Acta Psychologica 136 (2011) 390–398

Contents lists available at ScienceDirect

Acta Psychologica

journal homepage: www.elsevier.com/ locate/actpsy

Influence of head orientation on visually and memory-guided arm movements

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ARTICLE INFO

Article history:
Received 8 December 2009
Received in revised form 4 January 2011
Accepted 4 January 2011
Available online 2 February 2011

PsycINFO classification:
2330 Motor Processes
2340 Cognitive Processes

Keywords:
Drawing
Arm movement
Vision
Memory
Egocentric representation
Allocentric representation

ABSTRACT

In the absence of visual supervision, tilting the head sideways gives rise to deviations in spatially defined arm movements. The purpose of this study was to determine whether these deviations are restricted to situations with impoverished visual information. Two experiments were conducted in which participants were positioned supine and reproduced with their unseen index finger a 2 dimensional figure either under visual supervision or from memory (eyes closed). In the former condition, the figure remained visible (using a mirror). In the latter condition, the figure was first observed and then reproduced from memory. Participants' head was either aligned with the trunk or tilted 30° towards the left or right shoulder. In experiment 1, participants observed first the figure with the head straight and then reproduced it with the head either aligned or tilted sideways. In Experiment 2, participants observed the figure with the head in the position in which the figure was later reproduced. Results of Experiment 1 and 2 showed deviations of the motor reproduction in the direction opposite to the head in both the memory and visually-guided conditions. However, the deviations decreased significantly under visual supervision when the head was tilted left. In Experiment 1, the perceptual visual bias induced by head tilt was evaluated. Participants were required to align the figure parallel to their median trunk axis. Results revealed that the figure was perceived as parallel with the trunk when it was actually tilted in the direction of the head. Perceptual and motor responses did not correlate. Therefore, as long as visual feedback of the arm is prevented, an internal bias, likely originating from head/trunk representation, alters hand-motor production irrespectively of whether visual feedback of the figure is available or not.

1. Introduction

A functional association between head and hand/arm sensorimotor systems has been well demonstrated in sensorimotor tasks such as pointing towards remembered targets (Berger et al., 1998; Bresciani et al., 2002), drawing geometric figures (Guerraz, Blouin, & Vercher, 2003), arm pointing adaptation (Seidler, Bloomberg, & Stelmach, 2001) or even haptic adjustments (Kerkhoff, 1999; Guerraz, Luyat, Poquin, & Ohlmann, 2000; Luyat, Gentaz, Corte, & Guerraz, 2001). An effective way to investigate such a functional association with these tasks involves dissociating head and trunk orientations during the movement. Using this procedure, Guerraz et al. (2003) have shown that tilting the head towards a shoulder induces an overall rotation of the hand-drawn reproductions in the opposite direction to head tilt. Interestingly, when the gravitational cues are no longer present or relevant to the task (e.g. when performing the arm movement in the supine posture or in microgravity), deviations increase markedly (Berger et al., 1998; Guerraz et al., 2000, 2003). These findings therefore provide evidence for the importance of gravitational and neck afferent cues in the control of hand/arm movement in space.

The errors observed in both the pointing and drawing tasks when the participant's head is tilted sideways could indicate a bias in the internal representation of body configuration. This hypothesis is in line with the observations made by Knox and collaborators that rotation of the head towards the shoulder alters the perception of arm position (Knox & Hodges, 2005; Knox, Cordo, Skoss, Durrant, & Hodges, 2006). The errors induced by tilting the head on the trunk, which are usually in the opposite direction to the tilt, might reveal an over-estimation of the angle between the head and the trunk. Such misperception would be particularly prejudicial in sensory-impoverished contexts (absence of pertinent visual or gravitational cues) in which the trunk constitutes the main reference to control arm movement (Gurfinkel, Lestienne, Levik, Popov, & Lefort, 1993). It is worth noting that angular deviations in motor production would not be directly related to the orientation of the head relative to the trunk *per se* but rather to the conscious perception of head

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doi:10.1016/j.actpsy.2011.01.004

and body configuration (Knox et al., 2006, Mars, Honoré, Richard, & Coquery, 1998; Guerraz, Navarro, Ferrero, Cremieux, & Blouin, 2006).

In most of the aforementioned experiments, participants had the head aligned with the trunk and were first asked to inspect the position of the target (for reaching movements) or the contours of the geometric shape (for drawing movements) before closing their eyes. Then, participants had to wait for the orientation of their head to be dissociated from that of their trunk before either reaching the memorized target or reproducing the memorized shape (memory-guided action). Importantly, converging lines of evidence suggest that the availability of hand and target visual information has a strong influence on both the coding of target location and the control of spatially-oriented movements. For instance, the frame of reference (e.g., egocentric, allocentric) used to perform perceptivo-motor tasks is known to be a function of the type of visual information available during the movement (Bridgeman, 1991; Paillard, 1991; Blouin et al., 1993). Moreover, visually-guided movements are usually more accurate than memory-guided movements (Prablanc, Pélisson, & Goodale, 1986; Hesse & Franz, 2009; Heath, Westwood, & Binsted, 2004; McIntyre, Stratta, & Lacquaniti, 1998; Westwood, Heath, & Roy, 2001; Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006). The increased accuracy is related to the amount of visual feedback provided to the participants. For instance, Schettino, Adamovich, and Poizner (2003) reported that the performance in a grasping task is higher when feedback of both the hand and target is provided compared with conditions where the participants can only see the target. However, participants' performance is higher in the latter condition than when no visual feedback is available. Finally, it has been shown that when sight of the target is occluded during the task, the delay between the visual presentation of the target and the onset of the reaching movement is a determinant factor of performance (Elliott, 1986; Hesse & Franz, 2009).

