Human updating of visual motion direction during head rotations

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Running head: Updating of motion direction during head tilt

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Abstract

Previous studies have demonstrated that human subjects update the location of visual targets for saccades after head and body movements and in the absence of visual feedback. This phenomenon is known as spatial updating. Here we investigated whether a similar mechanism exists for the perception of motion direction. We recorded eye positions in three dimensions and behavioral responses in seven subjects during a motion task in two different conditions: when the subject’s head remained stationary, and when subjects rotated their heads around an antero-posterior axis (head tilt). We demonstrated that a) after head tilt subjects updated the direction of saccades made in the perceived stimulus direction (direction of motion updating), b) the amount of updating varied across subjects and stimulus directions, c) the amount of motion direction updating was highly correlated with the amount of spatial updating during a memory guided saccade task, d) subjects updated the stimulus direction during a two-alternative-forced-choice direction discrimination task in the absence of saccadic eye movements (perceptual updating), e) perceptual updating was more accurate than motion direction updating involving saccades, and f) subjects updated motion direction similarly during active and passive head rotation. These results demonstrate the existence of an updating mechanism for the perception of motion direction in the human brain that operates during active and passive head rotations and that resembles the one of spatial updating. Such a mechanism operates during different tasks involving different motor and perceptual skills (saccade and motion direction discrimination) with different degrees of accuracy.

**keywords:** motion direction, saccades, updating, head movements, reference frames.
Introduction

Humans and monkeys can accurately make saccades or pointing arm movements to the remembered location of stationary visual targets after intervening eye, head and body movements (Klier et al., 2005; Medendorp et al., 2002, 2003; Mergner et al., 1998; Karn et al., 1997; Mays and Spark, 1980; Hallett et al., 1976; Philbeck et al., 2001; Lewald et al., 2000; Blouin et al., 1997, 1998; Henriques et al., 1998). This ability, referred to as spatial updating, requires extraretinal signals related to the eye, body or head movements and retinal signals indicating retinal target position to be integrated during the computation of target location in space coordinates (Klier et al., 2005). Although spatial updating seems to be a very well established phenomenon in space perception, it remains less clear whether a similar mechanism also exists during the perception of motion direction. This is because the perceived motion direction and spatial position of objects can be dissociated from each other and has been suggested that different neuronal populations in the human brain are responsible for these two functions (Bulakowski et al. 2007). In the present study we test whether an updating mechanisms also exist during the perception of object motion. We additionally examine the possible role of an extraretinal signal (the efference copy of motor commands to rotate the head in space) in motion direction updating.

Previous studies have reported that extraretinal signals generated during eye movements influence the perception of visual motion (Wertheim, 1981; Pola and Wyatt, 1989; Brenner and van den Berg, 1994; Wertheim, 1987; Freeman et al., 2000; Turano and Heidenreich, 1996; Crowell et al. 1998). Wertheim (1981) proposed that retinal image motion carries no information about stimulus motion and therefore that perceived
motion, direction and velocity are relative concepts, i.e., they are relative to extraretinal signals. Supporting this view, Freeman and Banks (1998, 2000) demonstrated that information from retinal and extraretinal sources seems to affect speed perception during visual tasks. They developed a head-centric model of velocity perception that uses both retinal and extraretinal signals as well as errors in the signal estimates and experimentally confirmed the model’s predictions regarding the magnitude and direction of the Filehne illusion (illusory motion of a stationary background when pursuing a moving target, Filehne, 1922) and Aubert-Fleischl phenomenon (moving objects appear slower when pursued, Aubert, 1886; Fleischl, 1882).

More recently, Mitsudo and Ono (2007) have proposed that the human visual system calculates head-centered velocity by adding retinal and smooth pursuit velocity signals. In agreement with this idea, it has been shown that many MSTd motion sensitive neurons in macaque monkeys compensate for pursuit velocity, direction and speed, suggesting that such neurons use retinal and extraretinal signals during the computation of egomotion (Bradley et al., 1996; Shenoy et al., 2002; Lee et al.; 2007). Other studies also in macaques have examined the contribution of area MSTd neurons to the processing of retinal and extraretinal signals during egomotion and suggested that such neurons integrate vestibular and retinal inputs (Gu et al. 2006, 2007). Moreover, it has been shown that MSTd and MSTI neurons hold reference frame representations different from retina/eye centered (Fetsch et al., 2007; Ilg et al. 2004) and that the performance of these neurons at discriminating heading direction is comparable to behavioral performance (Gu et al., 2007). Interestingly, the latter authors demonstrated that behavioral and neuronal performance in the monkey deteriorates after labyrinthectomy, suggesting that at least a
considerable part of MSTd extraretinal inputs are of vestibular origin (Gu et al., 2007).

In humans, an electrophysiological study recorded Event Related Potentials (ERPs) while manipulating the intensity of the Filehne illusion during a smooth pursuit task and demonstrated that brain activity on a fronto-parietal network was solely determined by the subjective perception of visual motion irrespective of the physical attributes of the stimulus (Haarmeyer and Thier, 1998). This may suggest that although the brain integrates inputs from different extra retinal sources such as vestibular and proprioceptive resulting from body, head or eye-in-head motion with retinal inputs resulting from objects motion on the retina, the neural computations underlying the perception of visual motion are quite complex and may not always reflect the simple summation of sensory signals.

In a previous study Darling and Pizzimenti (2001) examined the reference frames used by the visual system during the perception of motion direction. Their subjects had to align the motion of a single dot to different axes that were differentially oriented relative to an earth fixed orthogonally oriented axis. Subjects made fewer errors when aligning the dot’s motion to an earth-fixed vertical in the vertical plane and to an external oblique line in the horizontal plane when head and trunk orientations were varied. They concluded that motion direction is encoded in an earth- or space-fixed frame of reference, supporting the view that extra retinal signals are taken into account during motion direction perception. However, in this study the authors used stimuli containing orientation information and the subjects made orientation judgments, leaving open the question of whether orientation and motion direction information were dissociated during
the task or whether they somewhat interacted (Krekelberg et al. 2003).

In the present study we determine the ability of human subjects to update the perceived direction of moving random dot patterns (RDPs) after head rotations and in the absence of visual feedback (cues). In the first of two experiments subjects reported the direction of a moving RDP presented on a circular computer screen. After the stimulus presentation subjects rotated their head and made a saccade in the perceived motion direction. In the second experiment subjects discriminated the direction of two moving RDPs presented before and after an intervening head rotation. In a third experiment we tested whether motion direction updating was similar during active and passive head rotations. This latter experiment will reveal the role of efference copy signals in direction of motion updating since during passive rotation such a signal cannot be the source of updating. Our results show that in the absence of additional visual cues and after intervening active or passive head rotations subjects updated the perceived motion direction of RDPs by different amounts. Such updating mechanism operates during a motor task involving saccades and during a perceptual task involving motion direction discrimination.

**Methods**

**Subjects:** Seven subjects participated in the study, two females and five males, aged between 22 and 39 years. Five were naïve to the purposes of the experiments. All subjects had normal or corrected to normal vision and gave a written consent for participating in the study. All the procedures used in this study were pre-approved by the ethics committee of the faculty of Medicine at McGill University.
**APPARATUS:** The experiments were conducted in a dark room. Subjects sat 57 cm away from a computer screen (resolution = 1280 x 1024 pixels and refresh rate = 75 Hz, 1 cm = 1 degree of visual angle). The subject’s head was fixed to a rotating ring using a bite bar (previously molded to their mouth). The ring allowed them to rotate the head counterclockwise around an anterior posterior axis oriented parallel to the earth and the bite bar position could be adjusted in such a way that the subject’s right eye was at the ring center which also was the center of rotation. A black cylinder of the same diameter as the ring (45cm) was positioned between the ring and the screen in such a way that subjects only visualized a circular area of the screen (**Figure 1a**). The cylinder did not move with the ring. This avoided visualization of the screen’s square edges or any other environmental cue that could be used as a reference for perceiving motion direction during the experimental trials. On top of the rotating ring, we positioned a graded scale and an adjustable mechanism that allowed us to stop the ring rotation at a given angle (e.g., 30 degrees, see setup pictures in supplementary material). During the first two experiments we positioned the mechanism at 30 degrees. The subject rotated the head from the straight position (0 degrees) to the point where rotation stopped (30 degrees to the left). These two points were considered as 0 head rotation (head straight) and 30 degrees head rotation (head tilted).

