The “motor oblique effect”: perceptual direction discrimination and pointing to memorized visual targets share the same preference for cardinal orientations.

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ABSTRACT

In previous studies we observed a pattern of systematic directional errors when humans pointed to memorized visual target locations in 2-D space. This directional error has also been observed in the initial direction of slow movements towards visual targets or movements to kinesthetically defined targets in 2-D space. In this study we used a perceptual experiment where subjects decide whether an arrow points in the direction of a visual target in 2-D space or not and observed a systematic distortion in direction discrimination known as the “oblique effect”. More specifically direction discrimination was better for cardinal directions than oblique. We then used an equivalent measure of direction discrimination in a task where subjects pointed to memorized visual target locations and showed the presence of a motor oblique effect. We finally modeled the oblique effect in the perceptual and motor task using a quadratic function. The model successfully predicted the observed direction discrimination differences in both tasks and furthermore the parameter of the model that was related to the shape of the function was not different between the motor and the perceptual tasks. We conclude that a similarly distorted representation of target direction is present for memorized pointing movements and perceptual direction discrimination.
INTRODUCTION

In previous studies we investigated the directional accuracy of planar pointing movements to visually presented targets using a memory delay paradigm (Smyrnis et al 2000; Gourtzelidis et al 2001). We showed that when subjects pointed to the location of previously seen targets, a systematic directional error was observed, that varied with target direction. This systematic directional error reflected a bias for movement endpoints to cluster towards the oblique directions between the cardinal axes. After excluding more trivial explanations for this error, relating to the mechanical properties of the arm, (Smyrnis et al 2000) we sought to explain this phenomenon as an effect of spatial working memory (Gourtzelidis et al 2001). More specifically we found that the same pattern of systematic directional errors has been observed in a series of studies of spatial working memory where subjects had to memorize the location of a dot within a circle and then use a pen to draw the dot in an empty circle (Huttenlocher et al., 1991). A model provided to account for the pattern of errors in both direction and amplitude, stated that these errors emerged from a strategy of subjects to categorize space, in order to help them memorize the spatial location of the targets. In a subsequent study (Theleritis et al 2004) we investigated the space categorization hypothesis, using a modified version of the memory pointing task. In this task subjects had to remember a series of target locations presented sequentially and then respond to a cue target, by moving to the next target in the previously presented series. Our hypothesis was that the increase in memory load in this task, as the number of targets to remember increased from two to four, would result in a more prominent space categorization effect and thus a larger systematic directional error. Surprisingly though we observed that the systematic directional error was the same
for all memory loads. This result therefore suggested that the space categorization strategy does not explain this phenomenon.

In another study Graaf et al (1991) instructed subjects to draw with a pen a line towards a visually presented target and proceed to do this very slowly. It was found that the initial movement direction, measured at the beginning of these slow pointing movements, consistently deviated from the target direction and the pattern of systematic directional errors that emerged, was surprisingly identical to the one we observed in fast pointing movements performed in memory conditions. It was also found that the same systematic directional errors were observed when subjects used a pointer to point in the direction of a target in 2-D space, suggesting that these errors might not be restricted to the execution of a movement. In a follow up study de Graaf et al (1994) showed that the same systematic directional errors were observed when targets were presented using kinesthetic instead of visual input. In a recent study of pointing movements, where the movement endpoints where defined by a passive positioning of the arm, in a location in 2-D space by a robot arm, Baud-Bovy and Viviani (2004) observed the same pattern of systematic directional errors. A similar systematic directional error pattern was observed when subjects used an isometric force manipulandum to produce force pulses to the direction of visually presented targets without feedback (Massey et al 1991).

A common theme in all these studies is that the individual has to specify the direction of a target in 2-D space without the presence of feedback. In all these cases then, the same qualitatively systematic directional anisotropy emerges, namely a trend of subjects to direct their movements away from the cardinal and towards the oblique directions in 2-D space. What is the origin then of this systematic directional error that is
observed in such diverse tasks both in terms of input (visual, kinesthetic), output (fast or slow movements, isometric forces, pointing with a pointer) and in terms of cognitive demands (memory movements, movements towards a visual target)?

In perception research there is a well described phenomenon of direction anisotropy called the “oblique effect”. This term has been used to codify the observed superiority in visual discrimination of the cardinal orientations as opposed to the oblique (Appelle 1972). The oblique effect was first demonstrated psychophysically by Jastrow in 1893. In these experiments subjects had to reproduce visually presented lines or had to set lines to predefined orientations. It was found that subjects performed better (were faster and more accurate) with horizontal and vertical as opposed to oblique lines. This effect in visual discrimination was observed not only for lines but for a series of visual stimuli that could be oriented. It was also not a particular characteristic of man but it was observed in other mammals and even in much more primitive animals such as the octopus (see review by Appelle 1972). It has also been shown that this effect in visual discrimination is already present in 6 week old infants (Leehey et al 1975).

