Illusory Motion Perception Is Associated with Contrast Discrimination but Not Motion Sensitivity, Self-Reported Visual Discomfort, or Migraine Status

Chongyue He, Bao Ngoc Nguyen, Yu Man Chan, and Allison Maree McKendrick

Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia

Correspondence: Allison M. McKendrick, C/O Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia 3010; allisonm@unimelb.edu.au.

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Purpose. Altered visual processing of motion and contrast has been previously reported in people with migraine. One possible manifestation of this altered visual processing is increased self-reported susceptibility to visual illusions of contrast and motion. Here, we use the Fraser–Wilcox illusion to explore individual differences in motion illusion strength in people with and without migraine. The motion-inducing mechanisms of the Fraser–Wilcox illusion are purported to be contrast dependent. To better understand the mechanisms of the illusion, as well as visual processing anomalies in migraine, we explored whether migraine status, susceptibility to visual discomfort, contrast discrimination, or motion sensitivity are related to quantified motion illusion strength.

Methods. Thirty-six (16 with aura, 20 without aura) people with migraine and 20 headache-free controls participated. Outcome measures were motion illusion strength (the physical motion speed that counterbalanced the illusory motion), motion sensitivity, and contrast discrimination thresholds (measured for each contrast pair that formed part of the illusory motion stimulus). Typical daily visual discomfort was self-reported via questionnaire.

Results. Motion illusion strength was negatively correlated with contrast discrimination threshold ($r = -0.271$, $P = 0.04$) but was not associated with motion sensitivity or migraine status. People with migraine with aura reported experiencing visual discomfort more frequently than the control group ($P = 0.001$). Self-reported visual discomfort did not relate to quantified perceptual motion illusion strength.

Conclusions. Individuals with better contrast discrimination tend to perceive faster illusory motion regardless of migraine status.

Keywords: visual illusion, motion perception, migraine, visual discomfort, contrast, interindividual differences

A visual motion illusion in peripheral vision that has been widely documented is the Fraser–Wilcox illusion,[1] or variants thereof, such as the peripheral drift illusion and the rotating snakes illusion.[2,3] These illusory stimuli are constructed of circular repetitions of a stationary stimulus consisting of discrete segments of different luminance, resulting in induction of the perception of rotatory motion.[1] (Fig. 2B provides an example of a variant of the Fraser–Wilcox illusion; readers may see illusory motion in their peripheral vision when viewing the fixation dot.) The direction of illusory motion depends on the order of the luminance gradients.[1] A common explanation for the perception of illusory motion in such stationary stimuli is that the neighboring differences in contrast are associated with differences in neural processing speed,[4] thus producing sequential neural responses similar to those for successive frames of physically moving stimuli.[2,5,6]

The exact neural circuits involved in the motion illusion have yet to be elucidated. In this regard, studying the factors that contribute to the substantial interindividual variability in reported motion illusion strength may provide insight into its underlying neural mechanisms. For the original Fraser–Wilcox illusion, 75% of 678 observers reported seeing illusory motion.[1] Rather than simply asking if illusory motion is present or not, the strength of illusory motion can be measured quantitatively by injecting physical rotation into the test stimulus and determining the speed required for an individual to effectively cancel the illusory motion.[7,8]

Self-reported susceptibility to illusory percepts induced by high-contrast striped patterns is greater in people with migraine than in non-migraine control groups.[9–13] Previous studies have attempted to quantify susceptibility to visual illusions by calculating a pattern sensitivity score, which is the total number of visual illusions reported when viewing a striped pattern. Individuals who experience migraine also report elevated subjective visual discomfort when viewing striped patterns.[14] It has been proposed that increased pattern sensitivity and elevated discomfort when viewing static striped patterns in people with migraine arise from abnormal cortical excitability,[15] which is considered part of migraine pathophysiology.[16] Consequently, both elevated pattern sensitivity and the level of subjective visual

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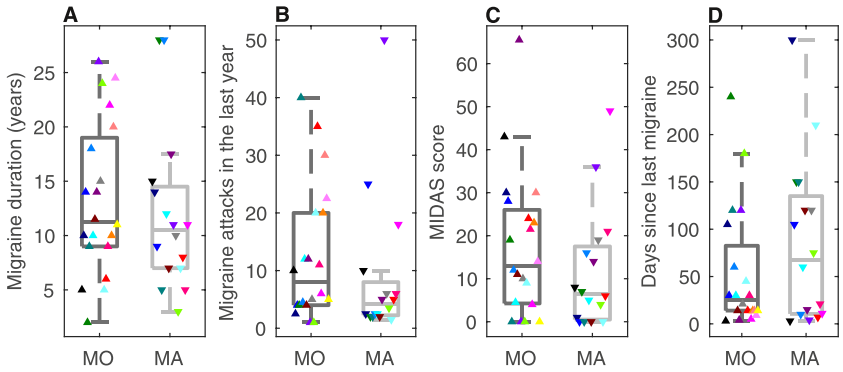

Figure 1. Demographics of the two migraine groups: migraine without aura (MO, upward-pointing triangle; $n = 20$) and migraine with aura (MA, downward-pointing triangle; $n = 16$). Marker color is consistent for each individual in Figures 1 and 4 to 7. (**A**) Years of migraine. (**B**) Migraine attacks in the past year. (**C**) Migraine Disability Assessment Score (MIDAS), where a higher score indicates greater headache-related disability. (**D**) Days since last migraine attack. Boxes describe median, 25th, and 75th percentiles. Each whisker extends to the data point nearest to 1.5 times the interquartile range.

discomfort have been considered analogs of cortical excitability,[17] although a direct mechanistic link between these phenomena is lacking.

