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Research report

Kinematic features of movement tunes perception and action coupling

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Abstract

How do we extrapolate the final position of hand trajectory that suddenly vanishes behind a wall? Studies showing maintenance of cortical activity after objects in motion disappear suggest that internal model of action may be recalled to reconstruct the missing part of the trajectory. Although supported by neurophysiological and brain imaging studies, behavioural evidence for this hypothesis is sparse. Further, in humans, it is unknown if the recall of internal model of action at motion observation can be tuned with kinematic features of movement.

Here, we propose a novel experiment to address this question. Each stimulus consisted of a dot moving either upwards or downwards, and corresponding to vertical arm movements that were masked in the last part of the trajectory. The stimulus could either move according to biological and or non-biological kinematic laws of pointing tasks. We compared subjects' estimations of the stimulus vanishing or final positions after biological and after non-biological motion displays. Subjects systematically overestimated the vanishing and final position for the two directions (up and down) and the two kinematics displayed (biological and non-biological). However, estimation of the final position decreased in precision and increased in variability for movements that violated the kinematic laws of arm pointing task.

The results suggest that motion inference does not rely only upon visual extrapolating mechanisms based on past visual trajectory information. We propose that motion estimation relies on internal models that contain specific kinematic details of vertical arm movement, which can be rapidly recalled during motion observation.

Keywords: Motion inference; Kinematics; Arm pointing; Internal models; Visual perception; Human

1. Introduction

Spatiotemporal discontinuity of the visual input, such as a moving object suddenly vanishing behind a wall, is an everyday occurrence that challenges motion extrapolation. A local mechanism in which the future trajectory is assessed through time integration of the visible part of the trajectory is one possibility to predict future state of the moving object. In most cases we are able to deduce objects' position that move out of sight, as for instance a falling object. Nevertheless, visual extrapolation of biological motion becomes considerably more challenging than non-biological motion relying on linear kinematic. Indeed, because of complex relationships between motor commands, musculo-skeletal system and external loads, kinematic of living object motion is mainly non-linear [34]. The remaining solution to overcome this difficulty would be to use extra-retinal input (e.g. prior experience and internal models) to reconstruct invisible part of the displacement.

Human and animal capacity for "object permanence", that is to say "the experience that objects persist through space and time despite the fact that their presence in the visual field may be discontinuous" [5] is an illustration of perceptual inference. Thus, static or moving object occlusion can lead to a strong impression of object or motion permanence even when the observer knows that there is no permanent object presents [26]. Perrett and co-workers [4,20], have found neurophysiological support to this idea. They reported perceptual cells in the superior temporal sulcus of monkey responding when a walker subject moves

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behind an occluder with many cells showing their highest levels of activity after object is completely hidden from view. The authors' conclusion was that such cells could contribute to perceptual capacity of object permanence and awareness maintenance. Neuronal activity in the absence of visual stimulus has also been observed in parietal cortex by Assad and Maunsell [3] during inferred motion trials in which moving target briefly disappeared and reappeared.

Interestingly, a population of motor neurons in the monkey's pre-motor area (area F5) has been found responding both to the execution and the sight of grasping an object, and continues to respond even if the final part of the action is occluded from the sight [42]. The authors pointed out the capacity of mirror neurons to be activated by hidden actions, provided that their outcome can be predicted and that visual extrapolation might be mediated by the action system. In other words, perception of visible and invisible biological motion seems to strongly depend on motor competence, an idea also supported by decade of research in psychology [26,43]. More recently, it has been demonstrated that visual cues can be used to make cognitive prediction, like to explicitly determine the forthcoming letter after a partial handwriting display [21].

Recent neurophysiological studies provide strong evidence that action observation and execution share common neural substrate [37]. According to the direct matching hypothesis, such motion permanence when visual input is transiently disrupted would result from cortical mechanisms that map an observed action onto an internal model of that action.

Nevertheless, the functionality of action-perception matching system has been mainly demonstrated for general aspect of the task (action meaning or intention understanding) and an important gap remains between this generality and the specificity of the motor program that allows action execution. For instance, we do not know if action observation can generate, beside high level of action representations, detailed kinematic parameters of the movement. Further, it is not clear to what extent the direct matching system implements motor programs equivalent to those used in action. Finally, what cues does the visual system use to categorize movement as biological or non-biological remains an open question (see Ref. [2]).

