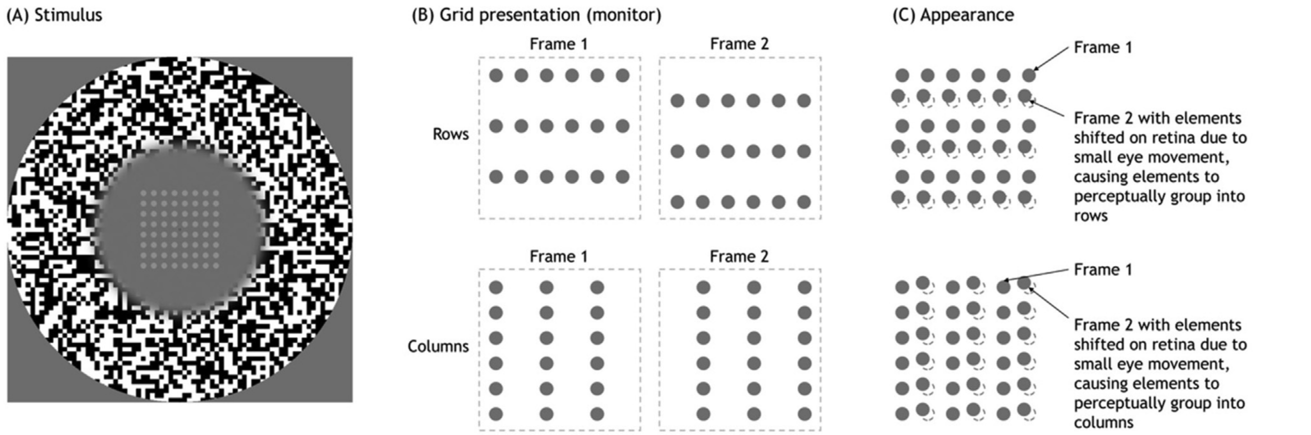

Fig. 1. Schematic of grid presentations used in the experimental stimulus. (A) On-line jitter illusion stimulus with regular grid presented in the central region, with a central red fixation spot. (B) The asynchronous presentation of alternate row (or column) elements presented on successive display frames. The dotted frames in the figure are for illustrative purposes only and were not present in the actual stimulus. (C) Example of the perceived arrangement of grid elements into rows (top) and columns (bottom) resulting from a diagonal shift occurring between the two presentation frames, respectively. Note that a 6 × 6 grid has been used to illustrate the presentation and appearance of the grid in (B) and (C), while experimental stimuli consisted of an 8 × 8 grid.

by changes in the spatial textures populating the two concentric regions (Park, Bedggood, Metha, & Anderson, 2017). This finding creates the opportunity to incorporate a novel test stimulus (with an altered spatial texture) for a particular visual task within the central region, and so test visual performance under conditions where perceptual stability is either present or absent for all elements involved in the visual task. Any differences in measured performance between these conditions can tell us whether perceptual stabilisation of small eye movements has a direct, measurable effect on visual function.

Our experiments extend those of Murakami (2004), by testing in a different visual function domain – that of spatial, rather than temporal, vision – and by using a task where performance is not contingent on a reference frame. We used a perceptual grouping task, where the grouping stimulus consisted of a regularly arranged grid of circular elements that were presented in physical alignment. On a given trial, alternate row (or column) elements were presented on two successive display frames, although the impression is of a single grid, briefly flashed in its entirety. Despite the apparent unified grid percept, observers are able to reliably group the grid into rows or columns in accordance with the temporally asynchronous stimuli presentations (Dakin & Bex, 2002; Usher & Donnelly, 1998; Wallis, 2005, 2006). This performance is due to small eye movements that occur between asynchronous presentations of alternate row (or column) elements, producing small spatial offsets between alternate grid elements (Wallis, 2006). Using eye tracking, Wallis (2006) showed fixational eye movement amplitudes were a good predictor of whether an observers' response would be affected by the temporal offset between alternate row or column elements. Our previous work has also systematically explored the relationship between retinal image velocity and grouping performance, revealing a largely linear relationship (Park, Metha, Bedggood, & Anderson, 2019).

For retinal-based stabilisation of small eye movements (Murakami & Cavanagh, 1998), the estimation of global image motion must occur over a narrow, but finite time window. Wallis posited that brief, temporally asynchronous stimuli could reveal the lower limit of the integration period in which global motion is calculated (Wallis, 2006). The failure to accurately estimate global motion means that the retinal slip occurring between the two presentation frames is not fully compensated for, thereby effectively introducing the spatial shift required for grouping to take place.

If perceptual stabilisation mechanisms were disabled, it remains unclear whether the perceptual manifestation of retinal slip arising from small eye movements (i.e. perception of "jitter") would enhance or be detrimental to grouping performance (or have no effect). We hypothesise that a jittery percept may be accompanied by improved grouping performance due to an effective increase in perceived shift between frames. It is also possible, however, that grouping is hindered due to judgements being made based on a jittery percept. Here we measure grouping performance with a concurrent nonflickering or flickering annulus, allowing grouping to be measured in the absence or presence of perceptual stability, respectively. Measured differences in performance between the two conditions will allow inferences to be made about whether grouping of temporally asynchronous stimuli is simply determined by the eye movements that occur between presentation frames, or whether it is also influenced by whether or not these eye movements are perceived.

2. General methods

Twelve healthy observers participated in the experiments. All subjects had visual acuity better than logMAR 0.10, and viewed stimuli using their habitual spectacle correction and natural pupils. The study followed the Declaration of Helsinki guidelines and was approved by our institutional ethics committee. All observers gave informed written consent prior to participation.

2.1. Stimuli

We presented stimuli on a calibrated computer monitor system (ViSaGe graphics card: Cambridge Research Systems, UK; Mitsubishi Diamond Pro 2070sb CRT monitor; resolution 1024 × 768, frame rate 120 Hz, subtending 41 × 31 deg at 55 cm) in a darkened room. Observers viewed the stimulus display monocularly with their non-preferred eye occluded by an opaque patch, with their heads stabilised by a chin rest.