During the third experiment (active vs. passive head rotation) we used a goniometer attached to the rotating ring to measure angular head displacement for different degrees of head tilt. The instrument was calibrated before each experimental session by rotating the head by different amounts and obtaining voltage values. A linear regression on the amount of rotation as a function of voltage allowed us to obtain the
amount of head rotation during each trial (Bouyer and Watt, 1996, see also figure 3 of supplementary material).

**STIMULUS AND TASK:** The stimuli were generated using an Apple Power PC computer using custom programmed software. The stimuli consisted of random dot pattern (RDPs) composed of white dots on a dark background. The dots could move (translate) either with 100% coherence (in one direction) or with 0% coherence (masking stimulus used in the second experiment). The area covered by the RDPs had the shape of an annulus with an inner diameter of two degrees and an outer diameter of 30 degrees. The dot size was 4 pixels$^2$ (2x2), one dot covered 0.003 degree$^2$ and the dots density was 1.2 dots/degree$^2$. The screen resolution was 32 pixels per degrees. The dot’s speed was 6 degrees/second and it was kept constant across the experiments. The luminance of the dots, 34.14 cd/m$^2$, was measured using a photometer (Konica Minolta LS-110). The luminance of the background was lower than 0.001 cd/m$^2$.

**SACCADE DIRECTION TASK:** This experiment was designed to determine subject’s ability to make saccades in the perceived motion direction of a RDP after active head rotations and in the absence of visual cues. Two experimental conditions were tested. In the first one (head tilted), subjects were required to make a saccade in the perceived RDP direction after an active head rotation. In the second one (head straight), subjects were required to make a saccade in the perceived RDP direction while keeping their head straight during the complete trial. We hypothesized that if subjects updated the perceived RDP direction after head tilt, saccade direction should be similar in both, head straight and tilted conditions. The two conditions were run in blocks presented in randomized order. Each block was composed of two different trial types randomly interleaved.
(direction trials (60) and memory guided saccade (60) trials). One block of 60 trials lasted approximately 15 minutes.

Direction trials consisted of the following sequence. A fixation point appeared at the center of the circular screen, after fixating on it the subject pressed the space bar to trigger the presentation of a RDP moving behind a virtual aperture during 400 ms (figure 1a, ‘1’). The aperture had the shape of a ring in order to avoid foveal tracking of individual dots, i.e., at the center of the ring only a circular shaped stationary fixation point was presented. From trial to trial, dots could move in one of ten possible directions, from 0 degrees (rightward) in steps of 10 degrees to 90 degrees (upward). We restricted the experiments to directions spaced every 10 degrees in the right upper quadrant because the duration of the sessions would have been very long if all the quadrants would have been tested with the same spatial resolution. The RDP offset was followed by a 2000ms interval in which only a dark screen was presented (figure 1a, ‘2’). Finally, a white ring of the same diameter as the RDP/aperture external border (30 degrees) appeared together with the fixation point during 2000 ms and the subject made a saccade (of approximately 15 degrees amplitude, i.e., the ring radius) toward the ring in the perceived RDP direction (figure 1a, ‘3’). During head tilted trials, subjects tilted the head 30 degrees to the left by applying a torque to the bite bar during the 2000ms interval after the RDP offset (figure 1b, ‘2’, observe VOR traces). After the saccade they rotated the head back to the original position (figure 1b, ‘4’). During these trials we mainly observed torso translations of about 3 to 6 cm (see last experiment and supplementary material (‘s8 head images’ and ‘torso analysis’)). During head straight trials subjects kept the head straight during the whole trial (figure 1c, ‘2’).
The trial sequence during the memory guided saccade task was very similar. However, here no moving RDP was presented and subjects made a saccade to the remembered location of a dot flashed during 400 ms at the beginning of the trial (figure 1b, ‘1’) either after tilting the head (head tilted trials) or after keeping the head straight (head straight trials) during the 2000ms period (figure 1b, c, ‘2’). The re-appearance of the fixation point after that period was the signal to initiate the saccade. The dot could be located at any of 10 different positions on the right upper quadrant separated by 10 degrees steps. In angular coordinates these positions corresponded to the direction of the RDP during the direction trials. The eccentricity of the dot was equivalent to the RDP radius. During these trials no ring was presented.

In the third experiment we tested subjects in a task similar to the one described in figure 1 but in this case the RDP direction of motion was fixed (40 degrees) and the amount of head rotation varied in different trials from 0 to 45 degrees. We tested the subjects under two different conditions. During the first condition, passive head tilt, the experimenter rotated the subject’s head by applying an amount of torque to the rotating ring. An external display, invisible to the subjects but visible to the experimenter, indicated to the latter the desired final amount of head tilt (0, 5, 10, 15, 20, 25, 30, 35, 40, 45). This paradigm proved to be successful to map the full desired range of head rotations (from 0 to 45 degrees, see figure 11). During the second condition, active head tilt, the experimenter instructed the subject, verbally at the beginning of the trial, the desired amount of head rotation. In order to make sure that subjects would cover the whole range of head rotations (0 to 45 degrees) we instructed them during training sessions on the meaning of the instruction (e.g., a 10 degrees head rotation means tilting the head 10
degrees away from the vertical). Most of our subjects did cover the expected range of head rotations following the verbal instructions. During the experimental sessions the subject did not receive any feedback regarding the final degree of head tilt. In both cases the amount of head rotation was randomized from trial to trial, avoiding that the subject could predict in advance the final head position. The peak velocities of the head movements and the final head positions were approximately equally distributed across the passive and active trials (see head velocity vs. head rotation in supplementary material).

In this experiment, as a control, we measured torso translations as a function of head rotation in 5 subjects (see ‘torso analysis’ and ‘s8 head images’ in supplementary material). We found that during leftward head rotations, subjects translated the torso to the right between 0.14 and 0.21 cm per degree of rotation. The largest translation was about 9.5 cm for a head rotation of 45 degrees. Torso rotations were almost negligible.

PERCEPTUAL UPDATING TASK: During the second experiment subjects compared the direction of two RDPs moving behind a circular aperture with the shape of a ring sequentially presented and separated by a 2000ms interval (figure 2). During the inter-stimulus interval an RDP with 0% coherence (random motion, figure 2, ‘2’) was presented in order to avoid retinal afterimages caused by the first RDP presentation. During the entire trial subjects maintained fixation on a circular color spot at the center of the display.

The first RDP was always presented when subjects had the head straight (figure 2a, ‘1’). The pattern could move in one of the following directions (61, 53, 49, 47, 45, 43, 41, 37, 151, 143, 139, 137, 135, 133, 131, 127). We intentionally used directions located
in the upper right and upper left quadrant in order to make difficult for the subjects to memorize the different pattern directions. We did not use the same directions as in the saccade direction task since these were 10 degrees apart and we needed to have different (smaller and larger) step sizes for the direction discrimination task used here. The second stimulus (chosen among the same set of stimuli) was presented either after the subjects kept the head straight during the 2000ms interval (head straight trials) or after they rotated the head 30 degrees to the left (head tilted trials) (figure 2a, ‘3’). The task for the subjects was to determine, in a two alternative forced choice (2AFC) paradigm whether the second stimulus direction was more to the right (clockwise) or to the left (counterclockwise) than the first one by pressing the right or left arrow key on a computer keyboard. During the inter-stimulus interval the fixation point color indicated whether they should tilt the head (blue) or keep it straight (white). After the final key press they tilted the head back to its original straight position (figure 2a, ‘4’).

We explored 16 different combinations of first and second pattern directions presented 8 times each in a block of 128 trials (30 minutes per block). Each subject ran each block 3 times. Data from different blocks were pooled. Before starting the data collection subjects were trained in the same task during 1-3 sessions. No feedback on performance was provided.