Elevated pattern sensitivity in people with migraine compared to controls has been associated with elevated contrast detection thresholds[9,18] and prolonged motion after effects.[11] This association between pattern sensitivity and both contrast and motion processing suggests that contrast and motion processing abnormalities are associated with visual discomfort. Here, we sought to further explore the proposed link between visual discomfort and visual illusions by presenting a contrast-dependent motion illusion (the Fraser–Wilcox illusion), from which we could quantify motion sensitivity and illusion strength. Contrast discrimination thresholds were measured for the specific differences in luminance between adjacent segments used in the illusory motion stimuli. We were additionally interested in whether migraine status and susceptibility to visual discomfort were related to illusion strength, given the previously proposed link between visual discomfort and susceptibility to visual illusions in people with migraine. Of the factors we studied that could influence the Fraser–Wilcox illusion, only contrast discrimination threshold was associated with motion illusion strength.

Methods

Participants

Twenty people with migraine without aura (MO; age, 18–46 years; median [interquartile range, IQR], 26 [24.5–35]; seven males), 16 people with migraine with aura (MA; age, 19–42 years; median [IQR], 27.5 [21.5–29.5]; nine males), and 20 headache-free control participants (age, 19–44 years; median [IQR], 25 [22–33]; 10 males) were recruited. There was no significant difference among the three groups in age (Kruskal–Wallis test, $P = 0.77$) or gender (χ^2 test of proportions, $P = 0.41$). MO and MA participants satisfied the criteria for migraine without aura and migraine with typical aura with headache, respectively, according to the International Classification of Headache Disorders, 3rd edition.[19] Migraine participants were tested at least 3 days after a migraine attack to ensure migraine medication washout and to avoid testing in the postdromal phase (see Fig. 1 for migraine demographics). Control participants did not regularly experience headache (fewer than four in the past year) and had never experienced aura symptoms consistent with migraine. Migraine participants completed the Migraine Disability Assessment Score (MIDAS) questionnaire[20] to provide an estimate of headache-related disability. Each participant was coded with a unique color–marker combination in the figures that show individual data.

All participants were required to meet the following inclusion criteria: monocular visual acuity of the testing eye better than or equal to 6/7.5 (0.1 logMar equivalent); refractive error within ± 5.00D sphere and less than –2.00D cylinder; clear ocular media on slit-lamp examination; and no history of ocular surgery, ocular disease, medications, or systemic conditions that can affect visual and cognitive functions (e.g., diabetes, antidepressant use). The experimental protocol was in accordance with the tenets of the Declaration of Helsinki and approved by The University of Melbourne Human Research Ethics Committee. All participants gave written informed consent. Each participant attended one session of approximately 2-hour duration and was allowed to take breaks in between tasks whenever needed.

Equipment

The experiments were conducted in a dim room. The stimuli were presented on a gamma-corrected ViewSonic G90fB CRT Monitor (ViewSonic, Brea, CA, USA), with a refresh rate of 80 Hz, resolution of 1232 × 923 pixels, and maximum luminance of 140 cd/m^2, via the ViSaGe graphics system (Cambridge Research Systems, Kent, UK). Stimuli were produced using custom software written in MATLAB R2010a (MathWorks, Natick, MA, USA) with the CRS Toolbox (Cambridge Research Systems). Responses were collected through a CB6 button box (Cambridge Research Systems). Participants maintained a working distance of 57 cm with a chinrest, and the left eye was occluded for all testing. Participants wore their own refractive correction unless it was a multifocal lens design. In that case, refractive correction appropriate for the working distance was provided in a spectacle trial frame. A small mirror was positioned below the monitor to allow the researcher to observe participants' fixation throughout the experiment.

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Visual Discomfort Questionnaire

The questionnaire (see Supplementary Materials) we developed to quantify subjective visual discomfort consisted of nine visual stimuli—direct sunlight; car headlights at night; shafts of light coming through trees or venetian blinds; sunlight on water, snow, or modern buildings; contrasting patterns on materials, wallpapers, or pictures; fluorescent lights; glare from computer, TV, or phone screens; particular colors; and other visual stimuli—based on items used in previous studies assessing self-reported visual discomfort.[9,11] Participants self-reported the frequency of experiencing (1) migraine, (2) headache, or (3) discomfort after viewing the listed types of visual stimuli. Control participants did not respond to the migraine-related component. Answers of "often," "sometimes," and "never" were scored 2, 1, and 0, respectively. The scoring system was also adapted from those used by Shepherd's group.[9,11] Three sum scores of migraine, headache, and discomfort were calculated for each participant, herein referred to as discomfort scores, headache trigger scores, and migraine trigger scores.

