Motion perception during saccadic eye movements

Eric Castet and Guillaume S. Masson

Centre de Recherche en Neurosciences Cognitives (CRNC), UPR 9012 du CNRS31, chemin J. Aiguier13402, Marseille cedex 20, France

Correspondence should be addressed to E.C. (castet@lnf.cnrs-mrs.fr)

During rapid eye movements, motion of the stationary world is generally not perceived despite displacement of the whole image on the retina. Here we report that during saccades, human observers sensed visual motion of patterns with low spatial frequency. The effect was greatest when the stimulus was spatiotemporally optimal for motion detection by the magnocellular pathway. Adaptation experiments demonstrated dependence of this intrasaccadic motion percept on activation of direction-selective mechanisms. Even two-dimensional complex motion percepts requiring spatial integration of early motion signals were observed during saccades. These results indicate that the magnocellular pathway functions during saccades, and that only spatiotemporal limitations of visual motion perception are important in suppressing awareness of intrasaccadic motion signals.

During saccadic eye movements, we do not perceive the world as moving. This observation is paradoxical because high-speed retinal motion can be detected with static eyes, provided it is produced by patterns with low spatial frequency[1]. Therefore, it is widely assumed that motion perception is 'switched off' during saccades. Based on psychophysical results reporting decreased intrasaccadic sensitivity (for instance, to contrast), two radically different theories account for the absence of conscious motion perception during saccades. The first approach postulates that extraretinal signals triggered by saccades actively suppress intrasaccadic motion processing[2,3]. Alternatively, some researchers propose that visual factors alone might be involved. For example, intrasaccadic information can be effectively masked by pre- and postsaccadic visual activations[4,5].

The general issue of intrasaccadic motion processing remains unclear. Notably, proposals concerning the physiological implementation of extraretinal suppression raise a number of problems. The visual system comprises two relatively independent pathways from the retina to the cortex. One pathway, which extends from the magnocellular subdivision in the lateral geniculate nucleus (LGN) to the parietal cortex, is thought to be important for assessing motion[6,7]. This 'magnocellular pathway' contains neurons responding optimally to gratings of low spatial and high temporal frequencies[8,9]. It is proposed, based on psychophysical results, that the magnocellular pathway is inactivated during the saccade by selective suppression in the LGN[10,11]. However, no physiological evidence supports this claim. Moreover, neurons in the middle temporal area (MT) of awake monkeys can be transiently activated by the visual flow created by fixational saccades[12], suggesting that precortical suppression of the motion pathway is unlikely. Furthermore, such suppression would be surprising, as there is reason to believe that the essential functions of the magnocellular stream are still needed during saccades, whether or not they contribute to conscious awareness[13]. Therefore, it was important to investigate how much intrasaccadic information is available in the magnocellular stream.

The ability to detect a two-frame displacement briefly presented during the saccade is well studied[14,15]. It is unclear if displacement perception involves activation of low-level motion detectors within the magnocellular pathway or a different process, like attentional tracking of a moving object's successive positions[16,17]. Attempts to assess intrasaccadic motion perception using stimuli more specifically linked to early cortical motion processing are scarce. Intrasaccadic retinal stimuli used in most studies do not optimally activate magnocellular motion detectors. As a result, human capacity for intrasaccadic motion processing is probably largely underestimated. In brief, visual functions that might be carried out by the magnocellular stream during saccades, including low-level motion processing, are currently poorly understood.

We present direct evidence for intrasaccadic motion perception mediated by low-level motion signals transmitted through the magnocellular pathway. Our experiments pinpoint the relevant visual factors that must be optimized to produce a clear, conscious sensation of visual motion during saccades.

RESULTS

Motion detection

The basic stimulus consisted of a vertical grating with low spatial frequency (0.17 cycles per degree) moving at a constant high speed (360° per s). With static eyes, the low-contrast grating (10%) was above the critical fusion frequency and was therefore invisible[18]. While the grating was continuously drifting, observers were required to make horizontal saccades between two fixation points whose spatial separation was varied across trials to alter eye velocity. The eye speed was concurrently measured in three observers who had to report whether or not grating motion was perceived during the saccade (yes/no task). Whenever saccades of moderate amplitudes (~6°) were made in the direction of the grating, a compelling perception of bars drifting in the direction of the grating occurred during the saccade. Mean velocity profiles of saccades of different amplitudes for one observer were plotted (**Fig. 1a**). The highest speed reached during a saccade increased