**EYE POSITION MEASUREMENTS:** During both experiments subjects wore a head mounted video-based eye tracker (Chronos Vision Inc, Berlin, Germany) that allowed on-line monitoring of the horizontal and vertical eye position components and offline calculation of the torsional component. The sampling frequency was 100 Hz. The eye position data as well as the stimulus parameters and timing were stored on a computer hard-drive. The
eye tracker used two different algorithms for converting the video images into eye-in-head position signals. The first one (pupil tracking) allowed determining the vertical and horizontal components. The second one (iris tracking) allowed determining the torsional component. During iris tracking we selected two or more iris segments that when tracked by the Chronos algorithm (Chronos Vision Inc, Berlin, Germany) gave us the torsional movements of the eye. Trials in which the two segments gave different readings were excluded from the eye position analysis (see experiments). Histograms of the included trials for all subjects (s1-s7) appear as supplementary material (see figure 1 supplementary material).

Each recording session started with a calibration procedure that was followed by the experimental blocks. For each subject, the order of the different blocks was randomized. The recording of the eye positions was synchronized with the stimulus presentation using an ITC-18 card (Instrutech Corp., Port Washington, USA) through which the stimulus presentation software automatically triggered and stopped the data recording at the beginning and end of every trial.

**DATA ANALYSIS:** In the first experiment, we plotted the horizontal, vertical and torsional eye position components as a function of time from trial onset (figure 1b, c). From these plots a trained observer examined the eye position signals and timing of events (trial onset and RDP presentation time) for each trial and marked the onset and offset of saccadic eye movements, i.e., time at which the first saccade after RDP offset started and ended (figure 2, supplementary material). The mean and standard deviation of the ending position components for each one of the different motion directions and conditions of experiment 1 was computed by separately averaging the horizontal and vertical landing
saccade positions across similar trials (RDP directions, figure 3). Before averaging across saccades we aligned all the movements to their starting position. These averages were converted from Cartesian into Polar coordinates by using equations 1 and 2:

\[
\begin{align*}
\text{(1)} & \quad Rho &= \sqrt{\text{horizontal}^2 + \text{vertical}^2} \\
\text{(2)} & \quad \text{theta} &= \arctan\left(\frac{\text{vertical}}{\text{horizontal}}\right)
\end{align*}
\]

*Rho* is the vector magnitude and *theta* the angle in degrees. The parameter *theta* was used as the measurement of the saccade direction.

Eye-in-head signals in angular coordinates were further transformed into eye-in-space angular coordinates by using equation 3:

\[
\text{(3)} \quad \text{theta}_{Eis} = \text{theta}_{Eih} + HR - OCR
\]

*Eis* is eye-in-space, *Eih* is eye-in-head, *HR* is head rotation and *OCR* is ocular counter roll. All the measurements are in degrees.

In the second experiment, eye position signals were also monitored. However since subjects were not required to make saccades, the eye position analysis was limited to examining the position traces in individual trials and determining: a) whether subjects made any eye movement during the trial, b) whether in trials in where subjects tilted the head, a VOR (vestibulo-ocular reflex) was elicited, and c) the amount of ocular counter roll (*OCR*) after head rotation. In general, the seven subjects tested did not make saccades during trials and we corroborated the presence of the VOR in all *head tilted* trials, therefore 100% of the trials were included in the analysis.

In order to compute the amount of *OCR* after the head tilt, we first determined the torsional eye-in-head position during two time periods of 1000ms each, immediately before and after the head tilt. These periods were selected by: a) plotting the eye position
data in all trials, b) visually identifying the beginning and end of the VOR, c) choosing the data segments (before and after the VOR) in which no eye movement was made, d) averaging the torsional eye position data within the segments, and e) subtracting the averages (after - before) in each individual subject (Figure 2). In order to have a second estimate of ocular counter roll to compare it against the other measurements in some subjects, we performed some additional measurements by running 20 additional trials of a task in which no RDP was presented. Here they were required to fixate a dot at the display center and in response to a color change, tilt the head 30 degrees to the left. Estimates of ocular counter roll were quite robust within subjects across different measurements.

We quantified the amount of updating for the different RDP directions after the head tilt in experiment 1 by computing an updating index \((UI\%)\) using equation 4:

\[
UI\% = \frac{(HR - OCR) + \Delta \Theta}{HR - OCR} \times 100
\]

\(HR\) is the amount of head rotation, \(OCR\) the amount of ocular counter roll and \(\Delta \Theta\) is the angular difference in degrees between the average saccade angle \((\Theta)\) with the head straight and tilted for the same RDP direction (i.e., head straight – head tilted). This index takes into account any possible bias the subjects could have in perceiving certain motion direction with the head straight since it uses \(\Delta \Theta\) instead of the differences between the RDP direction and the saccade direction.

In the second experiment, the number of times the subject pressed the left and right arrow key was also recorded and stored together with the trials parameters on a text file for offline analysis. For each experimental condition (head straight and tilted) and subject, we obtained a psychometric function by computing the proportion of times that
the subject pressed the left arrow key for a particular trial type and fitting these data with
the following function (equation 5):

\[ p(d) = \frac{1}{1 + e^{-(a_1 + a_2 d)}} \]  

Where ‘\( p(d) \)’ was the proportion of times subjects pressed the left arrow key (i.e., they
perceived the second RDP as moving more counterclockwise relative to the first) for a
given difference in direction ‘\( d \)’ (in degrees) between the first and second stimulus. ‘\( a_1 \)’
and ‘\( a_2 \)’ are the parameters of the function to be determined by the fitting procedure.
From the fitted values we computed the point of subjective equality (PSE), defined as the
‘\( d \)’, value at which subjects pressed the left key 50% of the times; and the direction
discrimination threshold, defined as the difference in degrees between the PSE and the
‘\( d \)’ value at which subjects pressed the left key 75% of the times. The latter provides a
measurement of subjects’ performance (figure 8).

We determine the amount of updating by computing an updating index (UI%) for
each subject using equation 6:

\[ UI\% = \frac{HR - OCR + (PSE_{ht} - PSE_{hs})}{HR - OCR} \times 100 \]

where \( HR \) is head rotation, \( OCR \) ocular counter roll, \( PSE_{ht} \) and \( PSE_{hs} \) are the points of
subjective equality with the head tilted and straight respectively. Observe that this
equation is very similar to the one used in the previous experiment for the saccade angle
\( \Theta \) (see above).
Results

**Direction of Motion Updating:** Figure 1 shows examples from one subject (s2) of horizontal, vertical and torsional eye position signals plotted as a function of time from trial onset for one head tilted (b) and one head straight trial (c) of the first experiment. We concentrated in the analysis of eye position traces during the saccade period (see methods and figure 2 of supplementary material). Figure 3a shows examples of saccade trajectories with the head straight (left column) and tilted (right column). Observe that the head tilted saccades recorded in head-centered coordinates have been rotated into space centered coordinates. Different colors represent saccades made to different RDP directions (numbers nearby landing positions). Notice that in this figure only saccades to 4 different directions have been plotted. In both conditions (head straight and tilted) the saccade trajectories appear very similar. This was also the case when analyzing data from the memory guided saccades trials (figure 3b).

In order to compare saccade direction between the two conditions we first computed the average horizontal and vertical landing position of saccades made toward the same direction and transformed both, head tilted and straight averages into space-centered coordinates. This is not trivial, since it requires computing the degree of retinal tilt for the former data set. Since we registered the amount of head tilt (30 degrees) as well as the torsional eye-in-head position we could compute the amount of ocular counter roll in head-centered coordinates induced by the tilt (Schworm et al. 2002). We then determined the exact retinal tilt in space-coordinates at the time when the saccade was initiated (see methods).
Figure 4 shows examples of torsional eye position signals from two subjects. The intervals at which the eye rotation occurred are indicated by the large signal deflections (torsional VOR). The histograms (b) display distributions of differences in torsional position before and after the head tilt (gray bars). The mean of these differences was 0.74 degrees for s2 and 0.82 for s3. When subtracting this amount from the amount of head tilt we found that the retinal tilt amounts in space coordinates were 29.26 for s2 and 29.18 for s3. For the rest of the sample the values were: s1= 28.27, s4= 28.46, s5= 27.43, s6= 25.39, and s7= 29.9 (see figure 1 of supplementary material).