Stimuli

The visual stimuli for both the motion illusion and contrast discrimination tasks were wheel patterns with 24 cycles of the luminance profiles. The original luminance profiles for clockwise and counterclockwise illusory motion stimuli, defined by the luminance ratio (*LumRatio*) as a function of location in an 8-bit lookup table (x), are shown in Equations 1 and 2, which were generated according to type 2a of the optimized Fraser–Wilcox illusion:[21]

$$LumRatio_{cw} = \begin{cases} 1, & 0 < x \le 32 \\ 0.66, & 32 < x \le 128 \\ 0, & 128 < x \le 160 \\ 0.33, & 160 < x \le 256 \end{cases} \quad (1)$$

$$LumRatio_{ccw} = \begin{cases} 0.33, & 0 < x \le 96 \\ 0, & 96 < x \le 128 \\ 0.66, & 128 < x \le 224 \\ 1, & 224 < x \le 256 \end{cases} \quad (2)$$

Gaussian blur with a standard deviation of 4 (on the x value) was applied to the original luminance profiles distributed in a 1×256 matrix to remove zigzag transitions between abrupt luminance steps matrices.[8] The smoothed luminance profiles for the motion illusion task are shown in Figure 2A. There were four stimulus conditions for the contrast discrimination task. The luminance profile for each condition consisted of two contrast levels at each contrast step for the motion illusion stimulus (Fig. 2C).

Procedures

A method of constant stimuli with a two-alternative forced choice was used to obtain estimates of motion illusion strength and contrast discrimination threshold. On each trial, the wheel patterns were displayed at 12° eccentricity for 500 ms on a white (140 cd/m^2) background with a black fixation dot (diameter = 0.224°). For the illusory motion task, the test stimulus was a single wheel injected with physical rotation, which could be in either the same or opposite direction as the illusory motion direction (Fig. 2B). Participants indicated whether the pattern appeared to rotate in a clockwise or counterclockwise direction by pressing a button. For the contrast discrimination task, there were two stimuli: (1) a reference pattern and (2) a test pattern of relatively reduced contrast (Fig. 2D). The two patterns were displayed at the same eccentricity as the motion illusion task. However, we chose to use a two-alternative forced-choice method (two patterns presented simultaneously at two different spatial locations) instead of a two-interval forced-choice method, as there was a potential for confounding after-effects when stimuli were presented one after the other. Note that this was not an issue for the motion illusion task, which presented only the stimulus in a single interval (with the observer being required to judge direction of rotation).

Participants indicated whether the higher contrast pattern appeared at the top or the bottom location by pressing corresponding button. An auditory tone was provided to indicate that a response had been received, but no feedback on whether the response was "correct" was provided. Participants were instructed to balance button presses when they could not decide the rotation direction, did not see any movement in the motion task, or could not distinguish the contrast between the two patterns in the contrast task.

All test sessions began with the motion illusion task. Each participant was given two practice runs to familiarize themselves with the task and allow determination of a suitable test range of rotation speeds for the main task. The practice runs consisted of nine rotation speeds for illusory motion pattern in both directions. Three repeats of the 18 conditions were block randomized in each run. The maximum real rotating speed of 3°/second was shown for the first practice run, which was then adjusted based on individual performance. A minority of participants required extra practice runs prior to formal data collection, as large saccades were observed by the researcher conducting the testing through the mirror setup. These participants received the instructions again and did not commence testing until stable fixation was demonstrated. Each participant then performed four runs, each with five repeats (resulting in 20 repetitions per stimulus intensity) of seven rotation speeds using a fixed speed range. The maximum testing speeds for all participants ranged from 2°/second to 3.5°/second, and a static condition (0°/second) was always included.

Contrast discrimination was measured after completing the motion illusion task. Each run consisted of eight block-randomized repeats of seven stimulus intensities ($\Delta LumRatio$; Fig. 2D), with half of the reference patterns at each intensity presented at the top location in each run. Participants completed three initial runs for training purposes and to aid in deciding each individual's test range. They then performed three runs (resulting in 24 trials per stimulus intensity) at their individual suitable test range, the results of which were used to compute a final threshold. After the total of six runs of one stimulus was finished, the same process was repeated for another test stimulus (four test stimuli in total; Fig. 2C). Stimuli were presented in a pseudorandom order to counterbalance learning and fatigue effects.

Fitting Psychometric Functions

Psychophysical data were fit to cumulative normal functions using pain-free Bayesian inference[22] through the psignifit 4 MATLAB toolbox.[23] The implemented formulas are provided