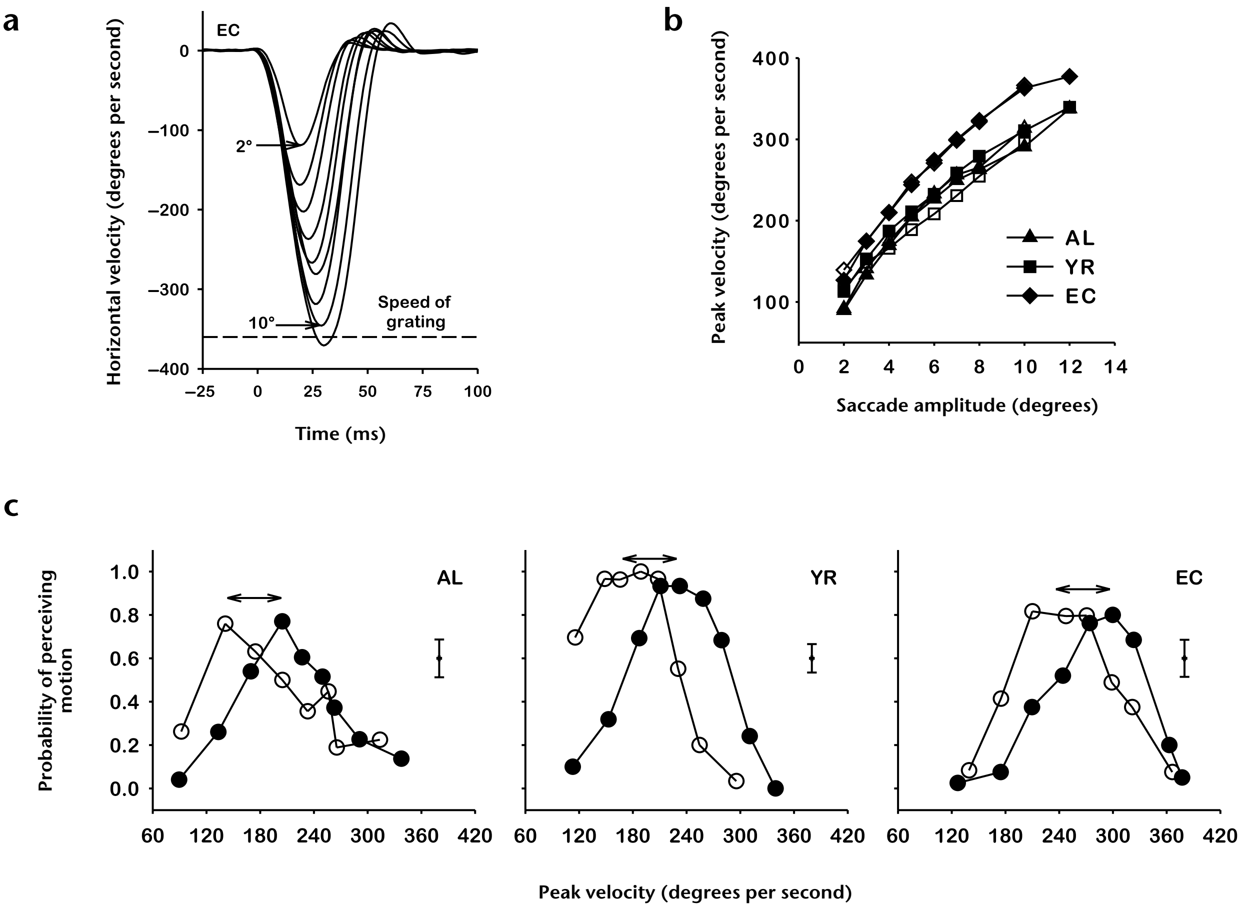

Fig. 1. Motion perception during a saccade in the same direction as a high-speed vertical grating (10% contrast). (**a**) Eye speed during leftward saccades (observer EC) as a function of time and saccade amplitude. Dashed line shows constant speed of a leftward-moving grating. For each saccade amplitude (two indicated by arrows), the mean velocity profile was obtained from aligning onsets of individual saccades and averaging their velocity profiles. (**b**) Dependence of peak velocity on saccade amplitude. For each combination of saccade amplitude and grating speed (solid symbols, 360° per s; open symbols, 300° per s), we measured the mean saccadic peak velocity by averaging individual peak velocities. (**c**) Probability of perceiving motion as a function of saccadic peak velocity for three observers. Gratings moving at either 360° per s (filled symbols) or 300° per s (open symbols) were presented in successive blocks. Error bars to right show average s.e. For all observers, the two inverted U-shaped curves were laterally shifted by 60° per s (horizontal arrows).

with saccade amplitude[19,20] (**Fig. 1b**). The probability of perceiving motion depended on this saccadic peak velocity (**Fig. 1c**). With gratings either at 360° per s (solid symbols) or 300° per s (open symbols), the data curves resembled an inverted U and were laterally shifted by a peak-velocity difference of about 60° per s (horizontal arrows). This value corresponded to the difference between the two grating speeds. These results strongly suggest that motion perception depends on the difference between the peak eye velocity and grating speed; the relevant factor is the speed (or temporal frequency) of the grating relative to the retina. This is best seen when data from Fig. 1c are replotted as a function of the retinal temporal frequency at the peak of the saccade (**Fig. 2a**). Here the two curves are superimposed, peaking between 10 and 25 Hz, depending on the observer.