The matching system activation appears strongly dependent on the visual context and on sophisticated visual analyses that lead to action meaning and intention understanding. Although it is clear that the matching system activation in monkey requires goal directed task [12] studies in human seem to be controversial. Fadiga et al. [10] and Maeda et al. [25] for instance found no differences in cortical–spinal excitability between transitive versus intransitive hand action. In contrast, a poor display [15], a hand reaching performed by a robot [40] or an observation in virtual reality condition [35] are all inadequate to elicit motor representation or do not fully activate the mirror areas [18,22,23]. Moreover, recording of eye movements performed during action observation suggests that the mirror system is activated only when observers view an object-oriented goal-directed task and not when the observer views only its kinematic components [11].

Actually the motor context given by the visual input (i.e. the physical presence of a goal in contrast to intransitive action where only movement without target to reach is displayed) seems determinant to match visual perception of motion onto the motor repertoire.

The current work tries to answer the two following questions: what is the capacity of human subjects to reconstruct the hidden part of a moving target? To what extent trajectory reconstruction is related to specific motor competence?

To this end we developed a new psychophysical experimental paradigm. Subjects were asked to estimate the vanishing position or the final position of a moving dot representing a hand reaching movement that was masked in the last part of its trajectory after biological and after non-biological motion display. Subjects' indications of the final positions in both types of displays were compared. A pure visual extrapolation mechanism will predict the same estimation of the final position for biological and non-biological movements. In contrast, according to the visual-motor linkage hypothesis, erroneous position judgement should occur when observed motion do not correspond to the subjects' motor repertoire.

2. Materials and methods

2.1. Apparatus and stimuli

For all experiments the stimuli were displayed on a colour flat screen (black background, resolution 1024 pixels × 768 pixels, where a pixel is a rectangle of 0.37 mm in length by 0.39 mm in height) connected to a PC. Each stimulus consisted in a white dot (five pixels in diameter, about 0.2° of visual angle) moving either upwards or downwards. This motion corresponded to arm movements performed in the vertical plane. The motion displayed on the screen corresponded only to the first 60% of the total arm pointing movement.

Four kinds of motion were displayed. For the first two kinds of motions, the dot moved on the screen upwards or downwards according to a normal biological rule (U for upward biological motion, D for downward biological motion), i.e. with their kinematic corresponding, respectively to the upward and downward velocity profiles recorded during vertical arm pointing movements [32]. Previous experimental data demonstrated finger invariant kinematic during vertical upward and downward arm pointing movements. More precisely, in contrast to analogous horizontal pointing movements, velocity profiles of vertical movements were asymmetric: upward displacement has a shorter acceleration phase compared to downward displacement of the same duration [30,32] (see Fig. 1).

In the two other motions, a conflict was introduced between motion direction and velocity profile. The upward motion was displayed with the velocity profile corresponding to a downward arm movement (UN for upward non-biological motion). Inversely, the downward motion was displayed with an upward natural velocity profile (DN for downward non-biological motion). The trajectories displayed were slightly curved with horizontal and vertical excursions, respectively of 11 mm (0.45° of visual angle) and 113 mm (10.4° of visual angle, see Fig. 2). The path length along the trajectories was 159 mm. Total movement duration was 1.21 s with a mean velocity of 131 mm/s (8.6° s) and a maximum velocity of 238 mm/s (15.6° s) (see Table 1).

2.2. Procedure and design

A total of 33 healthy subjects gave their informed consent and volunteered to participate in this study. Each participant sat at a comfortable viewing distance from the screen (about 70 cm) in a room with a dim lighting. Each subject was informed that the motion displayed on the screen corresponded to the motion of the finger extremity of the outstretched arm performing a pointing task in the sagittal plane (angular displacement equal to 65°). When a hair cross (10 pixels × 10 pixels) appeared at the centre of the screen, the subject should displace his sight and fixate the cross. After 1 s the cross disappeared and was followed by a random blank interval between 0.25 and 1.5 s. The subject should