As far as the origin of the oblique effect in visual discrimination is concerned, more trivial explanations such as eye movements, optical disorders and various dioptric characteristics, as well as the composition of the retinal mosaic, were found to be inadequate (Appelle 1972). On the other hand neurophysiological evidence suggested that at least some part of this perceptual phenomenon might rely on cortical mechanisms. Maffei and Campbell (1970) showed that the amplitude of the evoked potential for visually presented vertical and horizontal gratings was larger than that for oblique gratings. In a recent fMRI study it was also observed that the magnitude of the BOLD
response in area V1 for horizontal and vertical lines was larger than that for oblique lines (Furmanski and Engel 2000). These findings led to the hypothesis that the oblique effect is related to low level visual processing in primary visual cortex. In yet other studies that used haptically defined stimuli an oblique effect was also observed, in the sense that gravitationally defined horizontal and vertical axes were more accurately discriminated than oblique axes in blindfolded and blind adults, as well as in blindfolded children (Gentaz and Hatwell 1995, 1998). In yet another study Gentaz and Streri (2004) found a haptic oblique effect in 5-month old infants. A theoretical framework (Essock 1980) to consider the wealth of these findings proposes the existence of two classes of oblique effect, a purely visual one (class 1) related to low level visual processing in the primary visual cortex and a higher level oblique effect relying on extraretinal cues (vestibular, kinesthetic, haptic), that extends to cognitive and memory processes (class 2). In a recent study Krukowski and Stone (2005) found an oblique effect in smooth eye pursuit.

In this study we will try to establish a connection of the directional error pattern that has been observed in the pointing tasks described above, to the oblique effect in perception. We will first demonstrate theoretically how these two phenomena could be related. Let us assume that movements are made to neighboring targets and an observer has to use the distributions of endpoint directions to decide whether a particular endpoint is aimed at one target or its neighbor. In figure 1A we present the case where the observer would have to discriminate between a target T_1 located at a cardinal direction (90deg) and a neighbor target T_2, as well as between T2 and a target T_3 located at an oblique direction (45deg). The light shaded areas around T_1, T_2 and T_3 represent the spread of the distributions of movement endpoints around these targets respectively (S1, S2 and S3).
and the overlapping dark shaded area represents the part of the endpoint direction distributions where the observer would not be able to tell if the movement would be towards T₁ or T₂. The pattern of systematic directional errors that we previously described would correspond to a shift of T₂ to T₂a as shown in figure 1B. The effect of this shift would be a smaller overlapping dark shaded area between T₁ and T₂. Thus the observer would be more certain in discriminating T₁ from T₂. At the same time though this shift of T₂ would result in T₂a being closer to target T₃. Target T₂ shares now a shaded area (dark) with target T₃ and the observer would be less certain in discriminating T₂ from T₃. The end result then of the systematic directional error for a target T₂ presented between a cardinal and an oblique direction would be better direction discrimination from the cardinal and worse direction discrimination from the oblique direction, which is the definition of an oblique effect. A similar pattern of anisotropy in direction discrimination for the observer would be produced if instead of a shift in T₂, the spread of movement endpoints would increase with increasing directional deviance from the cardinal direction and towards the oblique as shown in figure 1C. It is noted here that the two phenomena described in figure 1B and 1C could theoretically be independent, canceling or adding to each other. In conclusion our theoretical analysis shows that the systematic directional error could indeed be related to differences in direction discrimination between cardinal and oblique directions thus reflecting an oblique effect in pointing.

In what follows we use a perceptual task of direction discrimination, where subjects have to decide whether an arrow is pointing in the direction of a visually presented target or not, to demonstrate a perceptual oblique effect. We will then use a
memory pointing task to the same target locations, to provide evidence of a motor oblique effect with similar properties to the perceptual one. We will finally show that the motor oblique effect is the result of the systematic directional error pattern that we have previously described for these movements.
METHODS

Subjects

Five healthy adults (age span: 28-38 years, 2 men) participated in the memory pointing experiment. Three of these subjects plus two new subjects (age span: 28-40 years, 2 men) performed the arrow pointing experiment. All participants were naïve to the purposes of this study and gave written informed consent for participation in the study after a detailed explanation to them, of the experimental procedures. The experimental protocol was approved by the Eginitio Hospital Scientific and Ethics Committee. All participants were right handed and performed the tasks using their preferred right hand.

Set up and procedure for the arrow pointing (AP) experiment

Subjects sat comfortably in front of a computer monitor (HITACHI CM630ET, 32.8cm horizontal x 24.5cm vertical) at a distance of approximately 60cm. The amplitude of the target stimuli was 6cm from the center target, thus the degrees of visual angle for all stimuli were 5.7deg. The subjects used two fingers of their right hand to press the left or right arrow key on the computer keyboard. Each trial started when a filled red disk (5mm diameter) appeared at the center of the screen (center target). After a variable period of 1-2sec, a second white filled disk (5mm diameter), the peripheral target, appeared at the circumference of an imaginary circle of 6 cm radius in one of 32 directions (11.25deg intervals) and a yellow arrow appeared originating at the center target that was either aligned with the target (50% of cases) or deviating 2.5 degrees away from the target either clockwise (25% of cases) or counterclockwise (25% of cases). The subject was instructed to use the right or left arrow key of the keyboard to respond either
“yes” if the arrow and the target had the same direction or “no” if the arrow direction deviated from the target direction. The arrow length varied among four values (15mm, 30mm, 45mm and 60mm).

Each subject performed one experimental session every day for six days. In each session the subject performed 4 repetitions for every arrow length, for every target direction in a randomized sequence, for a total of 512 trials (4 repetitions x 4 arrow lengths x 32 target directions). The total number of trials for each subject was 6x512 = 3072.

**Data processing for AP**

We excluded trials where the latency of the arrow key press was < 80 or > 5000ms. After application of these exclusion criteria we retained 15335 of the 15360 trials for all subjects (99.8%).

