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RESEARCH ARTICLE

Inference of complex human motion requires internal models of action: behavioral evidence

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Abstract Previous behavioral investigation from our laboratory (Pozzo et al. in Behav Brain Res 169:75–82, 2006) suggests that the kinematic features influence the subject's capacity to estimate the final position of simple arm movement in which the last part of the trajectory is hidden. The authors argue the participation of internal information, as the kinematic parameters, to compensate the lack of the visual input. The purpose of this report was to verify if the dependency of visual motion inference to biological displays can be generalized for intransitive and complex human motions. To answer this question, the subjects were asked to estimate the vanishing and final position of the shoulder trajectory of Sit to Stand (STS) or Back to Sit (BTS) motion performed in the sagittal plane, according to a biological or nonbiological kinematics. The last part of the trajectory (i.e., 35%) was occluded. We observed a kinematic effect on the precision of individuals' estimation. The subjects were more precise and less variable to estimate the end trajectory with biological velocity profiles. Moreover, impoverished visual information appeared sufficient to evaluate the final position of an intransitive complex human motion. These results suggest the participation of internal representations to infer the final part of complex motion. We discuss the results in the light of possible neural substrates involved during the inference task.

Keywords Motion inference · Internal models · Simulation · Mirror neurons · Complex intransitive motion

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Introduction

How do we visually extrapolate the final position of a biological motion like for instance the final position of a hand that reaches an object located behind a wall? In other words, what is the human ability to reconstruct and estimate the hidden part of a moving target? Neurophysiological evidence (Umiltà et al. 2001) suggests the participation of motor repertoires involving the mirror neurons (MNs) during observation of an occluded action. Localized in the monkey's pre-motor area (area F5), these neurons have the characteristic of discharging both during action perception of goal directed task and the production of the same action (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). The coexistence of motor and sensory properties in the same neuron suggests that the motor cortex not only executes actions but also participates in the construction of their representation (Fadiga et al. 2000). From this perspective, action observation would imply both in an implicit simulation and in implementation of motor programs necessary to perform the same action (Jeannerod 2001). Indirect evidences point to the existence of a human MN system within the ventral pre-motor cortex and inferior parietal lobule (for reviews see Rizzolatti and Craighero

2004; Rizzolatti 2005). The human visual perception should thus also be constrained by the knowledge of the biological rules that underlie motor performance (Viviani and Stucchi 1992; Chaminade et al. 2001).

In another line of evidence, many recent behavioral experiments suggested the involvement of the motor system during a motion perception or motion recognition task (Knoblich and Flach 2001; Verfaillie and Daems 2002; Casile and Giese 2006; Graf et al. 2007). For instance, Knoblich and Flach (2001) showed that during a throwing prediction task the participants were more accurate to estimate the consequences of their own movements. They interpret this result as an indirect evidence of the involvement of action system during a prevision task. Otherwise, Casile and Giese (2006) trained a new arm coordination pattern without visual feedback and demonstrated that the acquisition of new motor skills could selectively influence visual action recognition. Thus, the motor system, in absence of a prior visual experience, can directly constrain the perception of human motion. In a recent paper, Pozzo et al. (2006) demonstrated that when subjects are asked to estimate the final position of a moving dot corresponding to the index finger's vertical movement occluded in the last part of its trajectory, their precision decreases while variability increases when visual motion violates the kinematic laws. The authors suggested that inference process would not only rely on past visual trajectory information, but would imply in an implicit simulation of the motor program that supports this very same action. This precedent study is a behavioral evidence to support the visual–motor linkage hypothesis during motion inference process: weak differences between velocity profiles were shown to suffice to discriminate implicitly the biological from the nonbiological motion. Pozzo et al. (2006) concluded that transitive motion, without a physical target to reach in the visual scene, was sufficient to elicit the visual–motor linkage.

In contrast to the first investigation wherein subjects were asked to infer a transitive goal-oriented task, in the present study we sought to employ an intransitive, posture-dependent motion as in the case of Sit To Stand (STS) and Back To Sit (BTS) tasks. Indeed, the matching system activity seems to depend on the visual context for action understanding. In monkey, for instance, a goal-directed task is required (Gallese et al. 1996). In human, it seems controversial. Fadiga et al. (1995) found no differences in cortical-spinal excitability between transitive versus intransitive hand action. In contrast, a poor display (Grèzes et al. 2001) or a hand reaching performed by a robot (Tai et al. 2004) are insufficient to elicit motor representation and do not activate the frontal mirror area. To sum up, the observation of biological or alien effectors performing transitive or intransitive actions seems to affect the tuning of MNs.

Otherwise, during complex whole body motions like STS and BTS, trajectory of distal upper body part results in a complex dynamical context (large and multiple inertial interlimb interactive torques) in addition to equilibrium constraints. From this point of view, trajectory inference seems more demanding compared to a simple and almost straight finger path. Consequently, one might propose that the use of an internal model of limb dynamics rather than visual extrapolation mechanisms would be more complicated because of the task properties. Alternatively, one could suppose that in spite of the complexity of this motion, the inference process would use internal dynamic information. In fact, STS and BTS execution seem to use a similar internal model of gravity as for a simple arm reaching performed in the sagittal plane (Papaxanthis et al. 2003a). Thus, the acknowledged stability and robustness of the central representation of gravity (Pozzo et al. 1998) could facilitate the accurate recall of action to match the visual signal. In this case, anisotropy of upward and downward motion kinematics would influence the precision of motion inference.

