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RESEARCH ARTICLE

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Motion perception during involuntary eye vibration

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Abstract Retinal motion caused by reflexive or voluntary eye movements is rarely misinterpreted as object motion, as if the visual system discounted the contribution of these eye movements to retinal motion. Yet, involuntary eye movements caused by mechanical eye vibration is often interpreted as object motion unless the vibration has high frequency, in which case only image blur may be noticed. In these latter conditions, however, a light flickering above the fusion limit is vividly perceived to undergo oscillatory motion over its static surround. We determined the conditions of this phenomenon, showing that the perceived frequency of illusory oscillation equals the difference between flicker frequency and the frequency of vibration of the eyes. This outcome is explained as a result of the low-pass temporal frequency characteristic of vision, which further predicts that the same effect should occur if the flickering light is vibrated and observed with static eyes. This prediction was corroborated empirically. We also determined the minimal amplitude of oscillation required to perceive motion as a function of postural stability and the presence of static references, finding an amplitude threshold of ~1 arcmin with postural stability in dim-light conditions, which increases to ~2 arcmin with postural instability in the dark.

Keywords Motion perception · Illusory motion · Eye vibration · Displacement threshold

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Introduction

Visual perception of motion is crucial for visual animals, but retinal image motion is never an unequivocal indication that objects have moved in the environment: in the absence of object motion, retinal image motion may still occur as a result of eye movements, head motion, or locomotion. Proprioception and the efferent copy of voluntary eye movements are likely to provide the information required to distinguish retinal image motion caused by self motion from that caused by object motion. Indeed, human observers can detect and discriminate object motion that is imperceptible except during the brief duration of saccadic eye movements (García-Pérez and Peli 2001). Thus, our visual system seems to discount the contribution of eye movements to retinal image motion, interpreting the residual (if any) as object motion.

Alongside this exquisite ability to separate *voluntary eye motion* from object motion lies an equally astonishing propensity to mistake *non-reflexive involuntary eye motion* for object motion. For instance, humming transmits a vibration to the eyes that leads to the illusory perception of object motion (Rushton 1967; Wells and Evans 1968; Eastman 1969; Coats and McCrary 1979) and mechanical vibration of the eye muscles similarly evokes an illusory percept of object motion (Velay et al. 1997). The role of the efferent copy of voluntary eye movements in disambiguating retinal image motion seems established by the fact that proprioceptive clues alone cannot eliminate the illusory percept of motion that these passive eye movements evoke. In these circumstances, retinal image motion is vividly taken to represent object motion no matter how aware the observer may be that it is his/her eyes that are vibrating while the objects in the visual field are static.

Passive transmission of high-frequency and low-amplitude vibration to the eyes results in the perception of a small amount of blur that impairs vision, reducing acuity and the capability to identify alphanumeric characters (Lange and Coermann 1962; Dennis 1965; Griffin and Lewis 1978; Moseley and Griffin 1987; Harazin et al.

1996). Interestingly, this passive high-frequency eye vibration does not elicit the illusion of object motion, something that seems to have ecological advantages: besides constant ocular microtremor (Bolger et al. 1999), the eye vibrates in its cavity with every heel stroke during walking and, although the vertical vestibuloocular reflex may help reduce ocular vibration (Grossman et al. 1989), the visual system appears to have evolved to be invulnerable to the potential confounding effects of natural, involuntary eye vibration by designing a structure that resonates at a temporal frequency in the range 50–63 Hz (Harazin et al. 1996), a range that is filtered out by the low-pass characteristic of early visual processing (Levinson 1968). In spite of this, if the visual scene includes an intermittent display such as a cathode-ray tube or the flickering LED display of a night-stand digital clock, passive eye vibration at high frequencies induces a strong illusion of motion that only affects the intermittent part of the scene: image features of surrounding physical objects that are receiving continuous illumination do not appear to move. MacKay (1958) reported an analogous illusion of motion to occur when the eyeball is pressed intermittently in a stroboscopically lit room that contains self-luminous objects.