Since subjects made several saccades (at least 6 in each block) toward each one of the 10 RDP directions and dot positions, we were able to compute the mean landing horizontal and vertical position components for each direction and position, and convert these data into polar coordinates. In order to quantitatively test whether saccade direction was similar to RDP direction, we performed on each subject and condition (head straight and tilted) a linear regression procedure on mean saccade direction as a function of the RDP direction. If saccade direction was perfectly aligned with RDP direction then regression lines should have a slope of ‘1’ and an intercept of ‘0’. Figure 5a shows these data for head straight saccades in the saccade direction task. Visually, data and lines from different subjects show considerable overlapping suggesting that the results were somewhat similar across subjects. Figure 5b shows similar data for the head tilted condition. Although the data also overlap, they appear more variable as in ‘a’. However, when contrasting the head tilted data against the result predicted by the absence of updating hypothesis (straight line intercepting the ordinate at 30 degrees) all the data fell far away from that line and shifted toward the line with unity slope and zero intercept.
This suggests that subjects updated, at least to a certain degree, the perceived RDP direction after the head tilt.

**Figure 5** ‘d’ and ‘e’ shows similar data as in ‘a’ and ‘b’ but for the spatial updating trials. The results were very similar as the ones for the direction data. These observations, however, need quantitative testing. Therefore, we examined the intercepts and slopes of all the regression lines in the two conditions and for both, direction and spatial updating trials (Table 1 and 2).

For the intercept, the 95% confidence intervals for the intercepts in the head tilted condition do not overlap in any case with the predictions of the absence of updating hypothesis (30 degrees) confirming that all subjects updated both, the RDP motion direction, and the saccade target position after the head tilt (Tables 1 and 2 second column). This is not surprising for the spatial updating data (figure 5e, table 2), but this is a novel result in the case of motion direction updating (figure 5b, table 1).

Interestingly, many of the 95% confidence intervals for the intercepts in Tables 1 and 2 do not include the expected value of ‘0’ (see data marked with stars in the first two columns of Tables 1 and 2, upper section). For the head straight data (first column) this may suggest the presence of a response bias that is independent of any updating mechanism and that may change as a function of the stimulus direction, i.e., depending on the slope. For the head tilted data (second column) this could represent an updating mechanism that was not 100% accurate. The former possibility can be tested by fitting a straight line through the two data sets appearing in the ordinate of panels ‘a’, ‘b’, ‘d’ and ‘e’ in figure 5. If the regression lines had an intercept of ‘0’ and a slope of ‘1’ this would argue in favor of this possibility.
Figure 5 ‘c’ and ‘f’ plot saccade direction in the head tilted against the head straight condition. Again, the data points deviate from the prediction of the absence of updating hypothesis (solid line at 30 degrees in the ordinate). This gives additional support to the finding that subjects update the RDP direction and the target position. But more interestingly, in 3 subjects (out of 7), for the case of direction of motion updating and in 5 subjects (out of 7), for the case of spatial updating, the 95% confidence intervals for the intercept did not include ‘0’ (tables 1 and 2, intercept section, data marked with stars). This suggests that the bias present with the head straight cannot account for the observed results. Some of this variability must be explained, at least in part, by inaccuracies in the updating mechanism.

Concerning the line’s slope, some subjects showed deviations from ‘1’ (slope section, data marked with stars in tables 1 and 2). For the case of head straight vs. motion direction (figure 5a) or stimulus position (figure 5d) this suggests that subjects show biases in the perceived motion direction or position depending on the RDP direction or target location. For the head tilted data this could mean a bias that is either dependent on updating or that reflects the bias previously isolated with the head straight (slope section, data marked with stars in first column of tables 1 and 2). If the latter is true, the bias must disappear when plotting head straight vs. head tilted data since it should be present in both data sets, i.e., the slopes will not be different from ‘1’. This was clearly not the case, 3 subjects out of 7 for the saccade direction task and 5 subjects out of 7 for the memory guided saccade task, showed slopes that significantly differed from ‘1’ (figure 5 ‘c’ and ‘f’, tables 1 and 2 slope section, data marked with stars). Again, this
suggests that some of the variability in the amount of updating across different directions must be explained by inaccuracies in the updating mechanism.

The previous analysis provided us with a measurement of inter-subject variability in the estimates of the RDPs motion direction. In order to examine the within-subject variability in such estimates we plot in figure 6 the angular errors (see methods) for all trials as a function of motion direction in each one of the subjects. The circles represent data from individual trials, the bars represent the mean angular errors for all directions and the error bars the 95% confidence intervals. As we can appreciate in the figure, for some subjects such as s2, s5 and s6 the variability across directions was rather small, while for subjects s1 and s7 angular errors seem to be more variable. Data from subjects s3 and s4 appeared less variable than the ones from subjects s1 and s7 but more variable than for the rest of the subjects. An additional observation is that subjects were consistent in the angular error variability across different directions, e.g., subjects s1 and s7 show large variability and subjects s2 and s6 show small variability across almost all directions. We did not observe any consistent pattern across subjects relating response variability with motion direction suggesting that these two variables were not strongly related.

In order to examine updating accuracy more closely in our subjects, we computed an updating index for each direction of motion and target location (see methods). This index reflects the amount of updating after the head tilt in percentage after taking into account any possible bias present with the head straight. These data are shown in figure 7. For direction of motion updating (a), the index (ordinate) was quite variable across subjects and directions. In some subjects (e.g., s5 and s6) there was a clear trend to a linear change in the amount of updating as a function of motion direction (0 degrees
means motion to the right and 90 degrees means motion upward). However, other subjects show a different pattern with almost perfect (100%) updating for directions close to the vertical and horizontal and larger deviations either by over-updating (s2) or under-updating (s1) for directions in between. This may reflect different updating strategies across subjects. For the spatial updating data (figure 7b) the results were similar, however in this case the updating indices were less spread around the perfect updating prediction (100%). An interesting question that follows is whether direction of motion updating and spatial updating in the same subjects were correlated.

In order to answer this question, we performed a linear regression on updating indices for the saccade direction task as a function of updating indices for the memory guided saccade task. Figure 7c shows these data, the regression line has a slope of 0.87 +/- 0.23. The 95% confidence intervals include the unity slope, meaning that it was a positive correlation between the two updating indices within the same subjects (correlation coefficient r = 0.66). Interestingly, individual subjects seem to form clusters around the line. For example, data from subject 2 seem to group on the upper right while data from subject 1 on the lower left region and from subject 3 somewhere in the middle. The 95% confidence intervals for the intercept include the zero value. Together with the observations for the slope, this suggests that in both tasks subjects adopted similar updating strategies for similar motion directions and spatial positions.

PERCEPTUAL UPDATING OF MOTION DIRECTION: The results of the previous experiment suggest that subjects updated the perceived stimulus direction after actively tilting the head. However, one may argue that during stimulus presentation subjects planned a saccade toward a spatial location and when they rotated the head, they updated the spatial
representation of that location (i.e., spatial updating) instead of the perceived motion direction. In the latter case our results may reflect, at least in part, spatial updating instead of motion direction updating. In order to examine this possibility, we designed a task in which subjects were required to make a perceptual judgment regarding the stimulus direction before and after the head tilt without making a saccade toward a given spatial position.

We determined subjects’ ability to discriminate the direction of two RDPs presented before and after the head tilt (direction discrimination task, see methods and figure 2a). The experimental conditions were similar as in the previous experiment, head straight and head tilted. Figure 2b shows an example of eye position signals recorded during a head tilted trial. The two gray bars represent the first and second stimulus presentation times. The large deflections of the eye position traces indicate the VOR evoked by the head tilt (‘2’). Since in both conditions of this experiment we recorded the proportion of times that subjects perceived the second stimulus direction as deviated counterclockwise relative to the first, we could compute for each subject and condition a psychometric curve that reflects the subject’s direction discrimination performance.