The aim of this study was to verify if the dependence of visual motion inference on biological displays could be generalized for complex human motions like STS or BTS. In other words, can the sensibility to velocity profiles help to reconstruct the missing part of complex trajectories, as it is the case for a simple arm movement? To answer this question, subjects were asked to estimate the vanishing or the final position of a moving dot representing the shoulder trajectory of STS or BTS movements, partly occluded in the last part of the trajectory and according to biological or nonbiological kinematics.

Materials and methods

Apparatus and stimuli

The same methodology employed in our previous study (Pozzo et al. 2006), was used here. For all experiments, stimuli were displayed on a 17″ color flat screen (black background, resolution of 1,024 horizontal and 768 vertical pixels, where the pixel is a rectangle of 0.33 mm in length by 0.35 mm in height, with a refresh rate of 75 Hz) connected to a PC. Each stimulus consisted in a moving white dot (3 pixels in diameter) corresponding to a STS or BTS shoulder's trajectory. The display corresponds to the position of shoulder marker recorded in 3D at a frequency of 100 Hz (Elite System, BTS Bioengineering, Italy). For further details on the recording session, see Papaxanthis et al. (2003a). Because we previously observed a kinematic invariance characterizing the STS and BTS movements performed in the sagittal plane, we selected, for each direction,

one motion in agreement with the kinematic rules featured by Papaxanthis et al. (2003a) and we used it for the stimuli display. The authors recorded the kinematic of the shoulder (i.e., trajectory and velocity profiles) during a whole body motion (STS and BTS tasks) and demonstrated an anisotropy of the shoulder's velocity profiles. The velocity profiles were asymmetric depending on if movement was accomplished against the gravity (STS motion) or with the gravity (BTS motion). This observation corroborated previous results for arm motion (Papaxanthis et al. 1998, 2003b, 2005) and extended it to whole body motion (Papaxanthis et al. 2003a), suggesting that the central nervous system integrates the gravity force field in motor planning during arm or whole body motion performed in the sagittal plane. Thus, in this report the term "kinematic rules" refers to the asymmetry of velocity profiles of human movement performed in the sagittal plane.

The motion displayed on the screen corresponded only to the first 65% of the total movement, corresponding to the beginning of the deceleration phase of both shoulder tangential velocity profiles (see Fig. 1). If the past visual information were used to calculate the future of the trajectory, i.e., the end point (EP) position, visual extrapolation would be facilitated by the observation of a longer deceleration phase. In order to verify the role of the visual input in estimation precision this occurrence was chosen. Four kinds of movement were displayed. Two movements consisted in the dot motion on the screen depicting shoulder STS or BTS trajectories as recorded from the subjects' movement (we call these motions biological, since kinematics corresponds to movements with well-known motor laws). For the two other movements, a conflict was introduced on shoulder velocity profiles (see Fig. 1). Specifically, the STS motion of the dot was displayed according to the velocity profile corresponding to a BTS motion (violation of the biological motion, STS N) and the BTS motion of the dot was displayed according to STS velocity profile (BTS N).

The path lengths along the trajectories were 264 and 274 mm, and the total movement duration was 1.88 s with a mean velocity of 140 and 146 mm/s, respectively, for STS and BTS (see Table 1). For the STS trajectory, the horizontal and vertical excursions were, respectively, of 152 mm (12.5° of visual angle) and 124 mm (10.2° of visual angle) against 147 mm (12.1° of visual angle) and 126 mm (10.3° of visual angle) for the BTS. The shoulder path curvature displayed for upward and downward trajectories (vertical displacement, respectively, for STS and BTS motion) were calculated by using the ratio D_{max}/L (D_{max}: referred to the maximal perpendicular distance measured from the actual path to the straight line; L: corresponded to a straight line passing between the initial and final positions of the shoulder vertical displacement). This ratio showed that the upward part was more curved than the downward part: 0.21 vs. 0.18.