Within this framework, there are therefore reasons to believe that the effect of head tilt on the direction of the hand movements observed in previous studies could be limited to situations with impoverished visual information. Here we investigated this issue by having participants reproduce the contour of a geometric illustration with either the head aligned with the trunk or tilted towards a shoulder in different visual conditions: During the drawing movement, we prevented participants from seeing either both the illustration object and hand simultaneously (memory-guided) or only their moving hand (visually-guided). In the visually-guided task, as visual information of the illustration was available, the participant could update the properties of the geometric figure such as its shape or size during the drawing. In that respect, vision should be particularly beneficial for motor production as long as intrinsic characteristics of the object are concerned. Whilst being able to see the figure during the movement should allow participant to update their position relative to the figure, it should not however provide direct information relative to their body configuration. Whether this information would nevertheless be beneficial to the overall orientation of the motor production remains to be determined.

In addition to motor bias, tilting the head towards the shoulders induces perceptual illusions. For instance, when gravitational information is not relevant to the task, such as in the present study where participants were in a supine position, lines (*or objects*), which are oriented parallel to the trunk midline, are perceived as being tilted in the direction opposite to that of the head (Templeton, 1973, Parker, Poston, & Gulledge, 1983). Such perceptual illusion was evaluated in participants taking part in Experiment 1. However, because motor processes are largely immune to visual illusions (Aglioti, DeSouza, & Goodale, 1995; Bock, 1997; Glover & Dixon, 2001), we hypothesized that visually guided motor behaviour in condition of head tilt would not be correlated to the putative visual illusion induced by the head tilt.

2. Methods

2.1. Participants

Twelve and seven healthy participants took part in Experiments 1 and 2 respectively. Experiment 1 involved five women and seven men aged 19–32 years (mean 24.3, *SD* 3.5). Experiment 2 involved four women and three men aged 19–40 years (mean 26, *SD* 8.5) who did not take part to Experiment 1. They were all right handed according to the Edinburgh Inventory Test (Oldfield, 1971), naive to the aims of the study, and had no known history of vestibular, visual, or neuromuscular disease. Informed consent was obtained prior to the experiment according to the Declaration of Helsinki.

2.2. Procedure and apparatus

Participants were positioned supine on a thin mattress. Supine position (instead of seated position) was chosen to both minimize ocular-counter torsion which could have otherwise influenced the arm movement (see Ott, 1992; Wetzig & Baumgarten, 1990; Howard, 1986) and eliminate the contribution of the otoliths. A wooden board was positioned 50 cm above the participant in the horizontal plane (i.e., parallel to the participant's frontal plane). A mirror was placed at 45° between the participant's head and the board. The mirror reflected a geometric figure that was fixed on a board to the rear of the participant's head (see Fig. 1). The centre of the mirror was positioned at 40 cm from the geometric figure and at 40 cm from the participant's eyes. The use of a mirror allowed the participants to see the figure in the fronto-parallel plane at the level of their eyes without being able to see their hand. The figure represented a house composed of 5 luminescent segments (one horizontal line [the base], two verticals [the walls] and two segments oriented at 45° [the roof]). The base was 20 cm long. The remaining four segments were 14 cm long.

During the experiment, the lights in the experimental room were turned off so that only the luminescent object was visible to the participant. A device was used to position and secure the participant's head either aligned with the trunk or tilted 30° towards the left or right shoulder. Right index finger displacements were recorded in three dimensions with a Polhemus Fastrak. The receiver-coil of the 3-D magnetic sensor was fixed on the participant's fingertip. Output signals from the Fastrak were sampled at a rate of 120 Hz. As the figure to be drawn had two dimensions, only finger displacements in the horizontal plane were recorded.

2.3. The motor task

Participant's task was to reproduce the reflected geometric figure on the board above them using their right index finger without seeing their hand. The involvement of finger and wrist in drawing lines of such length has been shown to be minimal, the elbow and shoulder being the prime effectors for such movements (Lacquaniti, Ferrigno, Pedotti, Soechting, & Terzuolo, 1987). Nevertheless, in order to minimise large differences in the motor strategies between participants for line drawing, their wrist and index finger were secured in a fixed pointing position using a light splint. Prior to the experiment, subjects were required to familiarise themselves with the drawing task with the eyes open or closed. At the beginning of each trial, participants inspected the geometric figure for 10 s before receiving the instruction to position their index at the top of the right wall of the house and close their eyes. Then, the participant's head either remained aligned with the trunk (head-straight) or was slowly tilted by the experimenter towards the right (30°, head-right) or left (−30°, head-left) shoulder. After 10 s, participants were required to reproduce the figure either with their eyes closed (memory-guided condition) or with the eyes open (visually-guided condition). In the latter condition, the participants could only see the figure and had no

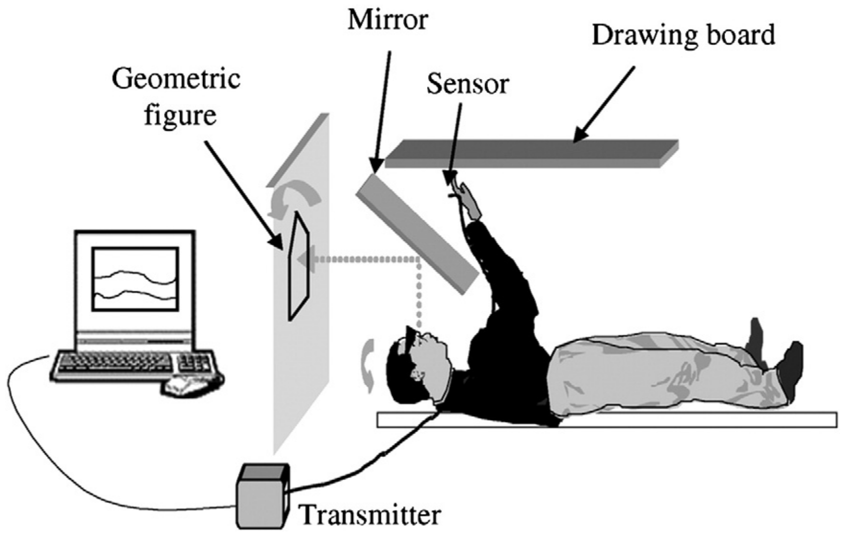

Fig. 1. Experimental setup.