We then computed a d-prime score for each target direction, each arrow length and each subject as follows. The total number of responses for one subject, one arrow length and one target direction, were grouped in four categories as indicated in table I. The correct detection of the same direction of arrow and target was defined as a hit. The probability of a hit was then:

\[
P(\text{Hit}) = \frac{N_1}{N_1+N_2} \quad (1)
\]

The false detection of the same direction of arrow and target was defined as a false alarm. The probability of a false alarm was thus:
\[
P(\text{FalseAlarm}) = \frac{N3}{N3+N4} \tag{2}
\]

The \( P(\text{Hit}) \) and \( P(\text{FalseAlarm}) \) were then transformed to z-scores and finally the d-prime, denoted as \( \text{dap} \) in the remaining of this manuscript, was computed:

\[
\text{dap} = z\text{-score}(P(\text{Hit})) - z\text{-score}(P(\text{FalseAlarm})) \tag{3}
\]

According to the arrow length we computed \( \text{dap15} \) (arrow length = 15 mm), \( \text{dap30} \) (arrow length = 30 mm), \( \text{dap45} \) (arrow length = 45 mm) and \( \text{dap60} \) (arrow length = 60mm).

**Set up and procedure for then emory pointing (MP) experiment**

Subjects sat in a darkened room and faced a wooden rectangular board covered with black paper. A digitizer tablet (Calcomp 2000) was laying underneath this wooden board and a mouse device that the subject grasped, using his/her right arm. The tablet height was adjusted at waist level for each subject. An LCD projector (TOSHIBA, TDP-140) was fixed on the room ceiling facing down at the wooden board. Visual stimuli as well as a cursor indicating the mouse position were produced by a PC computer program (using Delphi 7.0) and projected on the black paper surface on the board (40cm horizontally x 30cm), while the subject moved the mouse on the digitizer tablet below. Although the subject’s head was not fixed the distance of the subject’s eyes from the board was approximately 60cm and the amplitude of the stimuli was 6cm from the center
target, thus the degrees of visual angle were 5.7, as in the AP experiment. The mouse position was sampled at 100 Hz and was displayed on the board surface as a 2.5 mm diameter round white cursor. The ratio of arm movement to the cursor movement was 1.

Each subject performed trials of two tasks, a visual pointing and a memory pointing task (MP). Each trial started when a filled red disk (5mm diameter) appeared at the center of the screen (center target) and the subject moved the cursor in the center target. After a variable period of 1-2sec, a second white filled disk (5mm diameter), the peripheral target, appeared at the circumference of an imaginary circle of 60 mm radius in one of 32 directions (11.25deg intervals). In the visual pointing task the center target was turned off simultaneously, indicating to the subject to move the mouse controlled cursor as accurately as possible, to the peripheral target. In the MP task the peripheral target remained lit for 300ms and after a delay period of 3sec, the center target was turned off. This was the signal for the subject to move to the position of the previously shown peripheral target, by performing a single pointing movement. In this paper we discuss the results from the analysis of the directional error, at the end of the movement trajectory, for the MP task only. In the visual pointing task the error at the end of the movement trajectory was zero by definition, since the subject was required to place the cursor on the visible target. The directional error at various points in the trajectory for the two tasks, before the end of the movement, will be discussed in a separate paper. The subject in both tasks was instructed to hold the cursor at the target position for 2sec. Then the center target was turned on again, to signal to the subject to move to the center for the beginning of the next trial. Subjects were instructed to maintain head and trunk in an upright position during task execution and to use only shoulder and elbow movements to
move the mouse (no wrist or finger movements). No special equipment was used for stabilizing the trunk or head, but one of the authors was standing behind the subject giving instructions when he or she tended to change posture or use wrist or finger movements to perform the task.

Each subject performed one experimental session every day for six days (except from one subject that did not complete the first day session, missing 7 trials in the visual pointing task and 22 trials in the MP task). Within each session 4 repetitions for every target direction for every task thus a total of 256 trials were performed in a randomized sequence (4 repetitions X 32 directions x 2 tasks). Thus, every subject (except the one mentioned above) performed a total of 256x6= 1536 trials of which 768 were of the MP task.

**Data processing for MP**

The X-Y position data from the digitizer that were sampled were transformed to the location of the feedback cursor on the screen. Although the digitizer had a spatial resolution of 0.01mm the smallest movement that could be visualized as a cursor movement on the screen was 0.3mm (one pixel). We chose to use X-Y movement data of the cursor at the screen (lowest movement detected 0.3mm) to calculate the direction and amplitude of the movement. The same X-Y data were also used to calculate the instantaneous speed of the cursor by numeric differentiation. This speed was literally zero when the subject was waiting at the center target since very small movements of the arm that were less than 0.3mm did not result in cursor movement. An interactive program (programmed in Delphi 7.0) was used to compute and visualize the instantaneous speed
trace, to compute the movement onset (rise of instantaneous speed above zero for three consecutive measurements = 30ms) and the end of the first movement (return of instantaneous speed to zero and remaining zero for at least 100msec).