This effect might be a result of the nature of intermittent illumination and the low-pass temporal frequency characteristic of the visual system, as illustrated in Fig. 1. The *right panel* in Fig. 1 shows the predicted perceived appearance of the stimuli shown in the *left panel*. These predictions were obtained by temporal convolution of the stimuli with the typical temporal impulse response of the visual system (see Appendix). Because this temporal impulse response results in low-pass temporal filtering, flicker beyond the cutoff frequency is filtered out and only the average luminance remains. Thus, without eye vibration (Fig. 1a), a light source flickering at 52 Hz (*top trace*) has the same perceived appearance (except for luminance level) as a continuously illuminated source (*bottom trace*). When the eye vibrates sinusoidally at 60 Hz (Fig. 1b), the light sources are effectively swept back and forth over the retina according to the path of eye motion. As a result, the temporal pattern of flicker varies at each retinal location (i.e., along horizontal lines at different heights in the *left panel* of Fig. 1b), in each case describing a different complex waveform that is differently aliased by the low-pass filter. In these conditions, the output of the flickering light appears to undergo oscillation (*top trace*), whereas the continuous light simply appears blurred and motionless (*bottom trace*). When the frequency of eye vibration is kept constant, the frequency of illusory oscillation varies with flicker frequency (Fig. 1c) taking the value of the difference between flicker and vibration frequencies. As a result, no illusory motion will be perceived when the flicker and vibration frequencies are identical (*top trace*).

If this is the ultimate reason for the appearance of the illusion of motion, then the visual system has a remarkable ability to encode very small displacements of the retinal image and interpret them as image motion. Indeed, measurements of the displacement threshold for motion perception have yielded values between 0.1 and 1 min of arc (Tyler and Torres 1972; Westheimer 1979; Legge and Campbell 1981; Nakayama and Tyler 1981; Scobey and Johnson 1981; Levi et al. 1984; Buckingham and Whitaker 1985, 1986; Bedell and Johnson 1995). Yet, informal observations indicate that the illusory motion weakens and even disappears when the scene contains only an intermittent display (e.g., a flickering LED looked at in the dark). In other words, perception of this illusory motion is facilitated by the presence of a fixed reference on the retina, one that is provided by the anchored (however blurred) nature of visual features receiving continuous illumination.

The work described in this paper has two aims. Firstly, to test empirically the explanation for the illusory perception of motion illustrated in Fig. 1. Secondly, to determine, under different conditions of illumination and postural stability, the minimal displacement on the retina that is required for this illusory perception of motion to occur. The latter determination will serve to indicate the tolerance of the visual system to high-frequency vibration before illusory motion occurs while looking at intermittent displays. Some of these results have been presented in abstract form (Peli and García-Pérez 2000; García-Pérez and Peli 2002).

