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RESEARCH NOTE

Perception action interaction: the oblique effect in the evolving trajectory of arm pointing movements

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Abstract In previous studies, we provided evidence for a directional distortion of the endpoints of movements to memorized target locations. This distortion was similar to a perceptual distortion in direction discrimination known as the oblique effect so we named it the "motor oblique effect". In this report we analyzed the directional errors during the evolution of the movement trajectory in memory guided and visually guided pointing movements and compared them with directional errors in a perceptual experiment of arrow pointing. We observed that the motor oblique effect was present in the evolving trajectory of both memory and visually guided reaching movements. In memory guided pointing the motor oblique effect did not disappear during trajectory evolution while in visually guided pointing the motor oblique effect disappeared with decreasing distance from the target and was smaller in magnitude compared to the perceptual oblique effect and the memory motor oblique effect early on after movement initiation. The motor oblique effect in visually guided pointing increased when reaction time was small and disappeared with larger reaction times. The results are best explained using the hypothesis that a low level oblique effect is present for visually guided pointing movements and this effect is corrected by a mechanism that does not depend on visual feedback from the trajectory evolution and might even be completed during movement planning. A second cognitive oblique effect is added in the perceptual estimation of direction and affects the memory guided pointing movements. It is finally argued that the motor oblique effect can be a useful probe for the study of perception–action interaction.

Keywords Reaching movements · Arm pointing · Sensorimotor integration · Motor control · Spatial accuracy · Spatial representation · Human

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Introduction

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. In contrast, 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 predicts that perceptual phenomena would not necessarily contaminate the space representation for visuomotor processing.

A series of studies support the vision for perception versus vision for action dissociation in normal human subjects using different paradigms of visual illusions that affect perception of the location of objects in space or the size of objects. Bridgeman et al. (1981) showed that a perceived motion of a stationary target, thus a change in its location, induced by a surrounding moving frame did not affect reaching accuracy towards that target. Aglioti et al. (1995) showed that the "Tichener circles" size-contrast illusion in which the perceived size of a circular disk is affected by the size of disks surrounding it, did not affect the size of the hand grip aperture used to capture the disk. Subsequent studies that investigated the dorsal or egocentric versus ventral or allocentric reference frame segregation showed that this separation is not so clear cut as originally though and there is an interaction between these two modes of processing both for location and size. Gentilucci et al. (1996) showed that when pointing movements were performed in full vision of the arm, the "Muller-Lyer" illusion had no effect on pointing accuracy, while such an effect emerged when pointing was performed without vision of the arm, or using a memory delay. Hu and Goodale (2000) also showed that the size-contrast illusion had an effect when grasping of an object was performed after a delay. In a refinement of the action-perception dissociation theory Goodale and Westwood (2004) proposed 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. Another study has shown that the size-contrast illusion had a significant effect on the movement time for pointing to an object (van Donkelaar 1999). It seems then that there is no clear cut dissociation of allocentric and egocentric frames of reference but these different reference frames have a stronger or weaker contribution in the planning and execution of a movement depending on information available at the time. In a critical review of the hypothesis for the dissociation of vision for perception and vision for action Carey (2001) also focuses on the different mechanisms with which different visual illusions operate. In that sense the use of each visual illusion paradigm to study the perception action dissociation might be limited. Another complication in the theorizing for the dissociation of the two streams is the fact that they both stem from a single stream of visual processing in the brain that is the primary visual cortex and secondary visual areas. In a series of experiments Dyde and Milner (2002) showed that a perceptual illusion (simultaneous tilt illusion) produced in early visual processing of a stimulus, is also present in the visuomotor processing of that stimulus. On the other hand an illusion that affects late visual processing in higher order visual areas of the ventral stream (rod and frame illusion) has a minimal effect on visuomotor processing. In their view then a dissociation of perception and action is present only when the bias in perception is introduced at higher levels of visual processing while low level effects contaminate both perception and action. Finally other researchers suggest that there is no segregation between representations for perception and action and the differences observed are due to the incorrect matching of task demands in perceptual and motor tasks and measurement of perceptual effects (Franz 2001).

Another significant factor when considering the distinction between perception and action is the prominent role of on line control of movement. Since the pioneer work of Woodworth there has been a wealth of evidence for the effects of on line control in reaching and pointing arm movements (Desmurget and Grafton 2000; Elliot et al. 2001). It has been shown that the trajectories of fast arm reaching movements can be smoothly modified to accommodate for small displacements of target location that occur during the saccadic eye movement towards the target to be reached (Goodale et al. 1986; Prablanc and Martin 1992; Desmurget et al. 1999). Such on-line correction of the trajectory can start as early as 110 ms after movement onset that was roughly synchronous with the end of the ocular saccade (Prablanc and Mertin 1992). It has also been observed that online trajectory modifications can occur in the very early phase of movement just after movement onset (Bard et al. 1999). A theory of feed-forward control of arm movements postulates that an efferent copy of the planned movement trajectory is constantly updated during movement execution based on a forward estimation of the traveled trajectory of the arm towards the target location and incoming sensory information on the actual location of the arm (Wolpert et al. 1995). What this powerful control system needs then in order to start operating is the visual information for target location and an efferent copy of the motor command. Thus on-line correction of the motor plan can begin as soon as the movement starts (Desmurget and Grafton 2000).

A recent theoretical hypothesis extends the dichotomy of planning and on line control of arm movements to suggest the existence of two separate visual representations one sub serving movement planning that is prone to the effects of cognitive perceptual processes such as the visual context in which the movement will be performed and one sub serving on line movement control that is restricted only to computation of the kinematic parameters of the movement and is immune to context and other cognitive influences from perceptual systems (Glover and Dixon 2001; Glover 2004). This theory then replaces the distinction between perception and action with a distinction between movement planning and on-line control.