Figure 8 shows these curves for all subjects with the head straight (gray) and head tilted (black). If subjects perfectly updated the perceived direction after head tilt, we would expect that the two curves completely overlap. On the other hand, if subjects did not update the stimulus direction, the head tilted curve will approximate the flat dashed line crossing the ordinate at zero. This is because they would have always seen the second stimulus as moving more clockwise (to the right) than the first, i.e., the head rotation was 30 degrees counterclockwise and the second RDP never moved more than
16 degrees counterclockwise than the first. By examining the different panels in figure 8, it is easy to conclude that curves are clearly not flat, suggesting that subjects indeed updated the stimulus direction. However, in most subjects the curves do not completely overlap, suggesting that updating was not perfect. This somewhat resembles the results of the previous experiment.

In order to quantitatively test these observations we plotted the discrimination thresholds and the points of subjective equality (PSE) for all subjects and conditions (figure 9). The discrimination thresholds were not significantly different (figure 9a, p = 0.08, Wilcoxon rank sign test) suggesting that in both conditions discrimination performance was similar. The PSEs were far from the predictions of the absence of updating hypothesis (dashed line at 30 degrees in figure 9b) suggesting that subjects indeed updated the RDP direction. However, the PSE was significantly shifted toward the left (negative values) in the head tilted relative to the head straight condition (figure 9b, p=0.046, Wilcoxon rank sign test) suggesting that the subjects perceived the second stimulus as deviated toward the direction of the head tilt (left or counterclockwise) and therefore did not fully update the RDP direction after the head tilt.

In order to quantify the amount of updating, we computed an updating index for each subject (see methods). These data are plotted in figure 10. The white bars represent the updating indices for the different subjects. They are all above 80% and in four subjects they are above 95% meaning that they accurately updated the direction of the RDP after the head tilt. Interestingly, when removing the ocular counter roll from the computation of updating indices, the accuracy significantly increases toward 100%, i.e., the black bars are slightly but systematically higher than the white bars (p = 0.03125,
Wilcoxon rank sign test). On the other hand, when removing the head straight bias in the PSE from the computation of the updating indices \((OCR = 0)\), appearing in figure 10a (i.e., PSE with the head straight is considered to be zero), updating accuracy decreases considerably (figure 10b, \(p = 0.031\) in both cases, Wilcoxon rank sign test).

**Active vs. Passive Head Rotation:** The previous experiments demonstrated the existence of direction of motion updating during active head rotations in 7 human subjects. Since during the head tilted trials of these two experiments the final head position was always the same (30 deg counterclockwise) and subjects actively tilted the head two possible questions arise from these results. First, was the ability to update related to the fact that we used a similar amount of head rotation across trials? Second, Does updating accuracy change during passive head rotations?

In order to answer these questions we tested 6 subjects (4 of them participated in the previous experiments and 2 were new) in two different experimental conditions. In the first condition (passive head tilt) the experimenter rotated the head of the subject (after the moving RDP presentation and in complete darkness, see figure 1 and methods) to the left and by a different amount (between 0 and 45 degrees) in each trial. After the head rotation the stationary ring appeared on the screen and the subject made a saccade toward it in the perceived direction. In the second condition (active head tilt), the experimenter verbally told the subject at the beginning of each trial what was the desired amount of head tilt (between 0 and 45 degrees) and the subject actively tilted the head by applying a torque to the bite bar. The amount of head tilted was measured using a goniometer (see methods) coupled to the rotating ring. Since a main goal in this experiment was obtaining a wide range of head rotations for the same stimulus motion
direction in the *passive* and *active* conditions we used the same RDP direction (40 degrees) in all trials. By randomly changing from trial to trial the amount of head rotation we avoided that subjects could memorize or learn a unique final head position and use this knowledge to produce a response. This was a possibility in the first two experiments. We were not concerned with the subjects memorizing the RDP direction since this could only help them with the accuracy of the direction representation in retinal (eye-centered) coordinates. In order to produce an accurate representation of the RDP motion direction in space-coordinates the subject had to update different amounts of head rotation in each trial.

The scatter plots in **figure 11** shows data from all the subjects (s2, s3, s5, s7 and the two new subjects s8 and s9). Subjects s1, s4, and s6 were not available for testing. In these graphs the abscissa displays the amount of head rotation and the ordinate the angular direction of the saccade made in the perceived motion direction (see methods). The gray data points represent the data for the *passive* head tilt condition and the open symbols for the *active* head tilt condition. In both cases we can appreciate that the head rotation data cover almost all the desired range from 0 to 45 degrees (abscissa) and that the perceived direction was in many instances close to 40 degrees. But more important, for all subjects but s8, the data points for both conditions show considerable overlapping. We grouped the data in different bins according to the amount of head rotation (0-5, 6-15, 16-25, 26-35, 36-45) and computed the mean and standard deviation of the saccade direction for each bin. Except for s8, in all subjects and for most of the bins the error bars considerably overlap, suggesting that for most of the subjects the perceived direction within the same bin was very similar in both conditions.
In order to quantitatively test these observations we used the mean saccade direction in each bin to compute the bin’s updating index using equation 4 (see methods). In this specific case we used the mean saccade direction in the first bin (0-5 degrees of head tilt) as the perceived direction with the *head straight* (see methods). Unfortunately, in this experiment we could not obtain accurate measurements of OCR in each bin since the number of trials per bin that we could use for this analysis was relatively low and the variability of our torsional measurements was considerably higher than during the previous experiments in which only one amount of head rotation was tested. Thus, we considered the OCR as zero. This may have led us to slightly overestimate the degree of retinal tilt particularly for larger degrees of head rotation. However, this overestimation was the same for both, the *passive* and *active* conditions and the goal of this experiment was to compare the updating indices between these two conditions.

**Figure 12** shows the mean updating indices as a function of head rotation for the different bins in both conditions. We fitted a linear regression model to these data. The slopes of the lines were in all cases and conditions lower than zero (*active*: $s_2=-0.86$, $s_3=-0.61$, $s_5=-0.54$, $s_7=-0.81$, $s_8=-0.16$, $s_9=-0.26$; *passive*: $s_2=-1.42$, $s_3=-0.85$, $s_5=-0.18$, $s_7=-0.38$, $s_8=-1.01$, $s_9=-0.01$). For the individual subjects the slopes 95% confidence intervals for both conditions included the zero value. However, when compared the group data (group slopes) against the zero value, we found that for the entire group and in both conditions the slope was significantly lower than zero ($p<0.035$, Wilcoxon rank sign test). The comparison between the two conditions revealed no systematic differences ($p>0.8$, Wilcoxon rank sign test for paired data). These results suggest that it was a
systematic trend to a decrease in the updating index values with larger head rotations. This trend was similar in both the passive and active head tilt conditions.

We additionally compared the intercept of the lines (active: s2=96.5, s3=91.8, s5=112.5, s7=93.3, s8=109.8, s9=103.8; passive: s2=90.8, s3=95.1, s5=106.6, s7=88.2, s8=87.8, s9=99.2) against the 100% updating index value to determine whether it was any systematic bias to over- or under-update the RDP direction with the head straight (bin from 0 to 5 degrees of head rotation). There were no differences between the intercepts and the 100% value, neither for the individual subjects (95% confidence intervals included the 100% index value), nor for the group (p>0.1, for both active and passive data, Wilcoxon rank sign test). We also compared the intercepts values between the different conditions and found no significant differences (p>0.06, Wilcoxon rank sign test for paired data). These results were not surprising since both active and passive trials were virtually identical in the absence of head rotation.

In sum, the results of this last experiment demonstrate that a) for most of the subjects direction of motion updating was similar during active and passive head tilts, and b) for both, the active and passive conditions increasing the amount of head tilt produced a systematic decrease in the updating indices for the same RDP direction.
Discussion

The present study demonstrates the existence of an updating mechanism for the perception of motion direction in the human brain that can operate in the absence of visual cues and during active and passive head rotations. The accuracy of such a mechanism differs across different subjects and motion directions and is comparable to the one of spatial updating. We also demonstrated that motion direction updating operates at the perceptual level (i.e., perceptual updating) independently of the motor effector involved in a given task (saccade vs. key press).