visual feedback of either their arm or hand. They were instructed to reproduce the figure as accurately as possible (size and orientation of the different segments) without time constraints. The finger had to remain in continuous contact with the board. In order to facilitate analysis of each segment, participants were asked to pause movement at the end of each segment. Having completed the reproduction, participants removed their finger from the board. If the head was tilted during figure reproduction, the experimenter brought it back slowly to its primary, trunk-centred position. Only then could participants re-open their eyes in the memory condition. No feedback about reproduction accuracy was given to the participants during the familiarising session and the experiment.

Each participant performed 36 trials: 18 trials in the memory-guided condition and 18 trials in the visually-guided condition. In both conditions, 6 trials were performed for each head position (i.e. head-left, head straight, head right). The 36 trials were presented in a pseudo-random order. A rest period of 30 s with eyes open was inserted between consecutive trials.

2.3.1. Experiment 2

The apparatus and procedure were similar to those of Experiment 1 except that at the beginning of each trial, participants were required to close their eyes before their head either remained aligned with the trunk or was slowly tilted by the experimenter towards the right or left shoulder. Then participants opened their eyes to inspect the geometric figure for 10 s before receiving the instruction to position their index at the top of the right wall of the house. Then participants closed their eyes and reproduced the figure from memory (memory-guided condition) or started to reproduce the figure with the eyes open (visually-guided condition). This methodology ensured that in both conditions (visually and memory guided conditions) participants inspected the figure with their head positioned in the same orientation as in the reproduction task.

Each participant in Experiment 2 performed 24 trials: 12 trials in the memory-guided condition and 12 trials in the visually-guided condition. In both conditions, 4 trials were performed for each head position (i.e. head-left, head straight, head-right). The 24 trials were presented in a pseudo-random order.

2.4. Data analyses

The extrinsic and intrinsic characteristics of the each individual figure reproduction were analysed using different parameters: (1) mean segment orientation of the geometric figures (extrinsic) (2) the shape of the figures (angular deformation index; intrinsic) and 3) the length of the segments (size reproduction; intrinsic).

2.4.1. Mean segment orientation

Calculated on the basis of the orientation of the drawn segments ($n = 5$), the mean segment orientation constituted the main variable of the present study. Segment orientation was estimated using regression analyses fitting together the X−Y data points of each individual segment of the geometric shape. The number of data points varied from segment to segment (150 to 240 data points) according to the time taken by the participants to draw the figure (i.e. spanning between 1.25 s and 2 s). As can be seen in the sample trial presented in Fig. 2, the different segments of the figure were mostly linear. Therefore, first order regression equations best characterised these segments. This was confirmed by the high correlation coefficient of the regression analysis (r^2 values > 0.90) found for each individual trial in both the memory-guided and visually-guided conditions. The slope

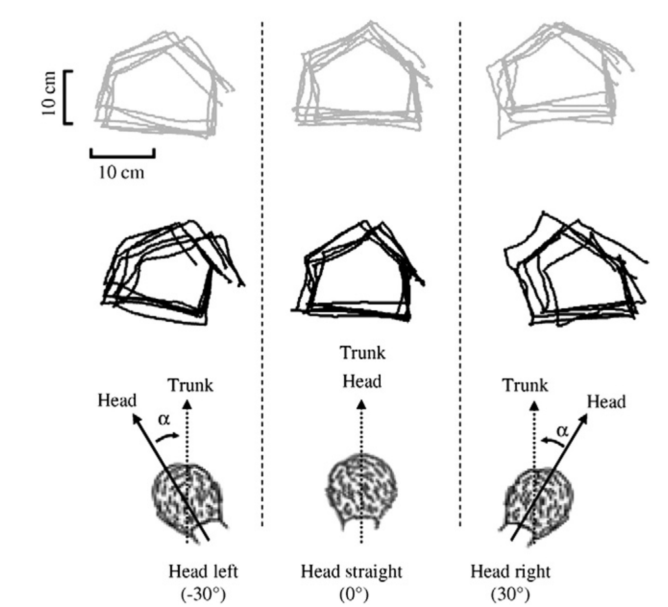

Fig. 2. Performance of a representative subject when reproducing the geometric figure in both the visually-guided (grey traces) and memory-guided (black traces) conditions as a function of head orientation. Traces represent single trials. The y-displacements of the index are plotted against the x-displacements.

values of the linear equation were then transformed into angular measures and then expressed in angular difference (normalisation) between the reproduced segment and the reference segment [vertical (0°), horizontal (90°) or oblique (±45°)]. The orientation of the geometric shape (mean segment orientation) was estimated by averaging the five normalised angles of each drawn figure. Negative and positive values indicate counter-clockwise and clockwise deviations of the drawn figure, respectively.