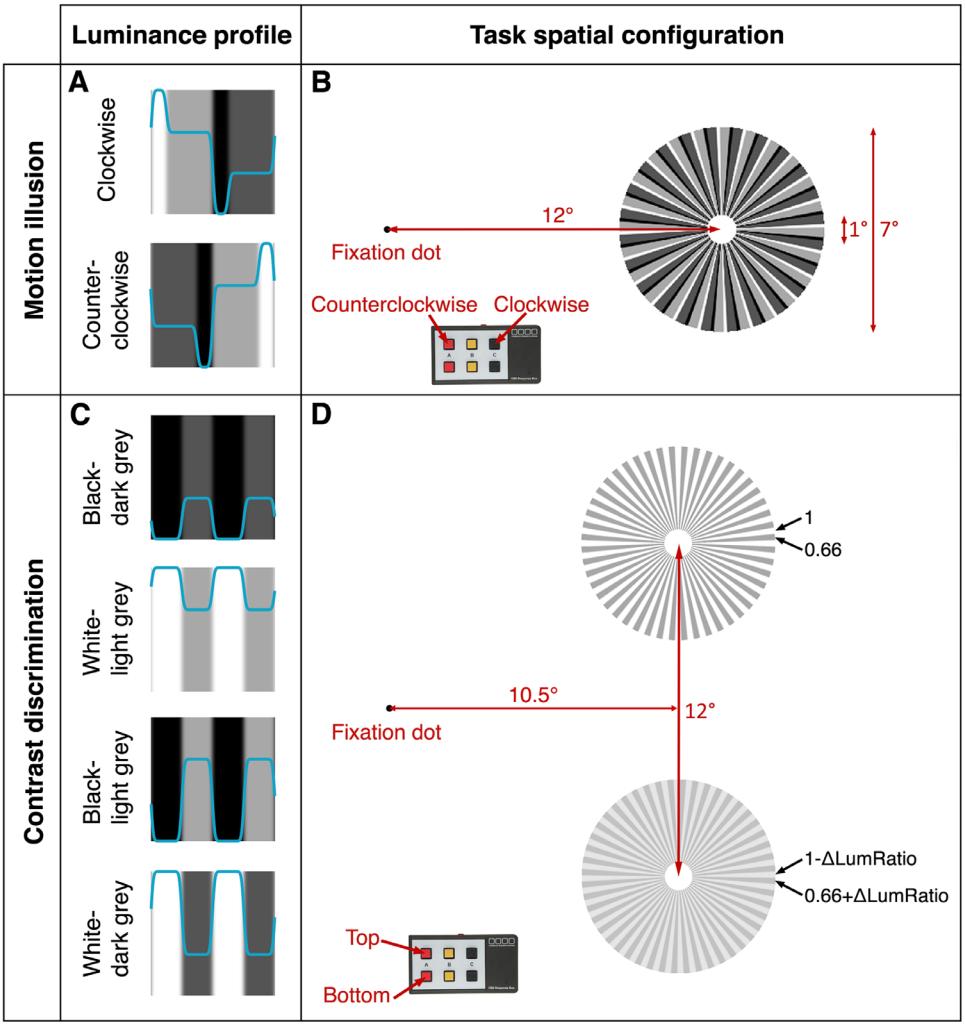

Figure 2. Stimuli for the psychophysical measurements. (**A**) Luminance profile of illusory motion patterns in the clockwise and counterclockwise directions. (**B**) Spatial configuration of the motion illusion task; a clockwise illusory motion pattern is given as an example. (**C**) Luminance profiles of the reference patterns for all four conditions. (**D**) Spatial configuration of the contrast discrimination task. A white–light gray luminance configuration is given as an example.

in Equations 3 to 5:

$$\psi(x; m, w, \lambda, \gamma) = \gamma + (1 - \lambda - \gamma) S(x; m, w) \quad (3)$$

$$S(x; m, w) = \Phi\left(C\frac{x - m}{w}\right) \quad (4)$$

$$C = \Phi^{-1}(0.95) - \Phi^{-1}(0.05) \quad (5)$$

For the motion illusion task, data were fit to the probability of choosing counterclockwise as a function of physical rotation speed, where the psychometric function (ψ) is a sigmoid function (S) scaled by upper (λ, the probability of choosing clockwise at infinitely high counterclockwise rotation speed) and lower (γ, the probability of choosing counterclockwise at infinitely high clockwise rotation speed) asymptotes. In this case, equal asymptotes were assumed ($\gamma = \lambda$). The cumulative standard normal function (Φ) is determined by the stimulus intensity (x, physical rotation speed), the threshold (m, the physical rotation speed at which $S = 0.5$), and the width (w, the difference between rotation speeds at which $S = 0.05$ and $S = 0.95$). The estimate of the cancellation speed for each luminance profile type was defined by half of the absolute difference between the means of psychometric functions of both patterns (Fig. 3). Motion sensitivity is defined as the mean of the widths (w) for the psychometric functions for both pattern directions, where a larger w reflects worse motion sensitivity.

For the contrast discrimination task, the response correct rate as a function of $\Delta LumRatio$ was fit to the psychometric function (ψ), which is a sigmoid function (S) scaled by upper (λ, error rate at infinitely large $\Delta LumRatio$) and lower (γ, correct rate at $\Delta LumRatio = 0.001$) asymptotes. As the tasks were two-alternative forced choice, γ was fixed at 0.5. Parameters of S are the stimulus intensity (x, $\Delta LumRatio$),

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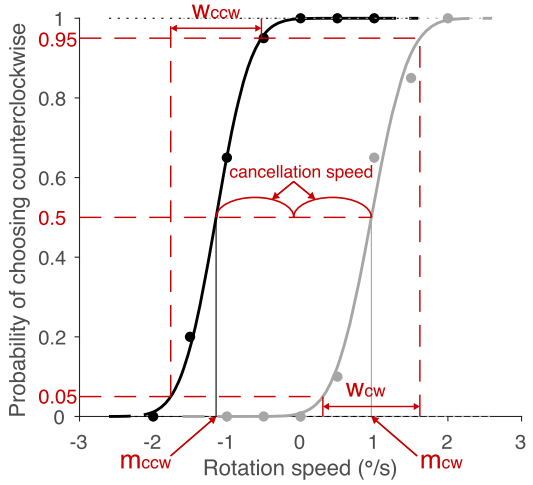