The test stimulus closely matched the spatial and temporal properties of the original on-line jitter illusion stimulus (see Murakami (2003)), with the exception of the central region (Fig. 1A). This region was populated with the perceptual grouping stimulus, which consisted of a regular grid of 64 circular elements (8 × 8) each 23.8 min arc in diameter, with regular horizontal and vertical spacings of 23.8 min arc. The entire grid subtended approximately 6 × 6 deg. Grid elements were grey (16 cd/m^2) on a uniform grey background (10 cd/m^2), giving a contrast increment of 60%, unless otherwise noted. We measured the persistence of the grid elements with a photodiode, and found their luminance decayed to 5% of peak values within 1 ms.

When a grid was not being presented, the central region remained uniform grey (10 cd/m^2). The grid elements varied depending on the

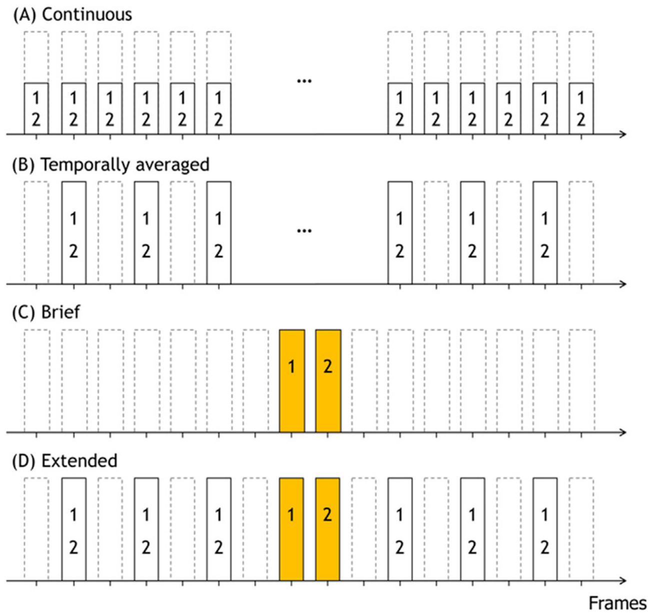

Fig. 2. The temporal properties of the grid stimulus presentation used in experiment 1. Conditions (A–D) correspond to the presentation description detailed in text. Each block represents a video display frame, the numbers within the blocks show the presentation of odd (1) and even (2) elements of the grid. Where alternate grid elements were presented (in yellow), alternate odd or even elements were presented first randomly in a given trial, unless stated otherwise in the methods. The height of the blocks represents the change in luminance of the grid elements from the background (10 cd/m^2), with the full height block being 6 cd/m^2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

condition being tested, and are detailed below and in Fig. 2.

A. Continuous: grid presented on every frame, with grid elements at half contrast (luminance of 13 cd/m^2)
B. Temporally averaged: alternate presentation between grid (16 cd/m^2) and uniform grey blank, giving the same apparent percentage luminance contrast as in the Continuous condition, above.
C. Brief: odd and even row (or column) elements (16 cd/m^2) on two successive frames, as used in Wallis (2006).
D. Extended: presentation of alternate grid elements as in the Brief condition (C), but preceded and followed by the presentation of temporally averaged grid presentation, as in the Temporally averaged condition (B).

Our extended condition (Fig. 2D) allowed for a protracted presentation of the grid stimulus in which to perceive eye movements, whilst keeping temporally asynchronous presentations of alternate grid elements confined to two successive display frames as used in Wallis (2006). We needed to establish that it was subject to illusory jitter, and was comparable in degree of perceived jitter to a continuous presentation of all grid elements without the inclusion of the temporally asynchronous grouping stimulus (Fig. 2A and B; continuous and temporally averaged conditions). The brief condition consisted of alternate grid elements being presented in isolation (Fig. 2C), as used in Wallis (2006). All four grid presentation conditions (A–D) were used in Experiment 1 for subjective ratings of illusory jitter, but only the brief and extended conditions (C and D) were used for measuring grouping performance in Experiment 3.

A central red fixation square (9 × 9 min arc) was always visible, except during the two-frame presentation of alternate grid elements in both brief and extended presentation conditions. The bordering region between the centre stimulus region and outer flickering annulus was blurred by a cumulative Gaussian shaped contrast modulator with a standard deviation of 40 min arc, as per the original on-line jitter illusion (Fig. 1A). The surround region was filled with a random dot texture, each dot 17 × 17 min arc wide, which consisted of 50% black (< 0.1 cd/m^2) and 50% (93 cd/m^2) white dots. A new random dot texture was generated for each trial and was flickered at 10 Hz, where all dots remained on during the 74.7 ms (9 frames) on-duty period and switched to mean luminance grey (10 cd/m^2) for 24.9 ms (3 frames) during the off-duty period.

2.2. Procedures

Rating task: Observers were asked to rate the magnitude of coherent motion (“jitter”) perceived in the centre region while maintaining fixation on the fixation square. A rating scale ranging 0–10 was used, with 0 corresponding to no jitter and 10 to jitter equivalent to the reference on-line jitter illusion (Murakami, 2003). The configuration of this reference stimulus was similar to that of the concentric stimulus used in this study (Fig. 1A) except for the central region, which was populated with a random texture consisting of Gaussian elements (see Murakami (2003) for details). For as long as the surround region was flickered, the central pattern, which was always displayed, appeared to move coherently in random directions. The reference illusion was demonstrated periodically (every 20 trials) to remind observers of what a rating of “10” looked like. Observers verbally reported their ratings after each trial, with the final value being the mean of 10 ratings for each observer for each test condition in Experiment 1.

Discrimination task: We used a method of constant stimuli paradigm for all discrimination tasks, where observers were forced to choose which stimulus pattern (rows or columns) had been presented on each trial. Observers indicated their response by button press, and auditory feedback was given for correct and incorrect responses for every trial. Of note is that the use (Usher & Donnelly, 1998) or non-use (Wallis, 2005, 2006) of feedback in perceptual grouping tasks appears to be based on the particular preference of the experimenters. Although absolute performance might be expected to improve if participants optimised their strategy to the grouping task based on the trial-by-trial feedback we provided, this should affect all conditions equally and so cannot explain the differences between conditions we report here.