In previous studies we investigated the directional accuracy of planar pointing movements to remembered visual targets (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. In our original study (Smyrnis et al. 2000) we showed that the systematic directional error varied with different memory delays between target presentation and movement execution. Thus when the delay was 0 seconds the systematic directional error was not present. At the delay of 2 s the error was significant but it was small in magnitude. Finally when the delay was 4 or 6 s the systematic directional error was large and highly significant.

In our original study (Smyrnis et al. 2000) we also explored the potential influence on this error pattern of the biomechanical properties of the moving arm and showed that such factors produced a very different type of directional error that correlated with the axis of maximum limb inertia. In a subsequent study (Gourtzelidis et al. 2001) we showed that this systematic directional error could be modified by the presence of an irrelevant visual cue in the vicinity of the target positions. Thus if an irrelevant visual cue was always visible in the vicinity of the previously seen visual targets then the directional error for those targets was dramatically reduced as if the irrelevant visual cue was used to cancel the directional error. Taken together these results suggested to us that this pattern of mean directional errors was not related to the biomechanical properties of the moving arm and it reflected some perceptually or memory driven process.

In a recent study (Smyrnis et al. 2007) we used an analysis of the change of mean directional error (a gain measure) introduced by Krukowski and Stone (2005) in their study on the estimation of direction of motion. By measuring the gain, that is the change of mean directional error between neighboring directions, we showed that the pattern of systematic directional errors in memory pointing reflects a space expansion in the vicinity of the cardinal directions (horizontal and vertical) and a space compression in the vicinity of the oblique directions. We also used a perceptual arrow pointing task and showed that this space distortion in the memory pointing task is equivalent to a better directional discrimination for targets presented around the cardinal directions as opposed to targets presented around the oblique directions in the perceptual arrow pointing task, a phenomenon that is known in perception research as the oblique effect (Appelle 1972). We further argued in that study that the “motor oblique effect” might originate in the perceptual system and then is transferred to the motor system. In this sense we could use the motor oblique effect as a tool to probe the perception-action dissociation hypothesis. The motor oblique effect is an interesting probe in that sense since it is not induced by a specific configuration of the visual stimulus such as those used in visual illusion paradigms (Carey 2001). The task design also is simple meaning that a single stimulus is used both for perceptual judgment and pointing, thus allowing for a better match between the motor and the perceptual tasks (Franz 2001).

In this study we used data from the movement trajectories of planar pointing in the memory and visual condition from our previous study (Smyrnis et al. 2007). We also used data from an arrow pointing experiment in which subjects had to point to a visually presented target on a computer monitor by adjusting the direction of an arrow using the computer keyboard keys. In order to measure the directional distortion in 2-D space we used the same measure of gain that was used in our previous study (Smyrnis et al. 2007). This measure reflects the distortion of space that is the result of the oblique effect, meaning increased gain (space expansion) for cardinal directions and decreased gain (space contraction) for oblique directions. Our original hypothesis based on the perception action distinction was that the motor oblique effect was the result of replacing an egocentric visuomotor representation with a perceptual allocentric representation of target direction in the memory condition. Under this hypothesis then the motor oblique effect would be absent in the visually guided pointing task at all points in the evolving trajectory while it would emerge in the evolving trajectory of the memory guided pointing task.

Methods

Subjects

Five healthy adults (age span 28–38 years, two men) participated in the visually and memory guided pointing experiment. Two of these subjects plus three new subjects (age span 28–40 years, two men) performed the arrow pointing experiment. All participants gave written informed consent 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 movement pointing experiment

The set up for this experiment is given in detail in our previous report (Smyrnis et al. 2007). Each subject performed arm movements on a digitizer tablet (CALCOMP 2000) using a mouse device. The tablet was lying underneath a wooden surface on which an LCD projector (TOSHIBA, TDP-140) projected the visual stimuli as well as a cursor indicating the mouse position on a surface area (40 cm horizontally × 30 cm). Stimuli were produced by a PC computer program (using Delphi 7.0). Although the subject's head was not fixed the distance of the subject's eyes from the board was approximately 60 cm and the amplitude of the stimuli was 6 cm from the center target, thus the degrees of visual angle were 5.7, as in the arrow pointing experiment that we describe below. 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 trial started when a filled red disk (5 mm 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 1–2 s, a second white filled disk (5 mm diameter), the peripheral target, appeared at the circumference of an imaginary circle of 60 mm radius in one of 32 directions (11.25° intervals). In the visually guided movement pointing task (MPv) 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 memory guided movement pointing task (MPm) after the same 1–2 s interval the peripheral target was turned on but the center target remained illuminated indicating to the subject that this was a memory trial. The peripheral target remained illuminated for 300 ms and then after an additional memory delay period of 3 s, the center target was turned off. This was the signal for the subject to move as accurately as possible to the position of the previously shown peripheral target, by performing a single pointing movement. After the movement completion the subject was instructed in both task conditions to hold the cursor at the target position until the center target was turned on again to signal to the subject to move to the center for the beginning of the next trial. MPv and MPm trials were randomly intermixed. 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 (to ensure that approximately the same arm movements were used by all participants for the pointing movements). A few practice trials were performed before data collection to ensure that subjects understood the instructions. An experimenter was monitoring task performance. Each subject performed six sessions (except from one subject that did not complete the first day session, missing seven trials in the MPv task and 22 trials in the MPm task). Within each session four repetitions for every target direction for every task thus a total of 256 trials were performed in a randomized sequence (4 repetitions × 32 directions × 2 tasks). Thus, every subject (except the one mentioned above) performed a total of 256 × 6 = 1,536 trials of which 768 were of the MPm 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 0.01 mm the smallest movement that could be visualized as a cursor movement on the screen was 0.3 mm (1 pixel). We chose to use *X–Y* movement data of the cursor at the screen (lowest movement detected 0.3 mm) 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 0.3 mm 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 = 30 ms) and the end of the movement (return of instantaneous speed to zero and remaining zero for at least 100 ms).