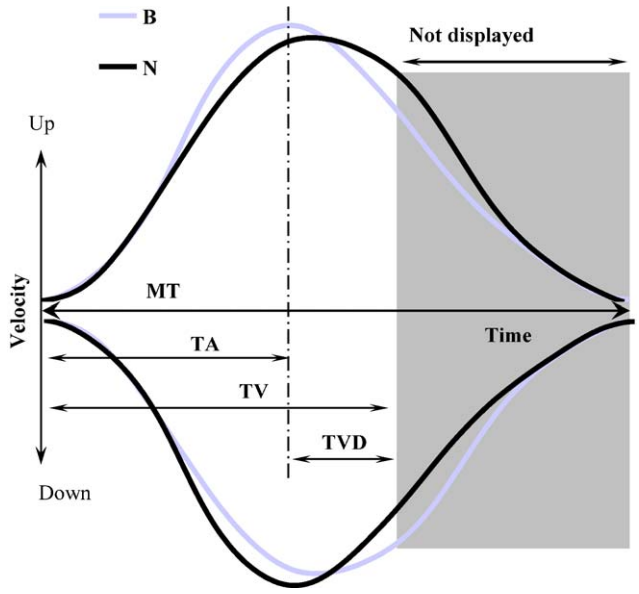

Fig. 1. Velocity profiles of the four kinds of moving stimulus used in the six experiments. For the first two kind of motions, the dot moved on the screen upwards or downwards according to a normal biological rule (biological displays, B-grey curves), i.e. with their kinematics corresponding, respectively to the upward and downward velocity profiles of the finger recorded during a vertical straight arm pointing movements. In the two other motions, a conflict was introduced between motion direction and velocity profile. The upward motion was displayed with the velocity profile corresponding to a downward arm movement and inversely for the downward direction (non-biological displays, N-black curves). The motion displayed on the screen corresponded only to the first 60% of the total arm pointing movement. Occluded part of the motion is indicated by a grey rectangle. Abbreviations of calculated kinematic parameters for the four displays: MT, total movement time of the display; TA, time of acceleration phase; TV, time of the visual input; TVD, time of the visible deceleration phase (see Table 1 for corresponding values).

continue to gaze at the centre until with appearance of the stimulus, which took place always on the right side of the screen. The end of the stimulus presentation was again followed by a random blank interval between 1.5 and 2.5 s. The subject gave his or her response by using the mouse.

This study consisted in six experiments: two experiments on position estimation (Experiments 1 and 2), two experiments on time estimation (Experiments 3 and 4) and two control experiments (Experiments 5 and 6). Experiment 2 (vanishing point (VP) estimation) was introduced in order to compare the estimation performance when the subjects were forced (Experiment 1) or not (Experiment 2) to actively infer the final position. Subjects participated either in Experiments 1, 3 and 5 or in Experiments 2, 4 and 5. The control Experiments 5 and 6 were always the last to be carried out (6 after 5) whereas the other two experiments were submitted in a random order. In all experiments the basic experimental design was a two factors (motion × direction) within subject design with 12 replications per cell. Both factors have two levels: biological versus non-biological for the motion factor, and downward versus upwards for the direction factor. Thus, each experiment was constituted by 48 trials. Experiments were conducted in accordance with ethical guidelines laid down by the Université de Bourgogne.

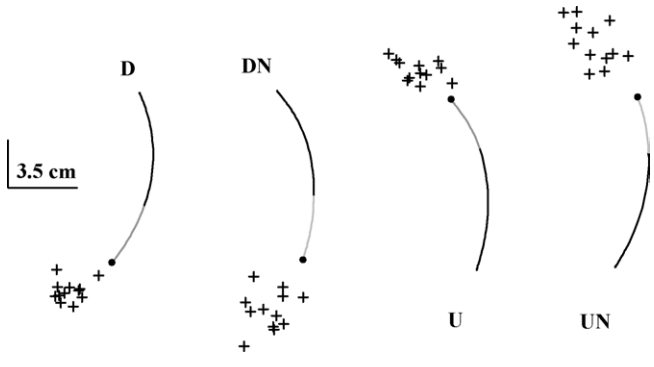

Fig. 2. End point estimation of one typical subject (Experiment 1). From left to right: downward biological (D), downward non-biological (DN), upward biological (U) and upward non-biological (UN) motions displayed. Black and grey curves show, respectively the visible and the hidden parts of the display. Black dots located at the end of the curve correspond to the ending position of the stimulus. Crosses correspond to the estimated end-points given by the subject by pressing on the mouse button.