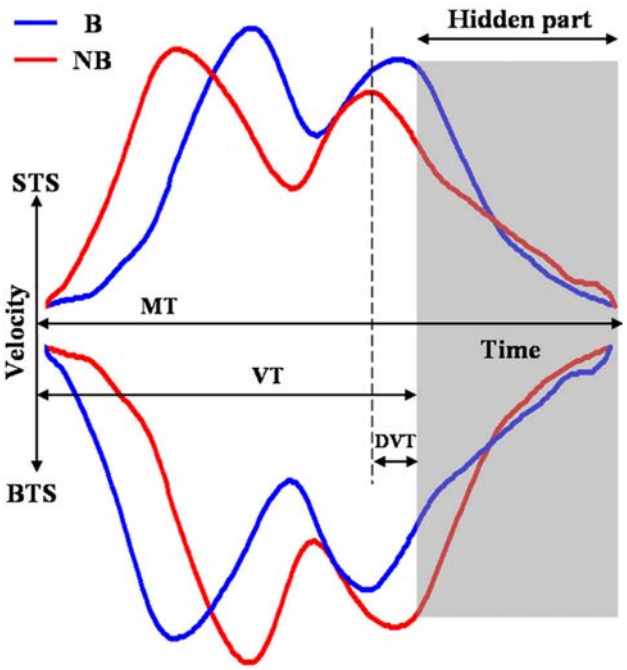

Fig. 1 Shoulder tangential velocity profiles of the four kinds of moving stimulus used in the experiments. For the first two kind of motions, the dot moved on the screen following STS or BTS trajectory according to a normal biological rule (Biological displays, *B-blue curves*), i.e., with their kinematics corresponding, respectively, to STS and BTS velocity profiles of the shoulder. In the two other motions, a conflict was introduced between direction and velocity profile. The STS motion was displayed with the velocity profile corresponding to BTS motion and inversely for the BTS motion (nonbiological displays, *NB-red curves*). The motion displayed on the screen corresponded only the first 65% of the total motion. Occluded part of the motion is indicated by a *gray rectangle*. Abbreviations of kinematic parameters for all displays: *MT* total movement time of the display, *VT* time of visual input, *DVT* time of the visible deceleration phase (see Table 1 for corresponding values)

Procedure and design

A total of 29 healthy subjects gave their informed consent to participate in this experiment. They had normal or corrected vision and were unaware of the purpose of the experiment. Each participant sat at a comfortable viewing distance from the screen (about 70 cm) in a darkened room. They were informed that the movement displayed on the screen corresponded to the shoulder trajectory during STS or BTS motion in the sagittal plane. When a crosshair (10×10 pixels) appeared at the center of the screen, the subject should displace his sight and fixate the cross. He initiated the movement using space bar of the keyboard and the cross disappeared. A random blank interval of between 0.2 and 1 s followed the disappearance. The subject continued to gaze at the center until the appearance of the stimulus presentation. The order of presentation of the stimulus pairs (STS, STS N, BTS and BTS N) was randomized for

Table 1 Parameters of the movements displayed

	MT (ms)	VT (ms)	DVT (ms)	ML (mm)	MV (mm/s)	VV (mm/s)
STS	1,880	1,222	61	264	140	244
STS N	1,880	1,222	156	264	140	169
BTS	1,880	1,222	156	274	146	177
BTS N	1,880	1,222	61	274	146	254

Motion information on the stimulus displayed for the two directions (STS and BTS) and the two kinematics (biological and nonbiological)

MT total movement duration/time, *VT* time of the visual input, *DVT* time of the visible deceleration phase, *ML* total length of movement, *MV* average velocity of motion, *VV* velocity of the stimulus at vanishing position

experiments 1 and 2. The subject responded by using the mouse.

This study consisted of four experiments: two experiments based on the position estimation (experiments 1 and 2) followed by two control experiments (control experiments 1 and 2). The basic experimental design consisted in two factors (Motion × Direction) with 12 repetitions for each factor combination. The motion factor had two levels: biological and nonbiological. The direction factor had two levels: STS and BTS. Thus, each experiment consisted of 48 trials. The experimental design with a small number of replications per condition (12) and the randomization presentation of the display prevented a possible learning effect.

All the participants gave their informed consent before the beginning of the experiment. The study was conducted in accordance with Declaration of Helsinki.

Experiment 1: end point estimation (EP)

Eleven subjects (five men, 27 ± 8 years) participated in the experiment 1. The experimental task consisted in evaluating where the motion would have stopped (spatial estimation) if it were completely displayed (remember that only the first 65% of the whole motion was visible). Subjects responded by displacing the crosshair cursor of the mouse on the final estimated position of the dot motion and validated it by clicking on the left button of the mouse. This response was automatically recorded by the computer.

Experiment 2: vanishing point estimation (VP)

Eleven subjects (four men, 27 ± 8 years) participated in the experiment. The experimental task consisted in placing the crosshair cursor exactly where the dot vanished; the rest of the procedure was similar with the experiment 1.

Control experiment 1

Subjects who performed the experiments 1 and 2 ($n = 22$) participated in this control. 99% of the motion length was displayed. After the disappearance of the dot, subjects were asked to place the crosshair cursor over where the dot disappeared; the rest of the procedure was similar with the experiment 1. They performed 24 replications: 12 tests per direction. This control permitted us to verify the subject's visuo-motor ability to point with the cursor in the context of the present experiment.

Control experiment 2

The aim of this control experiment was to obtain a rough estimation of the subject's sensibility to discriminate the weak differences appearing for kinematics (biological or nonbiological velocity profiles) used in the previous experiments.

Seven subjects (two men, 26 ± 8 years) participated in this experiment. The subjects watched the whole motion. Thirty pairs of movement were displayed. Six couplings were chosen: STS/STS N, STS/STS, STS N/STS N, BTS/BTS N, BTS/BTS and BTS N/BTS N. We used ten identical pairs, which corresponded to the same velocity profile: five similar pairs for STS (3 STS/STS plus 2 STS N/STS N) and five similar pairs for BTS direction (3 BTS/BTS plus 2 BTS N/BTS N). For the 20 other pairs, we applied for a same direction two different velocity profiles (biological vs. nonbiological) by using the same number of replications for each direction: ten pairs for STS direction (5 STS/STS N plus 5 STS N/STS) and ten pairs for BTS direction (5 BTS/BTS N plus 5 BTS N/BTS). It is important to stress that for a same direction (STS or BTS) the geometry of the trajectory is identical and independent of the applied velocity profiles (biological or nonbiological). The subject, after the presentation of two successive movements of the same direction, was asked to tell the experimenter if the movements displayed were identical or different. The subject had to evaluate 30 pairs of movements. The display of all pairs was randomized.