Spatial updating is a well-known phenomenon that has been investigated by behavioral and neuroimaging studies in humans (Hallet and Lightstone, 1976; Schlag et al., 1990; Blouin et al., 1998; Herter and Guitton, 1998; Smith and Crawford, 2001; Medendorp et al., 2002; Klier et al. 2005). Furthermore, physiological studies in non-human primates have reported spatial updating in several brain regions of macaques, including the extrastriate visual cortex (Nakamura and Colby, 2002), posterior parietal cortex (Duhamel et al., 1992; Batista et al., 1999; Colby and Goldberg, 1999) and frontal cortex (Goldberg and Bruce, 1990). However, the existence of spatial updating does not directly predict the existence of updating for visual motion attributes such as direction. This is because motion seems to have a system specially devoted to its processing in the primate brain (Merigan et al., 1993; Maunsell and Newsome, 1987; Maunsell, 1992) and perception of spatial position and motion attributes can be dissociated from each other (Wade 1994). Our results show the existence of an updating mechanism for the perception of motion direction in the human brain.
Such updating mechanism is not perfectly accurate, in many instances our subjects over- or under-updated different stimulus directions. This could reflect either a bias in the sensory processing of the visual stimulus and/or signals from other systems, such as vestibular and proprioceptive or in the motor/pre-motor response processing. The fact that similar biases were present during the memory guided saccade and saccade direction tasks (figure 7) favors the latter explanation, since the saccade direction and memory guided saccade tasks were similar in many respects except in the visual stimulus configuration. This is also supported by the findings shown in figure 10, which clearly demonstrate that during the perceptual updating task and in the absence of saccadic eye movements the updating accuracy was considerably higher (5 subjects have updating indices higher than 95%). Since in the perceptual updating task vestibular and proprioceptive signals were also present, one may hypothesize that processing related to saccadic eye movements substantially contributed to the variability in the amount of updating seen during the saccade direction task. Partially supporting this view, previous studies have reported considerable saccade endpoint variability during memory guided saccade tasks (Klier et al., 2007; Van Pelt et al., 2007), but psychophysical studies of motion direction discrimination have reported thresholds as low as 1.8 degrees in normal human observers (De Bruyn and Orban, 1988). These thresholds are comparable to the ones reported here for the perceptual updating task (figures 8 and 9).

A simple hypothesis of motion direction updating errors incorporated during processing related to saccades would assume that during both, the saccade and perceptual tasks retinal and vestibular signals undergo the same sensory and perceptual processing steps, and then they diverge between the two tasks when a motor effector must be chosen
to trigger behavior. For example, during the stages of saccade planning or execution specific biases could be incorporated to the response. We doubt that such biases are incorporated at the level where motor commands for the eye muscles are generated, i.e., at the level of the oculomotor nuclei (Sparks, 2002). This is because the heterogeneity of updating strategies across subjects (see figures 6 and 7) which suggests a more cognitive-related bias where subjects incorporate learned behaviors that could considerably change across individuals. Differences in motor strategies have been previously documented for related aspects of motor control such as head movement contribution during head unrestrained gaze shifts (Fuller, 1992).

To speculate about the neural structures where the bias could be incorporated is a much more difficult subject and one may start by answering the question of which neuronal populations could be active during the different components of each task according to what we already know about visuomotor processing in the brain.

There are several ‘good’ candidates areas. One is area MST (‘d’ and ‘l’ subdivisions, see also later during the discussion). During heading direction, a task that in many circumstances requires integration of vestibular and visual inputs as well as updating, MST seems to play an important role (Britten and van Wezel, 1998; Page and Duffy, 2003) and there is a general consensus that this area is a recipient of vestibular inputs (Gu et al. 2007). However, we are not aware of any study showing MST neurons reliably coding saccades or saccade goal. Thus, during both, perceptual and saccade tasks MST could combine the retinal and vestibular signals resulting from the visual display and the head rotation and provide a reliable signal for perception. During the perceptual task the resulting perceptual decision must be mapped onto a key press but during the
saccade task it must be mapped onto an eye movement with a wider range of behavioral choices than two keys. We do see why in the later case the response variability could be higher (i.e., errors from each choice may ‘add’ to each other), however, there is no apparent reason for systematic biases such as under or over-updating like the ones we have seen in our subjects during the saccade task.

There are also other candidate areas that at least during the saccade direction task could play an important role, such as LIP, in which neurons are motion direction selective, they encode saccade goal (Shadlen and Newsome, 2001), integrate vestibular signals (Andersen 1997), and contain efference copies of motor commands for eye movements (Heiser et al. 2005). LIP may be involved either in the perceptual decision and or in the mapping of that decision onto a saccade command. Furthermore, there are other neural pathways related to saccade processing that could be potentially recruited during the saccade task. For example, it is well know that vestibular signals can reach saccade related areas through at least two different pathways. The first one goes trough the ventrolateral thalamus and the parieto-insular vestibular cortex to the FEF (Grusser et al. 1990a,b; Guldin et al. 1992). The second one goes through projections to the thalamic nuclei and from there to parietal cortex, the FEF and SEF (Huerta et al. 1986; Huerta and Kaas, 1990). During the perceptual task these areas may not be recruited in the same manner as during the saccade task since in our experiments the subject could have ‘switched’ from one task mode to another. At least for the case of LIP, it has been demonstrated that responses of many neurons change as a function of the motor response (effector) involved in the task (Dickinson et al. 2003). Another structure that could potentially play a differential role in both tasks is the cerebellum due to its extensive
involvement in saccade planning and generation (Thier and Möck, 2005; Thier et al. 2002).

We should make clear, however, that the aforementioned possibilities remain highly speculative and that several aspects of this interpretation need extensive testing. First, we do not know which neuronal populations are involved in sensory and perceptual aspects of both tasks. Second, it is unclear why and how the recruitment of additional pathways during the saccade task could cause updating biases. For now, it seems reasonable to hypothesize that extra-processing steps implicating different motion direction and saccade selective populations could ‘bias’ the percept and/or behavioral response. An interesting question to explore in the future is whether during a task requiring direction of motion updating and which outcome is measured using both, key presses and saccades (during the same trials) similar or different updating biases would be present for both responses. This is however, beyond the scope of this work.

During the saccade task there is at least another source of variability that may directly influence the motor response. With the head tilted there is a degree of ocular counter roll that changes the initial eye-in-head position before the saccade relative to when the head is straight (see figure 4). In order to generate accurate directional saccades it is not sufficient to know the amount of head rotation but also how much the eyes roll back within the orbits. This will avoid systematic errors due to over-estimation of retinal tilt and therefore of saccade direction. However, given the small amount of counter roll we have seen in our subjects, the magnitude of the errors, and the fact that some subjects systematically under- while others over-updated the movement direction after the head rotation we consider this possibility unlikely. A similar study of visuo-spatial memory
computations during whole body rotations in roll has arrived to similar conclusions (Van Pelt et al. 2005).

Another interpretation of our results could be that the perception of motion direction in the absence of visual cues seems to occur in an allocentric (space-centered) frame of reference. This agrees with the results of Darling and Pizzimenti (2001), who reported that motion direction is perceived relative to an earth-fixed coordinate axis when the head is tilted. Importantly, in our study we eliminated any possible effect of orientation information during both updating tasks. We used circular shaped moving RDPs, which do not contain orientation information, therefore subjects had to purely rely on extraretinal signals and on their initial estimates of visual motion direction to solve the task. This becomes important when considering that orientation and direction information are preferentially processed in different pathways and/or cortical areas (Merigan and Maunsell, 1993).