Table 1
Durations of the different phases of the stimulus displayed for the two directions (up and down) and the two kinematics (biological and non-biological): MT, total movement time of the display; MT/AT, ratio of total movement time on acceleration time; TV, time of the visual input; TVD, time of the visible deceleration phase

	MT (ms)	MT/AT	TA (ms)	TV (ms)	TVD (ms)
U	1210	44.6	540	726	186
UN	1210	48.8	591	726	136
D	1210	48.8	591	726	136
DN	1210	44.6	540	726	186

2.2.1. Experiment 1—EP, end point estimation

Ten subjects (five men and five women, 24 ± 5) participated in the experiment. They had normal vision or were corrected for normal and were naïves to the purpose of the experiment. The experimental task consisted in placing the hair cross cursor where the motion would have stopped if it were completely displayed (remember that only the first 60% of the whole motion was visible!). Subjects confirmed their estimation by pressing the mouse button.

2.2.2. Experiment 2—VP, vanishing point estimation

Eleven subjects (five men and six women, 23 ± 2) participated in the experiment. They had normal vision or were corrected for normal and were naïves to the purpose of the experiment. The experimental task consisted in placing the hair cross cursor where the dot vanished. All the other experimental conditions remained the same/identical.

2.2.3. Experiment 3—ET, end point time estimation

The same subjects of Experiment 1 participated in this experiment. One subject was removed because was unable to accomplish the task. The experimental task consisted in a first pressing of the mouse button to initiate the display of the moving dot and, after the disappearing of the stimulus, in a second pressing to estimate when the motion would have stopped if it were completely displayed. All the other experimental conditions remained the same/identical.

2.2.4. Experiment 4—VT, vanishing point time estimation

The same subjects of Experiment 2 participated in this experiment. The experimental task consisted in a first pressing of the mouse button to initiate the display of the moving dot, and in a second pressing as fast as possible at the vanishing of the moving dot. All the other experimental conditions remained the identical.

2.2.5. Experiment 5—control

Twelve subjects participated in this experiment. They had normal vision or were corrected for normal and were naïves to the purpose of the experiment. They were divided in two groups: the first group saw solely partial motions whereas the second one saw full motion. Pairs of motion were displayed (one after the other) for each subject in a random order. The six possible combinations were: D/DN, D/D, DN/DN, U/UN, U/U, UN/UN. Thirty pairs were displayed among which 15 of these pairs were identical and the others 15 were different. The task consisted

in detecting if the pairs displayed (the two successively presented motions) were identical or different. The aim of this control experiment was to obtain a rough estimation of our sensibility in discriminating the weak differences in kinematics between the types of motions used in previous experiments.

2.2.6. Experiment 6—control

Almost all the subjects who participated in previous experiments (17) were tested in the control experiment (9 of Experiments 1–3 and 8 of Experiments 2–4). The full motion was displayed until it stopped. After the dot disappeared, the subjects were asked to place the hair cross cursor where the motion stopped. Subjects confirmed their estimation by pressing the mouse button.

2.3. Data analysis

Accuracy in estimating the end point (EP) stimulus position (position constant error, PCE) was defined as the difference between the actual position and the true position. Analogously, accuracy in estimating the stimulus time (time constant error, TCE) was defined as the difference between the estimated duration and the true duration for each motion. Subjects' precision in estimating the position of the stimulus end point (position variable error, PVE) was defined as the S.D. of the 12 replications measured for each of the two directions and two motions. Subjects' precision in estimating the stimulus duration (time variable error, TVE) was defined analogously. Vertical and horizontal PCEs and PVEs were separately analysed. The tangent line at the end point was used to evaluate inside or outside horizontal position estimation.

3. Results

3.1. Experiment 1—end point estimation

Fig. 2 illustrates the results of one typical participant. Generally, the final position of the dot overshoots for the two directions and the two motions. Vertical and horizontal PCEs and PVEs were separately analysed (see left and right panel of the Fig. 3).