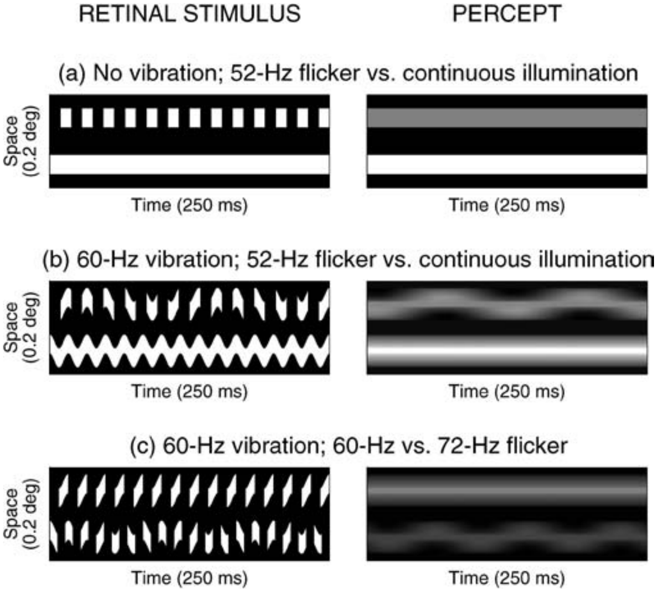

Fig. 1a–c Effects of eye vibration on the perceived appearance of a point light source on a dark background. **a** Light flicker at 52 Hz (*top trace*) versus continuous illumination (*bottom trace*) without eye vibration. **b** Light flicker at 52 Hz (*top trace*) versus continuous illumination (*bottom trace*) when the eye vibrates sinusoidally at 60 Hz. **c** Light flicker at 60 Hz (*top trace*) versus 72 Hz (*bottom trace*) when the eye vibrates sinusoidally at 60 Hz

Experiment 1

This experiment aimed at testing the validity of the explanation illustrated in Fig. 1 for the illusory oscillation. Subjects were presented with a flickering light that they looked at while their eyes vibrated at ~60 Hz. According to the explanation illustrated in Fig. 1, the frequency of the resultant illusory oscillation should equal the absolute value of the difference between the flicker frequency (which varied throughout the experiment) and the frequency of eye vibration (~60 Hz). Subjects reported the perceived frequency of illusory oscillation by setting the actual frequency of a continuously illuminated, oscillating light source until it matched the illusory frequency of oscillation of the flickering light. If the explanation is correct, a plot of the matching frequency established by the subjects against the flicker frequency of the light will have a V-shape with the vertex at an ordinate of zero and an abscissa equal to the frequency of eye vibration, whereas the arms should increase away from the vertex on either side with unity slope.

Materials and methods

Apparatus and stimuli

Head vibration was produced with a commercial percussion massager (HoMedics Inc., Commerce Township, MI, USA). The massager was set to operate at its highest speed, which results in a stand-alone vibration of ~63 Hz as measured with a stroboscope. That this head vibration transmits to the eyes was indirectly determined here by checking for the perception of illusory motion in a flickering display, but it had been objectively established by eye-position recordings (see García-Pérez and Peli 2003).

The stimulus consisted of two adjacent light sources located on the frontal plane of the observer: a sharp-edged circular light-emitting diode (LED, 4.5 mm in diameter) and a reflected laser beam (3.5 mm in diameter). The LED was made to flicker with a square waveform through custom-made circuitry driven by a model FG2 signal generator (Emerson Electric Co., Brea, CA, USA). Because the flicker rates required throughout the experiment were high and could not easily be determined with precision by reading the analog scale on the knob of the signal generator, the output signal was passed through a model 2245A oscilloscope (Tektronix, Beaverton, OR, USA) where accurate determination of the flicker frequency was made. This flicker frequency is the independent variable in the present experiment. The beam of a 640-nm laser pointer (RadioShack, Fort Worth, TX, USA) came reflected from a model G300PD front-surface mirror galvanometer (General Scanning Inc., Watertown, MA, USA) that was set to oscillate vertically with a triangular waveform by means of a model 166 signal generator (Wavetek, San Diego, CA, USA). The peak-to-peak amplitude of this vertical oscillation on the projection plane was initially set at 6–7 mm, although subjects could vary the amplitude if they felt this helped them carry out the task. The frequency of oscillation of the laser beam – adjusted by the subject to match the illusory oscillation of the LED – is the dependent variable, and its low values allowed direct reading from the analog scale on the knob of the signal generator with sufficient precision (±0.1 Hz).

Procedure

Subjects sat 1 m from the visual display and pushed the body of the massager up against their lower jaw. Held in this way, the heads of the massager pivoted freely without meeting resistance, and the resultant vibration at the body of the massager had constant amplitude and frequency. The subjects had their jaws locked so that vibration was transmitted up to the cranium and on to the eyes, which thus vibrated vertically. Prior to the session the subjects were familiarized with these postural requirements and were trained how to check for vertical eye vibration by judging the orientation of the illusory oscillatory path followed by the LED. Differences in pressure of the massager against the lower jaw as well as differences in locking pressure of the jaws affected the amplitude of vertical eye vibration, but did not alter its frequency as measured with a cancellation method (see García-Pérez and Peli 2003).