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 counter-clockwise deviation from the peripheral target was defined as positive DE. The DE was computed at five points along the movement trajectory, namely when the amplitude was 15, 30 and 45 mm from the center target and at the end of the first movement. In this paper we will discuss the results for the DE at 15, 30 and 45 mm amplitude within the movement trajectory.

We excluded from further analysis trials where the subject moved before the go signal and trials where the movement started earlier than 80 ms (anticipations), or later than 1,500 ms, after the turning off of the center target (late onset of movement). The choice of the upper limit was such that the highest 1% of reaction times was excluded. We also excluded trials in which the DE was $>22.5°$ or $<-22.5°$ at any one of the four points in the trajectory where it was measured. These values were selected to exclude the highest and lowest 0.5% of DE. The amplitude error was a measure of the difference in mm of the amplitude at a particular point in the movement trajectory minus the amplitude of the center of the peripheral target that was set to 60 mm. Thus a negative error corresponded to target undershoot and a positive error corresponded to a target overshoot. We excluded trials where the amplitude error for the first movement was <-15 mm or >15 mm in the MPm task. These values were selected to exclude the highest and lowest 0.5% of amplitude errors. Finally we excluded trials were the absolute value of the amplitude error was larger than 5 mm for the final movement endpoint in the MPv task (that was when the subject did not put the cursor in the target circle). After application of these exclusion criteria we retained 3,099 of the 3,833 trials for all subjects in the MPv task (80.8%) and 3,306 of the 3,818 trials for all subjects in the MPm task (86.6%). Table 1 shows the number of valid trials, the mean reaction time (plus standard deviation) and the mean movement time (plus standard deviation) for each task condition for each subject. It can be seen that movements were slow since the instruction to the subjects was to be as accurate as possible.

The direction at each of the three amplitudes within the trajectory was used to measure for each subject and each target direction the gain at 15, 30 and 45 mm. 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 (Smyrnis et al. 2007). Fig. 1 presents how this measure is derived. The figure plots the mean direction of movement 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 at the two neighbor targets $n-1$, $n+1$ and target n. This line is given by the equation:

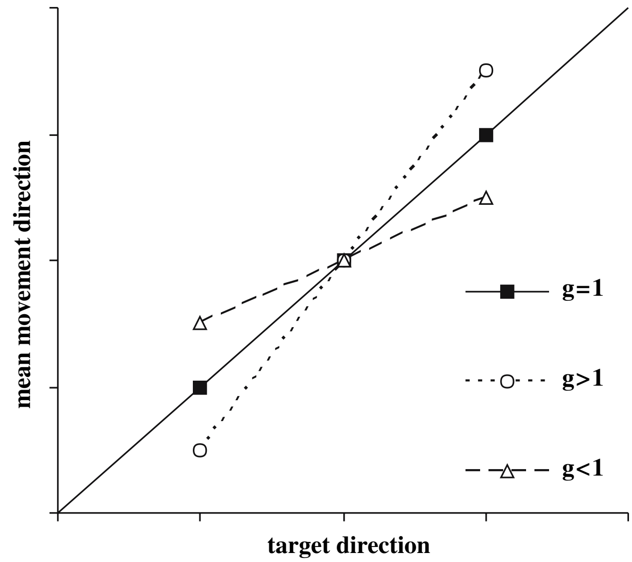

Fig. 1 Determination of gain for target direction n using the mean direction of movement at n, $n-1$ and $n+1$. Three cases are shown. In the first case (*filled squares* and *solid line*) the mean direction of movement for n, $n-1$ and $n+1$ equals respectively n, $n-1$ and $n+1$. The gain is 1. In the second case (*open circles* and *dotted line*) the mean direction of movement for $n-1$ is smaller than $n-1$ and for $n+1$ is larger than $n+1$ thus the gain is >1. Finally in the last case (*open triangles* and *dashed line*) the mean direction of movement for $n-1$ is greater than $n-1$ and for $n+1$ is smaller than $n+1$ thus the gain is smaller than 1

$$\text{Predicted mean movement direction} = \text{constant} + \text{gain} * \text{target direction}$$

In the hypothetical case of no anisotropy between target and movement direction (filled squares in Fig. 1), the gain for target n equals 1 (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 (open circles in Fig. 1), the gain will be greater than 1 (dotted line in Fig. 1). Thus the directional space for movement in the vicinity of target direction n is expanded (larger output difference for the same input difference). Finally, in the case where the movement for the neighbor target directions are shifted towards n (filled triangles in Fig. 1), the gain will be less than 1 (dashed line). Thus the directional space for movement in the vicinity of target direction 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° must be equal to 1.

Table 1 Reaction Times (RT) and Movement Times (MT) for each subject (1–5) at each on of the MPv and MPm tasks

	Mean RT	SD RT	Mean MT	SD MT	*N*
MPv task					
1	974.9	269.1	2,516.2	453.2	513
2	747.1	197.3	2,657.8	634.2	734
3	609.9	193.3	4,871.0	659.5	598
4	245.5	89.9	1,955.4	413.1	563
5	754.5	224.2	2,440.0	575.2	691
MPm task					
1	611.1	186.7	1,666.0	263.8	695
2	478.1	127.3	2,434.0	535.8	730
3	442.5	158.9	4,416.0	706.2	674
4	243.4	77.6	1,690.4	391.5	547
5	692.7	265.2	2,872.0	797.8	660

SD standard deviation, *N* number of trials

Setup and procedure for the arrow pointing experiment

Subjects sat comfortably in front of a computer monitor (HITACHI CM630ET) placed vertically at 60 cm distance from the subject. The subject used two fingers of her right hand to press on the left or right arrow of the computer keyboard. Each trial started when a filled red disk (5 mm diameter) appeared at the center of the screen (center target). After a variable period of 1–2 s, a second white filled disk (5 mm diameter), the peripheral target, appeared at the circumference of an imaginary circle of 60 mm radius in one of 32 directions (11.25° intervals) and a white arrow appeared with its origin at the center target facing at an angle >90° away from the peripheral target. The subject was instructed to use the arrow keys of the keyboard to rotate the arrow clockwise or counterclockwise so that it points to the target. Each left arrow key press corresponded to a counterclockwise rotation of the arrow of 1.4° and each right arrow key press corresponded to a clockwise rotation of the arrow of 1.4°. When the subject decided that the arrow pointed to the peripheral target she pressed the keyboard bar key to signal the end of the trial. The arrow length varied among four values (15, 30, 45 and 60 mm).