3.1.1. Horizontal displacement

The estimated EPs were consistently displaced inside the trajectory (i.e. on its convex side, see Fig. 2). Inward estimations were 97.5%, 95.8%, 94.2% and 95% of the total trials, respectively for D, DN, U and UN with an average PCE of 26.7 ± 3.5 mm (VE = 14.6 ± 1.1 mm). An ANOVA on horizontal PCE solely showed an effect of direction ($F(1,9) = 5.53$, MSE = 6381, $p = 0.043$). An ANOVA on horizontal PVE did not reveal any systematic effect.

3.1.2. Vertical displacement

For the vertical component of the estimated displacement there was a generalized overshoot. Overestimations were 75%, 83.4%, 84% and 88% of the total trials, respectively for D, DN, U and UN. The average PCE was 15.5 ± 4 mm (PVE = 10.6 ± 1.6 mm) that corresponded to 13.7% of the total vertical displacement. An ANOVA on vertical PCE showed an effect of motion ($F(1,9) = 14.37$, MSE = 4125, $p = 0.004$) and an effect of direction ($F(1,9) = 9.33$, MSE = 4386, $p = 0.013$). No interaction reached significance. From an ANOVA on PVE, only the motion factor reached significance ($F(1,9) = 10.7$, MSE = 74, $p = 0.009$). Fig. 3 (right panel) represents PCEs and PVEs with their dispersions in the four experimental conditions. From a post hoc analysis on PCE with the *Scheffe's test* all the pair wise comparisons reached the significance but U versus DN. In the whole, PCE was greater for upward (19.1 ± 4.5 mm) than downward motion (11.9 ± 4 mm) and PCE was greater for non-biological (19.8 ± 4.8 mm) than for biological motion (11.1 ± 3.3 mm).

3.2. Experiment 2—vanishing point estimation

3.2.1. Horizontal displacement

The estimated VPs were slightly displaced inside the trajectory (i.e. on its convex side). Inward estimations were, respectively 72.7%, 68.9%, 89.3% and 59.8% of the total trials for D, DN, U and UN with an average PCE of 4.2 ± 2.1 mm (PVE = 3.8 ± 0.3 mm). This value significantly differs from the value obtained in Experiment 1 ($F(1,19) = 25.3$, MSE = 920954, $p < 0.001$. An ANOVA on horizontal PCE solely showed an effect of motion ($F(1,10) = 5.2$, MSE = 9283, $p = 0.045$). An ANOVA on horizontal PVE did not reveal any systematic effect.

3.2.2. Vertical displacement

As in previous experiment a generalized overshooting of the VP was observed in all experimental conditions (overestimations were respectively 67.4%, 79.5%, 78%, and 72.7% of the total trials for D, DN, U and UN). The mean PCE was 8.9 ± 3.6 mm (PVE = 5.9 ± 0.6 mm), which is sensibly lesser than the value observed in the previous experiment without being statistically differ from it. An ANOVA on PCE did not showed any systematic effect. Fig. 4 (right panel) represents PCEs and PVEs with their dispersions in the four experimental conditions.

3.3. Experiment 3—end point time estimation

Mean TCE of ET was 298 ± 68 ms, which corresponds to 25% of the total duration, and the actual duration of the move-

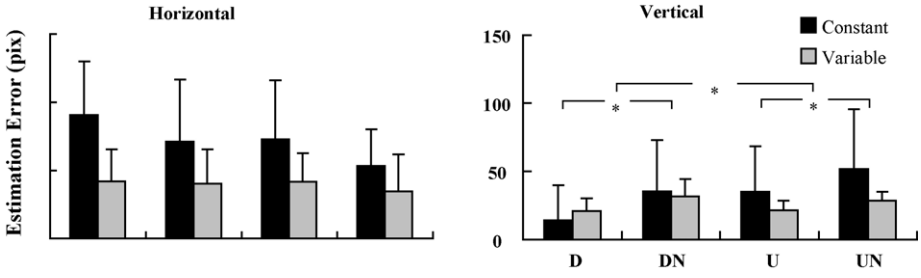

Fig. 3. Histogram of mean constant and variable errors in end point estimation (Experiment l) along horizontal (left panel) and vertical axes (right panel) for the two directions (down and up) and the two kinematics (biological and non-biological) of the display. Stars indicate significant statistical difference.