The cursor X-Y position at each point within each trial trajectory was transformed to conventional polar coordinates (direction and amplitude) with the origin at the center target. The directional error (DE) was the polar angular difference in degrees, of a particular point in the movement trajectory minus the peripheral target. A counterclockwise deviation from the peripheral target was defined as positive DE. The amplitude error (AE) was a measure of the difference in mm of the amplitude at a particular point in the movement trajectory minus the amplitude of the peripheral target that was set to 60mm. Thus a negative AE corresponded to target undershoot and a positive AE corresponded to a target overshoot. The DE was computed at five points along the movement trajectory, namely when the amplitude was 15mm, 30mm and 45mm from the center target and at the end of the first movement. In this paper we will discuss only the results for the DE of the first movement endpoint. The AE was measured at the end of the first movement.

We excluded from further analysis trials where the subject moved before the go signal and trials where the movement started earlier than 80ms (anticipations), or later than 1500ms, after the turning off of the center target (late onset of movement). We also excluded trials in which the DE was > 22.5 deg or < -22.5 deg at any one of the 5 points in the trajectory where it was measured. Finally we excluded trials where the AE for the first movement was < -15mm or > 15mm. After application of these exclusion criteria we retained 3036 of the 3818 trials for all subjects (86.6%).
The direction of the first movement endpoint in the MP experiment was used to measure for each subject and each target direction the following variables:

1. Gain (g)

Gain is a measure of the rate with which the direction of movement varies for different target directions and shows whether the directional space for movement endpoint direction is expanded or contracted with respect to the target directional space (see also Krukowski and Stone 2005). Figure 2 presents how this measure is derived. The figure plots the mean direction of movement endpoints on the Y axis (output) versus the direction of the target on the X axis (input). We called gain for target direction n, the slope of the best fitting regression line for movement endpoints at the two neighbor targets n-1, n+1 and target n. This line is given by the equation:

predicted mean movement direction = constant + gain * target direction (4)

In the hypothetical case of no anisotropy between target and movement direction (black filled squares in figure 2), the gain for target n equals 1 (black solid line). Thus in this case the movement directional space in the vicinity of target direction n is neither expanded nor contracted. In the case where the movement endpoints for neighbor target directions are shifted away from target n (red open circles in figure 2), the gain will be greater than 1 (red dotted line in figure 2). Thus the directional space for movement endpoints in the vicinity of target n is expanded (larger output difference for the same input difference).
Finally, in the case where the movement endpoints for the neighbor target directions are shifted towards n (blue filled triangles in figure 2), the gain will be less than 1 (dashed blue line). Thus the directional space for movement endpoints in the vicinity of target n will be contracted. Note that if directional space is expanded in one region (gain > 1) then it is obligatory that directional space will be contracted in another neighboring region (gain < 1) thus the mean gain for all directions around the total directional space of 360 degrees must be equal to 1. One value of gain was computed for each target direction for each subject.

2. Standard Deviation of DE (s)

In order to measure the spread of the distribution of DE for each target direction we calculated the standard deviation of the mean DE for movement endpoints, for each target direction, for each subject.

3. d-prime (dmp)

In figure 1 we showed that the differences in mean direction and the standard deviation of direction for movement endpoints around a specific direction define how well another target direction, in the vicinity of this target, would be discriminated.

If a target would be set to 2.5 degrees away from a particular target direction used in our experiment (that is the directional offset of the arrow in the arrow pointing experiment described above), then we can compute a z-score representing how many standard deviations away is this angular difference of 2.5
degrees from the target direction. This score is equivalent to the d-prime computed for the same directional difference of 2.5 degrees in the AP experiment. We will denote this d-prime for the memory pointing experiment as dmps in the remaining of this manuscript. Thus:

\[ \text{dmps}(\text{target direction}) = \frac{2.5 \text{deg/s}(\text{target direction})}{s(\text{target direction})} \]  (5)

where dmps is the z-score for discriminating a target at a 2.5 degree deviation from the mean direction of movement endpoints for the particular target direction and s is the standard deviation of DE for this target direction.

As we explained in the previous section in our definition of the gain measure, the discrimination of a target at 2.5 degree deviation from the mean direction of movement for this target will be also affected by the gain in the vicinity of the target. A gain larger than one would result in a shift of this hypothetical target away from the mean that would be equal to gain x 2.5 thus resulting in a better discrimination. If we thus take into account the gain in the vicinity of each target direction then:

\[ \text{dmp}(\text{target direction}) = \frac{2.5 \text{deg} \times \text{gain}(\text{target direction})}{s(\text{target direction})} \]  (6)

The discrimination then of a hypothetical target at 2.5 degrees away from a target direction will increase with increasing gain and decrease with decreasing variability of movement endpoint directions.
If the variance of movement endpoints remains the same independent of target direction and there are only mean endpoint shifts as shown in figure 1B then the differences in discrimination will depend only on the differences in gain for different target directions. To derive a d-prime measure that is independent of differences in s for different target directions we computed the mean s for all target directions pooled together that was 3.5 deg. We then derive the following d-prime:

$$dmpg(\text{target direction}) = \frac{2.5\text{deg} \times \text{gain(\text{target direction})}}{3.5\text{deg}}$$  (7)

Note that this last measure of discrimination is actually the gain multiplied by a constant thus one could use directly the gain for statistical analysis but we wanted to have equivalent measures of d-prime in our AP and MP tasks in order to directly compare them in our modeling.