Each subject performed a block of trials per day for a total of four days except for one subject that performed five blocks. In each block the subject performed four repetitions four each arrow length, for each target direction for a total of 4 × 4 × 32 = 512 trials.

Data processing for AP

The directional error (DE) was the difference in degrees of the final direction of the arrow and the peripheral target. A counter-clockwise deviation from the peripheral target was defined as positive DE.

We excluded trials where the reaction time of the first key press was <80 or >2,000 ms as well as trials with DE <−10° or DE >10° at any one of the arrow lengths. After application of these exclusion criteria we retained 10,598 of the 10,752 trials for all subjects (98.5%).

The DE at each of three arrow lengths (15, 30 and 45 mm) in the AP task was used to measure for each subject, each task, each target direction and each arrow length the mean DE, the gain (g) as described in the previous section for the MP task.

Data analysis

In order to answer the question of whether the gain is systematically modulated with increasing deviance from the cardinal direction in the MP and AP tasks we used the same data analysis as described in our previous work (Smyrnis et al. 2007). The data for each target direction were regrouped to correspond to a particular directional deviance from a cardinal direction within each one of eight hemi-quadrants as shown in Fig. 2. Every target direction corresponds to one of five directional deviances away from the cardinal direction within each hemi-quadrant: 0° (corresponding to the cardinal direction), 11.25, 22.5, 37.75 and 45° (corresponding to the oblique direction). Notice that in this regrouping of data, the values corresponding to 0° (cardinal) and 45° (oblique) direction of each quadrant are represented twice.

The task condition, distance within the trajectory (15, 30 and 45 mm) and the directional deviance from the cardinal direction as previously defined were introduced as within subject repeated measure factors in a repeated measure ANOVA for the MP task. The main effect of direction deviance on gain was analyzed along with the interaction of this effect with the task, trajectory length and the combination of task and trajectory length (three way interaction). All other effects (main effect of task, main effect of trajectory length and their interactions) are not meaningful since the mean gain for all directions is by definition 1 (if space is expanded in some directions it should be compressed in others so that the mean gain for all directions is 1). The arrow length and the directional deviance from the cardinal direction were introduced as

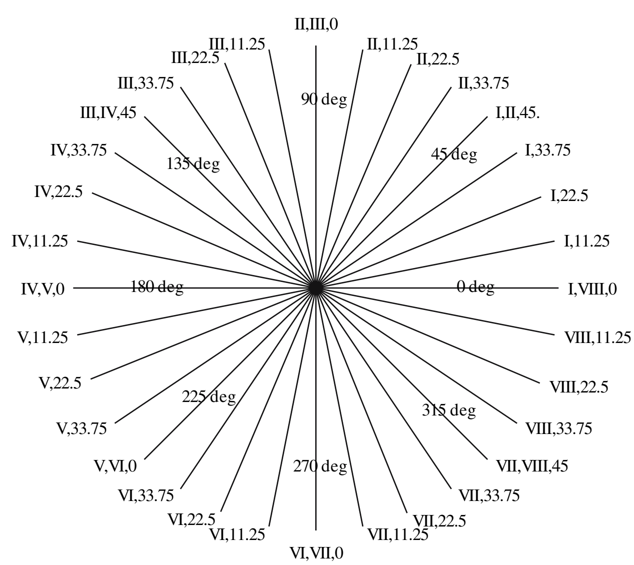

Fig. 2 Regrouping of data for each target direction to the corresponding directional deviance from a cardinal direction. Each target direction (*line*) corresponds to one of eight hemi-quadrants that are depicted with the Latin number that the line points to. The Arabic number corresponds to the directional 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 (0°) or oblique (45°) direction, two Latin numbers are shown corresponding to the two hemi-quadrants that share this cardinal or oblique direction

within subject repeated measure factors in a repeated measure ANOVA for the AP task. Again the main effect of direction deviance and its interaction with arrow length were analyzed.

A further analysis was used to derive the rate at which the gain deceases with increasing deviance from the cardinal direction that is directly equivalent to the magnitude of the oblique effect (Smyrnis et al. 2007). A multiple linear regression was performed for the data for each distance in the trajectory in the MPv and MPm tasks and each arrow length in the AP task. Individual subject data were pooled for this analysis. For all statistical analyses we used the STATISTICA 6.0 software (StatSoft Inc. 1994–2001).

Results

Gain modulation with direction

Figure 3 shows the modulation of gain with deviance from the cardinal direction for each subject in each task (MPv, MPm, AP). The ANOVA analysis confirmed that the gain decreased significantly with direction deviance from the cardinal direction in both MPv and MPm tasks (direction deviance main effect: $F_{4,140} = 27.24$, $P < 10^{-5}$). In our previous work we have named this modulation of gain with direction deviance from the cardinal direction as the "motor oblique effect" (Smyrnis et al. 2007). The motor oblique effect was larger in the MPm than the MPv task (direction deviance by task interaction: $F_{4,140} = 17.18$, $P < 10^{-5}$). Also the motor oblique effect varied with trajectory length (direction deviance by trajectory length interaction: $F_{8,280} = 3.89$, $P < 10^{-3}$). More specifically the motor oblique effect became less pronounced as the trajectory length increased. Moreover this decrease in the motor oblique effect with trajectory length was different between the two tasks (three way interaction, task by direction deviance by trajectory distance: $F_{8,280} = 1.88$, $P = 0.06$). As observed in Fig. 3 in the MPv task, the increase in trajectory length resulted in a steep reduction of the motor oblique effect leading to its disappearance at the length of 45 mm. In contrast in the MPm task the motor oblique effect reduction was much slower with increasing trajectory length and a clear motor oblique effect was still present at 45 mm. Finally the ANOVA showed no significant effect of the subject factor on these results.