2.4.2. Shape of the geometric figure: angular deformation & size reproduction

2.4.2.1. Angular deformation. The deformation was calculated on the basis of the orientation of the different segments relative to each other irrespective of the orientation of the figures as a whole in space. This *angular deformation index* was calculated as follows: for each of the five normalised segments (2 walls, 2 roofs, 1 base), we subtracted the mean segment orientation of the figure reproduction (parameter 1 described above). The results computed for each individual segment were then converted into absolute value of the deviations. The deformation index was then calculated as the average of the absolute deviations of the five segments. An index of zero value would then reflect a perfect reproduction independently of the overall orientation of the figure i.e. (1) the two "walls" being perfectly parallel to each other and perpendicular to the floor and (2) the two segments of the roof being perpendicular to each other and at 45° relatively to the walls. The higher the index value, the greater the deformation was.

2.4.2.2. Size reproduction. The size reproduction was computed as the ratio between the distance travelled by the finger from the first to the last data point and the perimeter of the reference figure. It was expressed in percentage.

2.5. The perceptual task

Following the motor reproduction task, we determined in participants participating in Experiment 1, the orientation of the figure required for the participants to perceive the median axis of the house as being parallel to their median trunk axis (body midline). The figure attached on the board to the rear of participant's head could be rotated around its centre by the experimenter. While participants had their eyes closed between two trials, the experimenter oriented the frame randomly 30° to the left (counterclockwise) or to the right (clockwise). Then participants opened their eyes and instructed the experimenter to rotate the house until they perceived it as being aligned with their median trunk axis. This was done without time constraints. Participants were tested in counterbalanced conditions with the head either tilted (30° right or left) or aligned with the trunk. The position of the head was maintained in that position during the entire trial. Four alignments of the frame were performed in the three head positions. For each trial, the perceptual deviation was calculated as the difference between the house's and the participant's median axes.

2.6. Statistical analyses

For all computed parameters concerning motor reproduction, the ANOVA model was a repeated measures design with "Head Orientation" (left, straight, right) "Vision" (visually- and memory-guided conditions) and trial order (trial 1 to 6 in Experiment 1 and trial 1 to 4 in Experiment 2) as within-subject factors. For perceptual adjustments, the ANOVA model was a repeated measures design with "head orientation" (left, straight, right) as a within-subject factor. Newman–Keuls method and Pearson coefficient were used for *post hoc* comparisons and correlation analysis, respectively. We used Student *t*-tests for occasional supplementary analyses. A 0.05 significance level was adopted throughout.

3. Results

3.1. The drawing task

3.1.1. Experiment 1

3.1.1.1. Mean segment orientation. Fig. 2 represents individual typical hand reproductions in both the memory-guided and visually-guided conditions with the head either straight or tilted sideways. As reported previously, the position of the head relative to the trunk significantly affected the mean segment orientation ($F(2,22)=28.2$, $p<.01$). With the head aligned with the trunk, participants accurately reproduced the orientation of the figure as confirmed by a mean segment deviation of only 1.2° ($SD=3.2°$) and 2.4° ($SD=3.5°$) in the visual and memory conditions, respectively. Head tilt induced a deviation of segment reproduction in the direction opposite to the tilt (see Figs. 2 and 3). With head tilted to the left, the deviation reached 7.9° ($SD=6.9°$) and 11.3° ($SD=7.2°$) in the visual and memory conditions respectively. With the head tilted to the right, deviations of −2.9° ($SD=3.6°$) and −3.1° ($SD=3.8°$) were observed in the visual and memory conditions respectively. The three head orientation conditions differed significantly from each other (*post hoc* $p<.01$). To test whether head-left induced larger deviations than head-right, we normalised the mean segment orientation with respect to that computed in the head straight condition. This was done by subtracting the orientation measured in the head straight condition from the orientation measured in the tilt conditions. Student *t*-test analysis based on these normalised deviations revealed that the difference between head tilted left and right was at the level of significance in the memory guided condition ($t(11)=2.2$, $p=.05$). No difference appeared in the visually guided condition ($t(11)=1,4$, $p>.05$).

As can be seen in Fig. 3, the mean segment deviation of the motor reproduction was smaller in the visual condition compared to the memory condition ($F(1,11)=11.9$ $p<.01$). However, as indicated by the significant Head Orientation×Vision interaction ($F(2,22)=7.3$ $p<.01$), the beneficial effect of vision depended on the orientation of the head relative to the trunk. Indeed, *post-hoc* comparisons revealed a significant difference between the visual and memory guided conditions only when the head was tilted left ($p<.05$).

The ANOVA did not reveal a significant effect of trial order neither as a main effect, nor in interaction with the other two factors on figure reproduction ($p>.05$).

Pearson's correlation analysis indicated that there was a strong linear relationship between the motor reproduction (mean segment orientation) in the memory-guided and visually-guided conditions (see Fig. 6 top panels). When the head was tilted either to the left or to the right, the correlation coefficients between the two reproduction tasks were $r=0.88$ and $r=0.91$, respectively ($p<.01$). These significant linear relationships persisted when the deviations in the head straight condition were subtracted from those in the head tilted conditions (head-left $r=0.85$; head-right $r=0.86$). When the head was maintained aligned with the trunk, a significant correlation of $r=0.87$ ($p<.01$) was noted. This indicates that participants whose reproductions were the most deviated in the memory condition produced the most deviated reproductions in the visual condition and *vice versa.*

3.1.1.2. Shape of the geometric figure (angular deformation and size reproduction). Analysis of angular shape deformation indicated that reproductions were significantly more distorted when the head was tilted either to the right (5.7° $SD=1.06$) or to the left (5.4° $SD=1.08$) than when it was aligned (4.7° $SD=0.84$) with the trunk ($F(2,22)=7.7$ $p<.01$, see Fig. 3B). The ANOVA also revealed a significant effect of