**Data Analysis**

For the analysis of each variable of interest in the AP and MP tasks the data for each target direction were regrouped to correspond to a particular directional deviance from a cardinal direction within each one of 8 hemi-quadrants as shown in figure 3. Every target direction corresponds to one of 5 directional deviances away from the cardinal direction within each hemi-quadrant: 0deg (corresponding to the cardinal direction), 11.25deg, 22.5deg, 37.75deg and 45 deg (corresponding to the oblique direction). Notice that in this regrouping of data, the values corresponding to 0deg
(cardinal) and 45deg (oblique) direction of each quadrant, are represented twice (figure 3).

The directional deviance and arrow length were introduced as within subject repeated measure factors in repeated measures ANOVA separate repeated measures ANOVA with directional deviance as the only within subject factor was then used to test the effect of directional deviance separately on dap15, dap30 and dap45 in the AP task. The same repeated measures ANOVA model was used to test the effects of directional deviance on g, s, dmp, dmpg and dmps in the MP task.

In another analysis a second degree polynomial was used to model the effects of directional deviance on each of the following variables: dmp, dmps, dmpg, dap15, dap30 and dap45. We used the non-linear estimation module of the STATISTICA 6.0 software (StatSoft, Inc. 1994-2001) to fit the polynomial to our data and estimate the linear and quadratic parameters of the model and their significance. The module uses the Gauss-Newton method for solving the nonlinear least-squares problem. In general, this method makes use of the Jacobian matrix J of first-order derivatives of a function F to find the vector of parameter values x that minimizes the residual sums of squares (sum of squared deviations of predicted values from observed values).

For all statistical analyses we used the STATISTICA 6.0 software (StatSoft, Inc. 194-2001).
RESULTS

AP task

Figures 4A, 4B and 4C show the modulation of dap15, dap30 and dap45 respectively with target direction. It can be seen that d-prime increases for cardinal directions and decreases for the oblique a phenomenon that is present for all subjects. Thus all subjects were more accurate at discriminating a 2.5 degrees deviation of the arrow from a cardinal direction and less accurate at discriminating this deviation from an oblique direction reproducing an oblique effect. Comparing of the figures also shows that discrimination efficiency (higher d-prime scores) increases with increasing arrow length as expected (for example the values of dap45 are generally higher than those for dap30 and in turn the values for dap30 are higher than those for dap15).

A repeated measures ANOVA confirmed a significant effect of directional deviance (F4,140 = 48.613, P <10^-5) and arrow length (F3,105 = 16.3, P <10^-5) on dap. The directional deviance by arrow length interaction was highly significant (F12,420 = 252.3, P <10^-5). The subject x directional deviance interaction was not significant (F16,140 = 1.53, P = 0.09) and the subject x arrow length interaction was also not significant (F12,105 = 0.55, P = 0.87). Finally the three way interaction subject x directional deviance x arrow length was also not significant (F48,420 = 1.13, P = 0.26).

We then analyzed separately the effect of direction deviance on dap for each arrow length. A repeated measures ANOVA confirmed a significant effect of directional deviance on dap15 (F4,140 = 52.8, P <10^-5), dap30 (F4,140 = 42.28, P <10^-5) and dap45 (F4,140 = 18.24, P <10^-5) while the subject x directional deviance interaction was not significant in all cases. Finally there was no significant directional deviance effect for
In conclusion this analysis showed the existence of a perceptual oblique effect in the AP task for all subjects that is modulated by arrow length.

**MP task**

Figure 5A shows the modulation of mean DE for each subject and the mean for all subjects for each target direction. The variation of mean DE produced a similar pattern as the one described in our previous work (Smyrnis et al 2001; Gourtzelidis et al 2002). Figure 5B shows the modulation of gain for each subject and the mean for all subjects for each target direction. It can be seen that the gain is generally higher in the cardinal target directions (0, 90, 180, 270deg) compared to the oblique. The repeated measures ANOVA showed a significant effect of directional deviance ($F_{4,140} = 54.1, P < 10^{-5}$) and a non-significant subject x directional deviance interaction ($F_{16,140} = 1.1, P = 0.35$).

Figure 5C shows the modulation of $s$ for each subject and the mean for all subjects for each target direction. There is a difference in $s$ with target direction but the expected decrease of $s$ for cardinal directions compared to the oblique is not present in all directional space. The repeated measures ANOVA showed a significant effect of directional deviance ($F_{4,140} = 3.8, P < 0.006$) and a non-significant subject x directional deviance interaction ($F_{16,140} = 1.4, P = 0.14$).

Figure 5D shows the modulation of $d_{mp}$ for each subject and the mean for all subjects for each target direction. A similar pattern as for the $d$-prime in the AP task can
be observed, namely that dmp was larger in the cardinal directions and smaller in the oblique, representing an oblique effect. Figure 6B shows the modulation of dmp with direction deviance and again the oblique effect is evident. The repeated measures ANOVA of dmp showed a significant effect of directional deviance ($F_{4,140} = 13.8, P < 10^{-5}$) and a non-significant subject x directional deviance interaction ($F_{16,140} = 1, P = 0.46$).

In conclusion this analysis showed a significant effect of directional deviance from the cardinal directions for gain, directional variance and the d-prime in the MP task. An oblique effect was evident in the case of d-prime for the MP task.