The phenomenon can be understood if we look at the effective spatiotemporal stimulus at the retinal level. The retinal speed (and temporal frequency) of the grating was high at the beginning of the saccade and decreased until the peak was reached. After the peak, retinal speed increased again (**Fig. 1a**). We propose that this constantly changing retinal temporal frequency partly explains the usual impairment of intrasaccadic motion processing. This derives from two fundamental spatiotemporal characteristics of motion detection. First, individual low-level motion detectors only respond to a restricted range of spatiotemporal frequencies[21–23], and second, they need a minimum amount of time to integrate motion energy[24]. Thus, for any spatial-frequency channel, the temporal frequency at the retinal level changes too rapidly to provide a reliable signal, at least during the early acceleration and late deceleration phases of the velocity profile. However, within a brief period during which the velocity peaks, retinal temporal frequency is relatively constant. It is during this critical period that motion detectors could be effectively activated, provided the spatiotemporal combination were optimal. This hypothesis is fully consistent with our motion effect. With small saccades, the temporal frequency of the grating relative to the retina was too high even when the peak velocity was reached (**Fig. 2a**). For instance, with a 2° saccade, the retinal temporal frequency at the peak was about 40 Hz (240° per s), much too close to the fusion frequency to produce a clear motion percept. With medium saccades, motion perception was

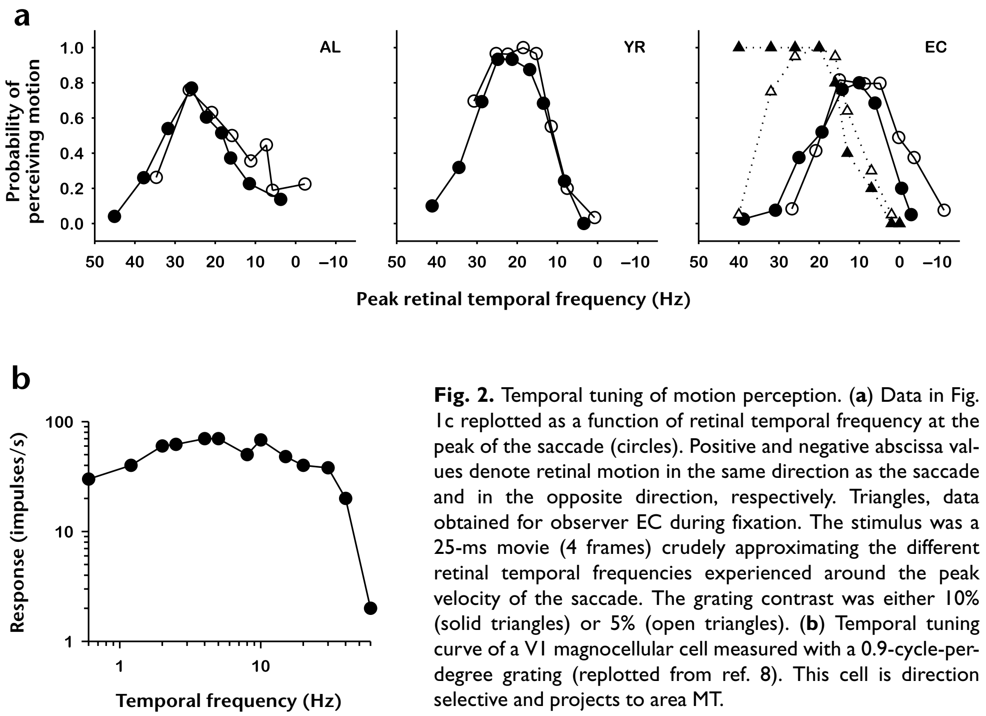

Fig. 2. Temporal tuning of motion perception. (**a**) Data in Fig. 1c replotted as a function of retinal temporal frequency at the peak of the saccade (circles). Positive and negative abscissa values denote retinal motion in the same direction as the saccade and in the opposite direction, respectively. Triangles, data obtained for observer EC during fixation. The stimulus was a 25-ms movie (4 frames) crudely approximating the different retinal temporal frequencies experienced around the peak velocity of the saccade. The grating contrast was either 10% (solid triangles) or 5% (open triangles). (**b**) Temporal tuning curve of a V1 magnocellular cell measured with a 0.9-cycle-per-degree grating (replotted from ref. 8). This cell is direction selective and projects to area MT.