Data analysis

For each trial, the accuracy in the estimation of the end point (EP) or vanishing point (VP) of the stimulus position

was defined as the difference between the position estimated by the subject and the true position (position constant error, PCE). Then, for each subject we calculated average PCE errors. Subjects' variability in estimating the position of the stimulus EP or VP was defined as the standard deviation (SD) of the 12 replications measured for each of the two directions and two motions (position variable error, PVE).

Deviation from alignment and overshoot PCEs and PVEs were separately analyzed. Deviation from alignment was measured with respect of *x*-axis for STS motion and *y*-axis for BTS motion. For overshoot, we used the *y*-axis data for STS motion and the *x*-axis data for BTS motion (see Fig. 2).

Subject responses were compared using ANOVA with repeated measures (2 directions × 2 kinematics × 12 repetitions). The significance level was $p < 0.05$. Scheffé post hoc was used to compare the effect of different levels within the same factor.

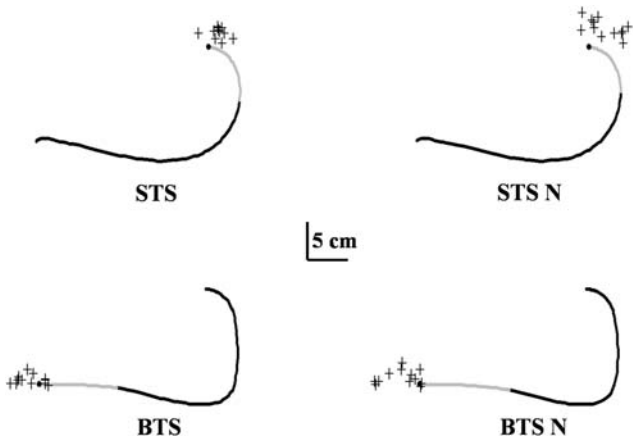

Fig. 3 End point estimation of a typical subject (experiment 1). From Left to Right and Top to Bottom: STS biological (*STS*), STS nonbiological (*STS N*), BTS biological (*BTS*) and BTS nonbiological (*BTS N*) motions displayed. *Black* and *gray curves* show, respectively, the visible and the hidden parts of the display. *Black dots* located at the end of the motion represent the ending position of the stimulus. *Crosses* correspond to the estimated end-points given by the subject by pressing the mouse button

Results

Experiment 1: end point estimation

In general, the final position of the dots was overestimated for the two motions and the two directions. Figure 3 illustrates the results collected from a typical participant.

Deviation from alignment

For the STS motion, the EPs were consistently displaced outside the trajectory. Outward estimations were 85.6 and 80.3% of the total trials, respectively, for STS and STS N with a PCE average of 22.3 ± 1.87 mm (PVE = 8.3 ± 1.54 mm). For the BTS motion we noted an upside displacement corresponding to 53.8 and 61.4% of the total trials, respectively, for BTS and BTS N with a PCE average of 15.5 ± 2.32 mm (PVE = 7.6 ± 0.89 mm).

An ANOVA for the PCE parameter revealed an effect of direction ($F(1,10) = 7.447$, $p = 0.02$): the deviation from alignment was always greater for STS motion compared to BTS motion. No significant effect was found for PVE. No significant difference was found between biological and nonbiological. No interaction effects were found.

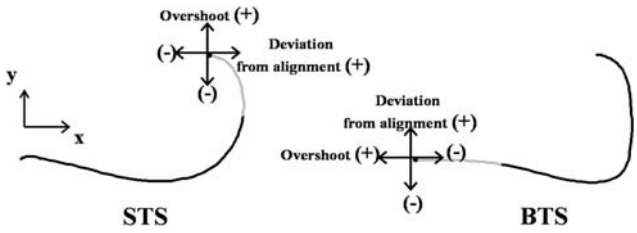

Fig. 2 Data analysis. *Left*, STS and *Right*, BTS motions are displayed. *Black* and *gray curves* show, respectively, the visible and the hidden parts of the display. *Black dots* located at the end of the motion represent the ending position of the stimulus. *Crosses* represent the axis of the deviation from alignment and the overshoot for the STS and BTS trajectories. Deviation from alignment is measured with respect to *x*-axis for STS motion and *y*-axis for BTS motion, whereas for the overshoot, we use *y*-axis data for STS motion and *x*-axis data for BTS motion

Overshoot

Subjects overshot when estimating the final position of motion. These overestimations represented 64.4, 69.7, 62.1 and 57.6% of the total trials, respectively, for STS, STS N, BTS and BTS N. The PCE average was 13.4 ± 1.98 mm (PVE = 6.9 ± 0.66 mm) for the STS condition and 14.5 ± 2.98 mm (PVE = 8.2 ± 0.74 mm) for the BTS condition. These values corresponded to 5.07% of the total trajectory length for STS direction and 5.5% of the total trajectory length for BTS direction.