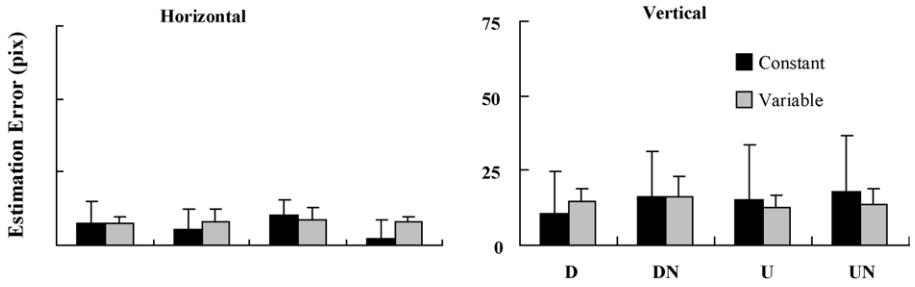

Fig. 4. Histogram of mean constant and variable errors for the vanishing point estimation (Experiment 2) along horizontal (left panel) and vertical axes (right panel) for the two directions (down and up) and the two kinematics (biological and non-biological) of the display.

ment was mainly overestimated (88%, 89%, 81.5% and 90% of the 108 trials were overestimated in D, DN, U and UN, respectively). Mean TVE was 170 ± 6 ms indicating a poor precision but a remarkable consistency among subjects (Fig. 5, right panel). An ANOVA on TCE and TVE did not reveal any effect. Mean intra-subjects variability was ± 150 ms.

3.4. Experiment 4—vanishing point time estimation

Mean TCE of VT was 232 ± 23 ms (VE = 69 ± 8 ms), which corresponds to 30% of the visible motion duration, occurrence of subject response being always after the vanishing point (Fig. 5 left panel). An ANOVA on TCE showed an effect of motion ($F(1,8) = 16.3$, MSE = 247394, $p = 0.004$).

3.5. Experiment 5—control

The mean percentages of correct responses were $48.3 \pm 10.6\%$ for the full motion group and $34.3 \pm 5.6\%$ for the partial motion group. Both values are below the chance level of correct responses (50%), indicating that subjects were very poor in detecting differences between motions.

3.6. Experiment 6—control

All subjects were very accurate and precise in their estimation, confirming that the PVE of previous Experiments 1 and 2 is not a side effect of memory and the different PCEs are a direct effect of experimental manipulations. Mean horizontal PCE was -0.07 ± 0.4 mm (VE = 2.1 ± 0.2 mm), and mean vertical PCE was -0.17 ± 0.4 mm (VE = 2 ± 0.1 mm). An ANOVA on TCE and TVE did not reveal any effect.

4. Discussion

In the present study, we assessed participants' capacity to estimate the vanishing point of a moving target or the final location of the target when an occluder interrupts the spatiotemporal continuity of target motion. We found a consistent overestimation in both vanishing and end point estimations. However, the main result obtained in our experiments is the significant effect of displayed kinematics on occluded motion estimation. The bias in end point estimation was increased by the non-biological displays while this variable had no consequences on the vanishing point estimation. The following discussion will consider successively the potential mechanisms involved in visual inference and the role of attention and implicit mechanisms involved in motion recognition.

4.1. Potential mechanisms involved in motion inference

We found systematic overshoot of position estimation for vanishing point estimations. This result is in agreement with previous observation made with apparent linear motion. Nijhawan [27,28] found that the perceived position of target moving with respect to the retina was extrapolated along its trajectory, leading the observer to perceive the target ahead of its actual position. This author explains this illusion by motion anticipation mechanism achieved in the retina that compensate for neuronal delay between the retina and visual areas. Similarly a recent study [1]