optimal, because these saccades yielded retinal temporal frequencies around the peak that fell within the optimal temporal range for motion detection[25]. With large saccades (when the peak velocity approaches the grating speed—null relative speed), static visual channels are optimally activated. Observers report that the sense of motion is lost and replaced by the perception of a 'flashed' grating. A previous study has shown that stabilizing the retinal image of a rapidly moving grating with a saccade produces a 'static flash' percept[26]. However, observers did not report motion perception, presumably because the single spatial frequency used (1 cycle per degree) was too high. Beside making stimuli non-optimal for the magnocellular pathway, high spatial frequencies present another problem: during a saccade, the range of retinal temporal frequencies swept through over a given period increases proportionally with spatial frequency. As a result, the restricted range of temporal frequencies required for motion processing within a single temporal-frequency channel is encountered for shorter periods as spatial frequency is increased. Thus, this period is approximately sixfold shorter in the previous study[26] than in ours, possibly accounting for the failure to perceive intrasaccadic motion with high spatial frequencies.

Processing intrasaccadic visual motion under our protocol requires integrating different speeds across time, presumably by some form of averaging, within a brief period of ~25 ms. We tested the ability to process this kind of visual stimulus with static eyes. For each saccade amplitude previously tested, a 25-ms stimulus with 3 different grating speeds was created to approximate the variation in speeds experienced near the saccadic peak velocity (see Methods). Again, subjects indicated whether or not motion was perceived. The results were qualitatively similar to that obtained during saccades: for low contrasts, probability of perceiving motion as a function of 'peak' retinal temporal frequency was an inverted U-shaped curve. Quantitative differences were demonstrated by observer EC (triangles, **Fig. 2a**). The leftward shift of the curve probably reflects the different perceptual criterion used for this task. Contrast sensitivity was also higher in the 'static eye' condition: with a 10% contrast grating (as in the intrasaccadic task), high temporal frequencies were not above fusion frequency and, therefore, produced motion perception (solid triangles). By halving contrast, motion perception was decreased for these high frequencies, yielding an inverted U-curve (open triangles). It is impossible to determine whether this sensitivity difference results from extraretinal or visual factors, mainly because the effective retinal stimulus differs between experimental conditions.

We showed that a saccade toward a high-speed grating of low spatial frequency could produce a clear motion percept: the grating briefly appeared to move in the direction of the saccade. This percept was optimal when the retinal stimulus was within the range for motion detection during the period including peak velocity. The optimal retinal temporal frequencies for motion detection (10–25 Hz; **Fig. 2b**) were consistent with the broad and high-cutoff tuning curves of direction-selective cells in primate striate cortex[8,9].

Direction discrimination

Possible inconsistency in criteria for motion percepts across observers and runs may be a weakness of the previous study. This may explain why peak values of the inverted U-curves differed for different observers (**Fig. 2a**). To overcome this, we also measured thresholds for direction discrimination. Because direction selectivity is an essential property of early motion detectors, a direction discrimination task further probed the involvement of motion pathways in intrasaccadic motion perception.

We predicted that perceived direction would oppose the direction of the saccade when the peak of the velocity profile exceeded the grating speed for a sufficiently long duration. To test this, a grating whose speed (or equivalent temporal frequency) was controlled by an adaptive-staircase procedure was presented on each trial as before. Observers made large saccades of constant amplitude (14°) and reported whether perceived motion was in the same direction as the saccade (forward response) or its opposite (backward response). Using 2 staircases, we could assess the grating speeds producing forward responses with probabilities of 0.29 and 0.71. Backward percepts appeared less vivid than forward percepts, presumably because of concurrent activation of static channels during the two brief periods when eye and grating speeds matched. The point of subjective stationarity (PSS) was determined by tracking the speed of a grating that produced a static percept (equiprobable forward and backward responses).

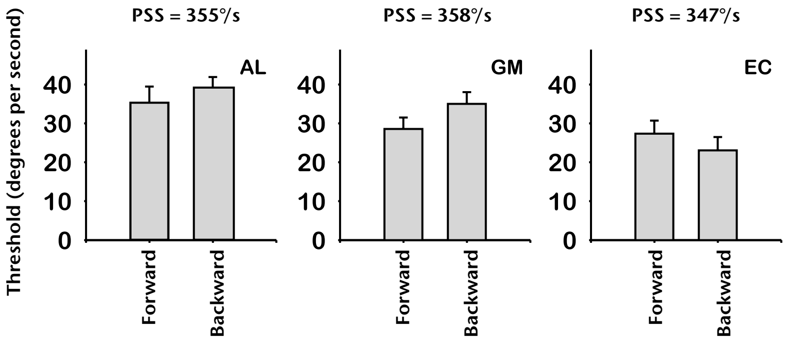

Fig. 3. Direction discrimination experiment. Thresholds for perceiving motion either in the direction of the saccade (forward) or in the opposite direction (backward). Forward and backward thresholds respectively correspond to grating speeds larger and smaller than the average saccadic peak velocity.