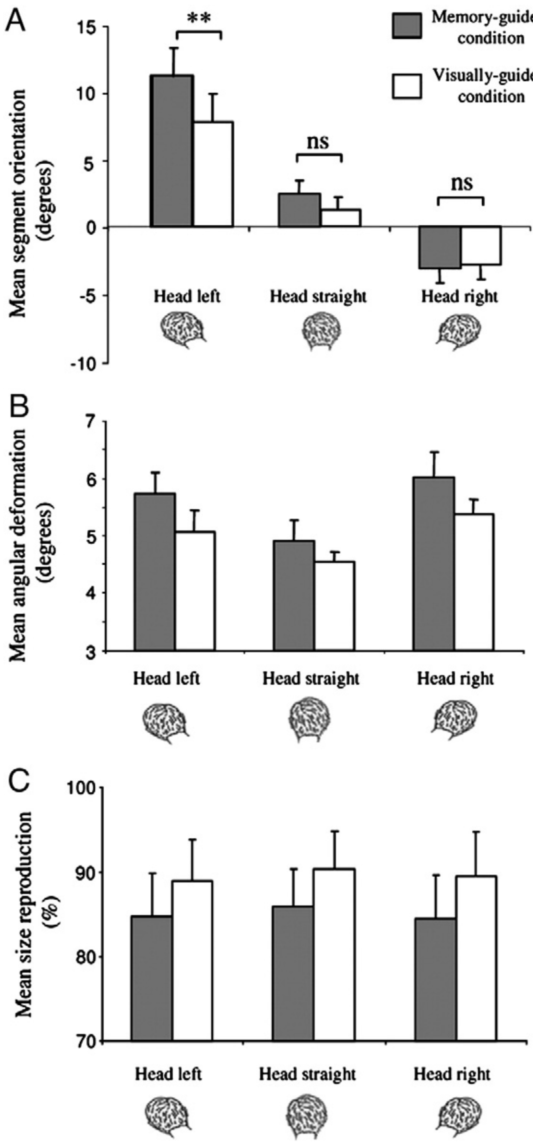

Fig. 3. Mean normalised segment orientation (A) mean angular deformation (B) and mean size reproduction (C) in the memory and visually-guided conditions respectively as a function of head orientation observed in Experiment 1. According to convention, counter-clockwise deviations are expressed as negative and clockwise deviation as positive. Error bars are standard errors of the mean.

Vision ($F(1,11) = 5.2$ $p < .05$), the deformation being slightly greater in the memory condition (5.6° $SD = 1.1$) than in the visual condition (4.9° $SD = 0.8$). The absence of a significant Head Orientation × Vision interaction indicated that vision of the figure during the drawing task was beneficial whatever the head orientation ($F(2,22) = 0.55$ $p > .05$). The trial order did not reach significance either as a main effect or in interaction with the other two factors ($p > .05$). Pearson's correlation analysis revealed a linear relationship between the magnitude of the reproduction deformation shown by the participants in visual and memory conditions when their head was either tilted (head-left : $r = .58$ $p < .05$; head-right: $r = .64$ $p < .05$) or aligned with the trunk ($r = .69$ $p < .05$).

Analysis of size reproduction indicated that the participants' reproductions were smaller than the actual figure with a mean contraction of ~14% when all experimental conditions were confounded. Size reproduction was not significantly affected by the Head Orientation factor either as a main effect ($F(2,22) = 1.05$ $p > .05$) or in interaction with Vision ($F(2,22) = 0.2$ $p > .05$). The main effect of the trial order reached significance ($F(5,55) = 5.03$ $p < .05$) with a mean contraction of figure reproduction that reduced gradually from ~18% for the first trial to ~10% for the sixth trial. This order effect did not interact with any other factor ($p > .05$). The main effect of Vision was also significant ($F(1,11) = 12.06$ $p < .001$). As can be seen in Fig. 3, whatever the orientation of the head, size reproduction was improved by ~5% in the visually-guided condition. Pearson's analysis also revealed a strong linear relationship between the size reproduction shown by the participants in the visual and memory conditions whatever the position of the head (titled left: $r = .91$; tilted right: $r = .97$ head straight: $r = .95$ $p < .01$).

3.1.2. Experiment 2

3.1.2.1. Mean segment orientation. Results of Experiment 2 were similar to the results in Experiment 1, showing that head tilt induced a rotation of the figure reproduction in the direction opposite to the tilt ($F(2,12) = 54$, $p < .01$, Fig. 4) with significant differences between the three head orientations in both visual conditions (post hoc tests