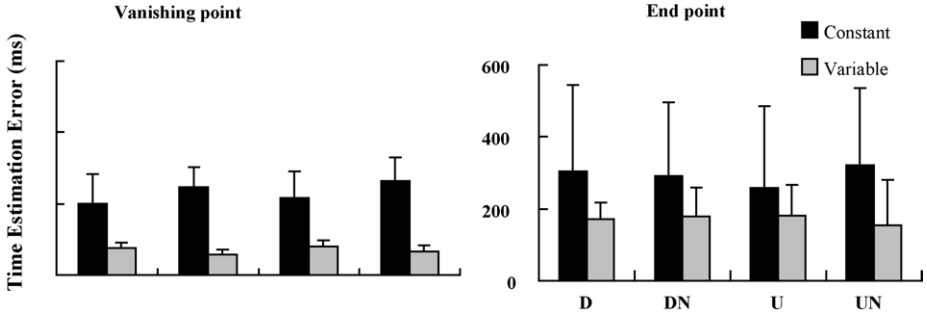

Fig. 5. Histogram of mean constant and variable errors in time estimation of the vanishing point (Experiment 4, left panel) and of the end point (Experiment 3, right panel) for the two directions (down and up) and the two kinematics (biological and non-biological) of the display.

that described such illusion at the starting point of a moving target also supports the idea of a low-level visual mechanism. Interestingly, the present overshoot was recorded with decelerating motion in contrast to constant velocity applied to previous visual stimulus. Past visual trajectory information may be used until the stimulus disappears on the basis of local visual measurements and temporal derivative operations. More surprising is the finding of a similar overshoot at end point estimation suggesting potential intervention of similar visual extrapolating mechanisms in position judgment.

Our results reveal that performance in estimating the final position of the target decreased in precision and increased in variability for displayed movements that violated kinematic laws. This result suggests that motion extrapolation does not rely exclusively on local visual input, and that end point estimation also result of external to internal signal interaction. In other words, the priming of the visual input by an internal model of arm pointing movement would allow for motion permanence after trajectory occlusion. Indeed, in the case of purely visual extrapolation, the visible part of the trajectory should determine end point estimation, especially the deceleration phase. Consequently, the displays presenting longer visible deceleration phase would lead to greater precision and accuracy in end point estimation than displays with shorter visible deceleration phase. Such prediction was neither confirmed for downward direction where estimation of display showed greater precision compared to DN display, nor for U motion that presented longer visible display and showed lesser precision compared to D display.

This result is in line with the idea of a close interconnection between perception and motor representation [19,37] and a "common coding" of perceptual and motor events [17]. A large body of experimental evidences demonstrated that visual perception elicits activation within a brain network closely related to that one that participates in motor behaviours (see Refs. [38,39]).

In the present experimental condition, we propose that the brain's motor system generates an internal representation of potential action related to the stimulus: as soon as the target disappears, the observer would simulate a reaching movement in the sagittal plane. The visual input would resonate with top down input only if the kinematic of the two inputs are sufficiently similar. Current observed velocity profiles would be compared to multiple stored kinematics engrams concerned with vertical motions covering different acceleration–deceleration ratios. The remaining difference would be projected back to the action system, in order to adjust the implicit motor simulation. From the simulated movement, the forward model that predicts the sensory consequence of the movement could be used to compensate the lack of visual input due to occlusion. Recent modelling [9,29] and experimental [13] studies support the plausibility of this view.

Note that our results strengthen the view that subjects are able to internally simulate, namely without making any movement, the dynamic context, that is the interaction of gravity with the moving limb. According to this, previous findings from our group [6,14,31,33], showed that subjects are able to accurately integrate gravity and inertial constraints during mental simulation of arm and whole body movements.

Brain imaging experiments could be designed to give neural meaning to this proposal. For instance, the correlation between the discharge of neurons in premotor cortex with biological and non-biological displays will reveal decisive information about the sensibility of mirror neurons to kinematic features of an action.

Eye movements can also contribute to subject's estimation of the final position of occluded target movement. In a similar study, Wexler et al. [44] showed a significant contribution of eye movement to the prediction of trajectories of moving objects. In the same way, Flanagan and Johansson [11] found that when subjects observe a reaching task, the coordination between their gaze and the actor's hand is predictive, rather than reactive, suggesting a direct matching between motor representation and action observation. On the basis of these studies one can hypothesize that the present differences in estimation are associated with tracking inefficiency because of irrelevant internal drive signal that cannot enhanced eye pursuit in the case of non-biological display. De'Sperati and Viviani 's finding [8] that passively observed biological trajectories are easier to track than trajectories following other velocities profiles supports this prediction.