**Modeling of the oblique effect in AP and MP**

Figure 6A shows the effect of directional deviance on the d-prime measures in the AP task and figure 6B shows the effect of directional deviance on the d-prime measures for the MP task. A steep decrease of d-prime close to the cardinal direction and then a plateau close to the oblique direction can be observed in most cases. A function that describes this decrease is a second order polynomial of the form:

$$d\text{-prime} = a + b \times (\text{directional deviance}) + c \times (\text{directional deviance})^2$$ (8)

Coefficient $a$, is related to the mean level of direction discrimination (d-prime). Coefficient $b$, is related to the magnitude of the oblique effect, that is how large is the decrease in d-prime between the cardinal and the oblique direction. The third coefficient, $c$, is related to the changes in the rate with which the d-prime decreases with deviance away from the cardinal direction. From figure 6A and 6B it is obvious that the mean level of direction discrimination, as well as the magnitude of the oblique effect, differ between the AP and MP tasks. The rate though of the decrease of the d-prime is rather constant.
such that the d-prime decrease reaches a plateau at approximately half the way between the cardinal and oblique directions (at 22.5 deg of direction deviance). This observation indicated to us that maybe what is very similar in both tasks is the relation between the linear component b and the quadratic component c in equation (8). That is, the larger the difference in d-prime between cardinal and oblique directions the steeper the decrease in d-prime away from the cardinal, so that the shape of the oblique effect function will scale with the magnitude of the oblique effect. Thus we hypothesized that the ratio of c over b is constant:

\[ r = \frac{c}{b} \] \hspace{1cm} (9)

By substituting c in equation (8) we get the final model that we tested:

\[ d\text{-prime} = a + b* (\text{directional deviance}) + b*r*(\text{directional deviance})^2 \] \hspace{1cm} (10)

The data for all subjects for each one of the d-prime measures were pooled for this analysis since the ANOVA analysis showed that no differences among subjects of the directional deviance effect (non significant interaction of directional deviance with the subject). The results are shown in Table II and the resulting model fits are shown for AP in figure 6A and for MP in figure 6B. It can be seen from table II that for both dap15 and dap30 all model coefficients were significant while for dap45 only coefficient a was significant indicating that in this case the coefficients b and r were not significantly different from zero and the model in equation (10) could be reduced to:

\[ d\text{-prime} = a \] \hspace{1cm} (11)

In the case of the MP task we tested the model on dmp, dmps and dmpg (see methods). Table II shows that for dmp and dmpg all model coefficients were significant while for dmps the model could again be reduced to equation (11).
Figures 7A, B, C show a comparison of the constant a, linear, b and ratio, r coefficients for dmp, dmpg, dap15, dap30 and dap45. The bars denote 95% confidence intervals for these coefficients. It can be seen in figure 7A that the constant a differed in all tasks and the 95% confidence intervals did not overlap. The linear coefficient b (figure 7B) differed between the AP and MP tasks while it was similar for the two small arrow lengths in the AP task (dap15 and dap30) where the 95% confidence intervals overlapped. **There was no linear coefficient for dap45 since the model in that case was reduced to equation (11) as previously described.** Finally the ratio coefficient r (figure 7C) was very similar for dap15, dap30 and dmpg and smaller for dmp but with overlapping 95% confidence intervals. **There was no ratio coefficient for dap45.**

We thus conclude that a quadratic function can be used to describe the oblique effect in both the AP and MP tasks. Furthermore in the MP task the predicted oblique effect by the model was not present when the d-prime computation did not take into account the effect of gain (dmps) but was present when the computation of d-prime was based solely on the variations of gain (dmpg). The oblique effect was smaller in magnitude in the MP task than in the AP task. Finally we showed that the shape of the oblique effect function normalized for the overall magnitude of the oblique effect (coefficient r in the model) was similar for the AP and MP tasks that is the oblique effect diminished as the deviance from cardinal direction increased to reach a plateau half way between the cardinal and oblique direction.
DISCUSSION

We argued in the introduction that the pattern of systematic directional errors that we observed in this and previous studies is theoretically equivalent to a better directional discrimination for targets presented around the cardinal directions as opposed to targets presented around the oblique direction, a phenomenon that is known in perception research as the oblique effect. In order to provide evidence for this argument we first used a task that required a perceptual discrimination of direction and observed a perceptual oblique effect that was very robust and did not vary significantly among subjects. We then used a memory pointing task and demonstrated the presence of a motor oblique effect that was also very robust and did not vary significantly among subjects. We successfully modeled the oblique effect using a quadratic function in both tasks. We also showed that although the perceptual oblique effect was larger in magnitude than the motor one, the shape of the oblique effect function, normalized for its overall magnitude, was similar for the AP and MP tasks. More specifically, the oblique effect in both tasks diminished with as the deviance from cardinal direction increased, to reach a plateau halfway between the cardinal and oblique direction.

We could argue that an oblique effect in the memorized motor representation of target direction could be the result of a shared reference frame between visual perception and memory movement. The existence of the motor oblique effect could be explained using two alternative hypotheses that are not mutually exclusive. The first hypothesis is that the direction representation in the motor system itself produces an oblique effect. This would imply, in analogy with the visual system, more neurons coding for cardinal directions than for oblique. This hypothesis does not seem to fit with current knowledge
on direction specificity in the motor areas. Georgopoulos and colleagues (1988) showed in the monkey primary motor cortex that directionally tuned neurons are homogeneously distributed with no underrepresented areas of directional space. There is though the possibility that other motor areas that are more related to visual processing would have a larger neural representation for cardinal directions compared to the oblique. Such an area for example could be the ventral premotor cortex where Schwartz et al (2004) have shown that neurons respond to the perceived and not the actual trajectory of an arm movement. Still we believe that the oblique effect in memory movements is not the result of an anisotropic neural representation of direction in the motor system. The main argument against this hypothesis is that we don’t find a significant oblique effect in the variance of directional error in memory movements. If more neurons would be encoding the cardinal directions compared to the oblique then we would expect that the coding for these directions would be less noisy thus resulting in less variable directional error. Still this hypothesis needs to be rigorously tested in future neurophysiological experiments.