For both rating and discrimination tasks, stimuli were presented for 2 s, followed by a minimum interstimulus interval (ISI) of 3 s during which observers responded. The minimum ISI was determined from pilot testing (data not shown), and ensured that the percept would not be affected by adaptation to flicker (Murakami & Cavanagh, 1998), or by afterimages from the preceding stimulus presentation. Where alternate grid elements were presented over two successive display frames in isolation (the *brief* stimulus condition described above), we centred the presentation of alternate grid elements within a 2-second temporal window to ensure stimulus presentation times were kept consistent across different conditions. Presentation of all stimuli conditions within each experiment were randomized unless stated otherwise.

2.3. Analyses

Statistical analyses were performed on paired data by using GraphPad Prism v5.01 (GraphPad Software, San Diego, CA), and are detailed in each Results section. Data were first checked for normality using the D’Agostino & Pearson omnibus normality test (Pearson, D’Agostino, & Bowman, 1977). Where data passed the normality test, parametric tests were used. Otherwise, an equivalent non-parametric test was used.

3. Experiment 1: Illusory jitter rating of grid

In this experiment, we examined the perceived illusory jitter of grid stimuli (see General Methods, above) within the central region of the on-line jitter illusion, to ensure visible jitter was present. Compared

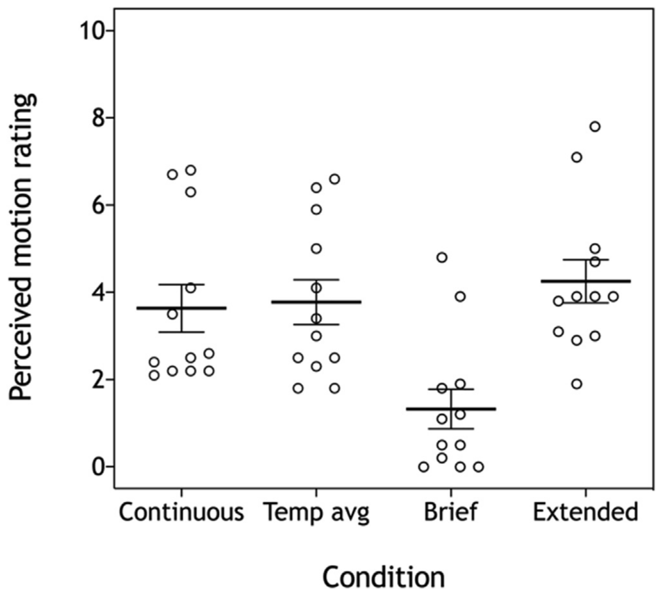

Fig. 3. Individual average ratings of illusory jitter (circle symbols) are shown, along with mean ratings ± 1 SEM (horizontal bars) for all grid presentation conditions presented in the central region of the on-line jitter illusion stimulus with concurrent flickering of the annulus region.

with the original online jitter illusion, we anticipated some reduction in jitter ratings of our test stimuli as central viewing of the illusion has been reported to reduce the illusory jitter (Murakami, 2003). However, the purpose of this experiment was to compare differences in illusory jitter between our presentation conditions, rather than to quantify any general reduction in jitter magnitude relative to the original online jitter illusion.

Perceptually, the continuous and temporally averaged presentations were similar in appearance, with both presentation methods having the same luminous contrast over time. We hypothesized that observers would perceive comparable illusory jitter for all protracted presentations of the grid, but perceive little to no jitter for briefly presented grid stimuli.

3.1. Results

Subjective jitter ratings are shown in Fig. 3. Brief presentations of grid stimuli were subject to very little jitter. Jitter ratings were comparable across all conditions where grid stimuli were presented for a protracted period, with an overall reduction in magnitude of jitter perceived relative to the eccentrically viewed reference stimulus (the “10” on the rating scale).

Ratings were significantly different between grid presentation conditions (Repeated measures (RM) one-way ANOVA; $F(3,33) = 19.55$, $p < 0.0001$), with post-hoc testing showing it was the brief presentation condition that differed from the others (Bonferroni corrected pairwise comparisons, $p < 0.0001$); all other pairwise comparisons were not significant.

A small “twinkle” was apparent in the extended presentation condition at the temporal junction of the temporally averaged and alternate grid element presentations of the grid. “Transient twinkle perception” has been reported for stimuli presentations at flicker frequencies above the CFF for humans (Nakajima & Sakaguchi, 2015). The perceived jitter of the extended grid stimuli was unaffected by the presence of the twinkle, indicated by comparable jitter ratings with continuous and temporally averaged grid stimuli that should not induce a twinkle percept.

Overall, we find that a flickering surround induces a reliable, albeit slightly reduced in magnitude, percept of illusory jitter in our grid stimulus provided it is presented for a protracted period.

4. Experiment 2: Visibility of temporally asynchronous presentation

Temporal offsets of as little as a few milliseconds can be reliably detected by observers, possibly due to triggering mechanisms for motion detection (Westheimer & McKee, 1977). Usher and Donnelly (1998) investigated whether perceptual grouping of temporally asynchronous stimuli was mediated by implicit motion computation. The authors reported that a 16 ms temporal asynchrony in alternate grid element presentation (corresponding to a total time cycle of 32 ms) resulted in “a perfectly steady [grid] percept with no flicker or motion reported by subjects” (Usher & Donnelly, 1998). Wallis (2006) also described that his naïve subjects reported the temporally asynchronous grid stimuli was single and stationary. However, it is not apparent whether this was quantitatively examined in his study.

Therefore, we designed an experiment to quantitatively demonstrate that the temporal offset between alternate grid elements was imperceptible, particularly for our novel extended grid condition. Observers were asked to judge the order of alternate grid element presentation of the temporally asynchronous grid stimulus – i.e. whether odd or even grid elements were presented first. We hypothesised that if the temporal offset in presentation was reliably perceived by observers, the ability to judge the order of presentation would be better than chance.

4.1. Methods

In each trial, there was equal chance of odd or even alternate grid elements being presented first. Testing blocks alternated between row and column conditions for brief and extended grid conditions. Within a testing block of 30 trials, presentations were either all rows or all columns. All observers completed the brief condition first, followed by the extended condition. A practice run (30 trials) for each condition was completed before commencing data collection (90 trials for each condition).

4.2. Results

The mean performance for all presentation conditions was not significantly different from chance (theoretical mean of 0.50) (one-sample *t*-test, $p > 0.05$ for all conditions) (Fig. 4).

