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Time perception of visual motion is tuned by the motor representation of human actions

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Several studies have shown that the observation of a rapidly moving stimulus dilates our perception of time. However, this effect appears to be at odds with the fact that our interactions both with environment and with each other are temporally accurate. This work exploits this paradox to investigate whether the temporal accuracy of visual motion uses motor representations of actions. To this aim, the stimuli were a dot moving with kinematics belonging or not to the human motor repertoire and displayed at different velocities. Participants had to replicate its duration with two tasks differing in the underlying motor plan. Results show that independently of the task's motor plan, the temporal accuracy and precision depend on the correspondence between the stimulus' kinematics and the observer's motor competencies. Our data suggest that the temporal mechanism of visual motion exploits a temporal visuomotor representation tuned by the motor knowledge of human actions.

The perceived passage of time often does not match the physical temporal length of an event and time estimation, like visual perception of length or shape, is frequently subject to several types of illusions. It is well known that duration perception of rapidly moving stimuli is distorted and causes a subjective time dilation. For instance, time distortion can be induced by velocity[1–3], visibility[4], temporal frequency[5] and complexity[6,7]. Moreover, there is no dedicated sensory organ to directly measure the passage of time, which appears to be a subjective quantity evaluated using the perception of change from several sensations. However, sensory stimulation signals rely on processes of different speeds and different cortical areas providing heterogeneous time measurements, and all these inconsistencies may cause potential perceptive biases in duration judgments[8].

These limitations are in strong discrepancy with the high precision of human interaction with moving objects. Indeed, common daily life gestures (e.g. hand shaking), as well as sport activities require temporal judgment about changes in position over time and at last the translation of the temporal estimation to an appropriate motor output. How can the brain compensate for these sensory limitations to efficiently interact with the environment?

One possibility to improve temporal estimation is to rely on priors or top down influences. For instance, it has been demonstrated that the sense of time works through Bayesian inference and expectations of change in the natural environment[9]. It has also been hypothesized that the motor representation of human actions calibrates the temporal perception of visual events[10,11]. However, to date, this possibility has not been demonstrated yet, although some works have proven that visualizing a whole body motion e.g.[11–14] or the execution of an action prior a visual stimulation e.g.[15] can alter subjective time. This idea implies a common temporal representation between the action and vision systems, a possibility that still remains controversial.

The present investigation aims at verifying whether a specific visuomotor mechanism relying on the motor representation of human actions (or internal models of action) can mediate our perception of time. Most of the previous protocols, although interesting for examining the perception of time, present several limitations to address this question. Indeed, a pure perceptual task, a rare situation encountered during daily life activity, artificially disconnects the perception phase from the following motor output phase. Thus, to verify the existence of a functional relationship associating the time estimation process to the motor system, we manipulated both the visual stimulation and the task.

Concerning the visual stimulation, we designed a protocol (Figure 1a,b) to exploit the invariance of the kinematics of human movements in order to understand the role of motor representations in time perception.

Therefore, the two conditions reflected the kinematic properties of the visual stimulus that reproduced or not natural human arm movements. Thus, we took advantage of the well-known subjective time dilation[1–3,5–7] that is induced by the stimulus high velocity (a greater density of events[5] with respect to a visual stimulus moving at a slower velocity for the same space). Consequently, we were able to test whether the temporal estimation of a fast moving object improves when it accelerates and decelerates according to human movement's kinematic rules (to simplify hereafter called Bio) compared to a stimulus displayed at constant velocity (to simplify hereafter called NBio). If our hypothesis is true, the accuracy of participants' responses should depend on the compatibility between the kinematics displayed and the motor repertoire.

Regarding the tasks, observers were asked to replicate the duration of a dot moving in the vertical plane by moving their right arm along the vertical plane or by holding down a key. In this way we were able to investigate whether the temporal judgment was task dependent or corresponded to a general mechanism linking the temporal analysis of visual motion to the motor system. One can expect a priori a better temporal estimation for a motor response mimicking the visual stimulus (arm movement, hereafter called Task A) compared to a task (key press, hereafter called Task K) completely unrelated to the stimulus' motion. Conversely, a similar performance in timing the duration of external events in the two tasks would indicate the presence of a general sensorimotor mechanism tuning the temporal estimation of the observed motions. The results show that the temporal mechanism of visual motion exploits a temporal visuomotor representation calibrated by the motor representation of human actions.

Results

Time Reproduction experiment: the accuracy and precision of time perception are influenced by the observed motion's kinematics independently of the tasks. In the *Time Reproduction experiment* (Figure 1a,b) participants were asked to reproduce the duration of a moving dot with the kinematics encoded (Bio) or not (NBio) in the human motor rep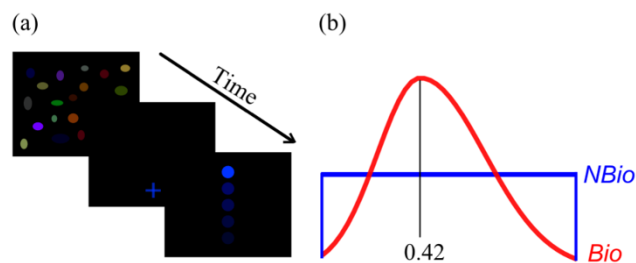ertoire displayed at six different mean velocities/durations. Participants had to replicate its duration through two different tasks differing in the motor plan: an arm movement (Task A) or a button reproduction (Task K). First of all we checked in both tasks, and for all stimuli durations, whether the participant's temporal reproduction (i.e. accuracy and precision) was significantly influenced by the observed motion's kinematics. Thus a preliminary data evaluation by a three factors mixed-model analysis of variance (Task, Stimulus and Time) was conducted on accuracy and precision. Where the three factors considered as sources of variability were: Task (A and K), Stimulus (Bio, NBio), and Time (6 durations/mean velocity of the stimulation).