The experiment was carried out in a single session of 30 trials. The room was lit with incandescent light. On each trial, the flicker frequency of the LED was set at a random value within 5 Hz from a rough estimate of the frequency of eye vibration obtained at the beginning of the session with a cancellation method (García-Pérez and Peli 2003). The subject then adjusted the frequency of oscillation of the laser beam until it appeared to match the illusory oscillation of the LED. This task turns out to be very easy to perform given that (1) the illusory oscillation of the LED and the actual oscillation of the laser beam are similar in waveform, (2) the temporal frequency of either oscillation when they match is below 5 Hz, and (3) even if the two oscillations were out of phase, when they are matched in temporal frequency they keep a constant relative lag. Each trial produced a pair of values: the flicker frequency of the LED and the matching frequency of oscillation of the laser beam, which is expected to be at the unsigned difference between the flicker frequency of the LED and the constant frequency of eye vibration.

Participants

Four subjects took part in the experiment, who signed informed consent forms that were approved by the institutional review board in compliance with the US National Institutes of Health (NIH) guidelines and regulations.

Results and discussion

Figure 2 shows perceived frequency of oscillation as a function of flicker frequency. Except for subject #2, the data confirm the hypothesis that the illusory frequency of oscillation increases with a unity slope as flicker frequency moves away from the frequency at which the eyes vibrate. The data from subject #2 clearly depart from unit-slope lines, but they are far from random and increase with a slope of 0.5, consistent with the conjecture that this subject (a musician) was producing a half-cycle of actual oscillation of the laser beam for each full cycle of illusory oscillation of the LED.

Overall, then, the data confirm that the illusory oscillation is a simple result of the basic low-pass temporal frequency characteristic of the early stages of visual processing. The illusory oscillation occurs at the difference frequency between flicker and vibration. As indirectly determined by the horizontal location of the vertex of the V-shaped functions in Fig. 2, the frequency of eye vibration induced by the massager was ~60 Hz for all subjects.

Additional observations using the same experimental setup revealed that the amplitude of the illusory oscillation varies, all else being equal, with lighting and postural conditions. In particular, turning off the light produces a

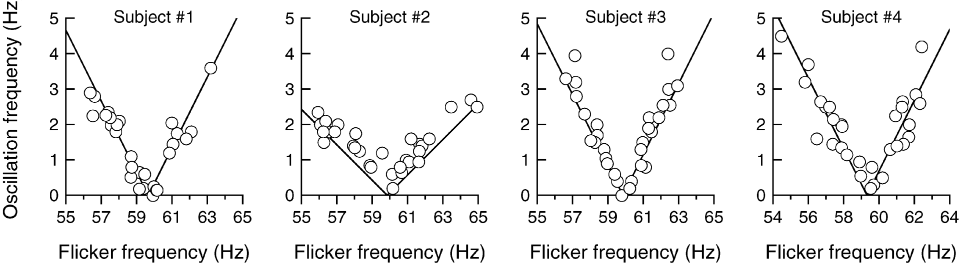

Fig. 2 Results of experiment 1, showing perceived frequency of oscillation as a function of flicker frequency. The location along the horizontal axis of the V-shaped function was determined by a least-squares fit. The only free parameter was the location along the horizontal axis, as the slope was constrained to be unity for all subjects except #2, whose data suggest a slope of 0.5