Our results provide formal support for the previous qualitative statements of Wallis (2006) and Usher and Donnelly (1998) that brief temporally asynchronous grid stimuli do not contain reliable perceptual cues. This lack of cues also applies to our extended presentation condition. As temporal offsets are not visible, they cannot account for the perceptual grouping of briefly presented temporally asynchronous grid stimuli as reported by Wallis (2006), as well as in the extended presentation used to assess grouping performance in the experiments to follow.

5. Experiment 3: Influence of perceptual stabilisation on grouping

The aim of this experiment was to measure grouping performance with a concurrent flickering or nonflickering annulus, thereby measuring grouping performance under conditions where perceptual stabilisation of the grid was or was not allowed to occur. Differences between the two conditions would suggest that perceptual grouping of temporally asynchronous stimuli is not simply determined by eye movements occurring between presentation frames, but also whether these eye movements are perceived. In this experiment, observers were required to make judgements of whether the grid (brief or extended) was perceptually grouped into rows or columns.

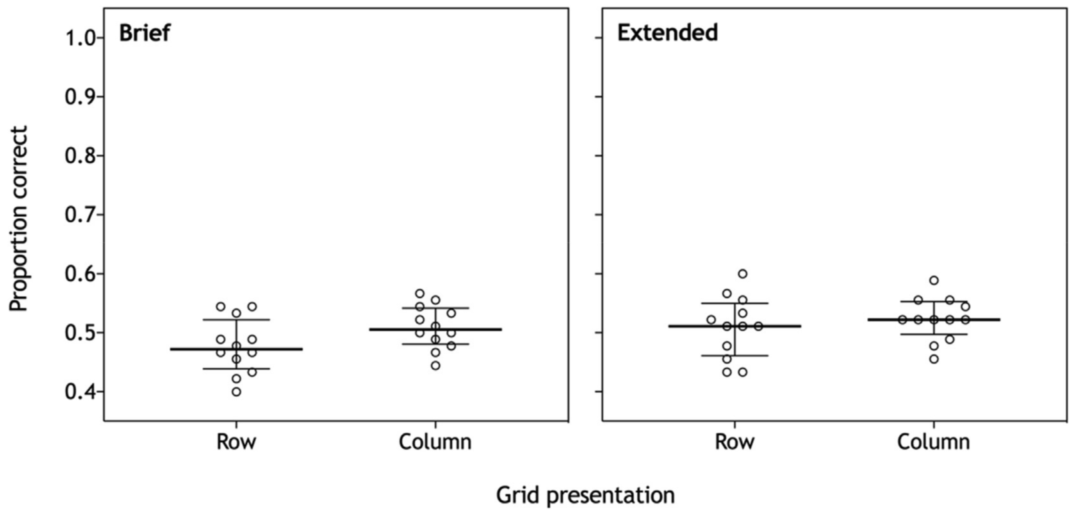

Fig. 4. Visibility of temporal presentation order of the grid stimulus. Brief (left) and extended (right) grid presentation conditions showing individual performance (circle symbols) and group mean ± 1 SEM (horizontal bars).

5.1. Methods

Training was first performed for brief and extended grouping stimuli. One test run consisted of 30 trials, where there was equal chance of row or column elements being presented. The ordering of alternate grid element presentations – i.e. whether odd or even elements were presented first – varied randomly between trials. For the *brief* presentation condition, all observers completed two practice runs (60 trials). Grouping performance was then assessed every 3 practice runs against a performance criterion of 65% correct, which was conservatively set based on the 70% average performance reported in Wallis (2006). If the performance criterion over the 3 runs was not achieved, a further 3 practice runs were given and performance reassessed, up until a maximum of 15 practice runs. Only four (out of twelve) subjects met this criterion with less than 15 practice runs. For the *extended* presentation condition, observers performed the same number of practice runs as they undertook in the brief presentation condition.

Perceptual grouping performance was then measured for both brief and extended conditions with a concurrent flickering or nonflickering surrounding annulus. All observers performed a further practice run for each condition before data collection. Testing consisted of 4 blocks of 12 runs (30 trials) each. Each block consisted of either all brief or all extended grid presentations, with the order of blocks counterbalanced. Within each block, test runs alternated between flickering and nonflickering conditions. In total, each condition had 360 trials.

5.2. Results

The results (Fig. 5) showed that for the brief condition, there was no difference in grouping performance between flickering and nonflickering surround conditions (Wilcoxon matched-pairs signed rank test, $p = 0.68$). However, for the extended condition, observers performed better in the presence of a flickering surround compared to when the surround is static (Wilcoxon signed rank test, $p = 0.02$).

The results suggest perceptual grouping performance for briefly presented stimuli is unaffected by disabling perceptual stabilisation mechanisms. This is not surprising, as the perceived appearance of the briefly presented grid stimuli are likely to be equivalent whether perceptual stabilisation mechanisms are active or not, given the stimulus is likely too brief for such mechanisms to be effective. However, the results for the extended condition demonstrate grouping performance to improve, as hypothesised, when eye movements are perceived. There are two further noteworthy points. Firstly, grouping of perceptually stabilised extended stimuli were not significantly different from chance (Wilcoxon signed rank test, $p = 0.09$), while this was not the case for the flickering annulus. Secondly, there was large variability in grouping performance evident across observers. Anecdotally, it appeared that those with more experience in psychophysical observation tended to have poorer performance. We speculated that more experienced observers might have better fixation, and so have poorer performance due to smaller shifts between presentations of alternate grid elements. Therefore, we examined this in the next experiment.

6. Experiment 4: Small eye movement statistics and grouping

We measured small eye movements while observers passively viewed videos approximately matching stimulus conditions from Experiment 3, to test the following hypotheses. Firstly, we hypothesised that eye movement statistics remain unchanged under viewing of different stimulus conditions – i.e. that viewing different stimuli did not entrain different eye movement patterns. Secondly, we hypothesised that variation in grouping performance between observers could be explained by differences in observer eye movement statistics. Specifically, we hypothesised that those with larger variation in fixation – i.e. eyes that move more on average – are more likely to introduce retinal shifts between presentation of alternate grid elements, which will manifest in this task as better grouping performance.