An ANOVA for the PCE parameter revealed a velocity profile effect ($F(1,10) = 25.1$, $p = 0.0005$). A Scheffé post hoc analysis showed a significant difference between STS versus STS N ($p = 0.038$), BTS versus BTS N ($p = 0.026$) and STS versus BTS N ($p = 0.001$), for which the velocity profile was the same while the direction differed. In all cases, the subjects were always more precise to estimate the biological end position. An ANOVA on PVE revealed also an effect of motion ($F(1,10) = 8.2868$, $p = 0.016$) indicating that the variability increased for nonbiological displays.

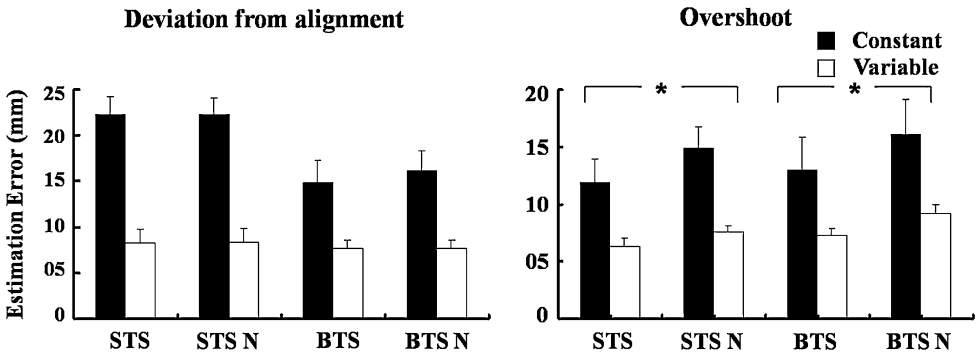

Fig. 4 Histogram of mean constant and variable errors for the end point estimation (experiment 1) for deviation from alignment (*left panel*) and overshoot (*right panel*) for the two directions (STS and BTS) and the two kinematics (biological and nonbiological) of the display. *Stars* indicate statistical difference ($p < 0.05$)

In short, PCE was greater for nonbiological motion (15.5 ± 2.4 mm) than for biological motion (12.3 ± 2.5 mm). Figure 4 (right panel) represents PCEs and PVEs with their dispersions in the four kinds of display. All subjects showed a tendency to be more precise for the inference of biological movement (see Table 2).

Experiment 2: vanishing point estimation

Similar to experiment 1, the vanishing position was overestimated for the two motions and the two directions. Figure 5 illustrates the results of a typical participant.

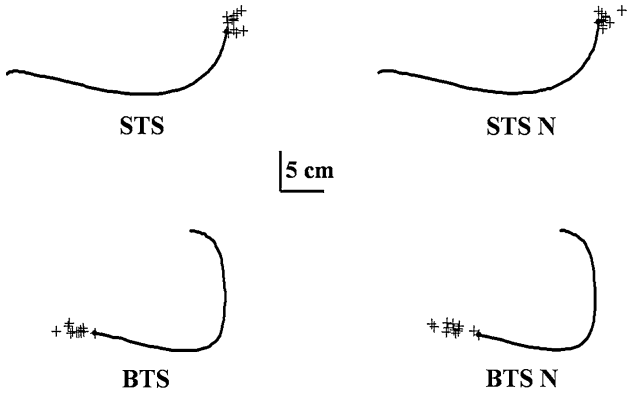

Fig. 5 Vanishing point estimation of one typical subject (experiment 2). From Left to Right and Top to Bottom: STS biological (*STS*), STS nonbiological (*STS N*), BTS biological (*BTS*) and BTS nonbiological (*BTS N*) motions are displayed. *Black curves* show the visible parts of the display. *Black dots* located at the end of the motion represent the vanishing position of the stimulus. *Crosses* correspond to the vanishing points estimation

Table 2 Results of subjects' end point estimation in function of the velocity profiles displayed

	STS	BTS
S 1	9.8	10.8
S 2	15.3	11.1
S 3	16.8	−2.5
S 4	6.6	18.1
S 5	3.9	10.4
S 6	4.5	−6.7
S 7	10.8	1.9
S 8	18.6	27.4
S 9	−0.7	19.8
S 10	7.8	1.9
S 11	3.0	11.3

Difference between nonbiological and biological displays for each subject (S) and each direction (STS and BTS) recorded in the experiment 1 (EP). The present values are expressed in pixels. The values of STS column are the results of the subtraction between the STS N average and the STS average for each subject. The values of BTS column are the result of the subtraction between the BTS N average and the BTS average for each subject. A positive value means that the subject was more precise while estimating the final position of a biological movement

Deviation from alignment

The STS condition showed a slight displacement outside of the trajectory. Outward estimations were 50.75 and 56.8% of the total trials, respectively, for STS and STS N with a PCE average of 3.43 ± 0.35 mm (PVE = 2.5 ± 0.3 mm). For the BTS condition, we noted an upward deviation corresponding to 77.3 and 91.6% of the total trials, respectively, for BTS and BTS N with a PCE average of 6.6 ± 0.9 mm (PVE = 3.2 ± 0.34 mm).