The ANOVA in the AP task confirmed that gain decreased significantly with direction deviance from the cardinal direction (direction deviance main effect: $F_{4,140} = 93.5$, $P < 10^{-5}$). This modulation of gain with direction deviance was due to the known oblique effect in perception. The perceptual oblique effect was dependent on

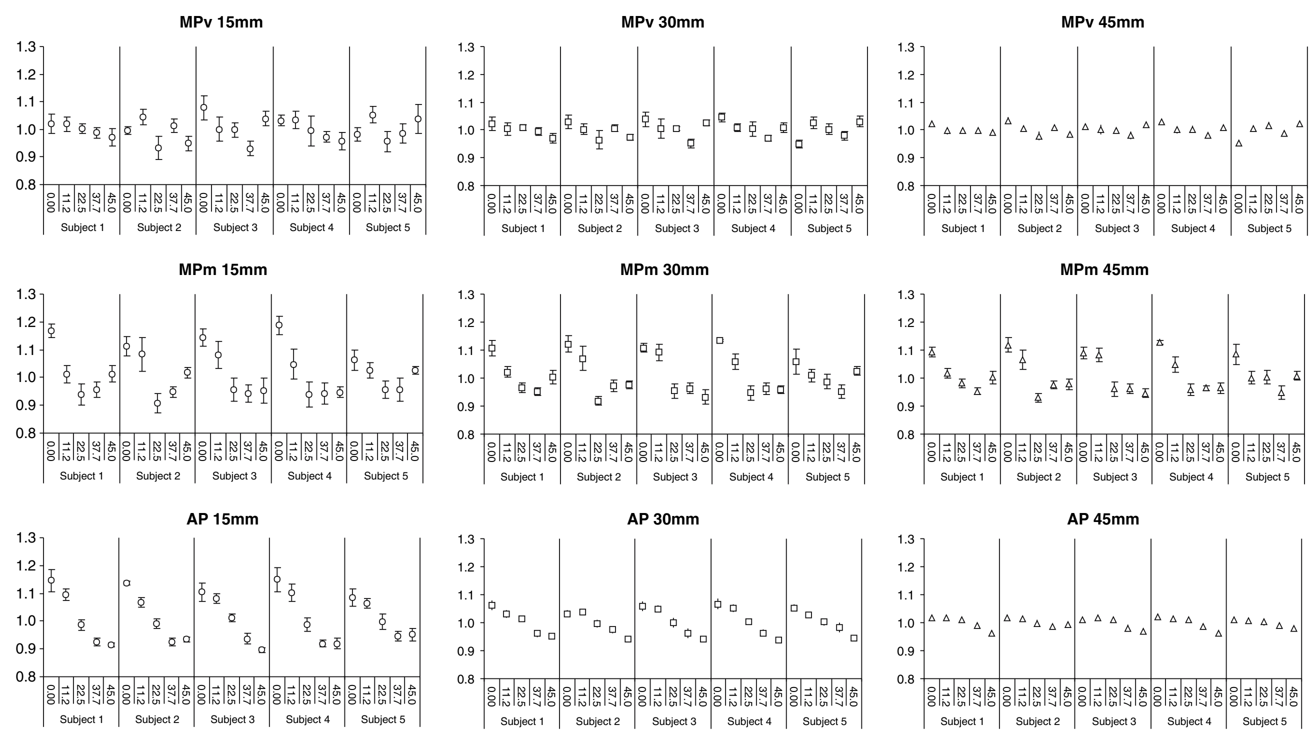

Fig. 3 Modulation of gain with deviance from the cardinal direction for each subject (*error bars* indicate standard error of the mean) for the visual movement pointing task (MPv), the memory movement pointing task (MPm) and the arrow pointing task (AP) at each one of the three distances in the trajectory in MPv and MPm tasks (15, 30 and 45 mm) and the three arrow lengths in the AP task (15, 30 and 45 mm)

the arrow length (direction deviance by arrow length interaction: $F_{8,280} = 44.6$, $P < 10^{-5}$). As shown in Fig. 3 the perceptual oblique effect was larger with small arrow lengths and decreased as the arrow length increased. Finally the ANOVA showed no significant effect of the subject factor on these results.

Magnitude of the oblique effect

A linear regression model was applied to the data for each one of the three distances of the movement trajectory for the MPv and MPm tasks (15, 30 and 45 mm) and for the three arrow lengths in the AP task (15, 30 and 45 mm). For this analysis the data for all subjects were pooled since it was already shown in the ANOVA analysis that there was no significant difference among subjects of the gain modulation with direction deviance. The results of these regression analyses are presented in Table 2. For the MPv task the regression showed a significant motor oblique effect at 15 mm in the forming movement trajectory while at 30 and 45 mm the effect was no longer significant. For the MPm task the regression showed a significant motor oblique effect at all distances in the forming movement trajectory. The absolute value of the slope of the regression line is an indicator of the magnitude of the motor oblique effect (the larger the slope the larger the modulation of gain with direction deviance from the cardinal direction) Table 2. The absolute value of the slope decreased with increasing distance but this decrease was small. Table 2 also shows that the absolute value of the slope in the MPm task was much larger than those observed in the MPv task at the small distance of 15 mm suggesting that even at the beginning of the movement the motor oblique effect is more prominent in the memory guided movement pointing task. Finally the regressions showed a very significant oblique effect in the AP task for all arrow lengths. The absolute value of the slope decreased dramatically with arrow length indicating that the magnitude of the oblique effect was very strongly influenced by the amount of perceptually available direction information (Table 2). It can also be observed that the magnitude of the oblique effect (absolute value of regression slope) in the MPv task corresponds to the 45 mm of arrow length in the AP task and the magnitude of the oblique effect in the MPm task corresponds to values between the 15 and 30 mm arrow length in the AP task. A comparison of the absolute value of the regression slopes in all tasks is graphically presented in Fig. 4.