6.1. Methods

Stimuli videos were presented on a Dell U2711b 27″ monitor (resolution 2048 × 1152, frame rate 60 Hz, subtending 43.4 × 25.2 deg at 75 cm) in a dimly lit room. Observers heads were stabilised by a chin and forehead rest during recordings. Eye movements were recorded with a desktop mounted EyeLink 1000 (SR research, Mississauga, Ontario, Canada) at 1000 Hz. For all subjects, viewing and recording were performed monocularly, consistent the Experiments 1–3, above.

The videos were generated offline using MATLAB, and closely approximated our previously presented stimuli. Observers were instructed to maintain fixation on the spot at the centre of the screen, which remained visible for the entire duration of recording. Each video was preceded by a fixation spot appearing on a uniform background for 1 s. We presented videos for the following conditions, in a counterbalanced fashion: (A) original Murakami on-line jitter illusion, (B) fixation spot only, (C) flickering surround and brief grid presentation, (D) flickering surround and extended grid presentation, (E) static surround and brief grid presentation, and (F) static surround and extended grid

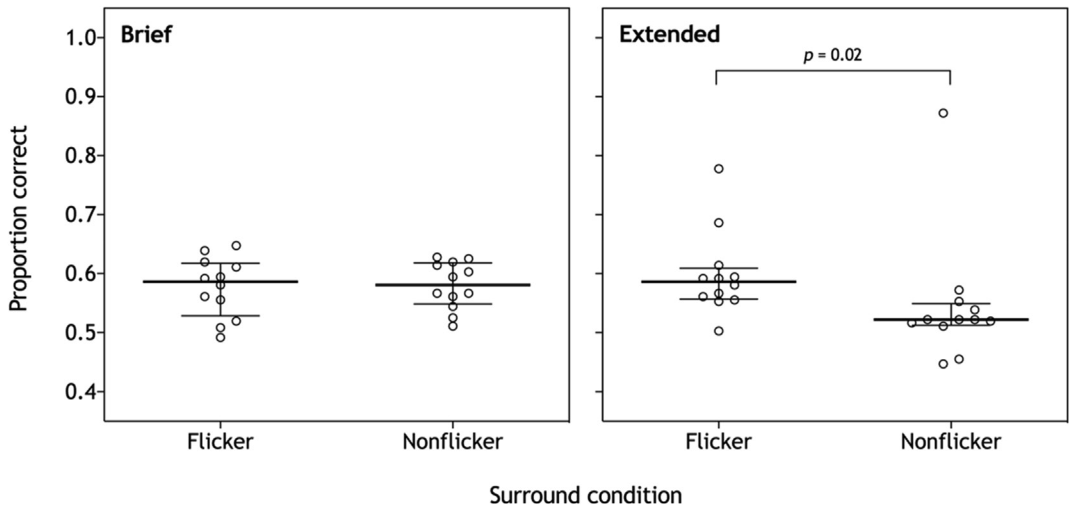

Fig. 5. Grouping performance in the presence and absence of perceptual stabilisation, denoted by flicker and nonflicker conditions, respectively. Individual grouping performance (circle symbols) for brief (left) and extended (right) presentation conditions. Group median ± IQR (horizontal bars) shown.

presentation. All videos were 10 s in duration, although we analysed only the central 2 s of all eye movement recordings to keep timings closer to those used in previous experiments. We repeated our eye movement recordings six times per condition.

A sample report was generated by Data Viewer (SR research Ltd, Mississauga, Ontario, Canada), which extracts and pre-processes the raw eye movement data for each trial. A custom MATLAB program then sorted the data based on blink- and velocity-based criteria detailed below, prior to performing statistical analyses.

Blink: Blinks were automatically identified by the eye tracker via an unknown, proprietary method. As it has previously been reported that the initial and final parts of the blink can be missed by the EyeLink 1000 software due to the pupil being only partially occluded by the lid (Costela et al., 2014), we excluded a further 100 ms period (100 samples) before and after the blink period identified in the sample report.

Velocity: Resultant velocities were first calculated using the x and y velocities in the sample report, and resultant velocities (the total vector calculated from x and y velocity values using Pythagorean theorem) exceeding 90 deg/s then excluded. As the velocity-amplitude relationship for microsaccades and saccadic eye movements fall on a continuum (Zuber, Stark, & Cook, 1965), the peak velocity corresponding to a 1 deg saccade was determined from the main sequence (Bahill, Clark, & Stark, 1975) to be 90 deg/s. This amplitude upper limit of 1 deg was chosen as it has been shown to capture the vast majority (> 90%) of microsaccades (Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008) while excluding most voluntary saccades (Engbert, 2006; Martinez-Conde, Macknik, Troncoso, & Hubel, 2009).

We also excluded samples within a 54 ms temporal window centred about those sample excluded by our velocity criterion (see Fig. 6 for the processing of an example eye trace). We determined this window by calculating the duration of a 15 deg saccade (Carpenter, 1977), being a saccade equivalent to the diameter of the central region of our stimulus. Visual inspection of eye traces indicated no saccades of this magnitude occurred for any of the observers during all recording conditions. As such, the temporal window was guaranteed to capture all samples exceeding the velocity criteria.

6.2. Results

All observers had less than 5.6% of samples excluded before the below analyses, except for one observer who had a higher proportion excluded (16.6%) due to blinks. Analyses of standard deviation of x and y velocities and stimulus condition showed no significant interaction between stimulus condition and standard deviation of eye velocities in the x and y direction (RM two-way ANOVA; $F(5,66) = 1.38$, $p = 0.24$) (Fig. 7). Overall, the mean standard deviation for vertical ($\mu_y = 3.56$) and horizontal ($\mu_x = 3.46$) velocities were similar. There was no effect of direction ($F(5,66) = 0.78$, $p = 0.38$) and stimulus condition ($F(5,66) = 1.23$, $p = 0.30$) on standard deviation of velocities.

There was no correlation between the standard deviation of the resultant velocity and grouping performance (determined in Experiment 3 flicker condition) for either brief or extended stimulus presentations, as shown in Fig. 8 (Spearman correlation, $r_s = 0.01$, $p = 0.98$ and $r_s = 0.26$, $p = 0.42$ respectively). It is possible that fixation variability – as measured by the standard deviation of resultant velocity – may be heavily influenced by the inclusion of microsaccades in our dataset due to their relatively large amplitudes. Therefore, we reanalysed the data after having excluded microsaccades using the microsaccade detection algorithm of Engbert and Kliegl (2003). We found that there was still no correlation between grouping performance and fixation variability for either brief or extended stimulus presentations (Spearman correlation, $r_s = -0.36$, $p = 0.26$ and $r_s = -0.01$, $p = 0.97$, respectively). Microsaccades typically occurred only once or twice during the 2 s fixation period across all conditions and observers, consistent with previous work (Ciuffreda & Tannen, 1995).