Figure 3. Example psychometric functions from one participant showing the calculations of cancellation speed and motion sensitivity. The cancellation speed was calculated as half of the absolute difference between the mean of the psychometric functions of the clockwise (m_{cw}) and the counterclockwise (m_{ccw}) patterns. Motion sensitivity was defined by the mean of the width of psychometric functions of the clockwise (w_{cw}) and the counterclockwise (w_{ccw}) patterns. *Gray*, clockwise pattern; *black*, counterclockwise pattern. Positive rotation speed corresponds to the counterclockwise direction.

the threshold (m, the $\Delta LumRatio$ at which $S = 0.5$), and the width (w, the difference between $\Delta LumRatio$ values at which $S = 0.05$ and $S = 0.95$). The contrast discrimination threshold was the $\Delta LumRatio$ at which $\psi = 0.75$. The contrast discrimination thresholds for each stimulus condition were ranked in ascending order, resulting in four rank numbers for each participant. The mean of the four ranks was calculated for each participant as their individual contrast discrimination rank.

Statistical Analysis

All analyses were conducted using SPSS Statistics 23 (IBM, Armonk, NY, USA). Shapiro–Wilk normality tests were conducted for each measure to determine the appropriate statistical tests for between-group comparisons and correlations between tasks. Where the data were normally distributed, ANOVA was used. Kruskal–Wallis tests were used to replace one-way ANOVA for non-normally distributed data. Data were log transformed when mixed ANOVA was needed for non-normally distributed data. Tukey's post hoc test was used to determine the significant pairs from a mixed ANOVA. Because non-normally distributed data were involved in all correlation tests, Spearman correlations were performed to determine the relationships between measurements; $P < 0.05$ was considered significant. The unstandardized effect size of a significant pairwise comparison was reported as the mean difference with 95% confidence interval (CI) of the difference for normally distributed data and as median difference (within subject) or difference in median (between subject) for non-normally distributed data. The standardized mean difference effect size for within-subject design (Cohen's d_{av}) was also reported for differences between stimulus conditions, as there was only a significant main effect of conditions in the mixed ANOVA.

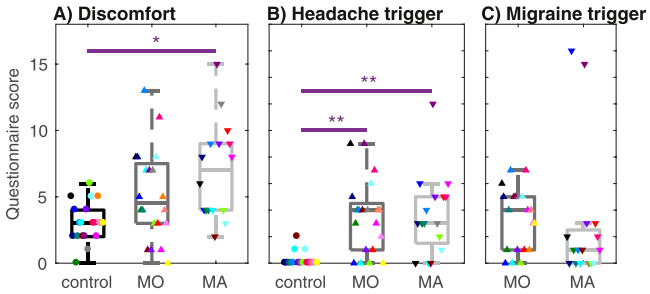

Figure 4. Group and individual questionnaire scores. Control (circle), $n = 20$; MO (upward-pointing triangle), $n = 20$; and MA (downward-pointing triangle), $n = 16$. Marker color is consistent for each individual in Figures 1 and 4 to 7. (**A**) Discomfort score. (**B**) Headache trigger score. (**C**) Migraine trigger score. $^{*}P < 0.5$; $^{**}P < 0.001$. Boxes describe median, 25th, and 75th percentiles. Each whisker extends to the data point nearest to 1.5 times the interquartile range.

Results

Visual Discomfort Questionnaire

Figure 4A shows a significant group difference in discomfort related to visual stimuli (Kruskal–Wallis test; $\chi^2[2] = 12.69$; $P = 0.002$). The discomfort score in the MA group was higher than in the control group (Dunn–Bonferroni post hoc pairwise comparison; $P = 0.001$; difference of median = 4), but the scores were similar between the MO group and control participants ($P = 0.11$) and between the MO and MA groups ($P = 0.36$).

There was also a group difference in headache trigger score (Kruskal–Wallis test; $\chi^2[2] = 23.68$; $P < 0.001$) (Fig. 4B). As expected, control participants reported significantly fewer headaches triggered by visual stimuli (MO, $P < 0.001$; MA, $P < 0.001$); however, the two migraine groups did not differ significantly in headache trigger score ($P = 1.00$). The MA and MO groups also did not differ significantly in migraine trigger score ($\chi^2[1] = 3.64$; $P = 0.06$). There was no significant difference between MO and MA participants in any self-reported interictal visual related symptoms. The MIDAS questionnaire score was significantly correlated with discomfort score (rho = 0.51, $P = 0.002$) and headache trigger score (rho = 0.51, $P = 0.001$) with Holm–Bonferroni correction for multiple comparisons considered.

Motion Illusion Strength

Cancellation speed and motion sensitivity are plotted in Figure 5 for each group. There was no significant difference between groups in either cancellation speed (ANOVA, $F_{2,53} = 0.52$, $P = 0.60$) or motion sensitivity (Kruskal–Wallis, $\chi^2[2] = 5.64$, $P = 0.06$). The results suggest that people with migraine, regardless of aura status, did not perceive faster illusory motion nor did they exhibit poorer motion sensitivity than the headache-free control participants.