The alternative hypothesis is that the oblique effect in the motor system originates in the perceptual system. An anisotropic perceptual representation of directional space is thus transferred to the motor system. In a recent study Krukowski and Stone (2005) measured how well subjects discriminated the direction of a moving target when this deviated from a cardinal direction compared to an oblique direction while subjects followed the moving target with smooth eye pursuit movements. The authors, by transforming the direction of smooth eye pursuit into a binary decision to match the perceptual decision, showed that both the perceptual discrimination of target motion and the discrimination based on smooth eye pursuit shared the same qualitatively oblique
effect, namely a better discrimination for cardinal than oblique directions. This result is very similar to our finding of a shared oblique effect in a memory pointing task and a perceptual decision task (the arrow pointing task). Krukowski and Stone (2005) furthermore decomposed the oblique effect in smooth eye pursuit in two components, one related to changes in the variance of pursuit direction between cardinal and oblique directions of target motion and one related to changes in the gain. In striking resemblance to our results they observed that the oblique effect in smooth eye pursuit was the result of a modulation in gain and not variance. We also observed that our model of the oblique effect in the AP and MP tasks was successful when the d-prime in the MP task was computed based only on the gain variations with direction but was not successful when the d-prime was computed based only on the variance variations with direction. It is interesting to note here the very close similarity of the shape factor of the model for the oblique effect based on gain variations (dmpg) and the perceptual oblique effect (see figure 7C). In their study Krukowski and Stone (2005) postulate that an anisotropic visual representation of direction is transferred to motion processing areas in the brain. Our findings suggest that this representation might also be transferred to arm movement related areas of the brain.

We could further refine the hypothesis of a similar representation of directional space between perceptual and motor systems and ask whether the perceptual oblique effect that is transferred to the motor representation in memory movements is a class 1 or class 2, effect. A class 1 oblique effect suggests a distorted representation of visual space produced in primary visual cortex that is reflected later on in all visuomotor transformations. This hypothesis though can not explain the findings of Baud-Baudry and
Viviani (2004), namely the presence of the same pattern of directional errors, suggesting the presence of the same motor oblique effect, in a motor task where subjects had to move their arm to a position that was instructed by a prior passive movement of the arm. In fact the presence of the same oblique effect in smooth eye pursuit, memory pointing with visual input and pointing with kinesthetic input suggest that a class 2 oblique effect contaminates eye and arm movement in all these conditions.

A prominent theory on the dissociation of ventral and dorsal streams proposes an anatomical and functional segregation between vision for perception and vision for action (Goodale and Milner 1992). In this view the representation of visual space in the dorsal stream involves accurate representations of spatial locations based on egocentric frames of reference that are used to guide movements of the eye and arm. On the other hand the representation of visual space in the ventral stream involves relative representations of spatial locations that are prone to the effects of visual illusions, thus are inaccurate, and use allocentric reference frames. These representations are used to detect objects in the visual world, categorize them and give abstract properties to them like a name. This theory then would predict that perceptual phenomena would not contaminate the space representation for visuomotor processing. In this study we have evidence for such a contamination by the oblique effect in the specification of the direction of memory pointing movements. Is this result against the theory? In a refinement of the action-perception dissociation Goodale and Westwood (2004) propose that this dissociation is present only when reaching and grasping of objects is performed in real time. When delays are introduced in reaching and grasping the memory trace of the object that is used is more related to the ventral perceptual stream. This memory representation then is prone
to perceptual phenomena such as visual illusions while the representation for reaching and grasping under visual guidance is not (Goodale and Westwood 2004; Hu and Goodale 2000; Goodale et al 2003). In accordance with this theory we observed that the memory representation of target direction is affected by a perceptual distortion, the oblique effect. The prediction of this theory then would be that this oblique effect would not be present in the programming and execution of direct pointing movements to a visual target. We will fully investigate this hypothesis in a paper that will follow.

In conclusion we showed that memory pointing movements and visual perception share an oblique effect in direction discrimination that is reflected in a distorted representation of directional space and implies similarity in the processing of directional information in these conditions.
ACKNOWLEDGMENTS

This work was partly supported by the “Kapodistrias 2004-2005” program of research support from the National and Kapodistrian University of Athens.
REFERENCES


LEGENDS TO TABLES AND FIGURES

**Table I:** This table shows the grouping of responses to each type of stimulus in the AP task.

**Table II:** The results of the application of a second order polynomial model to the d-prime scores for the AP experiment (dap15, dap30, dap45) and the MP experiment (dmp, dmpg) are presented. The first column shows the r value for the fit of the model and the following columns show the value of each coefficient (a: constant, b: linear, c: non-linear) and the corresponding t-value and p-value for the significance test for the coefficient.