reduction in the perceived amplitude of the oscillation, which under certain conditions tends to disappear completely: subjects who had reported seeing the LED in motion 100% of the times when the eyes were vibrated in the light reported the same illusory motion percept less than 40% of the times under identical conditions in the dark. Similarly, activities that cause postural variations (walking, head movements, etc) seem to reduce and even completely eliminate a perception of illusory motion that would otherwise be vivid. These observations are consistent with the notion that known or presumed eye movements constitute "noise" above which object motion has to be perceived (MacKay 1958; Kinchla and Allan 1969; Murakami and Cavanagh 1998, 2001). The next experiment explores the effect of these conditions on the perception of illusory motion as a function of the amplitude of vibration. Yet, the setup for experiment 1 does not lend itself to such study with rigorous control of the amplitude of vibration transmitted to the eyes by means of the massager. Interestingly, informal examination indicated that the perceived appearance of the flickering LED under eye vibration used in experiment 1 was thoroughly analogous to its appearance when the vibration was applied to the stimulus itself and the eyes were static. Thus, it is the spatiotemporal stimulus pattern at the retina that matters, whether produced by the eye vibrating while looking at a flickering light or by the flickering light actually being vibrated and viewed with static eyes. This equivalence allows us to transfer the vibration to the stimulus, which provides a better control of frequency and amplitude. In these rigorously controlled conditions, the next experiment aimed at determining what amplitude the vibration has to have for subjects to perceive illusory motion under different lighting and postural conditions.

Experiment 2

The stimulus for this experiment was created so that its projection on the retina when the eyes are static was identical to the retinal stimulus created by light flicker and eye vibration. The light source was a laser beam that was made to flicker by an interposed shutter, and was further made to oscillate by reflecting it on an oscillating mirror. As a result, the amplitude of the oscillation was under precise control and subjects were asked to detect motion as a function of the amplitude of this oscillation. Psychometric functions were measured for various postural/lighting conditions and it is expected that the minimal amplitude of oscillation needed to achieve a fixed performance criterion increases as stable retinal references weaken.

Materials and methods

Apparatus and stimuli

A 633-nm He-Ne laser beam (model GLG5261, NEC, Tokyo, Japan) was used, which rendered an elongated shape 4×8 mm (2.5×5 min of arc at the viewing distance of 5.5 m) on the projection plane. The laser beam passed through a model OD-8813A acousto-optical modulator (NEC) driven to produce square-wave flicker of adjustable frequency by means of a model F33 signal generator (Interstate Electronic Co., Anaheim, CA, USA). The flickering beam was subsequently reflected on a model G300PD front-surface mirror galvanometer (General Scanning Inc.) that was set in sinusoidal oscillation at 55 Hz by means of a model 4011A signal generator (BK Precision, Placentia, CA, USA). The half-peak bandwidth of the galvanometer was 96 Hz, and the amplitude of oscillation (which is the independent variable in this experiment) could be varied. The apparatus was calibrated to produce prescribed amplitudes of displacement of the laser beam along its axis of elongation on the projection plane, and during the sessions a model 465 oscilloscope (Tektronix) was used to help set the signal levels required to obtain those amplitudes.

Procedure

Subjects were 5.5 m away from the projection plane, and there were three conditions, which only differed as to the lighting and postural setting, under which the measurements were made. In one condition, subjects sat using a headrest and the room was dimly but sufficiently lit with a DC source so as to allow visible fixed references within the field of view; in another condition, subjects sat similarly but without the headrest and the room was in complete darkness; in the third condition, subjects were also in complete darkness and stood on only one foot to produce postural instability (which turned out to be substantial, according to the subjects' informal reports). Thus, in the first condition subjects could use stable visual references as well as proprioceptive information to aid