Contrast Discrimination

Group and individual contrast discrimination thresholds for each condition are shown in Figure 6. A 3 × 4 mixed ANOVA—(group: control, MO, or MA) × (conditions: black–dark gray, white–light gray, black–light gray, or white–dark gray)—was performed on the log contrast discrimination

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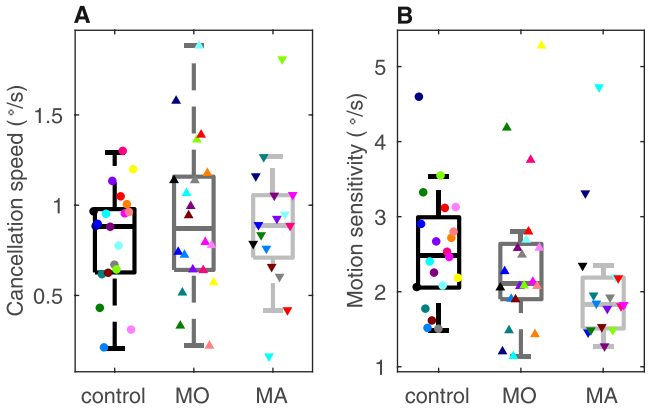

Figure 5. Group and individual results for (**A**) cancellation speed and (**B**) motion sensitivity. Control (circle), $n = 20$; MO (upward-pointing triangle), $n = 20$; and MA (downward-pointing triangle), $n = 16$. Marker color is consistent for each individual in Figures 1 and 4 to 7. Boxes describe median, 25th, and 75th percentiles. Each whisker extends to the data point nearest to 1.5 times the interquartile range.

threshold data. There was a significant effect of stimulus type ($F_{3,159} = 54.21$, $P < 0.001$) but no main effect of group ($F_{2,53} = 1.60$, $P = 0.21$) or interaction between group and stimulus type ($F_{6,159} = 1.98$, $P = 0.07$). Tukey's post hoc tests showed that the contrast discrimination threshold for black–dark gray (type 1) was significantly smaller than for white–light gray (type 2; $P = 0.002$; mean difference on log threshold = 0.08; 95% CI, 0.03–0.12; $d_{av} = 0.42$). The contrast discrimination threshold for white–light gray (type 2) was significantly smaller than for black–light gray (type 3; $P < 0.001$; mean difference on log threshold = 0.13; 95% CI, 0.09–0.18; $d_{av} = 0.76$) and for white–dark gray (type 4; $P < 0.001$; mean difference on log threshold = 0.15; 95% CI, 0.11–0.19; $d_{av} = 0.88$). The contrast discrimination thresholds for black–light gray (type 3) and white–dark gray (type 4) were not significantly different from each other ($P = 1$). These results suggest that migraine or aura status did not affect contrast discrimination thresholds.

Correlations Between Measures

Spearman correlations were performed to determine the relationships between measurements. Because illusion strength was not statistically different between groups, participants were pooled into a single group for the correlation analysis. Cancellation speed was not significantly correlated with discomfort score (all participants included: rho = 0.19, $P = 0.16$; migraine participants only: rho = 0.07, $P = 0.69$), headache trigger score (all participants included: rho = 0.15, $P = 0.25$; migraine participants only: rho = 0.18, $P = 0.30$), migraine trigger score (rho= –0.05, $P = 0.78$), or motion sensitivity (rho = –0.12, $P = 0.38$). However, there was a weak negative correlation between contrast discrimination rank and cancellation speed (rho = –0.27, $P = 0.04$) (Fig. 7). The results suggest that people with lower contrast discrimination thresholds tend to perceive stronger motion illusion. Correlations among psychophysical measures were additionally tested for the control group only, and none of them reached conventional statistical significance (all $P > 0.05$).

Discussion

The current study confirms previous reports of considerable inter-individual differences in the strength of the Fraser–Wilcox motion illusion. Given the proposed critical role of the temporal properties of contrast/luminance response functions on the Fraser–Wilcox illusion,[2,5,6] contrast perception was expected to be associated with illusion strength. This is supported by our finding that individuals with lower contrast discrimination thresholds tended to perceive faster illusory motion. To our knowledge, ours is the first study to directly quantify motion illusion strength in people with migraine. One study indirectly compared motion illusion strength between people with and without migraine by presenting a chromatic version of the Fraser–Wilcox illusion using virtual-reality goggles.[24] In that study, people with migraine exhibited greater postural sway than the control group after viewing the stimulus; however, the subjective rating of the illusion strength was not significantly different between the two groups.[24]

We used a similar method to quantify the motion illusion strength as previously described,[7,8] specifically determining the speed of physical injected rotation that cancelled the illusory motion. Individual psychometric functions (Fig. 3 as an example) were able to demonstrate that responses to the static stimulus (0 rotation speed) were consistent with the proposed illusory motion direction, and that stimulus with different injected motion speeds, including the static condition, were perceived as a monotonic continuum. While this measure provides an estimate of illusion strength, it is not clear at which stage in the motion processing pathway the illusory motion is cancelled by the physical motion. If the motion induced by the Fraser–Wilcox illusion has already become non-distinguishable from real motion before reaching motion processing regions, then motion sensitivity should not affect the average perceived motion speed but rather the accuracy of perceptual judgments. Indeed, this is consistent with our results, because we did not find a correlation between motion sensitivity and illusion strength.