Dependence of oblique effect magnitude on RT and MT

It was found that the motor oblique effect in the MPv task disappeared very fast after movement onset, faster than what was observed in the AP task. In order to investigate the dynamic properties of the oblique effect in the MPv task we divided each subject data to four categories based on the mean reaction time (RT) and the mean movement time of each subject (MT). The first category included trials with RT and MT smaller than the mean (fast RT and fast MT). The second category included trials with fast RT and MT larger than the mean (slow MT). The third category included trials with RT larger than the mean (slow RT) and fast MT and the fourth category included trials with slow RT and MT. In the following analysis all movements from each category were pooled for all subjects and a linear regression model was applied to the data for each one of the three distances of the movement trajectory for the MPv task (15, 30 and 45 mm). The results from this

Table 2 Regression model results of the oblique effect (modulation of gain with direction deviance from a cardinal direction) at 15, 30 and 45 mm distance in the evolving trajectory of the visual movement pointing task (MPv) and the memory movement pointing task (MPv) and at 15, 30 and 45 mm arrow length for the arrow pointing task (AP)

Gain (mm)	r	$F_{(1,38)}$	P	Slope
MPv 15	0.32	4.3	0.04	−0.0010
MPv 30	0.27	3.0	0.09	−0.0005
MPv 45	0.14	0.8	0.4	−0.0001
MPm 15	0.62	24.3	$<10^{-3}$	−0.0036
MPm 30	0.73	42.9	$<10^{-3}$	−0.0030
MPm 45	0.75	50.6	$<10^{-3}$	−0.0029
AP 15	0.86	108.8	$<10^{-3}$	−0.005
AP 30	0.90	169.6	$<10^{-3}$	−0.0028
AP 45	0.59	20.5	$<10^{-3}$	−0.0007

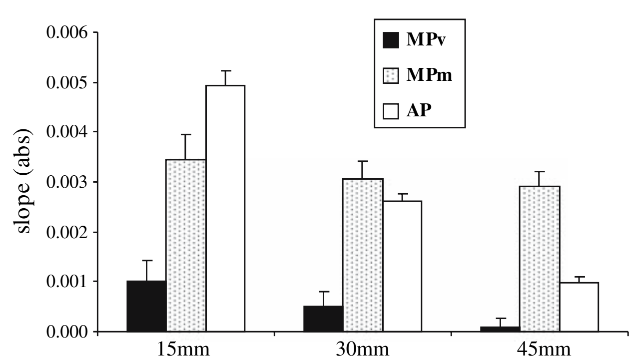

Fig. 4 Absolute value of the regression slopes indicating the magnitude of the gain modulation (magnitude of the oblique effect) at the three distances in the trajectory for all the movements in the MPv task (*black bars*), the fast movements in the MPv task (*black dotted bars*), all movements in the MPm task (*bars with horizontal lines*) and the three arrow lengths in the AP task (*white bars*)

Table 3 Regression model results of the oblique effect (modulation of gain with direction deviance from a cardinal direction) at trajectory distance of 15, 30 and 45 mm for four categories of trials based on reaction and movement times in the MPv task

Gain (mm)	r	$F_{(1,38)}$	P	Slope
RTfMTf 15	0.30	3.94	0.05	−0.0011
RTfMTf 30	0.24	2.43	0.12	−0.0005
RTfMTf 45	0.16	1.07	0.30	−0.0002
RTfMTs 15	0.33	4.86	0.03	−0.0016
RTfMTs 30	0.27	3.06	0.09	−0.0007
RTfMTs 45	0.07	0.21	0.64	−0.0001
RTsMTf 15	0.11	0.48	0.49	−0.0006
RTsMTf 30	0.17	1.09	0.30	−0.0004
RTsMTf 45	0.27	3.08	0.09	−0.0006
RTsMTs 15	0.27	2.99	0.09	−0.0011
RTsMTs 30	0.26	2.78	0.10	−0.0006
RTsMTs 45	0.21	1.81	0.18	−0.0002

RTfMTf fast reaction time and fast movement time; *RTfMTs* fast reaction time and slow movement time; *RTsMTf* slow reaction time and fast movement time; *RTsMTs* slow reaction time and slow movement time

analysis are presented in Table 3. It can be seen that the motor oblique effect is significant at the beginning of the trajectory for movements with fast RT compared to movements with slow RT where the oblique effect is not significant at any point along the evolving trajectory. It was also observed that the motor oblique effect was larger for movements with slow MT compared to movements with fast MT.

Discussion

In this study we analyzed the directional errors of pointing movements towards visual and remembered targets in 2-D space, at the beginning of the trajectory (one-fourth of the distance from peripheral target location), in the middle of the trajectory (half the distance from peripheral target location) and towards the end of the movement (three-fourths of the distance from peripheral target location). In the memory guided pointing task we observed that the mean direction at all three points in the evolving trajectory varied in a systematic fashion such that the gain (rate of direction variation) was larger for cardinal directions than for oblique directions. This directional distortion corresponds to an expansion of space at cardinal directions and contraction of space at oblique directions and reproduced the directional distortion that we described for the movement endpoint directions in the same memory guided pointing task in our previous study (Smyrnis et al. 2007). In that study we named this directional distortion of space as the motor oblique effect and we provided evidence that this space distortion is equivalent to the well known perceptual oblique effect (Appelle 1972) that is defined as better direction discrimination for cardinal directions compared to oblique. The current study showed that the motor oblique effect was present at different points along the evolving trajectory of the pointing movement towards the memorized location of the target and suggested that this distortion of directional space might be already present in the programming of pointing movements to memorized target locations.