An ANOVA for the PCE parameter indicated an effect of direction ($F(1,10) = 14.0876$, $p = 0.0037$) and motion ($F(1,10) = 40.5869$, $p = 0.0001$). The deviation from alignment was always greater for BTS condition (6.6 ± 0.9 mm) as compared to STS condition (3.4 ± 0.34 mm). The accuracy for the biological conditions was higher (4.4 ± 0.57 mm) than for the nonbiological displays (5.6 ± 0.67 mm). An ANOVA on PVE revealed a significant interaction between direction and motion ($F(1,10) = 12.3670$,

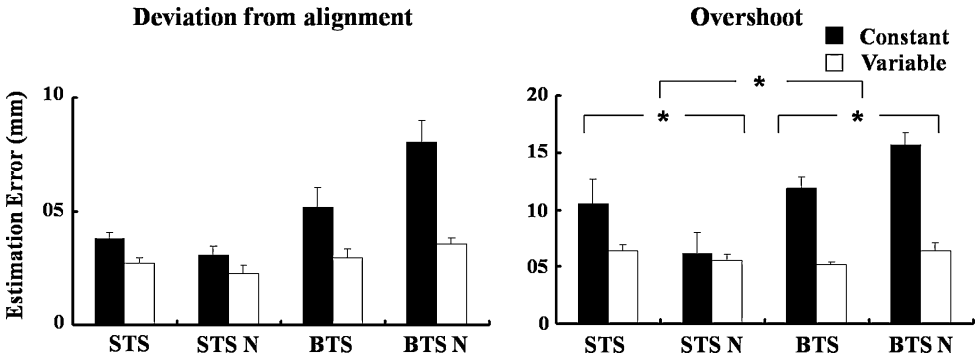

Fig. 6 Histogram of mean constant and variable errors for the vanishing point estimation (experiment 2) for deviation from alignment (*left panel*) and overshoot (*right panel*) for the two directions (STS and BTS) and the two kinematics (biological and nonbiological) of the display. *Stars* indicate statistical difference ($p < 0.05$)

$p = 0.005$). Figure 6 (left panel) represents PCEs and PVEs with their dispersions in the four conditions.

Overshoot

We observed a consistent overshoot in every experimental condition. Overestimations were 86.4, 79.5, 97.7 and 99.2% of the total trials, respectively, for STS, STS N, BTS and BTS N. The PCE average was 9.7 ± 1.7 mm (PVE = 4.7 ± 0.54 mm) for the STS condition and 13.9 ± 0.94 mm (PVE = 5.6 ± 0.45 mm) for the BTS condition. An ANOVA for the PCE parameter confirmed an effect of direction ($F(1,10) = 9.5354$, $p = 0.01$). The precision to estimate the VP was better for STS (9.7 ± 1.74 mm) than BTS condition (13.9 ± 0.94 mm). ANOVA test revealed a significant interaction between direction and motion for PCE ($F(1,10) = 57.6526$, $p = 0.00002$) and PVE ($F(1,10) = 9.0111$, $p = 0.013$). To conclude, the accuracy was higher when the vanishing velocity was lower. For instance, when the vanishing velocity of STS motion equaled 244 mm/s the PCE mislocalization was 10.5 ± 2.2 mm (PVE = 6.4 ± 0.6 mm) vs. 6.1 ± 1.9 mm (PVE = 5.5 ± 0.26 mm) for a vanishing velocity of 169 mm/s (see Table 1 for corresponding values). Moreover, the variability of subjects' VP estimation decreased for STS condition. Figure 6 (right panel) represents PCEs and PVEs with their dispersions in the four conditions.

Control experiment 1

All subjects were very precise in their estimation. Overshoot mean PCE was -1.8 ± 0.74 mm (PVE = 3.48 ± 0.52 mm) and -0.54 ± 0.94 (PVE = 3.92 ± 0.54 mm) which corresponded to 0.7 and 0.2% of the total trajectory length, respectively, for STS and BTS. The deviation from alignment of PCE was -2.77 ± 0.78 mm (PVE = 3.65 ± 0.64 mm) for STS and 0.34 ± 0.97 (PVE = 2.46 ± 0.42 mm) for BTS. This confirmed that the effects observed in the experiments 1 and 2 were the results of experimental manipulations and not a side effect of memory.

Control experiment 2

The mean of correctness in this experiment was of 12.7 ± 2.98 (which represents $42.4 \pm 9.9\%$ of correct responses). This result was lower than the chance level (15 correct responses).

We noted that when the subject observed an identical pair (biological and biological or nonbiological and nonbiological) the average percentage of correct responses was of $70 \pm 14.1\%$. Interestingly, during the observation of different pairs (biological vs. nonbiological) this percentage dropped to $28 \pm 12\%$ (result statistically different from the observation of an identical pair: test t, $p = 0.0008$). This percentage was lower than chance level (50% correct responses) suggesting that the subjects were unable to discriminate the weak kinematic differences between the conditions. More interestingly, none of the seven subjects were able to discriminate upper chance threshold of the differences between the velocity profiles for a same direction. After the experiment, we performed a debriefing of the participants, which confirmed that the subjects did not discriminate weak differences between the velocity profiles. Accordingly, this observation supports the control results and suggests that the biological effect observed in experiment 1 (EP estimation) proceeds from an implicit mechanism (not becoming aware).

Discussion

In the present report, we evaluated the subjects' capacity to reconstruct the hidden part of the shoulder trajectory during a whole body STS task.