Thresholds for all observers lay within a 25°–35° per s range (4–6 Hz): 'forward' differential thresholds correspond to the difference between 0.71 and 0.50 levels, and 'backward' thresholds correspond to the 0.50–0.29 difference (**Fig. 3**).

For comparison, we also measured these direction-discrimination thresholds during fixation. The stimulus was a 25-ms movie of 4 frames simulating 3 successive speeds around the peak of a 14° saccade. We varied the average speed from a few degrees per second to the left to a few degrees per second to the right. Measured thresholds (observers E.C., G.S.M., data not shown) were four- to sixfold lower than those during saccades (**Fig. 3**). However, it is impossible to assess whether this decrease was related to extraretinal signals or to visual factors alone, especially as retinal stimuli differed between conditions. One clear difference was that, because of the large saccade, the effective stimulus width for the intrasaccadic condition was narrower (about 12°) than the full screen available during the fixation condition (27°). As a result, spatial integration mechanisms could not be as efficient as during fixation. Moreover, the screen edges sweeping over peripheral retina may produce lateral masking. Intrasaccadic thresholds may also be inflated by variability in peak saccade speed across trials, as we used average, rather than trial-by-trial, eye speed. Therefore, investigating the relative influence of visual versus extraretinal factors on direction discrimination during saccades requires further research.

Here, the relevant difference between fixation and intrasaccadic thresholds concerned the PSS. During saccades, the PSS (above each graph in **Fig. 3**) was smaller than the average saccadic peak velocity (370° per s), so the corresponding retinal speed averaged over 25 ms was close to zero (mean, –6° per s). This suggests that stationarity is perceived when retinal speeds within ~25–30 ms are of opposite directions and thus approximately average to zero, consistent with our measurement of the PSS during fixation at nearly 0° per s.

In summary, the intrasaccadic ability to discriminate between 'forward' and 'backward' directions supports our hypothesis that direction signals relevant to the task are indeed extracted during a short period in which eye velocity peaks.

Direction-specific adaptation

Although the spatiotemporal selectivity of these motion effects suggests the involvement of early motion detectors, one could argue that the percept is merely due to static mechanisms recruited to detect a temporal change of position[16,17]. To rule out this possibility, we used a classic protocol for direction-specific adaptation[27]. A vertical high-contrast adapting grating (12 Hz, 0.17 cycles per degree, 72° per s) covering the whole screen was presented while observers stared at a fixation point. Its temporal frequency was chosen to optimally activate motion detectors[25]. During the test period, a vertical grating (50 Hz, 0.17 cycles per degree, 300° per s) of variable contrast presented in the top or bottom half of the screen was moved either in or opposite to the adapting direction. Observers were required to make saccades in the same direction as the test grating and to indicate the part of the screen in which the intrasaccadic motion was perceived. The saccade amplitude for each observer was chosen to optimize motion perception (as assessed in the first experiment). Contrast thresholds were dramatically increased when the adapting and test gratings were in the same direction, whereas adaptation in the opposite direction had only a slightly detrimental effect (**Fig. 4**; comparison of across-observer means, $t_2 = 8$; $p = 0.015$). This direction-specific threshold elevation is a classic signature of an early direction-sensitive mechanism[27]. In primates, direction selectivity is a visual property that starts at the level of the primary visual cortex[28]. Therefore, this finding is at odds with suggestions that the activity of the magnocellular pathway (constituting the dominant input to motion detectors[6,7]) is suppressed at a precortical level during saccades[10,11].

Two-dimensional motion perception

In the experiments above, the perceived direction of the intrasaccadic percept always matched the axis of the saccade itself. This coincidence raises the possibility that the percept was actually determined by an extraretinal signal associated

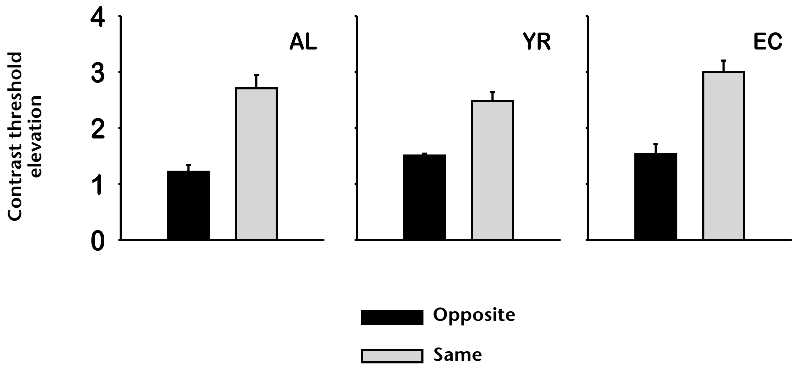

Fig. 4. Direction-selective adaptation. Observers made horizontal saccades and detected whether a horizontally moving test grating was located in the top or bottom half of the screen (spatial 2AFC). Contrast sensitivity was measured with or without adaptation to a moving grating. The data clearly show direction-selective adaptation: contrast-threshold elevation (relative to the unadapted condition) was larger when the adapting grating was in the same rather than in the opposite direction.