In line with our hypothesis, the results establish that eye movement statistics remain unchanged under different stimulus conditions. However, contrary to our proposed explanation for inter-individual variability, differences in eye movement statistics were unable to predict each observer's grouping performance.

7. Discussion

Our principal finding is that perceptual stabilisation of small eye movements can have a small, but measurable effect on perceptual grouping of temporally asynchronous grid stimuli of extended duration. The results suggest that disabling perceptual stabilisation mechanisms can effectively increase the perceived shift between alternate grid elements and facilitate grouping under conditions where these eye movements can be perceived (i.e. extended stimulus presentations). However, correlation between fixational eye movement statistics and grouping performance show that overall (i.e. time averaged) measures of fixation instability are poor indicators of performance. For brief presentation of the grid stimuli, grouping performance was unaffected by whether perceptual stabilisation mechanisms were active or not.

A key finding from the subjective ratings of illusory jitter was that protracted presentations of the grid stimuli were reported to jitter, while brief presentations resulted in little to no perceived jitter. As

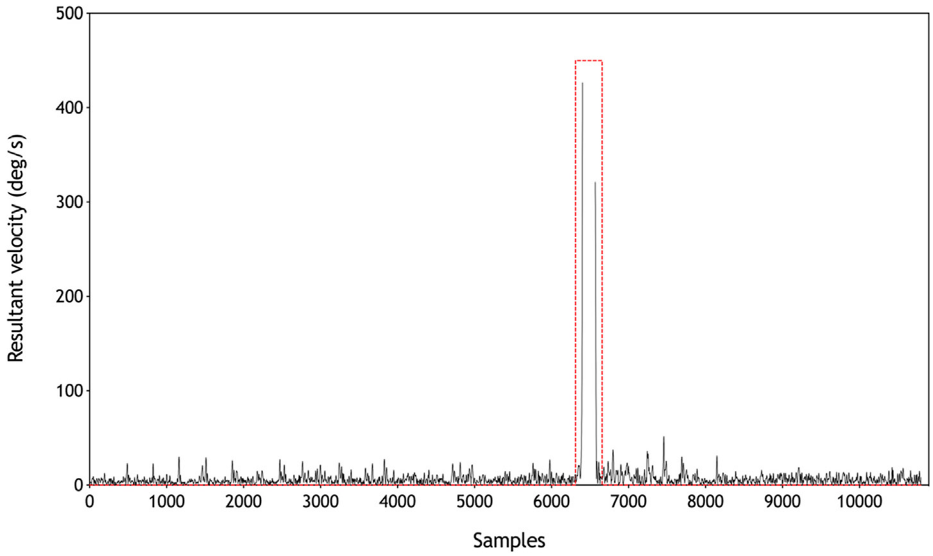

Fig. 6. Example of raw eye trace during passive viewing of the fixation spot only condition for one observer. Exclusion criteria for blinks and velocity threshold (90 deg/s) applied and exclusion shown (red dashed line) for one blink episode. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

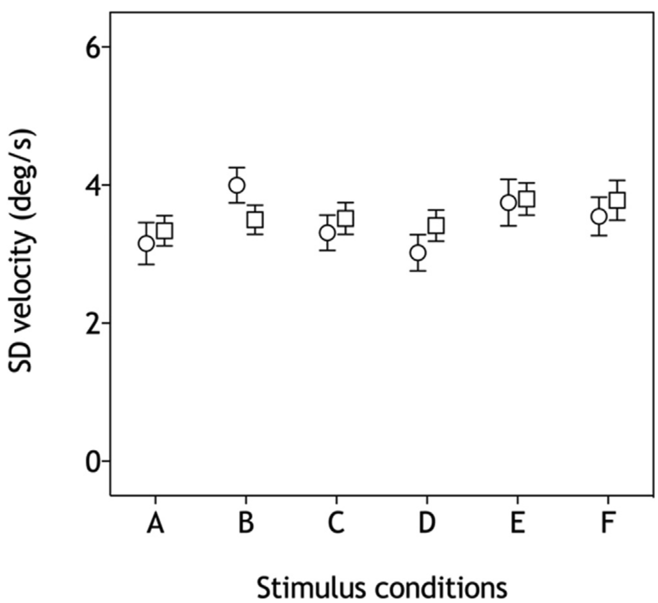

Fig. 7. Standard deviation of x (circle symbols) and y (square symbols) velocities for all observers under different stimulus conditions: (a) original Murakami on-line jitter illusion, (b) fixation spot only, (c) flickering surround with briefly presented central grid, (d) flickering surround with extended presentation of central grid, (e) static surround with briefly presented central grid, and (f) static surround with extended presentation of central grid. Error bars denote ± 1 SEM. X and y data points have been horizontally offset to allow for comparisons.

retinal slip arising from small eye movements follow a self-avoiding random walk (Engbert, Mergenthaler, Sinn, & Pikovsky, 2011; Herrmann, Metzler, & Engbert, 2017), one would anticipate that, at best, a motion displacement of the grid stimulus may be perceived during the brief period that the grid is presented. Based on the characteristics of small eye movements, the maximum displacement experienced by the eye between two display frames would be around 0.012 min arc, 0.66 min arc, and 2.8 min arc for drift, tremor, and microsaccades respectively (Wallis, 2005). When these displacements are converted to spacing ratios (ratio of horizontal to vertical spacing between elements), the grouping performance measured in this present study are in good agreement with grouping performance (around 50–65%) for equivalent spacing ratios when grid elements are physically displaced (Ben-Av & Sagi, 1995). Although encouraging, this good agreement needs to be treated with caution. The displacements reported by Wallis (2005) may not apply to our experimental set-up, and it is noteworthy that somewhat greater displacements might be anticipated in our experiment given that we stabilised our participants' heads with a chin rest alone. Furthermore, the displacements given by Wallis are the *maximum* displacement expected between frames, which presumably do not manifest on every stimulus presentation. One might therefore anticipate that overall grouping probability across an experiment would be somewhat less than that predicted by a calculation based on maximum displacement.