Our results agree with the ones of Melcher and Morrone (2003) who described spatiotopic temporal integration of motion signals during saccades. This latter result can be seen as evidence in favor of the existence of a space-centered representation of motion signals in the human brain. The existence of direction of motion updating reported in this paper also agrees with a model proposed by Wade and Swanston (1996) in which motion signals are combined at different stages with extraretinal inputs resulting in a geocentric representation of visual motion. In fact, multiple reference frame representations for gaze coding have been found in areas such as the Supplementary Eye Fields (SEF) of primates (Martinez-Trujillo et al., 2004; Olson and Gettner, 1996). Whether SEF contains similar representations for motion direction remains unclear.
The existence of such reference frame representations implies that different signals from different sensory systems, such as visual, vestibular and proprioceptive, as well as efferent copies of motor commands for moving the eyes must be combined somewhere along the sensorimotor pathways (Soechting and Flanders, 1992; Roll et al., 1991). Interestingly, Shaikh and coworkers (2004) have reported the existence of multiple reference frame representations of self-motion in the cerebellum of non-human primates suggesting the convergence of at least vestibular and proprioceptive signals in this structure. Moreover, Page and Duffy (2003) have demonstrated the convergence of visual and vestibular inputs in motion processing area MST of macaques suggesting that extraretinal signals play a critical role in the neural computations underlying optical flow perception. Corroborating this suggestion, Gu and coworkers recently reported the contribution of vestibular signals to the responses of MSTd neurons and to behavioral performance during heading perception in monkeys (Gu et al., 2007).

In our task, updating could have taken into account extraretinal signals from at least three sources: the vestibular system, proprioception and an efferent copy of the motor command for tilting the head (Crowell et al. 1998). The results of our last experiment (figures 10 and 11) could be interpreted as evidence against a necessary role of the efference copy signal as a main source of directional updating. This is because during active and passive head rotations the updating was very similar, except for one subject. However, this aspect of our results may need further testing since there exist the possibility that our subjects could produce ‘online’ efference copy signals based on constant feedback from neck proprioceptors and they may have had somewhat contributed to the direction of motion updating. We have at least three arguments against this
possibility. First, during passive head rotations the subjects could not have predicted in advance the final amount of rotation. Second, the head velocities were very similar during the passive and active conditions. Third, the experimenter did not subjectively sense any resistance to the head rotation by the subject, who was told in advance not to do so. Nevertheless, future studies must determine the specific contribution of the different extraretinal signals to direction of motion updating.

Our results agree with the ones of previous studies of spatial updating during passive (Klier et al. 2005) and active (Medendorp et al. 2002) head/body rotations since our subjects were able to update different amounts of head tilt in both conditions. As in the study of Klier et al. (2002) our results also show variability among different subjects suggesting that updating strategies may differ across individuals. This idea is supported by the fact that updating errors showed large variability in some subjects, while in others the variability was substantially lower (see figure 6). One possibility is that updating strategies depend on the ability of the subjects to use the signals available for updating and such ability may be shaped by factors such as previous training or experience in different tasks. For example a jet pilot may be more accurate than an average person in updating motion direction after a head rotation. This may also apply to less extreme cases of variability.

Considering the existing electrophysiological evidence already mentioned, probably the best candidates for being the recipient of vestibular and proprioceptive signals and for performing the computations needed to perceptually update motion direction are areas MSTd and MSTl for the following reasons: a) they contain direction selective visual neurons with tuning curves for linear motion that are similar to the tuning
curves of MT neurons (Lagae et al. 1994), b) as mentioned before, they contain extraretinal signals related to the vestibular and perhaps other sensory systems (Page and Duffy, 2003; Ilg et al. 2004; Fetsch et al., 2007; Gu et al., 2007), and c) lesions of this area impair the encoding, storage and retrieval of motion direction information during memory tasks (Bisley and Pasternak, 2000). The latter is an important argument since during the head rotation period motion direction information must have been stored and/or retrieved before the extraretinal signals were available for the computations underlying updating. This hypothesis also matches results from physiological studies in monkeys demonstrating that many MSTd neurons compensate for gaze rotation, whether produced by eye-in-head or head-in-world rotation (Shenoy et al., 1999; Andersen et al., 2000).

Posterior parietal cortex (PPC) including the ventral intraparietal area (VIP) could also play a role in updating of motion direction since they contain different distributed representations of the stimulus in body and space coordinates (Brotchie et al., 1995; Bremmer et al., 1997; Merriam and Colby, 2005; Schlack et al., 2005; Duhammel et al. 1997). Finally, area LIP is also a recipient of different signals that could be used during updating (Andersen, 1997). Future electrophysiological studies are needed in order to determine the role of different motion processing areas in the motion direction updating phenomena described here.

One interesting finding in our experiments is that during perceptual updating, when the ocular counter roll was not taken into account ($OCR = 0$), performance significantly improved (figure 10). One explanation for this result is that when subtracting the $OCR$ from the amount of head tilt, the retinal tilt decreases (retinal tilt =
head tilt - OCR) and consequently the amount of under-updating relative to the retinal tilt increases (see equation 6 methods). As we have stated earlier in the discussion the interpretation of this observation is not straightforward since it may mean that subjects either updated the motion direction in head-centered coordinates or that they did it in retinal coordinates and they simply made errors. Our data does not allow distinguishing between these possibilities.

We have found previous reports of effects of eye position signals on spatial updating (Tanaka, 2005) and of systematic errors in the direction of saccades that is also subject dependent in tasks where the amount of ocular counter roll is manipulated (Henriques et al., 1998). The latter authors have hypothesized that this may be due to the fact that when humans orient themselves, usually they hold the head in an upright position, minimizing the amount of OCR and that this may be avoided if subjects undergo extensive training. Our subjects were indeed trained during several sessions, thus they may have ‘learned’ to update the 30 degrees head tilt instead of the eye-in-space tilt (30 degrees – counter roll). Some authors have also used active head rotations during an updating paradigm and intentionally avoided ocular counter roll (Van Beuzekom et al. 2001). Thus, OCR seems to affect both spatial and motion direction updating, however until which degree as well as the exact mechanisms by which it does so remain unclear.

In summary, we have described and behaviorally characterized a mechanism for updating of motion direction in the human brain. Further studies in human and non-human primates would be needed in order to reveal in more detail the behavioral constraints and the exact neural basis of this mechanism.
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Figure legends

Figure 1
a) Design of experiment 1 (direction of motion updating, head tilted trial). 1) RDP presentation, 2) head tilt, 3) saccade toward the static ring (represented by the white circle) in the perceived motion direction, 4) and 5) head rotation back to the original straight position.

b) and c) Eye position traces for the horizontal (red), vertical (blue) and torsional (black) components (ordinate) as a function of time from RDP onset (abscissa) for a head tilted (b) and a head straight (c) example trial from subject s2. The vertical dashed lines indicate the different trial periods. The arrows indicate the stimulus direction in each trial.

Figure 2
a) Design of experiment 2 (perceptual updating) for head tilted trials: 1) first RDP presentation (100 % coherence), 2) masking RDP presentation (0% coherence) and head tilt, 3) second RDP presentation (100% coherence) and response (key press). b) Eye position signals (ordinate) as a function of time from first RDP onset (abscissa) during a head tilted trial in subject s2, horizontal in red, vertical in blue and torsional in black. The shaded areas represent the 100% coherence RDPs presentation times and the numbers correspond to the different trial periods.

Figure 3
a) Example subject (s3) saccade trajectories for different RDP motion directions in space-centered coordinates. The different colors and the correspondent numbers indicate different RDP directions for head straight (first column) and head tilted trials (second column). The abscissa indicates the horizontal and the ordinate the vertical eye position
components in degrees. b) Saccade trajectories in the same subject during memory guided saccade trials in *head straight* (first column) and *tilted* (second column) trials. In all panels the circle indicates the position of the stationary ring and the radial lines the motion direction of the RDP (see also numbers’ color) or the target position.

**Figure 4**

a) Torsional eye position signals (ordinate) as a function of time from RDP onset (abscissa) in *head tilted* trials from subjects s2 and s3. The shaded areas indicate the periods used during the computation of ocular counter roll. VOR: vestibulo ocular reflex. 
b) Histograms of the differences in torsional eye position between the shaded areas for each subject across trials. The vertical short line at the top indicates the mean and the horizontal line the 95% confidence intervals for the mean. The line at zero indicates the point of no difference.