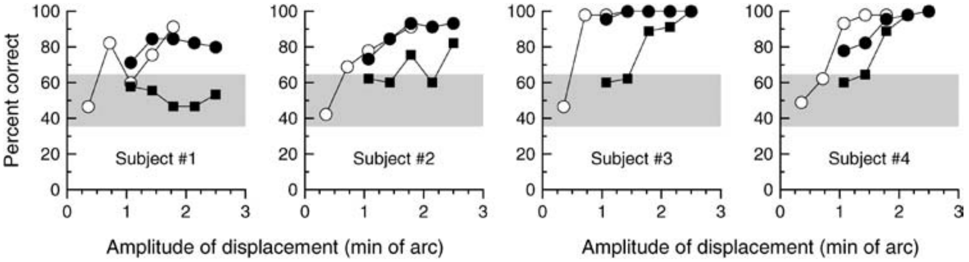

Fig. 3 Results of experiment 2, showing percentage of correct responses as a function of displacement amplitude under three postural/lighting conditions. Percentage of correct responses in the forced-choice task is plotted as a function of the actual amplitude of oscillation, separately for the conditions of postural stability in the light (*open circles*), postural stability in the dark (*solid circles*), and postural instability in the dark (*solid squares*). *Gray shading* marks the region where the percentage correct does not differ significantly (at α=0.05) from the chance level of 50%, given the 45 trials per data point

judgments of object motion; in the second, lack of visual references implies that only proprioceptive information was available to aid this judgment; in the third, visual references were not available either, and proprioceptive information indicates a substantial amount of head movement that should impair the detection of small displacements of the stimulus.

A session consisted of 15 trials at each of five amplitudes of oscillation. The order of these 75 trials was randomized. Three separate sessions were run for each postural/lighting condition for a total of 45 trials per amplitude per condition. Each trial, whose beginning was signaled by an audible beep, presented a temporal two-alternative forced-choice task in which the acousto-optical modulator was set to square-wave flicker at 60 Hz in one of the intervals (chosen at random with equal probability) and at 600 Hz in the other. Presentation duration in each of the intervals was 2 s, with an interleaved blank lasting 1 s. Given the constant 55-Hz oscillation of the mirror galvanometer, one of the intervals resulted in the laser beam actually appearing to undergo sinusoidal oscillation at a detectable 5 Hz while the other resulted in an undetectable oscillation at 545 Hz, which simply appeared perceptually as continuous illumination without motion. The subject's task was to indicate in which of the two intervals the beam had oscillated, and the response was recorded as correct or incorrect. The data thus gathered were binned to obtain percentages of correct responses as a function of the amplitude of the oscillation.

Participants

The same four subjects of experiment 1 took also part in this experiment.

Results and discussion

Figure 3 shows percentage of correct responses as a function of displacement amplitude in each of the three postural/lighting conditions. Consistent with the observations described above, the results of this forced-choice task indicate smaller displacement thresholds in the condition of postural stability in the light (*open circles* in Fig. 3). With postural stability in the dark (*solid circles*), different subjects appeared to be differently affected by the lack of visual references: some subjects performed about equally as well as in the light, whereas others failed to see motion occasionally at displacements where they always saw it in the light. Finally, postural instability in the dark (solid squares) resulted in the worst performance overall, usually resulting in a lack of motion perception with displacements at which this motion was clearly visible in other postural/lighting conditions.

On a psychometric function for two-alternative forced-choice tasks, threshold is usually defined as the stimulus level rendering 75% of correct responses. From the data in Fig. 3, the displacement threshold is about 1 min of arc for all subjects when viewing is in the light (*open circles*), increases slightly when viewing is in the dark (*solid circles*), and increases further up to about 2 min of arc when viewing is in the dark and with postural instability (*solid squares*), although the threshold for subject #1 in this latter condition seems to be even further up beyond the range of displacements considered in this experiment.

General discussion

The results of experiment 1 confirmed that the illusory oscillation is governed by the mechanism illustrated in Fig. 1, thus being a direct consequence of the ability of the visual system to interpret small displacements of the retinal image as evidence of image motion. The illusory perception of motion is more vivid when there is a nearby, static visual reference. As illustrated in Fig. 1b, a nearby light that is continuously illuminated appears blurred but static under eye vibration, so providing an anchor point in the visual field that facilitates the detection of positional changes over time.