**Figure 1:** This figure presents graphically the origin of the motor oblique effect as described in the introduction. Target T1 is presented at a cardinal direction (90deg) and the spread of directions of movement endpoints around it is shown as S1 with a light shaded area target. The same presentation was used for targets T2 that is in between a cardinal and an oblique direction and T3 that is at an oblique direction (45deg) with corresponding spreads S2 and S3. The shaded areas in the three parts of the figure show the overlapping spread of movement endpoints which represents ambiguity in discrimination between neighboring targets. In figure 1B the result on ambiguity of a shift in T2 direction (to location T2a) is shown and in figure 1C the result of an increase in the spread of the distributions on ambiguity is shown.
**Figure 2:** Determination of gain for target direction n using the mean direction of movement endpoints at n, n-1 and n+1. Three cases are shown. In the first case (filled squares and solid line) the mean direction of movement endpoints for n, n-1 and n+1 equals respectively n, n-1 and n+1. The gain is 1. In the second case (open circles and dotted line) the mean direction of movement endpoints for n-1 is smaller than n-1 and for n+1 is larger than n+1 thus the gain is greater than 1. Finally in the last case (open triangles and dashed line) the mean direction of movement endpoints for n-1 is greater than n-1 and for n+1 is smaller than n+1 thus the gain is smaller than 1.

**Figure 3:** Regrouping of data for each target direction to the corresponding directional deviance from a cardinal direction. Each target direction (line) corresponds to one of 8 hemi-quadrants that are depicted with the Latin number that the line points to. The Arabic number corresponds to the directional deviance in degrees of this target direction from the cardinal direction for this hemi-quadrant. In the case of a target direction that corresponds to a cardinal (0deg) or oblique (45deg) direction, two Latin numbers are shown corresponding to the two hemi-quadrants that share this cardinal or oblique direction.

**Figure 4:** A: plot of d-prime scores for each target direction for arrow length of 15 mm in the AP experiment (dap15). The large solid circles represent the mean score for each target direction for the 5 subjects while the small open circles represent the scores of individual subjects. In B and C the d-prime scores for each target directions are plotted for arrow lengths of 30 (dap30) and 45mm (dap45) respectively.
Figure 5: A: plot of mean directional error for each target direction in the MP experiment. The large solid circles represent the mean DE for each target direction for the 5 subjects while the small open circles represent the mean DE of individual subjects. In B, C and D are shown the gain, standard deviation of directional error (s) and d-prime (dap) for each target direction in the MP experiment.

Figure 6: A: Plot of the d-prime variation with directional deviance in AP. The squares, circles and triangles represent mean d-prime for arrow lengths of 15mm (dap15), 30mm (dap30) and 45mm (dap45) respectively (error bars: standard error of the mean). The solid dashed and dotted lines represent the model fit for d-prime for arrow lengths of 15, 30 and 45mm respectively. B: Plot of the d-prime variation with directional deviance in MP. The squares represent the mean d-prime (dmp), the circles represent the gain component of d-prime (dmpg) and the triangles represent the variance component (dmps) in the MP task respectively (error bars: standard error of the mean). The solid, dashed and dotted lines represent the model fit for dmp, dmpg and dmps respectively.

Figure 7: Histograms comparing the model coefficients for the d-prime of the MP task (dmp), the gain component of d-prime of the MP task (dmpg), the d-prime for the arrow length of 15mm of the AP task (dap15), the d-prime for the arrow length of 30mm of the AP task (dap30) and the d-prime for the arrow length of 45mm of the AP task (dap45). In A the comparison is for the model constant a, in B the comparison is for the linear component b and in C the comparison is for the ratio factor r.
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<td>The subject responds “yes”</td>
<td>The arrow points to the target</td>
</tr>
<tr>
<td>, the arrow points to the target</td>
<td>N1</td>
</tr>
<tr>
<td>The subject responds “no”, the arrow points away from the target</td>
<td>N2</td>
</tr>
</tbody>
</table>

| The arrow points 2.5 deg away from the target      | N3                                                                        |
|                                                   |                                                                           |
|                                                   |                                                                           |
Table II: Modeling of the oblique effect in AP and MP tasks

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model r</th>
<th>a</th>
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<td>dap15</td>
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<td>-0.106</td>
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<td>dap30</td>
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<td>3.5</td>
<td>27.1, &lt;10^{-5}</td>
<td>-0.082</td>
<td>-6.02, &lt;10^{-5}</td>
<td>-0.011</td>
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<td>dap45</td>
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<td>3.84</td>
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<td>-0.012</td>
<td>-2.7, &lt;0.01</td>
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<tr>
<td>Dmps</td>
<td>0.16</td>
<td>1.09</td>
<td>27.2, &lt;10^{-5}</td>
<td>-0.002</td>
<td>-0.45, &gt; 0.6</td>
<td>0.01</td>
<td>0.15, &gt; 0.8</td>
</tr>
<tr>
<td>Dmpg</td>
<td>0.74</td>
<td>0.798</td>
<td>136.6, &lt;10^{-5}</td>
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Figure 4: Variation of dap15(A), dap30(B) and dap45(C) with target direction.

A

B

C

A: plot of d-prime scores for each target direction for arrow length of 15 mm in the AP experiment (dap15). The large solid circles represent the mean score for each target direction for the 5 subjects while the small open circles represent the scores of individual subjects. In B and C the d-prime scores for each target directions are plotted for arrow lengths of 30 (dap30) and 45mm (dap45) respectively.
Figure 5: Variation of mDE(A), g(B), s(C) and d'pr (D) with target direction in MP.

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<td>N4</td>
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