An assumption of this method is that the measured cancellation speed reflects the true speed that would be perceived for the Fraser–Wilcox illusion had it been presented for the same stimulus duration (500 ms) without injected motion. Backus and Oruç[6] measured the physical rotation speed for a non-illusory pattern that matched the illusory rotation speed of a stationary Fraser–Wilcox stimulus for durations ranging from 50 to 1000 ms in six observers. The physical matching speeds as a function of stimulus duration were fit to the sum of two exponentials.[6] That study concluded that the perception of the Fraser–Wilcox illusion consisted of both a brief fast motion and a sustained slow motion separating at approximately 250 ms after the stimulus onset.[6] The cancellation speeds measured in the current and previous studies[8,25] are generally consistent with the reported matching speeds in Backus and Oruç[6] corresponding to the late, sustained motion component.

Backus and Oruç[6] suggested that the dynamic adaptation function for each luminance element creates a neural image similar to that for the phase shift of a drifting sinusoidal grating. Based on neurophysiological contrast response functions for the first 200 ms post-stimulus onset,[26] Backus and Oruç created theoretical phase position functions for a series of stimulus contrasts up to 6 seconds after the stimulus onset. A greater difference in contrast levels was associated with a larger difference in phase positions (except at around

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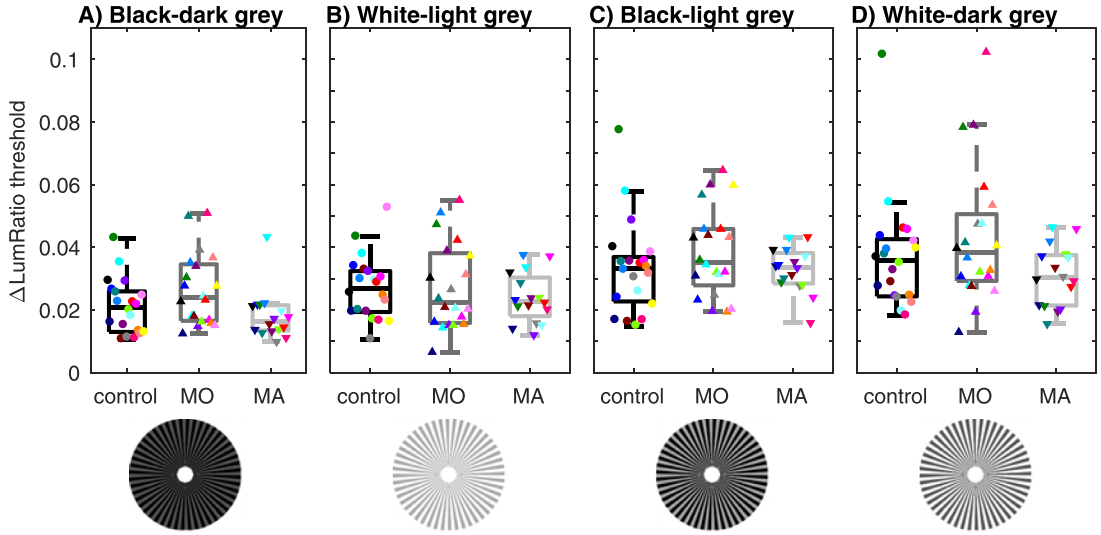

Figure 6. Group and individual contrast discrimination thresholds for the four stimulus types (**A** to **D**) tested in this study. Control (circle), $n = 20$; MO (upward-pointing triangle), $n = 20$; and MA (downward-pointing triangle), $n = 16$. Marker color is consistent for each individual in Figures 1 and 4 to 7. Boxes describe median, 25th, and 75th percentiles. Each whisker extends to the data point nearest to 1.5 times the interquartile range.

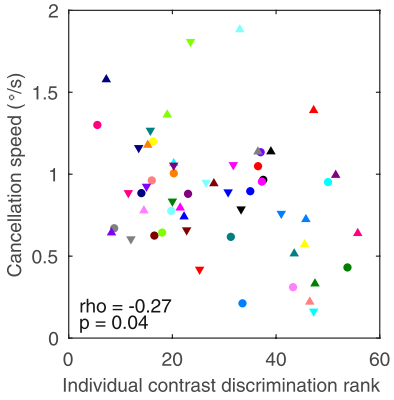

Figure 7. Cancellation speeds as a function of individual contrast discrimination rank, which was the average for all four stimulus conditions in participants from all groups ($n = 56$). Circle, control; MO, upward-pointing triangle; and MA, downward-pointing triangle. Marker color is consistent for each individual in Figures 1 and 4 to 7. Higher rank indicates worse contrast discrimination.

90 ms after stimuli onset when the response to each contrast level reached its maximum).[6] This association is consistent with a previous finding that the subjective rating of Fraser–Wilcox illusion strength increases with stimulus contrast.[27] According to their model, the correlation between cancellation speed and contrast discrimination threshold in our results suggests that individuals with lower contrast discrimination thresholds perceived larger phase shifts in the illusory motion.