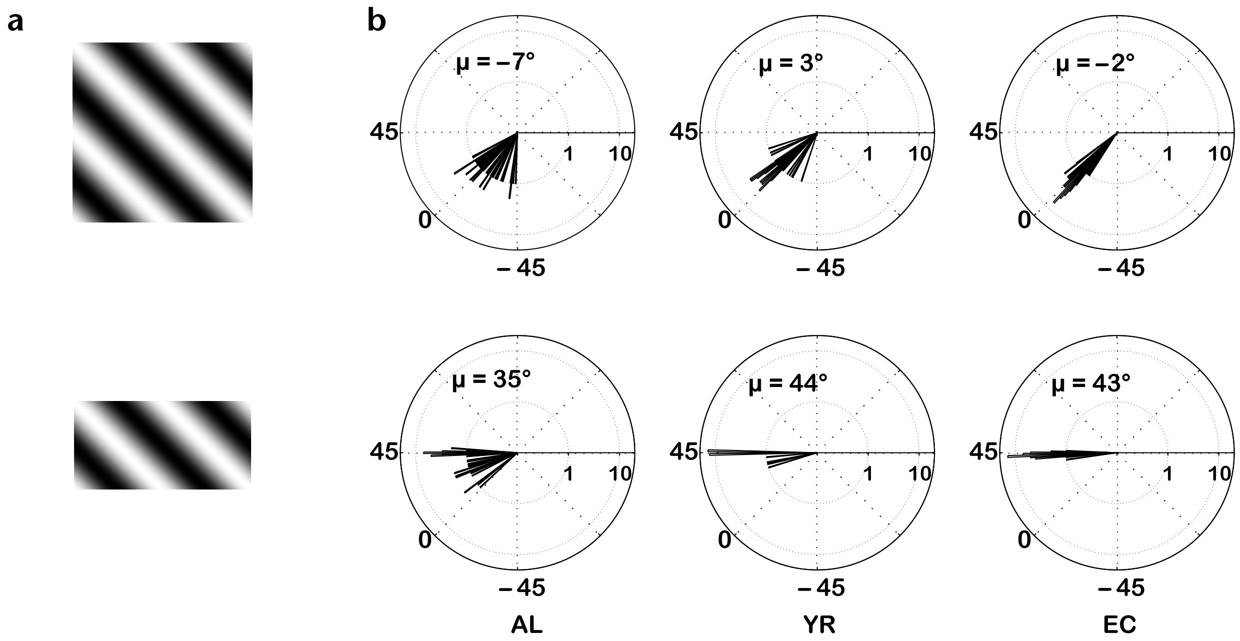

Fig. 5. Perceived direction of two-dimensional motion. (**a**) Stimuli were oblique (45°) moving gratings (contrast 30%; temporal frequency as before) presented within square (20° × 20°) or rectangular (20° × 10°) apertures. As before, observers made horizontal saccades of optimal amplitude and then rotated an arrow in the middle of the screen to indicate the direction of perceived intrasaccadic motion. (**b**) Distributions of perceived directions in polar coordinates. The origin (0°) of the angular axis represents the motion component perpendicular to the bars of the grating. The radial axis plots, in log coordinates, the number of observations collected for each direction. Mean direction is given by μ. With a square aperture, perceived directions cluster around the perpendicular component. With a rectangular aperture, perceived directions are parallel to the long axis (barber-pole illusion).

with the saccade[14]. To avoid this confounding effect, we used the display from the first experiment but rotated the moving grating by 45° and presented it within a large square aperture (**Fig. 5a**, top). Observers made horizontal saccades of optimal amplitudes, and then adjusted the direction of an arrow presented on the screen to report the perceived direction of the intrasaccadic percept. The distribution of the perceived directions was centered around the grating direction (**Fig. 5b**, top), as would be expected if motion detectors with the preferred oblique orientation matching the grating orientation were activated in this condition.

Furthermore, motion perception of real complex objects requires the spatial integration of different local motion signals that are not in the direction of the eye movements[29,30]. If early motion signals are not suppressed during saccades, as suggested by previous experiments, one could argue instead that integration of these signals into a two-dimensional velocity signal is actively suppressed. A classic stimulus used to study motion integration is the barber-pole illusion[31]: when an oblique grating moves within a rectangular, rather than square, aperture, its perceived motion is parallel to the long side of the aperture. This phenomenon, which indicates the importance of the motion signals elicited near aperture borders[32,33], was also tested. The height of the aperture used before was simply halved to obtain a horizontal 'barber-pole' (**Fig. 5a**, bottom). All observers perceived the classic barber-pole illusion—here, in a horizontal direction (**Fig. 5b**, bottom). Intrasaccadic motion perception based on activation of low-level detectors tuned to all possible directions followed by integration of the resulting signals, presumably at a second stage[29,34,35], is therefore possible during saccades.