In contrast to position estimation, time estimation (Experiment 3) did not differ with respect to the direction (up versus down) or the motion (biological versus non-biological). Because of equal motion duration in the four conditions tested (U, UN, D and DN) this result seems a priori reasonable. However, one can also expect higher variability in time estimation for NB display under the hypothesis of improves motion inference due to internal model matching. Nevertheless, in the present experimental conditions precise time estimation of short duration visual events (1 s) is difficult (the CE was about 25% of the total duration) and could mask a significant effect of motion display. This possibility could be verified with experiments showing movement displays with longer durations.

Our results indicate a better precision in end point estimation for downward motion compared to upward motion. This result may be the consequence of a visual effect due to the different velocity profiles displayed for the two directions. Because upward biological display presented longer visible deceleration phase compared to downward display (186 ms and 136 ms, respectively), this hypothesis seems not acceptable. Alternatively, the direction effect could be due to asymmetries in the representation of upper and lower portions of the visual field [7,36]. According to these authors, lower visual field would be more efficient in visual signal processing for the control of many goal directed movements. Moreover, it has been argued that attention has a higher resolution in the lower as compared to the upper visual field [16,41]. Together these differences in attention and perception processes across the vertical extent of the visual field might explain the greater error in EP estimation for upward than downward motion.

4.2. Implicit motion recognition

Our results demonstrate that motion reconstruction was possible despite a poor visual context where spatial relation between

effectors and target to reach is broken (object to grasp or target to reach). This demonstrates that a low-level visual attribute of motor activity such as the kinematic features of a simple dot is used by the visual system to categorize movement as biological or non-biological and thus reaches (or not) the motor system of the observer. Interestingly, we found that subjects were not able to explicitly recognize biological and non-biological motion (see Experiment 5) suggesting that fast processing pathway leads to immediate link between prediction of upcoming events and a representation of corresponding motor programs. Kinematic laws constraining action or object motion in the vertical plan could facilitate an automatic matching between perception and action. Indeed, kinematics in the vertical plane from living (i.e. arm or whole body movement, see [30,32]) and non-living object (i.e. a ball projected upward or falling down) present drastic differences (asymmetric velocity profiles with successive acceleration and deceleration phases versus constant acceleration or deceleration phases). This means that in terms of frequently occurring features, a clever viewer that grew up on earth (in a gravitational force field) would not be surprised at the observation of vertical motions. Thus, the perceptual expertise of the observer cannot be excluded to explain the different precision estimation of biological and non-biological displays. During the observation of a simple dot, these limited kinematic features could also lead to immediate recall of a forward model that contains specific trajectory details of whole arm movement in the sagittal plane.

The results show a significant effect of velocity profiles on end point estimation but not for the vanishing point estimation. Difference in the task demand may explain the lack of effect in the VP experiment. In most of the previous investigations, subjects were either asked to estimate the vanishing or the flashing point of moving objects and the response was given as soon as the target disappeared. In contrast, during the present end point estimation, expectation activity appears because the response is delayed after the moving target disappears. Moreover, the subjects were forced to actively reconstruct the end position of the hidden part of the trajectory. These aspects of the task could implement attentional mechanism facilitating selection of one out of possibly several corresponding motor primitives and the modulation of visual receptive visual field by attentional load. By the same token, attentional stress would boost up the resonating between visual input and internal models of action in several part of the brain that have been demonstrated to be involved in both perception and action events.

This assumption is supported by anatomical considerations showing horizontal connections of the visual system within areas, and higher areas providing feedback, that result in dynamic changes in receptive field properties [24]. Such a recurrent processing from higher visual area could pre-activate neurons with vertical motion receptive field in primary visual cortex and beyond, and accelerate the perception–action matching process. The present report suggests that internal brain state like attention facilitates overlapping of perception onto action representation.

5. Conclusion

The present study quantifies the human ability to reconstruct and estimate the missing section of the trajectory of a decelerating visual stimulus. Our results indicate that kinematic features of the motion provide a memory template for motion recognition. The motion display of a single dot that respects biological laws is sufficient to evoke implicitly internal model of action. The finding of a rapid mechanism that converts kinematic terms of the visual scene into potential motor representations would give a strong biological advantage when reaching moving preys that suddenly disappears.

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