Earlier studies have suggested our ability to detect displacements to be limited by the spatial resolving power of the eye (Johnson & Leibowitz, 1976). However, displacement thresholds substantially less than 0.5 min arc have been reported (Stratton, 1902), with thresholds as low as 10 sec arc reported for line and sinewave grating targets (Westheimer, 1978). This places our ability to detect such small displacements amongst the hyperacuities (Westheimer, 1975) where sensitivities are not fundamentally limited by retinal photoreceptor spacing. Whilst these spatial limits suggest that we should be able to detect shifts arising from small eye movements, motion displacement detection is also constrained by temporal limits. This temporal limit represents the minimum duration that is required for motion to be detected – meaning motion occurring within durations less than this temporal limit are unable to be detected, regardless of the magnitude of displacement, or the velocity of the motion. This minimum motion duration was reported to be around 35 ms (Tayama, 2000), placing the duration of the brief presentation (16.6 ms for two display frames) used in the experiments well below this temporal limit.

When we measured grouping performance with a briefly presented grid in the presence or absence of a flickering annulus, performance remained unchanged. This was consistent with expectations from our phenomenological results in Experiment 1, and the inability of the human visual system to detect motion over such brief durations as mentioned above. The resulting percept of the briefly presented grid is unlikely to differ whether perceptual stabilisation is disabled or remains intact, as grouping should manifest from the failure in compensation of the retinal slip occurring between the two presentation frames. For the extended presentation of the grid, however, the measured difference in performance between flicker and nonflicker conditions suggest that disabling of perceptual stabilisation mechanisms can facilitate grouping. This is in agreement with the hypothesis that perceptual manifestation of retinal slip can lead to an increase in perceived shift in the arrangement of alternate grid elements, thereby improving grouping performance. Furthermore, our results suggest that perceptual

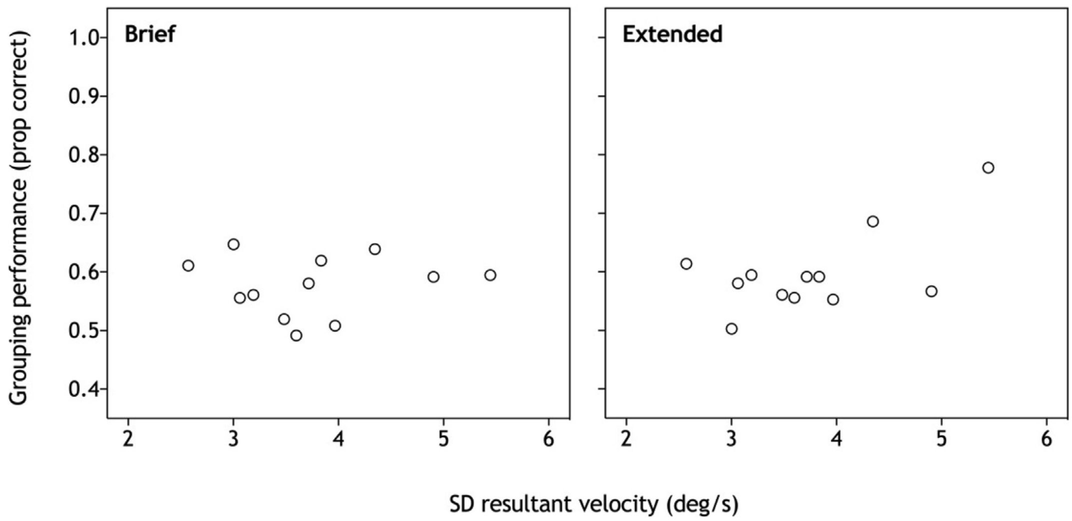

Fig. 8. Correlation between grouping performance for brief (left) and extended (right) presentations of grid stimuli from Experiment 3 (flicker condition) and standard deviation of resultant velocity for the fixation spot only condition (stimulus condition B).

grouping occurs at a processing stage subsequent to perceptual stabilisation. Should perceptual stabilisation occur at a processing stage subsequent to perceptual grouping (or in a parallel stage that is independent of grouping), grouping performance in our flicker and nonflicker conditions should be identical as the retinal shifts under these conditions are identical. It is only subsequent to the application of a perceptual stabilisation stage that the effective image shift differs between conditions.

7.1. The possible role of stimulus uncertainty

Of note is that some observers made unsolicited reports about the grouping task being more difficult for the extended grid, noting that the twinkle percept was less salient, or at times absent for the extended grid presented with a static annulus. As the twinkle percept occurred at the temporal junction of the temporally averaged grid and the asynchronous grouping stimulus, it could potentially signal to the observer, the occurrence of the grouping stimulus. Given that poorer grouping performance was measured under this condition, the decreased saliency of the twinkle percept could provide an alternative explanation for the pattern of results observed, based on the uncertainty model proposed by Pelli (1985). It is possible that the reported reduced salience of the twinkle percept in the static condition increases temporal uncertainty and drive thresholds up under this condition. However, the fixation spot disappeared at the time of the alternate grid element presentations, which provided a highly salient cue signalling the presentation of the grouping stimulus. Subsequent testing of the detection of the fixation spot disappearance in a subset of observers demonstrated that they were able to reliably detect this for extended grid stimuli with or without a flickering annulus (> 90% detection performance for both conditions; data not shown). In the presence of this highly salient and demonstrably reliable cue, it is unlikely that the perceptually variable, and less salient, twinkle percept can explain the poorer grouping performance of the extended grid presented with a static annulus. Therefore, we conclude that altered uncertainty is very unlikely to account for the difference in grouping performance observed for the extended grid where perceptual stabilisation mechanisms remained intact or were disabled.

7.2. Eye movement statistics and perceptual grouping performance

We found that observers' fixational eye movement statistics were unaffected by factors such as the presence and absence of salient flicker in the surround, and brief or extended presentations of the grid stimuli centrally. This suggests that any differences in performance found are not due to changes in eye movement statistics across the different conditions. The findings are in agreement with previous findings that eye movements are not entrained by spatial and temporal properties of the stimuli (Murakami, 2003), and that intrinsic changes in eye movements are not observed with changes in stimulus properties. However, our results cannot rule out the idea that observers adopted different eye movement behaviours when performing our experiments which were then abandoned when passively viewing the stimuli during eye movement recording. Unless such adopted behaviour were systematically different for our different stimulus conditions, they cannot explain the differences in grouping performance we find between different conditions, however.