The main question raised in this study was whether this directional distortion is present in the evolving trajectory of pointing movements towards visual targets. There is a wealth of evidence that in conditions of delayed movement the effects of perceptual distortions on movement become prominent suggesting a transition from an egocentric visuomotor frame of reference to an allocentric perceptual frame of reference (Gentilucci et al. 1996; Goodale and Westwood 2004). In previous work we showed that the direction distortion that is causing the motor oblique effect was not present at the final movement endpoint when the memory delay was 0 s (Smyrnis et al. 2000). The directional distortion was larger for a delay of 2 s but still the largest effect was for delays of 4 and 6 s. It has already been shown that for delays of up to 2 s the accuracy of reaching movements does not decay suggesting that visual information about the target remains for that period of time (Elliot and Madalena 1987). Based on these previous results our initial hypothesis was that the motor oblique effect influences the memory representation of the target location and not the visual representation in accordance with the dissociation of vision for perception and vision for action (Fig. 4a). Thus the motor oblique effect would be absent in the evolving trajectory of the movement towards the visual target and present in the evolving trajectory of the movement towards the remembered target location. Our choice of memory delay of 3 s ensured that the memory period would be long enough for the visual representation of the target to have decayed.

We observed that the motor oblique effect was present in the evolving trajectory of the memory guided pointing movements as expected but it was also present during visually guided pointing at the beginning of the movement trajectory. Its magnitude though was smaller than that observed for memory guided pointing and even smaller than that observed for perceptual directional judgment in the perceptual arrow pointing experiment.

We will discuss two theoretical models that could be used to explain these results based on the current discussion on the perception action dissociation. According to the first model the basic dissociation is not between perceptual and action systems but between two stages in the motor system itself, a stage of motor planning and a stage of online motor control (Glover 2004). In the first stage of motor planning a representation of the target is formed based on a large array of visual and cognitive information. In the second stage of online control another representation of the target is used to guide the moving arm that is based on the absolute movement metrics. We could hypothesize then that the motor oblique effect influences only movement planning and is then corrected by the online control representation of the target derived from vision that is accurate (Fig. 5b). This theoretical model explains why the motor oblique effect is present early on during the visually guided pointing movement and then is corrected. It also explains why there is no such correction for memory guided pointing where the online visual representation of the target is not available. This model though cannot explain adequately why the motor oblique effect is larger in the memory guided pointing task. Finally the major problem that rises with this model is that it would predict that the motor oblique effect would be smaller with shorter reaction times where the planning stage would be small and larger with larger reaction times where the planning stage would increase in time. It would also be larger with shorter movement times where the online control system has less time to correct the effect present in the planning stage. Our analysis though on the effect of reaction time and movement time on the motor oblique effect showed the exact opposite results.

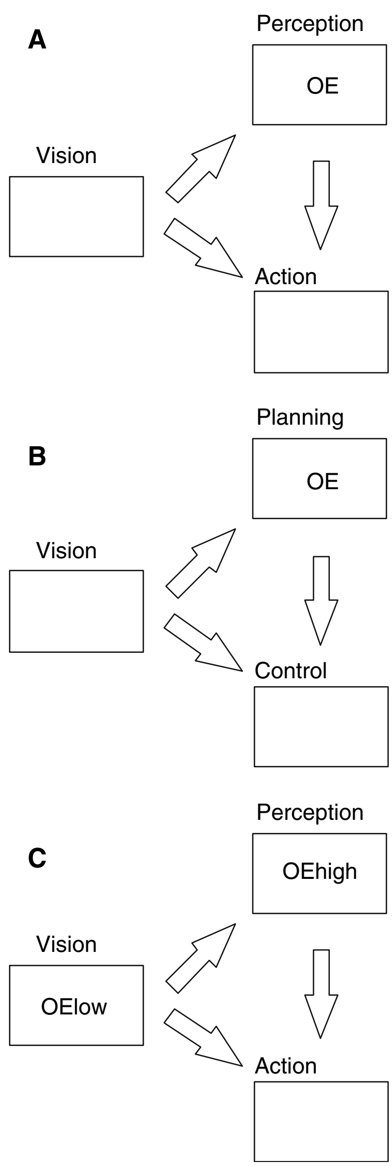

Fig. 5 Three theoretical models for the introduction of the motor oblique effect in movement pointing. **a** The perception versus action dissociation model. **b** The movement planning versus control model. **c** The perception and action integration model (*OE* oblique effect)

An alternative theoretical model to explain our results could be based on a refinement of the perception-action dissociation hypothesis. The model assumes that there are two types of oblique effect as suggested by Essock (1980). The first is a low level visual oblique effect resulting from visual processing in primary visual areas. In higher order perceptual processing areas this low level oblique effect is magnified by a second high level cognitive oblique effect that is not solely confined to vision but is also present with other inputs such as proprioception (Gentaz and Hatwell 1995). Early visual processing of the target location introduces the low level visual oblique effect. This effect is transmitted to the visuomotor processing areas were correction mechanisms start to operate (Fig. 5c). In the case of memory guided pointing movements the low level oblique effect is not corrected and it is also enhanced by the introduction of a high level cognitive oblique effect. This model then can explain the presence of a small oblique effect in visually guided pointing movements and a larger oblique effect in memory guided movements. This effect is even larger in the perceptual task (where the high level cognitive oblique effect is fully present).