Experiment 2 tested the role of static references and fixation accuracy in the displacement threshold for motion perception. Earlier studies on the displacement threshold (defined as the smallest instantaneous target displacement that can be detected) have yielded a diversity of results that are relevant in this context. Legge and Campbell (1981) measured the displacement threshold for a dot subtending 0.45 min of arc, obtaining values in the range 1.05–2.17 min of arc (averaging 1.42 min of arc) across subjects when the task was carried out in the dark, and in the range 0.28–0.61 min of arc (averaging 0.43) when the task was carried out in the light and with a structured background that provided fixed visual references. Performance was thus above the spatial resolution limit (which is ~1 min of arc) in the dark, but revealed hyperacuity in the light. Considering that the dot subtended 0.45 min of arc, the reported displacement thresholds imply a jump about three times the width of the stimulus when in the dark, and about the width of the stimulus when in the light. Bedell and Johnson (1995) measured the displacement threshold for a dot subtending 2 min of arc that was under horizontal sinusoidal oscillation at various temporal frequencies in the dark. Best performance occurred when the temporal frequency of oscillation was 8 Hz, and yielded displacement thresholds ranging from 0.4 to 0.9 min of arc across subjects.

Other studies using alternative stimuli (lines or gratings) yielded displacement thresholds of diverse magnitudes. Tyler and Torres (1972) reported displacement thresholds of 0.5 and 1 min of arc (for each of two subjects) for an isolated vertical line 1 min of arc wide that was sinusoidally oscillated horizontally at 2 Hz; addition of a static vertical line 10 min of arc distant decreased the displacement threshold to 0.1 and 0.3 min of arc respectively for each subject. Westheimer (1979) reported displacement thresholds of about 0.2 min of arc for detecting the sudden horizontal jump of a vertical line, but neither the width of the line nor the lighting conditions were reported. Nakayama and Tyler (1981) measured the amplitude threshold for detecting the sinusoidal deformation of a vertical line in the light, reporting thresholds of 0.08 or 0.3 min of arc (for different subjects) under optimal spatial and temporal frequencies of the sinusoidal deformation. Scobey and Johnson (1981) used a vertical line 1 min of arc wide that underwent translational motion in the light at different speeds, finding a minimum displacement threshold of 1 min of arc for speeds at or above 2 min of arc per second. On the other hand, Levi et al. (1984) found that the displacement threshold for gratings with visual references was 0.67–1 min of arc, whereas Buckingham and Whitaker (1985) reported displacement thresholds of 0.5 min of arc for 2-cycle/deg gratings in the dark and oscillating at optimal temporal frequencies (above 5 Hz).

In our experiment 2, the stimulus had a width of 5 min of arc in the direction of oscillation, which had a temporal frequency of 5 Hz. Results of Nakayama and Tyler (1981) (see their Fig. 4) indicate a three-fold increase in threshold at this frequency compared with the optimal frequencies (up to 1 Hz) that yielded the values mentioned in the preceding paragraph. Our results reveal a (peak-to-peak) displacement threshold of about 1 min of arc in the light and about 2 min of arc in the dark with postural instability or, in relative terms, an oscillation that respectively implies 0.2 and 0.4 times the width of the stimulus. Our thresholds are thus above the resolution limit, and they are also larger than those reported in the studies mentioned above, but our stimulus was considerably larger and resulted in smaller relative thresholds when compared with stimulus size.

It should be stressed that our experimental setup enabled us to completely eliminate visual references when performed in the dark, because we used a laser beam in a completely darkened room. In the studies mentioned above the stimulus was presented on a monitor whose glow makes the edges visible, thus serving as an anchored visual reference especially when the subjects are dark-adapted (see Tyler and Torres 1972). Therefore, our thresholds in the dark (*solid circles* in Fig. 3) are more likely to represent performance in unreferenced conditions than those obtained in other studies. With the lights on and visual references available within the field of view (*open circles* in Fig. 3) motion thresholds were similar, except for a minimally lower one for one of the subjects. It thus appears that performance in the light is not much better than in the dark, perhaps because our relatively long presentation durations allowed subjects to correct for inter-trial eye drift and hold fixation even in the dark, or because the displacement threshold for targets oscillating at 5 Hz (as in our experiment) is not affected by luminance level (Buckingham and Whitaker 1985) or the presence of static references (Buckingham and Whitaker 1986). Yet, motion thresholds increased considerably with postural instability in the dark, possibly reflecting that the continual posture variations required to maintain equilibrium when standing on one foot disrupted fixation accuracy or the reliability of retinal motion as an indicator of object motion. Thus, our results appear to confirm the conjecture of Legge and Campbell (1981) that factors that decrease fixation accuracy might increase displacement thresholds. In any case, the small differences that we found at threshold between performance in the dark and in the light do not carry over to conditions of suprathreshold displacements, as discussed next.