An alternative explanation for the motion illusion has been provided by Conway et al.,[5] who proposed a contrast-dependent neural latency model that is likely to reflect the early, brief motion component proposed by Backus and Oruç.[6] In direction-selective macaque primary visual cortex and middle temporal visual area neurons, Conway et al.[5] demonstrated a 10- to 20-ms latency difference between responses (timing of peak of neuronal firing rate since stimulus onset) to high (black and white) and low (dark gray and light gray) contrast bars presented for 27 ms on a mid-gray background. The brief presentation of each contrast stimulus (e.g., black next to dark gray) was able to elicit direction-selective responses consistent with the global direction of the illusory motion (black → dark gray → white → light gray), in both human behavioral (stimulus duration for 200 ms) and single-neuron electrophysiological (stimulus duration for 50 ms) measurements.[5] Conway et al.[5] suggested that the latency difference between adjacent elements created motion signals in similar mechanisms as apparent motion and reverse phi motion for low-contrast (black–dark gray, white–light gray) and high-contrast (black–light gray, white–dark gray) element pairs, respectively. It seems that the illusion strength determined by the early component might also be associated with contrast discrimination thresholds measured from each adjacent element pairs for short durations. However, it is difficult to interpret our results in the context of the model of Conway et al.[5] without a better understanding of how the early and late components of the motion illusion are related.

In our study, we did not directly assess the subjective discomfort induced by the motion illusion stimulus used in the experiments, but instead used a more generalized questionnaire rating of visual discomfort. There are other anecdotal reports of visual discomfort being acutely induced by variants of the Fraser–Wilcox illusion covering a larger visual area,[2] but we cannot comment on the presence or absence of specific discomfort to our mid-peripheral stimuli other than the informal observation that participants appeared comfortable throughout the experiments and did not cease testing prematurely. One possibility is that the acute discomfort induced by visual stimuli may not be dependent on its "illusory" nature. To test whether pattern-induced discomfort is dependent on local illusion strength, a future study might assess subjective discomfort to images with more spatial

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repetition of the Fraser–Wilcox illusion and quantify illusion strength at each location compared to a control condition using non-illusory wheels with physical rotation.

Previous studies have used a variety of psychophysical tests to indirectly infer information regarding potential cortical excitation abnormalities associated with migraine. Some have reported altered performance in migraine participants, while others have not found significant differences between their migraine and control groups (for review, see O'Hare and Hibbard[28]). It should be noted that in addition to marked differences between task requirements, there are also considerable differences in the migraine features, severity, and age of participants between studies. Our results have added two further tasks to the list of those that have not revealed significant differences between migraine and control groups—namely, illusory motion direction discrimination and contrast discrimination.

We did not observe poorer motion sensitivity in our cohort of migraine participants. In previous studies that have demonstrated elevated motion detection thresholds in people with migraine relative to control participants, either the stimuli were presented at near-threshold duration[29] or the studies measured motion coherence thresholds (the ability to discriminate coherent motion signal from noise),[30–37] whereas our suprathreshold stimuli were presented for a longer duration (500 ms) and without the addition of external noise. One possible explanation for the lack of significant difference between migraine and non-headache groups on certain visual tasks is that the stimulus signal-to-noise ratio might be an important factor in revealing between-group differences. As suggested by O'Hare and Hibbard,[28] if people with migraine are proposed to have higher internal noise levels, then their overall noise level would be expected to be more different from the control systems when input signals are weak or contain large amounts of external noise.[28] Given that the stimuli used in this study had abundant input signals, they might not be optimized to reveal subtle differences in noise tolerance.

Another reported finding in previous literature is a stronger and prolonged motion after-effect in people with migraine,[12,38–40] except when the motion after-effect strength is assessed through a nulling technique.[29] It is not clear how inter-individual differences in motion after-effect strength relate to performance on our illusory motion task. There are highly significant differences in the nature of the visual stimuli used to explore these effects, with the most obvious being the time course of motion after-effect stimuli. Motion after-effects are typically generated after at least 30 seconds of initial adaptation.[12,29,38–40] Our stimuli were 500 ms in duration and therefore not expected to evoke the same responses as longer duration motion after-effect presentations.

Previous studies exploring contrast perception in migraine have yielded more equivocal results than those of motion processing. Some studies have reported impaired contrast sensitivity in migraine,[9] some have reported no group difference,[41] and others have even found better sensitivity in migraine participants.[42] As contrast sensitivity is dependent on both the eccentricity and spatial frequency of the stimuli,[43] our peripheral wheel pattern makes it difficult to directly compare our contrast stimuli to many other studies that have typically concentrated on measuring foveal vision. A future approach to considering the relationship between visual motion and contrast tasks would be to collect data using a battery of tasks in large groups of people with migraine and controls. A difficulty, however, with this approach is that the data would have to be collected on the same day in people with migraine because visual performance can fluctuate with duration post-migraine.[44]

In conclusion, the current study demonstrates a wide range of individual differences in the strength of the Fraser–Wilcox motion illusion. A negative correlation between the motion illusion strength and contrast discrimination threshold was found, which might indicate a primarily deterministic or secondarily modulatory effect of contrast perception on perceived motion speed. People with migraine with aura reported greater susceptibility to visual discomfort compared to the control group; however, we did not find evidence in support of a link between self-reported visual discomfort and visual illusion strength.

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Author/s:
He, C;Chan, YM;McKendrick, AM;Nguyen, B

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