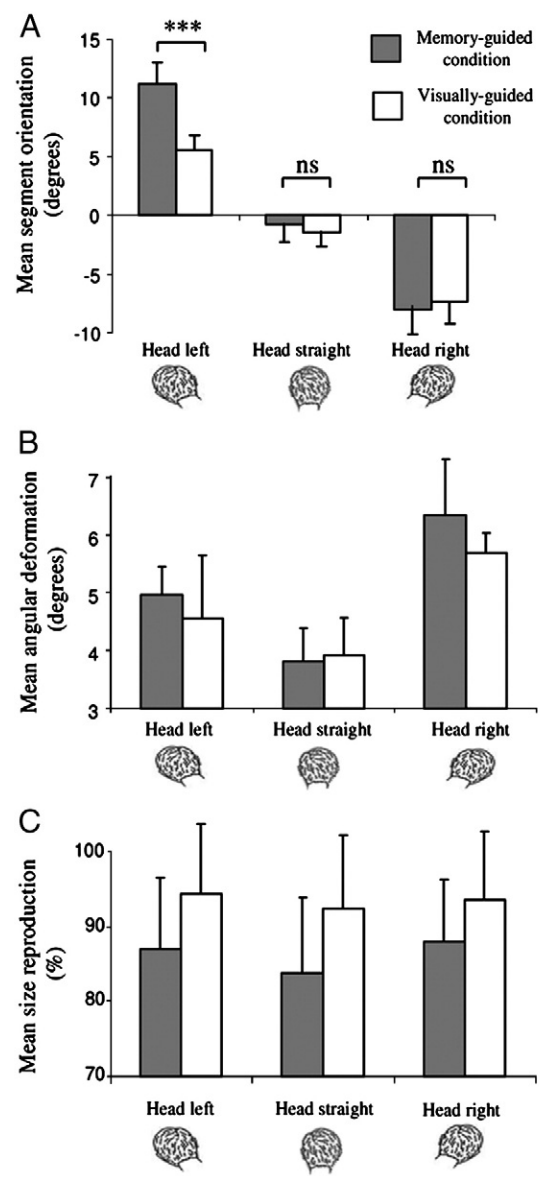

Fig. 4. Mean normalised segment orientation (A) mean angular deformation (B) and mean size reproduction (C) in the memory and visually-guided conditions respectively as a function of head orientation observed in Experiment 2. According to convention, counter-clockwise deviations are expressed as negative and clockwise deviation as positive. Error bars are standard errors of the mean.

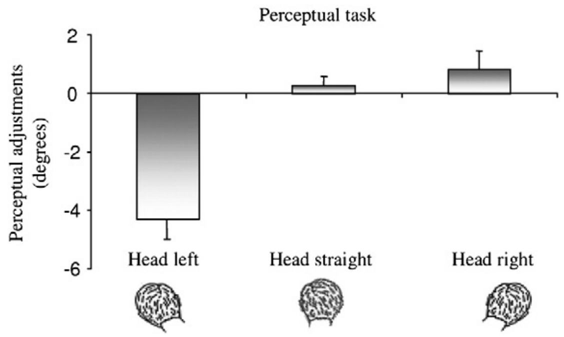

Fig. 5. Mean perceptual deviations (in degrees) as a function of head orientation. Counter-clockwise deviations are expressed as negative and clockwise deviation as positive. Error bars are standard errors of the mean.

$p<.01$). Absolute deviation values were significantly greater when the head was tilted to the left than when it was tilted to the right in the memory-guided condition ($t(6)=2.1$, $p<.05$) but not in the visually-guided condition ($t(6)=0.4$, $p>.05$). Vision also affected significantly the figure reproduction ($F(1,6)=6.1$, $p<.05$) with a beneficial effect only when the head was tilted to the left ($p<.01$). The trial order did not reach significance either as a main effect or in interaction with the other factors ($p>.05$). Pearson's correlation analysis indicated that the two reproduction tasks (visual and memory guided tasks) correlated when the head was tilted left ($r=.60$), right ($r=.78$) and when aligned with the trunk ($r=.68$). Pearson's correlation analysis based on relative deviations (i.e. deviation measured in head straight condition subtracted from deviations measured in head tilted conditions) revealed similar results (head-left $r=0.53$; head-right $r=0.75$ $p<.05$).

3.1.2.2. Shape of the geometric figure (angular deformation and size reproduction). The ANOVA indicated a significant effect of Head Orientation ($F(2,12)=12.2$, $p<.01$) with a greater mean angular deformation when the head was either tilted leftwards (4.7°, $SD=2$) or rightwards (6.1°, $SD=1.7$) than when it was aligned with the trunk (3.8°, $SD=1.4$) (see Fig. 4). In contrast to Experiment 1, the ANOVA did not reveal a significant effect of Vision either as a main effect ($F(1,6)=0.55$, $p>.05$) or in interaction with the head orientation factor ($F(2,12)=0.34$, $p>.05$). The trial order had no significant effect (p>.05).

Size reproduction was not significantly affected by the Head Orientation factor either as a main effect ($F(2,12)=1.8$, $p>.05$) or in interaction with Vision ($F(2,12)=2$, $p>.05$). In contrast, the effect of vision was significant ($F(1,6)=5.95$, $p=.05$) indicating that whatever the orientation of the head, the mean contraction of figure reproduction was reduced in the visually-guided condition. Finally, the mean contraction tended to reduce from the first to the forth trial but this effect did not reach significance ($p=0.12$). The trial order did not significantly interact with the other two factors ($p>.05$).

3.2. The perceptual task (participants of Experiment 1)

Head orientation significantly affected perceptual adjustments ($F(2,22)=5.01$ $p<.05$). With the head tilted towards the left shoulder, participants perceived the figure as being aligned with their median trunk axis when it was actually tilted by an average of −4.3° ($SD=5.2$) towards the tilted head (Fig. 5). The deviation was smaller with the head tilted right (0.8 $SD=4.8$). When the head was aligned with the body, the participants accurately perceived the orientation of the figure (0.26° $SD=1.1$). *Post hoc* comparison indicated that the deviations observed with the head tilted left were significantly different from the other two conditions ($p<.05$), the deviations of which were not significantly different from each other ($p>.05$).

To assess the relationship between the motor and perceptual tasks, the correlation coefficients between the mean segment orientation in the motor task and the mean perceptual deviation were calculated. As depicted in Fig. 6 (lower panels), whatever the orientation of the head, there was no significant linear relationship between the motor and perceptual performances ($p>0.05$). Correlation analysis based on the relative deviations in the head-left and head-right conditions (calculated as the difference between head-tilted and head straight conditions) confirmed the absence of linear relationship between the perceptual and motor tasks when the head was either tilted right ($r=0.27$, $p>.05$) or tilted left ($r=-0.02$, $p>.05$). Similarly, there was no significant correlation ($r=-0.21$, $p>.05$) between the mean head