When the LED was viewed under eye vibration (using the massager) in an illuminated room, the illusory motion was vivid and its amplitude was suprathreshold. Yet, this illusory motion seemed to disappear when the room lights were turned off. The results of our experiment 2 indicate that differences in suprathreshold perception are not accompanied by similar variations in threshold (compare *open* and *solid circles* in Fig. 3). Thus, although displacement thresholds in the dark are similar to those in the light, the perceived magnitude of suprathreshold motion is reduced in the dark. The reason for this may lie in procedural differences between the criterion-free forced-choice task used to determine displacement thresholds in our experiment 2 and the subjective judgments involved in the suprathreshold task just mentioned; in the latter case, proprioceptive information indicating some amount of head and eye motion combines with the lack of visual references (when in the dark) to raise the subjective criterion for motion perception, whereas the blank interval in the forced-choice task under similar conditions provides a comparison stimulus that allows referenced judgments.

To determine that this difference is not due to the ambient illumination level, we illuminated the room with a stroboscope operating at about 55 Hz. The room appeared stable when viewed from the inside even when the eyes were vibrated. The reason for the lack of effect of eye vibration in these conditions is that the entire retinal image is oscillating, so there is no external visual reference that can signal the presence of this retinal oscillation (MacKay 1958; Kinchla and Allan 1969; Murakami and Cavanagh 1998, 2001). Yet, the oscillation could be perceived if part of the visual field received continuous illumination (e.g., when an additional continuous source lit some objects in the room, or when the interior of the stroboscopically illuminated room was viewed through the door from the continuously illuminated outside and with the door frame in view). This fact illustrates that the visual system assumes that overall, rigid retinal image motion is a result of self motion, and only differential image motion is interpreted as object motion. This assumption serves well in the continuously illuminated world where visual systems have evolved.

Appendix

The spatiotemporal output g in the *right panels* of Fig. 1 was obtained from the input f in the corresponding *left panel* through temporal convolution with the temporal impulse response h of the visual system, i.e.,

$$g(x,t) = \int_{-\infty}^{t} f(x,\tau)h(t-\tau)d\tau.$$

We used the same temporal impulse response as in García-Pérez and Peli (2003), namely,

$$h(t) = \begin{cases} \frac{a(t/\tau_1)^{n_1-1}\exp(-t/\tau_1)}{\tau_1(n_1-1)!} - \frac{b(t/\tau_2)^{n_2-1}\exp(-t/\tau_2)}{\tau_2(n_2-1)!} & \text{if } t > 0 \\ & \text{otherwise} \end{cases}$$

with n_1=9, n_2=10, a=1, b=0.4, τ_1=5 ms and τ_2=7 ms (see Fig. 4). The precise values of these parameters are immaterial: other values compatible with the reported integration time of the overall visual system under varying conditions (Ikeda 1986; Swanson et al. 1987) give rise to the same qualitative result, namely that the frequency of illusory oscillation equals the unsigned difference between flicker frequency and the frequency of eye vibration.

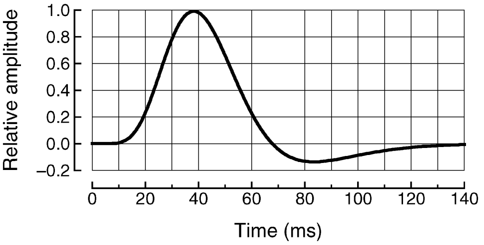

Fig. 4 Temporal impulse response used to produce the output in the *right panels* of Fig. 1

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