The model proposed in Fig. 5c could also explain the modulation of the motor oblique effect with reaction time and movement time. Since the oblique effect is present in low level visual processing it is always introduced in the initial stages of visuomotor processing. It could then be corrected by feed forward mechanisms that do not use visual feedback from the cursor location. These mechanisms might start operating even before movement onset since they do not require visual feedback. In a previous study it has been shown that changes in target location can have an effect already at movement onset if the reaction time is greater than 200 ms (van Sonderen et al. 1988). In our case then when RT was larger the feed forward correction process might be completed even before movement onset. On the other hand the movement time might also be preprogrammed by this feed forward mechanism. If that was the case the correction of the oblique effect might be slower when the subject plans a slow reach and faster when the subject plans a fast reach thus a larger initial oblique effect would be present with slower movement times. What kind of information other than visual feedback could be used then to correct the motor oblique effect? A source of such information could derive from a learning process based on previous movements to the same target location. Since each subject performed many movements to the same target locations, a form of learning could be used for the feed forward prediction of the trajectory path and thus for appropriate corrections on the initial visual representation of the target.

A final point concerns the very long movement times that were observed in this study. We asked individuals to make accurate movements and we did not require that movements should also be fast. This fact could explain the very long movement times in this study. The long movement times though limit the results of this study in that they can not be generalized to all pointing movements that are usually much faster.

In conclusion our results favor the hypothesis that the interaction of perceptual and motor systems in the computation of direction is complex and continuous (Gentilucci et al. 1996). It also suggests that distortions in visual perception can be introduced at different levels of visual processing having varying effects on the specification of direction for reaching to a visual target. Looking at the predictions of alternative hypotheses concerning this interaction our results seem to favor the hypothesis that the separation of vision for perception and vision for action or the separation of planning and control might be oversimplifications for an actual continuous stream of visual information processing arising in early visual areas that is then transmitted to higher processing areas becoming more and more specialized either for action or for perception (Milner and Dyde 2003: Gaveau and Desmurget 2004). Finally we consider the motor oblique effect as a useful probe to study the interaction of perceptual and motor systems that is not the result of the presentation of a complex visual stimulus giving rise to a visual illusion.

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References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Appelle S (1972) Perception and discrimination as a function of stimulus orientation: the "oblique effect" in man and animals. Psychol Bull 78:266–278

Bard C, Turrell Y, Fleury M, Teasdale N, Lamarre Y, Martin O (1999) Deafferentation and pointing with visual double-step perturbations. Exp Brain Res 125:410–416

Bridgeman B, Kirch M, Sperling A (1981) Segregation of cognitive and motor aspect of visual function using induced motion. Percept Psychophys 29:336–342

Carey DP (2001) Do action systems resist visual illusions? Trends Cognit Sci 5:109–113

Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST (1999) Role of the posterior parietal cortex in updating reaching movements to a visual target. Nat Neurosci 2:563–567

Desmurget M, Grafton S (2000) Forward modelling allows feedback control for fast reaching movements. Trends Cognit Sci 4:423–431

Dyde RT, Milner AD (2002) Two illusions of perceived orientation: one fools all people some of the time; the other fools all of the people all the time. Exp Brain Res 144:518–527

Elliott D, Helsen WF, Chua R (2001) A century later: Woodworth's (1899) two-component model of goal directed aiming. Psychol Bull 27:342–357

Elliott D, Madalena J (1987) The influence of premovement visual information on manual aiming. Q J Exp Psychol A 39:541–559

Essock EA (1980) The oblique effect of stimulus identification considered with respect to two classes of oblique effects. Perception 9:37–46

Franz VH (2001) Action does not resist visual illusions. Trends Cogn Sci 5:457–459

Gaveau V, Desmurget M (2004) Do movement planning and control represent independent modules? Behav Brain Sci 27:35–36

Gentaz E, Hatwell Y (1995) The haptic "oblique effect" in children's and adults' perception of orientation. Perception 24:631–646

Gentilucci M, Chieffi S, Daprati E, Saeti MC, Toni I (1996) Visual illusion and action. Neuropsychologia 34:369–376

Glover S (2004) Separate visual representations in the planning and control of actions. Behav Brain Sci 27:3–78

Glover S, Dixon P (2001) Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. J Exp Psychol Hum Percept Perform 27:560–572

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Goodale MA, Pelisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. Nature 320:748–750

Goodale MA, Westwood DA (2004) An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. Curr Opin Neurobiol 14:203–211

Gourtzelidis P, Smyrnis N, Evdokimidis I, Balogh A (2001) Systematic errors of planar arm movements provide evidence for space categorization of multiple frames of reference. Exp Brain Res 139:59–69

Hu Y, Goodale MA (2000) Grasping after a delay shifts size-scalling from absolute to relative metrics. J Cogn Neurosci 12:856–868

Krukowski AE, Stone LS (2005) Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. Neuron 45:315–323

Milner DA, Dyde RT (2003) Orientation and disorientation: illusory perception and the real world. In: Johnson-Frey SH (eds) Taking action cognitive neuroscience perspectives on intentional acts. Bradford Book, MIT Press, Cambridge, MA, London, England, pp 4–28

Prablanc C, Martin O (1992) Automatic control during hand reaching at undetected two-dimensional target displacements. J Neurophysiol 67:455–469

Smyrnis N, Gourtzelidis P, Evdokimidis I (2000) Systematic directional error in 2-D arm movements increases with increasing delay between visual target presentation and movement execution. Exp Brain Res 131:111–120

Smyrnis N, Mantas A, Evdokimidis I (2007) The "motor oblique effect": perceptual direction discrimination and pointing to memorized visual targets share the same preference for cardinal orientations. J Neurophysiol 97:1068–1077

van Donkelaar P (1999) Pointing movements are affected by size-contrast illusions. Exp Brain Res 125:517–520

van Sonderen JF, Denier van der Gon JJ, Gielen CCAM (1988) Conditions determining early modification of motor programmes in response to changes in target location. Exp Brain Res 71:320–328

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269:1880–1882