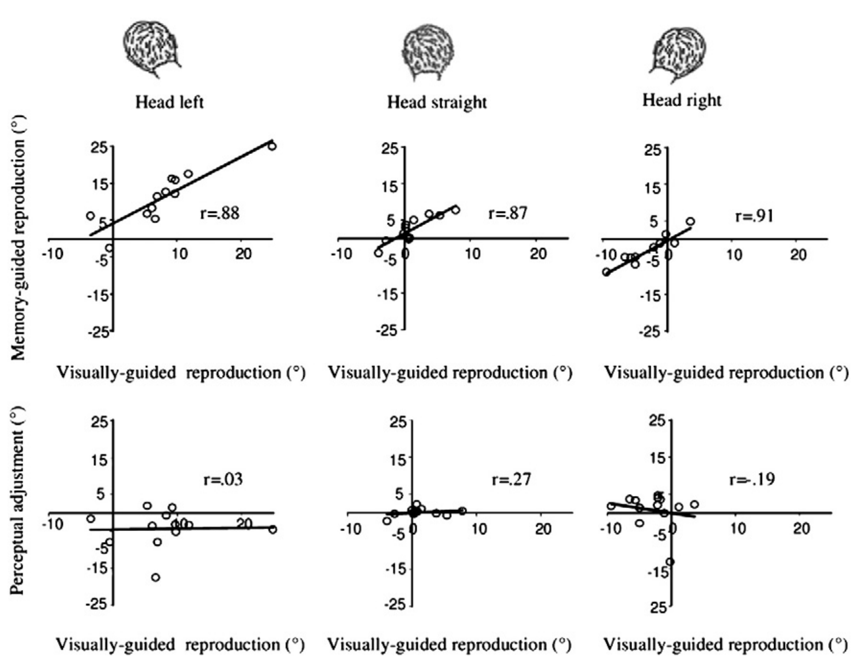

Fig. 6. Top panels show individual mean segment orientation (calculated as the average of 6 trials per condition) of memory reproductions (*Y* axis) plotted against visual reproductions. Lower panels show individual deviations of perceptual adjustments (*Y* axis) plotted against visual reproductions (*X* axis).

tilt effect in perceptual adjustments (calculated as the difference between head-left and head-right conditions) and the mean head tilt effect in visually guided reproduction.

4. Discussion

In the present experiments, we investigated whether the deviation in motor reproduction of memorized figures in condition of head tilt (e.g., Berger et al., 1998; Guerraz et al., 2003) would persist when visual feedback of the figure (but not of the hand) remained available during the drawing task. Firstly, corroborating previous findings, we found in Experiments 1 and 2 that head tilt towards the shoulders induced systematic deviation of segment reproduction in the direction opposite to the tilt. Not documented in previous studies, we also noticed significant deformations of the reproductions. In contrast, head tilt did not affect size reproduction. The salient finding of the present study is the better reproduction of extrinsic (mean segment orientation) as well as intrinsic (shape and size) characteristics of the figure in the visually guided condition.

We ensured in Experiment 2 that in both the visually and memory guided conditions participants inspected the figure with their head positioned in the orientation in which they had to reproduce the figure. Indeed, the change in the retinal image of the house (mainly its orientation) between the head-straight and head-tilted situations in Experiment 1 could have provided the brain with additional information about how much the head had been turned; information unavailable in the memory-guided condition. Results of Experiment 2 provided however similar results to those of Experiment 1, that is, a reduced effect of tilting the head left in the visually open-loop drawings. This suggests that the change in the retinal image of the house when the participants first saw the figure with the head-straight and then with the head tilted was not the key information used for improving the orientation of the reproductions in Experiment 1.

The bias in the figure reproduction, induced by tilting the head sideways, was observed in both the memory and visually guided conditions with strong linear relationships between each other. As such, this suggests common underlying processes whether or not visual feedback from the figure is available during drawing. Information related to the figure must be transformed into an intrinsic muscle-based frame of reference to produce the hand movements. The drawing task therefore involves transformations of information that is coded into different frames of references (e.g., eye-, head-, body- or hand-centered) (Soechting & Flanders, 1992; Pouget, Ducom, Torri, & Bavelier, 2002). Errors observed during the drawing movement could occur at any of these steps. Considering the dissociation between head and trunk alignment in the present experiments, the drawing deviations observed in Experiment 1 and 2 are likely the consequence of errors of transformation from head to body centered of reference due to a bias in the internal representation of body configuration (Guerraz et al., 2006). As long as visual feedback of the arm is prevented, this bias would alter hand-motor production irrespectively of whether visual feedback of the figure is available or not.

Interestingly, reduced deviations were observed in Experiments 1 and 2 when participants had visual feedback of the figure with head tilted left. Different non-exclusive reasons could account for the better drawing performance observed when visual feedback of the figure was available. It has been reported that individuals perceive with a better accuracy their gaze (Blouin, Gauthier, & Vercher, 1995, Blouin, Amade, Vercher, Teasdale, & Gauthier, 2002) and head (Becker & Saglam, 2001) directions in the presence of retinal signals (even when these signals are spatially non-informative). Therefore, vision of the figure may have made extra-retinal and neck proprioceptive information perceptually more meaningful and interpretable compared to the condition without retinal inputs. This may have resulted in a more accurate internal representation of the head–trunk configuration, and in an attenuated effect of head tilts with visual feedback. However, this improvement of the internal representation of the head–trunk configuration appears to be short lived. Indeed, in contrast to Experiment 1, participants in Experiment 2 observed the figure with the head already tilted just before being asked to reproduce it either from memory or with eyes open. Results revealed a significant difference between these two visual conditions (at least with the head tilted left) indicating that the beneficial effect of vision on the internal representation of the head–trunk configuration does not persist when the participants close their eyes. Similarly, the deviation in the memory-guided condition was of similar magnitude in Experiments 1 and 2 although in the former, participants did not have at any time the opportunity to observe the figure while their head was tilted. This might alternatively suggests that vision provides the brain with additional information about how much the head had turned only when those visual cues are integrated on-line with proprioceptive afferents and/or motor command of the arm. Finally, it must be mentioned that although seeing the figure during the movement does not provide direct information relative to body configuration, it might however provide indirect cues. Indeed, because the house was systematically presented in the same orientation with respect with participant's trunk, retinal orientation of the house could have provided cues about the relationship between the head and trunk/arm. This alternative explanation of the visual effect in drawing task deserves further experiments in which the orientation of the figure is systematically changed.