**Figure 5**

Linear regression for all subjects (different symbols) and conditions (different panels) of experiment 1. a) Saccade direction with the *head straight* (HS, ordinate) as a function of RDP direction (abscissa). b) Saccade direction with the *head tilted* (HT, ordinate) as a function of RDP direction (abscissa). c) Saccade direction with the *head tilted* (ordinate) as a function of saccade direction with the *head straight* (abscissa). d-f) Spatial or memory guided saccade task. d) Saccade direction with the *head straight* (ordinate) as a function of target location (abscissa). e) Saccade direction with the *head tilted* (ordinate) as a function of target location (abscissa). f) Saccade direction with the *head tilted* (ordinate) as a function of saccade direction with the *head straight* (abscissa). The line
crossing the ordinate at 30 degrees in the two lower rows represent the predicted result if subjects would have not updated the RDP direction or target position.

**Figure 6**

Angular error as a function of motion direction for each one of the subjects. The circles represent data from every trial, the bars the mean angular error for each direction and the error bars the 95% confidence intervals for each direction.

**Figure 7**

a) and b) Linear regressions of updating indices (ordinate) as a function of RDP direction (abscissa in ‘a’) or target position (abscissa in ‘b’). The different symbols represent the different subjects. The solid line at 100 represents perfect updating. c) Updating indices in the saccade direction task (ordinate) as a function of updating indices in the memory guided saccade task (abscissa). The parameters of the regression as well as the predicted values (line) are shown.

**Figure 8**

Psychometric functions for all subjects in experiment 2. The abscissa represents the differences in direction (degrees) between the first and second stimulus in space-centered coordinates and the ordinate the proportion of times the subjects perceived the second stimulus moving counterclockwise (CCW) relative to the first stimulus. The black dots represent *head tilted* and the gray dots *head straight* data. The vertical lines indicate the PSE for the corresponding curves and the horizontal dashed line the absence of updating hypothesis prediction.

**Figure 9**
a) Direction discrimination thresholds (ordinate) with the *head straight* and *tilted* for all subjects (different symbols in ‘b’). The lines join data points from the same subject. b) PSE for all subjects in degrees (ordinate) again with the *head straight* and *tilted*. The dashed line illustrates the predicted result if subjects would not have updated the RDP direction after the head tilt.

**Figure 10**

Updating indices in experiment 2. a) White bars are indices computed taking into account the *head straight* condition bias as well as the OCR, black bars are indices computed removing the OCR, i.e., $OCR = 0$. b) Similar data as in ‘a’ but computed without taken into account the PSE in the *head straight* condition, i.e., $PSEhs = 0$.

**Figure 11**

*Passive* vs. *active* head rotation experiment data. Scatter plots of head rotation (abscissa) vs. saccade direction (ordinate) for all subjects. The solid gray symbols represent passive head rotation trials and the open circles active head rotation trials. The lines join the mean of the perceived direction in different bins. The error bars represent standard deviations.

**Figure 12**

Linear regression of the updating indices in the different bins as a function of head rotation for the different subjects. The symbols are the same as the ones used in figure 11. The lines equations are shown. The colors correspond to the color of the symbols (gray is passive and black active). X axis: amount of head rotation, Y axis: updating index.
Figure 2

a) Perceptual updating task

b) Eye-in-head position (deg) vs. Time from first stimulus onset (ms)
Figure 3

Horizontal eye-in-head position (deg)

Vertical eye-in-head position (deg)
Figure 7

a) Saccade direction task

b) Memory guided saccade task

c) intercept = 15.682 +/- 23.833
slope = 0.870 +/- 0.235
r = 0.661
Figure 8

Difference in direction first - second (deg)

Proportion of CCW responses

-16 -4 0 4

s1  s2  s3  s4

s5  s6  s7

head straight
head tilted

Difference in direction first - second (deg)
### Table 1. Linear regression results (directional updating)

<table>
<thead>
<tr>
<th></th>
<th>Head straight</th>
<th>Head tilted</th>
<th>Head straight vs tilted</th>
</tr>
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<tbody>
<tr>
<td><strong>Subjects</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
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<tr>
<td>s1</td>
<td>-6.43 +/- 4.20 *</td>
<td>-0.81 +/- 4.13</td>
<td>6.10 +/- 6.66</td>
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<tr>
<td>s2</td>
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<td>-7.76 +/- 3.28 *</td>
<td>-3.45 +/- 6.75</td>
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<tr>
<td>s3</td>
<td>-13.13 +/- 4.87 *</td>
<td>-11.13 +/- 5.71 *</td>
<td>2.20 +/- 2.81</td>
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<tr>
<td>s4</td>
<td>2.03 +/- 4.92</td>
<td>4.56 +/- 5.64</td>
<td>2.84 +/- 5.34</td>
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<tr>
<td>s5</td>
<td>3.39 +/- 2.78 *</td>
<td>8.44 +/- 2.62 *</td>
<td>6.12 +/- 2.63 *</td>
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<tr>
<td>s6</td>
<td>-3.09 +/- 3.85</td>
<td>14.71 +/- 4.73 *</td>
<td>17.37 +/- 5.51 *</td>
</tr>
<tr>
<td>s7</td>
<td>2.14 +/- 5.06</td>
<td>2.14 +/- 5.06</td>
<td>9.04 +/- 4.79 *</td>
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</table>

<table>
<thead>
<tr>
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<th>Head straight</th>
<th>Head tilted</th>
<th>Head straight vs tilted</th>
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<tr>
<td><strong>Subjects</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
<td><strong>Coefficient +/- 95% CI</strong></td>
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<tr>
<td>s1</td>
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<td>1.06 +/- 0.07</td>
<td>0.95 +/- 0.12</td>
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<tr>
<td>s2</td>
<td>1.12 +/- 0.09 *</td>
<td>1.06 +/- 0.06</td>
<td>0.92 +/- 0.11</td>
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<tr>
<td>s3</td>
<td>1.17 +/- 0.09 *</td>
<td>1.18 +/- 0.10 *</td>
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<tr>
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<td>0.98 +/- 0.09</td>
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<td>0.99 +/- 0.09</td>
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<tr>
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<td>0.70 +/- 0.04 *</td>
<td>0.70 +/- 0.04 *</td>
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<tr>
<td>s6</td>
<td>1.01 +/- 0.07</td>
<td>0.74 +/- 0.08 *</td>
<td>0.72 +/- 0.10 *</td>
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<tr>
<td>s7</td>
<td>1.16 +/- 0.11 *</td>
<td>0.90 +/- 0.09 *</td>
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**Table 2.** Linear regression results (spatial updating)

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<tr>
<th>Subjects</th>
<th>Intercept</th>
<th>Coefficient +/- 95% CI</th>
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<tbody>
<tr>
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<tr>
<td>s2</td>
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<td>-3.86 +/- 2.23 *</td>
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<td>s3</td>
<td>1.87 +/- 1.49 *</td>
<td>1.55 +/- 3.50</td>
<td>-0.35 +/- 3.55</td>
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<tr>
<td>s4</td>
<td>3.35 +/- 2.66 *</td>
<td>8.29 +/- 3.04 *</td>
<td>5.19 +/- 3.25 *</td>
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<tr>
<td>s5</td>
<td>5.34 +/- 1.37 *</td>
<td>4.28 +/- 3.00 *</td>
<td>-0.34 +/- 3.27</td>
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<tr>
<td>s6</td>
<td>0.95 +/- 2.23</td>
<td>9.05 +/- 3.70 *</td>
<td>8.47 +/- 4.47 *</td>
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<tr>
<td>s7</td>
<td>-6.71 +/- 1.61 *</td>
<td>4.72 +/- 1.70</td>
<td>10.65 +/- 1.42 *</td>
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<table>
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<th>Head straight vs tilted</th>
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<td>s1</td>
<td>0.97 +/- 0.063</td>
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<td>0.89 +/- 0.07*</td>
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<tr>
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<td>0.94 +/- 0.04*</td>
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<tr>
<td>s3</td>
<td>0.86 +/- 0.02 *</td>
<td>0.89 +/- 0.06 *</td>
<td>1.03 +/- 0.07</td>
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<tr>
<td>s4</td>
<td>0.90 +/- 0.05 *</td>
<td>0.87 +/- 0.05 *</td>
<td>0.96 +/- 0.06</td>
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<td>s6</td>
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<td>1.05 +/- 0.03 *</td>
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<td>0.87 +/- 0.02*</td>
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