The innovative aspect of our protocol leads us to investigate the respective contribution of visual information and internal representation of action to reconstruct the missing part of a complex and intransitive human movement. We used an impoverished visual context (only one light dot is displayed) describing a complex human trajectory.

The main result is an effect of the motion displayed on EP estimation in contrast to VP estimation, where the

ability to estimate the position of the moving targets depended only on target velocity. The following discussion will deal with the internal models of action and visual extrapolation mechanisms involved in the estimation of the vanishing and the final positions of a whole body motion.

VP experiment

We found a constant overshoot concerning the estimation of the vanishing position. This overshoot increased with respect to the velocity of the visual stimulus but was not related to the kinematics of the display (biological or not biological). For instance, we found that during STS while the velocity of the visual stimulus at the VP was greater for the biological display compared to the nonbiological display, precision in estimation decreased. In this case, visual processes seem to play a decisive role in target estimation.

A similar overshoot was found during vanishing position estimation experiments performed with constant velocity display where the shift in estimation increased according to the velocity (Mitrani et al. 1979; Kerzel et al. 2001; Actis-Grosso and Stucchi 2003). Nijhawan (1994) interpreted this result as a consequence of a visual extrapolation of the moving target's instantaneous location to compensate for the processing delay. The present investigation demonstrates the robustness of this mechanism for nonlinear motion display with successive acceleration and deceleration phases.

The present forward shift could also be the result of eye movement planning prior the disappearance of the target (Kao and Morrow 1994). Because of the processing delays of visual information (~100 ms, see De Valois and De Valois, 1991) the control of eyes' movement must be predictive to match the eyes with the moving target. Otherwise, when a moving target disappeared suddenly during a smooth pursuit task, the eye velocity decreased exponentially within 200–300 ms (Mitrani and Dimitrov 1978; Barnes et al. 2000) after its disappearance. During this delay the residual eye velocity toward the occluded target could contribute to the mislocalization of the VP. Accordingly, Kerzel et al. (2001) demonstrated a reduction of the forward shift during a nonpursuit condition experiment while subject's eye was fixed on a stable point.

We also found that the precision of the VP estimation was better for STS compared to BTS trajectory (experiment 2). Differences in curvature in upward compared to downward motion can explain these results. Indeed, a decay of speed pursuit and a lag in the pursuit is recorded for curved trajectories (Mrotek et al. 2006). During STS the dot disappeared near the maximal trajectory curvature, where pursuit velocity decreases. In contrast, for BTS movement, the dot vanished after this maximal when the trajectory is almost straight, and where the smooth pursuit is easier. In this latter condition, predictive mechanisms would facilitate the overshoot.

EP experiment: motor inference process

In contrast to VP experiment, precision in EP estimation was affected by displayed motion (biological vs. nonbiological). We found that the subjects' precision in motion inference was greater for displays that respected the kinematic law (see Fig. 3). Interestingly, for STS the duration of visible deceleration phase, on which motion extrapolation can be computed, was shorter during biological display compared to nonbiological display. Consequently, past visual input seems not to be the main information used to infer the invisible part of the trajectory. This result corroborates the preceding observations (Pozzo et al. 2006) and extends it to a complex and nontransitive whole body motion.

The superior sensibility to biological versus nonbiological displays demonstrated here supports the idea that motion inference would use internal information such as the implicit knowledge of motor laws required to perform the experimental task. In other words, during the reconstruction of hidden complex trajectories, the subject would retrieve motor informations to compensate for the lack of visual input. The general idea of a close interconnection between perception and motor representation, of late, has come to be increasingly accepted by several authors (Jeannerod 1994, 2001; Decety et al. 1997; Prinz 1997; Hari et al. 1998; Cochin et al. 1999; Rizzolatti et al. 2002; Fadiga et al. 2005; Kilner et al. 2007). Furthermore, the idea that during observation of action specific neural networks subserving that particular movements already tuned for action are retrieved is now recurrent in neurosciences (for an overview see Giorello and Sinigaglia 2007).

Thus, even if no recording of cerebral activity is provided here, we propose, using recent neurophysiological evidences and computational models, that the fronto-parietal mirror circuit is one candidate among the neural substrates, involved in the visual inference process that matches perception onto action system. Indeed, the functional characteristics of the mirror system (Rizzolatti and Craighero 2004; Buccino et al. 2004) would facilitate the recall of motor information to infer the hidden part of the trajectory. The multiple anatomical interconnections existing between the inferior parietal lobule and the premotor cortex would facilitate such interaction (Rizzolatti et al. 1998; Rizzolatti and Luppino 2001). Thus, one possible schema, operating probably within the parieto-frontal connections, is that the visible part of the trajectory would elicit an inverse internal model that translates the visual information into a motor plan (Miall 2003; Iacoboni 2005). This later corresponds to the plan that the subject uses to perform the STS or BTS motions.

From the motor plan, a forward model that predicts the future state (dynamic forward model) of the motor command (Miall and Wolpert 1996) would be used to predict the hidden part of the shoulder trajectory. The effect of shoulder kinematic observed here could illustrate the reduced efficiency of such inverse model to elaborate a motor plan for a nonbiological display. Indeed, the violation of a biological rule might introduce a conflict between the kinematics of the visual input and the kinematics of movement probably stored in the inferior parietal lobule (Kalaska et al. 1990; Erlhagen 2003).