DISCUSSION

We show that making saccades in the direction of a rapidly moving grating produced clear motion percepts when retinal image motion (averaged over a critical period around the saccadic peak velocity) was within the motion-detection range. Observers could distinguish between retinal motion in the direction of the saccade and retinal motion in the opposite direction, and perceived a static grating when retinal speed averaged over ~25–30 ms was close to null. Adapting during fixation to a low spatial and high temporal frequency grating produced a direction-specific reduction in contrast sensitivity to intrasaccadic motion perception. Additionally, spatial integration of early motion signals leading to two-dimensional motion perception was still observed during saccades. We conclude that these intrasaccadic motion percepts revealed the activation of direction-selective mechanisms tuned to low spatial and high temporal frequencies within the magnocellular pathway.

We designed the stimulus to optimize intrasaccadic motion perception. First, as the grating was invisible at the beginning (and at the end) of each saccade, there was no pre- or post-saccadic visual information that might have produced forward or backward masking[4,5,36,37]. Moreover, in contrast to studies using a two-frame sequence, the grating was not abruptly presented during the saccade. Instead, it was continuously displayed on each trial. This point was crucial: the gradual transitions between a retinal temporal range above fusion frequency and an optimal range for motion detection minimized the temporal energy spread and the intrusion of masking transient signals. This optimization allowed a study of motion detection *per se* rather than displacement detection. The involvement of early motion processing is unclear in numerous studies of intrasaccadic displacement perception[14,15]. Two-frame presentations used in displacement studies are weak stimuli for motion processing. As a consequence, it is possible that performance in these studies might rely exclusively on visual processes that detect changes in position over time[16,17].

In our experiments, intrasaccadic motion perception was easily experienced when magnocellular motion detection was optimized. In primates, the first stage of motion processing takes place in the striate cortex (V1). The one-dimensional edge-motion signals extracted in V1 are thought to be integrated at a later stage into a two-dimensional velocity signal within the middle temporal area[34,35]. There is ample evidence that motion perception depends on the activity of MT cells[38–40]. In addition, MT cells of alert monkeys consistently respond to directional signals induced by randomly directed small-amplitude (about 0.8°) saccades while monkeys fixate[12]. MT neurons transiently increase their firing rates when these fixational saccades induce a retinal flow in the neurons' preferred direction, whereas neuronal responses are mildly suppressed when saccades induce null retinal flow. In this framework, the spatiotemporal characteristics of the effects in experiments 1–3 suggest the involvement of direction-selective V1 neurons[8,9], whereas motion integration observed in experiment 4 was probably related to MT responses.

Our findings suggest that visual factors are the essential determinants of suppression of consciousness of motion during saccades[4,5,36,37]. Clearly, extraretinal signals do not switch off motion processing. Studies suggesting such suppression actually measured the visibility of static gratings (0 Hz)[10,11], and therefore are not inconsistent with our study, which used spatiotemporal stimuli optimized for motion detection by the magnocellular pathway (with low spatial and high temporal frequencies).

Our results also pertain to the issue of perceptual stability during eye movements in relation to extraretinal signals[14,15]. In our experiments, it was striking that a static flash percept occurred when the eye peak velocity equaled the speed of the moving grating. Such a static appearance was inconsistent with the idea that extraretinal signals are used to compensate for the effect of eye movements, as generally assumed with smooth eye movements[41–44]. This hypothesis would predict high-speed motion perception of the grating. Therefore, it seems that saccadic eye movements invoke other mechanisms to achieve perceptual stability[13,45]. Alternatively, it is possible that a recalibration process due to extraretinal signals acts more slowly than the actual saccadic eye movements[46], or that extraretinal signals carry a damped representation of eye position[47].

Here we showed that the magnocellular pathway functions during saccades. Indeed, suppression of the magnocellular-dominated stream would have important adverse effects[48]. For instance, the role of the parietal cortex in visual attention[49] makes it well suited to alert and orient the visual system toward a peripheral transient signal detected during the saccade. Given the high frequency of saccades in normal vision, future research should examine the behavioral importance of processing intrasaccadic visual information.

Our findings do not rule out the possibility that an extraretinal signal alters intrasaccadic visual motion processing. However, we clearly showed that such a putative extraretinal signal does not suppress motion perception during saccades. Therefore, it is more parsimonious to interpret the usual absence of intrasaccadic motion perception as the result of visual and/or attentional factors alone.