The absence of a correlation between the standard deviation of fixational eye movement velocity and grouping performance suggests that averaged retinal shift – a global estimate of fixational eye movement behaviour – cannot accurately predict an observer's performance in this task. This may first appear to contradict the findings in Wallis (2006) where eye movement magnitudes were shown to be a good predictor for grouping performance. However, the difference may be due, in part, to eye movement recordings and psychophysical experiments being carried out separately in the current study. The eye movement recordings in Wallis (2006) were performed concurrently with the psychophysics, allowing for the post-hoc extraction of instantaneous – rather than average – eye movement amplitudes during the presentation of grid stimuli. In our experiment, eye movement statistics (standard deviation of resultant velocity) over a longer period of 2 s were used, thus any information about instantaneous eye movement at the time of presentation of grid stimuli is absent from our data. Despite this, it is not unreasonable to assume that eyes that move more on average are also more likely to be moving at the time of the stimulus presentation. Recent work has established the average relationship between retinal slip and grouping performance over a wide range of target velocities (Park et al., 2019 (in press)), although how this relationship might vary between individuals is yet to be explored.

In summary, incorporating a perceptual grouping task within the on-line jitter illusion has allowed for the influence of perceptual stabilisation of small eye movements on perceptual grouping to be directly tested. Our findings demonstrate that grouping performance is facilitated when retinal slip arising from eye movements can be perceived. Perceptual stabilisation mechanisms therefore not only influence our perception, they also have small – but measurable – effects on spatial visual function.

References

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences, 24*(3), 191–204.

Ben-Av, M. B., & Sagi, D. (1995). Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelations. *Vision Research, 35*(6), 853–866.

Carpenter, R. H. S. (1977). *Movements of the eyes.* London: Pion.

Ciuffreda, K. J., & Tannen, B. (1995). *Eye movement basics for the clinician.* Mosby.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43*(9), 1035–1045.

Costela, F. M., Otero-Millan, J., McCamy, M. B., Macknik, S. L., Troncoso, X. G., Jazi, A. N., ... Martinez-Conde, S. (2014). Fixational eye movement correction of blink-induced gaze position errors. *PLoS One, 9*(10), e110889.

Dakin, S. C., & Bex, P. J. (2002). Role of synchrony in contour binding: Some transient doubts sustained. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 19*(4), 678–686.

Engbert, R. (2006). Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research, 154*, 177–192.

Engbert, R., Mergenthaler, K., Sinn, P., & Pikovsky, A. (2011). An integrated model of fixational eye movements and microsaccades. *Proceedings of the National Academy of Sciences of the United States of America, 108*(39), E765–770.

Herrmann, C. J. J., Metzler, R., & Engbert, R. (2017). A self-avoiding walk with neural delays as a model of fixational eye movements. *Scientific Reports, 7*(1), 12958.

Johnson, C. A., & Leibowitz, H. W. (1976). Velocity-time reciprocity in the perception of motion: Foveal and peripheral determinations. *Vision Research, 16*(2), 177–180.

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Hubel, D. H. (2009). Microsaccades: A neurophysiological analysis. *Trends in Neurosciences, 32*(9), 463–475.

Murakami, I. (2003). Illusory jitter in a static stimulus surrounded by a synchronously flickering pattern. *Vision Research, 43*(9), 957–969.

Murakami, I. (2004). Correlations between fixation stability and visual motion sensitivity. *Vision Research, 44*(8), 751–761.

Murakami, I., & Cavanagh, P. (1998). A jitter after-effect reveals motion-based stabilization of vision. *Nature, 395*(6704), 798–801.

Nakajima, Y., & Sakaguchi, Y. (2015). Transient twinkle perception is induced by sequential presentation of stimuli that flicker at frequencies above the critical fusion frequency. *Attention, Perception, & Psychophysics, 77*(8), 2711–2727.

Park, A. S. Y., Bedggood, P. A., Metha, A. B., & Anderson, A. J. (2017). Masking of random-walk motion by flicker, and its role in the allocation of motion in the on-line jitter illusion. *Vision Research, 137*, 50–60.

Park, A. S. Y., Metha, A. B., Bedggood, P. A., & Anderson, A. J. (2019). The influence of retinal image motion on the perceptual grouping of temporally asynchronous stimuli. *Journal of Vision, 19*(4), 1–11.

Pearson, E. S., D'Agostino, R. B., & Bowman, K. O. (1977). Tests for departure from normality: Comparison of powers. *Biometrika, 64*(2), 231–246.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 2*(9), 1508–1532.

Stratton, C. (1902). Visible motion and the space threshold. *Psychological Review, 9*, 433–447.

Tayama, T. (2000). The minimum temporal thresholds for motion detection of grating patterns. *Perception, 29*(7), 761–769.

Troncoso, X. G., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008). Microsaccades drive illusory motion in the Enigma illusion. *Proceedings of the National Academy of Sciences of the United States of America, 105*(41), 16033–16038.

Usher, M., & Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. *Nature, 394*(6689), 179–182.

Wallis, G. (2005). A spatial explanation for synchrony biases in perceptual grouping: Consequences for the temporal-binding hypothesis. *Perception & Psychophysics, 67*(2), 345–353.

Wallis, G. (2006). The temporal and spatial limits of compensation for fixational eye movements. *Vision Research, 46*(18), 2848–2858.

Westheimer, G. (1975). Editorial: Visual acuity and hyperacuity. *Investigative Ophthalmology & Visual Science, 14*(8), 570–572.

Westheimer, G. (1978). Spatial phase sensitivity for sinusoidal grating targets. *Vision Research, 18*(8), 1073–1074.

Westheimer, G., & McKee, S. P. (1977). Perception of temporal order in adjacent visual stimuli. *Vision Research, 17*(8), 887–892.

Zuber, B. L., Stark, L., & Cook, G. (1965). Microsaccades and the velocity-amplitude relationship for saccadic eye movements. *Science, 150*(3702), 1459–1460.