Moreover, STS and BTS tasks are characterized by large vertical and horizontal body trajectories with two bimodal velocity profiles generating a double successive acceleration and deceleration phases. This task that presents geometrical, mechanical and equilibrium constraints much more important than for a simple arm movement and requires a sophisticated motor control (Mourey et al. 1998; Patton et al. 2000; Papaxanthis et al. 2003a). Despite this difficulty, subjects' capacity to estimate the hidden part of the trajectory remained adequate. One proposal would be that the more the movement is complex and the more information on biological motion is provided, the stronger is the tuning for motor simulation. Indeed, the complexity of the visual pursuit for STS or BTS motion, with several changes of directions, could best facilitate the recall of internal information based on motor repertoires.

Otherwise, STS and BTS motions are strongly constrained by a motor law applicable both to arm or body motions performed with or against gravity force field and illustrated by a typical asymmetric velocity profile (Papaxanthis et al. 1998, 2003a, b, 2005). Such constraint could facilitate the linkage between perception and action systems and more precisely with an internal representation of gravity (McIntyre et al. 2001). In support of this assumption, Indovina et al. (2005) suggest that this internal representation of gravity can be activated by visual motion that appears to be coherent with natural gravity. In this way, the recall of motor representations based on kinematic parameters during inference process could be facilitated. However, invariant characteristics of biological motion performed in the vertical plane might correlate to visual features that can be extracted without resimulating the whole dynamics. Likewise, this hypothesis requires deeper investigation.

Among the different modeling of action to perception matching system proposed in the literature the following schema is recurrently proposed (Miall 2003; Rizzolatti and Craighero 2004; Iacoboni 2005; Oztop et al. 2006). The model is built upon a visual feedback circuit involving the parietal and motor cortices, with a predictive role assigned to MNs in ventral premotor area (Oztop et al. 2005).

Accordingly, the MNs circuit would permit an online implicit simulation process of the observed motion, mainly based on the kinematic parameters (Gangitano et al. 2001, 2004) that would allow the subject to elaborate his estimation. However, a hand reaching movement (the classic experimental paradigm used in action-observation studies) provides visual input on hand trajectory that could simplify the matching process between vision and motor components of the task. In contrast, during a STS or BTS task a subject does not see his/her shoulder trajectory.

The absence of visual information about our own body displacement could however be compensated by the observation of conspecifics performing STS or BTS. In this case, the recall would not concern the STS motor plan but external visual input based on the observation of other individuals. Thus, the role of the visual experience of daily life tasks in motion inference cannot be excluded. It is possible that subjects store visual input extracted from usual behaviors that also contributes to motion recognition as it is the case for locomotion (Vaina et al. 2001) or face (Puce et al. 2003) recognition, for instance. The recent demonstration of the sensitivity of the superior temporal sulcus area (STSa) to visual experience of biological motion (Grossman and Blake 2001) supports such possibility.

This eventuality does not exclude the potential contribution of STSa to fronto-parietal (Fp) loop where mental imagery of whole body motion might be stored (Grossman and Blake 2001) and used during a partial (Thompson et al. 2005) or a total occlusion of the visual scene (Baker et al. 2001). Consequently, STSa could feed the Fp loop by characterizing the kinematics of the visual stimuli and send it to the posterior parietal MNs (Miall 2003; Iacoboni 2005). An fMRI study (Saygin et al. 2004) employing a biological motion recognition paradigm support such possibility. The authors (Saygin et al. 2004) demonstrated the recruitment of STSa and fronto-parietal complex during the observation of a meaningless action. Moreover, a recent experiment established that the activation of MN system during the action observation evoked a purely motor representation that could not be explained by the visual experience (Calvo-Merino et al. 2006). Indeed, they recruited a female and male population of professional dancers and demonstrated a greater activity of the fronto-parietal areas for the movement observation in agreement with the motor expertise of each gender group. The authors argued that this activity is a proof of a motoric response of MNs network and not the result of the motion visual knowledge. An interpretation supported by a behavioral study of Daprati et al. (2006) which demonstrated that subjects' performance during a hand motion recognition task does not depend on morphological cues. Thus, when the subject saw a virtual hand rendered as a simple stick diagram, the authors showed a minor role of visual expertise compared to the influence of kinematic templates in motion recognition. In our experimental design, to limit the influence of shape

recognition process, we applied similar trajectories that only differed with respect to their velocity profiles. If subjects' responses depended only on the visual experience to estimate the final position of the motion we could hypothesize a similar estimation between biological or nonbiological kinematics. However, we noted a kinematic effect on subjects' evaluations: they were more accurate and less variable to infer the final position of the biological motion even when the availability of the visual information was greater for nonbiological motion (see the STS motion). This result suggests the participation of internal information to elaborate the motion prediction. Mataric et al. (1998) claimed that motor primitives could be recalled by only using the visual tracking of the end point and that little visual information appears sufficient to map internal movement primitives onto the observed motion. This agrees with our experimental paradigm, where the subjects saw, uniquely, one light dot.

For all these reasons, it seems difficult to support the visual experience assumption to explain the present result. In contrast, we speculate that the lack of the visual input induces an implicit motor simulation of the observed motion, which would be tuned according to movement kinematic rules.

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