METHODS

Psychophysics. Stimuli were displayed on a 21-inch Sony color monitor (GDM-4011P) driven by a display controller (Cambridge Research System VSG 2/3F, Rochester, UK) with a 160-Hz frame rate. At a viewing distance of 68 cm, the average horizontal separation between adjacent pixels subtended 0.035° of visual angle. The screen subtended 27° × 21°. A lookup table in the software was used to linearize the intensity response of the screen phosphors at an 8-bit luminance resolution.

Stimuli displayed during saccades. On each trial, a moving grating of low spatial frequency (0.17 cycles per degree) was displayed for 2 s. During the first 500 ms, the contrast increased using a raised cosine function from 0% to the desired level, which was kept constant for 1000 ms. The contrast then decayed to 0% using the same function during the last 500 ms. A low-pitch sound indicated that the contrast had reached the desired level, prompting saccades. A high-pitch sound, presented when the grating disappeared, prompted observers to respond. The temporal frequency was either 50 Hz (300° per s) or 60 Hz (360° per s) except in the second experiment (direction discrimination), where it was varied with an adaptive procedure. The mean luminance of the grating was 22 cd per m^2 (4.5 cd per m^2 in the second experiment). Observers AL and YR were naive as to the purpose of the experiments.

Stimuli displayed with static eyes. A 25-ms movie was presented at 3 different speeds during fixation by displaying 4 frames of a grating whose spatial phase was appropriately shifted. For each saccade amplitude (tested in the first experiment), 3 retinal speeds centered on the saccadic peak velocity were calculated from the saccadic velocity profiles over 25 ms. For instance, for a 2° amplitude, the 3 successive retinal speeds of the grating were S1, 270° per s (6 ms before the peak), S2, 240° per s (at the peak) and S1 again (6 ms after the peak); average speed, 260° per s.

Measurement of eye movements. Horizontal movements of the right eye were recorded using a high-resolution infrared scleral-reflectance system (IRIS Skalar, Delft, Netherlands). Analog signals were digitized at 500 Hz with a 12-bit resolution ADC. A bite bar was used to restrain head movements. Two points of different colors indicated the size and the direction of the saccade to be made. On each trial, a sound instructed observers to make the saccade. Data were analyzed off line. Inappropriate saccades were discarded from the analysis.

Direction discrimination. Across trials of the same block, the direction of the saccade (14° amplitude) was constant (leftward or rightward). Observers were required to indicate whether perceived motion of the grating was in the same direction as the saccade (forward) or in the opposite direction (backward). The grating (20% contrast) covered the whole screen and had its temporal frequency controlled by one of 3 staircases with steps of 0.5 Hz[50]. One staircase (starting value, 360° per s; – 60 Hz) converged on a 0.50 threshold indicating the speed at which the grating appeared static. The two other staircases tracked the 0.29 and 0.71 thresholds. Their starting values, which were 300° per s (50 Hz) and 420° per s (70 Hz) in the training period, were respectively increased and lowered as performance improved across blocks. The actual starting values were randomly chosen within a range of 2 Hz centered on the above values. The end of a block occurred when a minimum of nine reversals had been completed in each staircase. The three thresholds were then estimated by averaging the six last reversals in each staircase. The 'same direction' differential threshold (DT) was defined as the difference between the 0.71 and 0.50 levels, and the 'opposite direction' DT as the difference between the 0.50 and 0.29 levels.

Direction-specific adaptation. Required saccade direction (leftward or rightward, in the direction of the test grating moving at 300° per s) was randomly alternated across trials. For each observer, a constant saccade amplitude was chosen from results of the first experiment to optimize motion perception (4° for EC and 3° for AL and YR). The contrast of the test grating was adjusted with an adaptive staircase procedure converging on a 0.71 threshold (steps of 0.4% contrast)[50]. Two staircases, each assigned to a grating direction, were randomly interleaved within a block.

Contrast thresholds were measured with or without adaptation to a moving grating (80% contrast), which covered the whole screen and had the same spatial frequency as the test grating and a temporal frequency of 12 Hz (optimal for motion detection of low spatial frequencies[25]). The adapting grating, whose direction was constant within any block, was presented for one minute at the beginning of each block. Observers were then exposed to cycles of test periods (during which one saccade had to be made within 1500 ms) and 10-s adapting periods. Test gratings were presented either in the upper or lower part of the screen (spatial 2AFC). A block ended when a minimum of eight reversals had been completed in each staircase. The two thresholds were then estimated by averaging the last six reversals in each staircase.

Two-dimensional motion perception. For a given saccade direction (leftward or rightward), the orientation of the grating was randomized so that the motion component perpendicular to the bars was either above or below horizontal. The two different saccade directions were presented in distinct blocks. The perceived directions plotted in Fig. 5b were averaged over the four possible quadrants (two for each saccade direction). The square and rectangular aperture conditions were randomly interleaved within each block.

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