The effect of vision was however limited to the left head tilt condition in both Experiments 1 and 2. As mentioned above, the figure reproductions were more deviated in the left tilt condition than in the right tilt condition in both Experiments. Vision might therefore be beneficial only for large angular errors such as those observed with head tilted left but not for the smaller deviations observed in condition of head tilted right or head straight. Although reported in other motor or perceptual tasks (Guerraz, Poquin, Luyat, & Ohlmann, 1998; Guerraz, Poquin, & Ohlmann, 1998; Guerraz et al., 2006), this asymmetry does not emerge systematically (Guerraz et al., 2003; Luyat et al., 2001 Funk, Finke, Müller, Utz, & Kerkhoff, 2010). It must be noticed however, that when present, the difference between left and right head tilt is always in favour of a greater effect of left tilt (Guerraz, Poquin, Luyat, et al., 1998; Guerraz, Poquin, & Ohlmann, 1998; Guerraz et al., 2006; Funk et al., 2010). The reason for the greater effect of left tilt is currently unknown. It could be related to an internally mediated postural asymmetry that has been reported by Previc (1991,1994) and Putnam, Noonan, Bellia, and Previc (1996) in a large number of individuals. These authors examined whether the orientation of the head deviates from vertical in participants instructed to stand in a natural upright position. They found that the percentage of right-head-tilted individuals was more than twice that of the left-head-tilted group. Although speculative, the limited bias in motor production in the head tilt-right condition might be, to some extent, related this postural asymmetry.

Vision also allowed participants to reproduce the intrinsic characteristics of geometric figures (angular and size deformation index) with more accuracy than in the memory condition when either the head was tilted sideways or aligned with the trunk (see Fig. 3B,C). This effect did however not reach significance in Experiment 2 when the deformation index was concerned. The reduced drawing performance in memory condition is compatible with the hypothesis that different representations are involved according to which task the participant undertakes: an accurate representation used for guiding and controlling movements when the object is visible and a second representation, less accurate but useful in order to execute movements when the object is not visible. Vision of the visually-structured illustration may have allowed the participants to specify movement parameters in a stable retinal-based allocentric frame of reference (Bridgeman, 1991; Paillard, 1991; Blouin et al., 1993). The covariant changes in the retinal inputs when the head was tilted may have enhanced such a frame of reference, limiting the detrimental impact of the head position on the drawing performance. The absence of visual information in the memory-guided condition did not favour the use of an allocentric frame of reference. In this condition, movement parameters were more likely to be specified in an egocentric, more volatile, frame of reference (Bridgeman, 1991; Paillard, 1991; Blouin et al., 1993). Here the motor production would be more vulnerable to body motion and changes of body configuration. It must be stressed, however, that we cannot rule out the possibility that participants in the present study had access to the same representation in both visual tasks. Indeed, when either the angular or size deformation index was considered, strong linear relationships between the visual and memory conditions were observed. Therefore, although vision improved drawing performances, participants might access to the same representation in both tasks. The diminished capacities in reproducing the intrinsic properties of the figure in the memory condition would then be related to some sort of decay of the visuomotor information used for movement execution (Hesse & Franz, 2009; Franz, Hesse, & Kollath, 2009).

Following the sensorimotor task in Experiment 1, participants were required to align the median axis of the house parallel to their median trunk axis. The participants in the condition of head tilt to the left perceived the figure as being aligned with the trunk when it was actually tilted in the direction of the head. This effect is similar to the well known Aubert effect (Aubert, 1861; Dichgans, Diener, & Brandt, 1974; Howard, 1986; Wetzig & Baumgarten, 1990; Guerraz, Poquin, Luyat, et al., 1998; Guerraz, Poquin, & Ohlmann, 1998). This indicates that when aligned with the trunk, as it was in the motor task, the figure was likely perceived as tilted in the direction opposite to the head. This perceptual illusion could therefore be at the origin of the deviations observed in the same direction in the visually-guided condition. However, the absence of correlation between the perceptual and the motor tasks does not support such hypothesis (see Fig. 6 lower panels). It must be noticed that different factors related to motor execution (such as biomechanical factors) may play a role and mask such relationship. In addition, the fact that the perceptual and motor tasks were not performed at the same time may be a limiting factor of the correlation analyses.

In contrast to the absence of correlation between the motor and perceptual tasks, a strong and systematic relationship was noticed between motor performances in the memory and visually guided conditions when the mean segment deviation, the angular deformation, and size deformation were considered. While such correlations are compatible with the use of common processes in the visually and memory-guided reproductions, they do not support the hypothesis of direct links between visual illusion and visually-guided reproductions. This is in line with previous studies showing that motor processes, such as online control of goal-directed hand movements, are immune to perceptual illusions (Aglioti et al., 1995; Bock, 1997; Glover & Dixon, 2001).

In summary, our results confirm the important head–hand relationship in sensorimotor tasks such as drawing. In addition, these results show that vision of the figure improves the reproduction of both intrinsic (shape and size) and extrinsic (orientation relative to the participant) characteristics of the figure. However, the effect of head tilt on the angular deviation of the overall figure (extrinsic characteristic), although reduced, persists when vision of the object (but not the hand) is available. This provides evidences for a bias in the internal representation of body configuration in the head tilt condition.

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