Figure 2a represents participants' accuracy in replicating the visual event duration (ΔE) as a function of the stimuli mean velocity. A decreasing exponential model was applied to fit the data ($R^2 > 0.92$ in all experimental conditions). The statistical analysis for the accuracy, as illustrated in Figure 2a, shows that the two tasks (Task A, Task K) do not differ significantly, whilst there is an interaction between Stimulus (kinematics: Bio, NBio) and Time (or mean velocity, see also Figure 2b for a linear representation of the same data in terms of durations), responsible for marked differences in participants' responses $(F(5,36) = 131.7, p < 0.0001)$. The significant differences concern the sub-second interval of time (velocity: 52–131°/s), where the fast stimulus motion[1,2,3,5,6] induced a systematic subjective time dilation in NBio conditions (blue trace), but not in the Bio
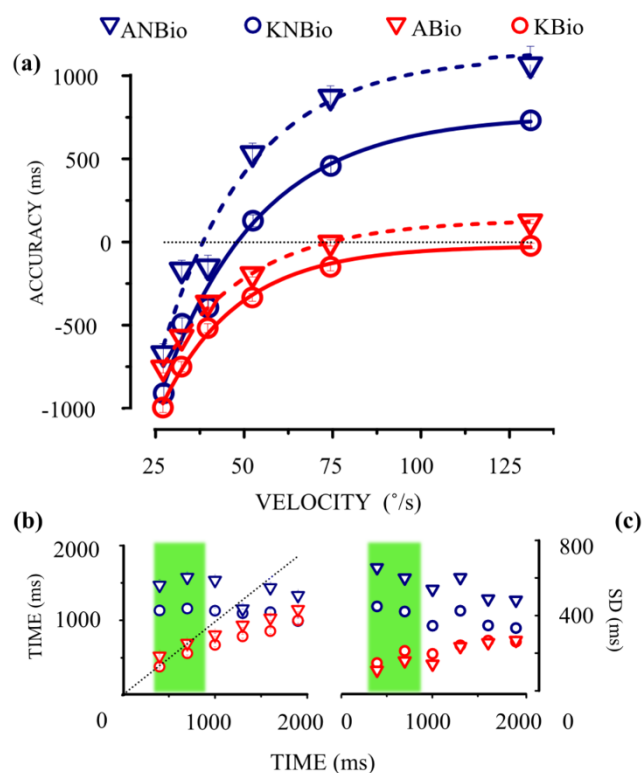

Figure 1 | Experimental procedure. Stimuli sequence (a) and velocity profiles of the dot displayed (b). Each trial started with a mask of two-dimensional randomly distributed small discs, randomly variable in luminance and colors (with diameters between 2° and 20°) covering an area of about 100° in diameter. Then a blue cross indicating motion starting position appeared. The cross was replaced by a blue dot moving upward according to the biological law of motion (Bio, bell-shaped velocity profile, Figure 1B, red line) or violating it (NBio, constant velocity, Figure 1B blue line). When the dot vanished participants had to reproduce the duration of the visual stimulus in two different ways: by moving their right arm along the vertical plane (Task A) or by holding down a key (Task K). Thus in Task A, participants were instructed to point to the cross preceding the appearance of the dot with their right arm, to keep the arm in this position while observing the dot motion, and to perform an upward arm movement of the same duration as soon as the stimulus vanished. Instead in Task K, participants had to watch the dot motion, and, when it disappeared, to hold down a keyboard button as long as they had perceived the duration of its motion.

Figure 2 | The visual kinematics modulates the temporal estimation. Each symbol indicates the mean value (±standard error). The colors code the Stimulus (red - Bio kinematics, blue-NBio constant motion), whereas the shape codes the Task (circle-key K, triangle–arm A). The green zone highlights the region where stimulus duration was close to the natural arm movement duration. (a) Accuracy. ΔEstimation (ms, y-axis)-as function of the stimulus velocity (°/s, x-axis). In each experimental condition ΔE was calculated as the mean difference between time reproduction responses and stimulus durations. (b) Time Reproduction. Time (ms, y-axis) as a function of the -stimuli durations-Time (ms, x-axis). The black line indicates a perfect time reproduction. (c) Precision. Standard Deviation (y-axis) - as function of the -stimuli durations- Time (ms, x-axis).

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conditions (red traces) where this effect disappeared, as confirmed by the results of the Post-Hoc Newman-Keuls comparisons. In fact, in the sub-second interval of time, the stimulus significantly affected the performance (at each level of factor Time, all $p < 0.001$), while in the supra-second range of time (velocity $< 52°/s$) no significant differences appeared.

The response precision - standard deviation - is represented in Figure 2c as a function of the time (stimulus duration). A visual inspection (Figure 2a,b,c) shows that the precision and the accuracy seem to be modulated by the stimulus' duration and kinematics in a similar way (in particular comparing Figure 2a,b with Figure 2c). The statistical tests confirm this observation, showing a significant interaction between factors Stimulus and Time ($F_{(5,35)} = 13.46$, $p < 0.0001$). The post-hoc Newman-Keuls comparisons reveal that for the sub-second durations, the precision associated with Bio motions was significantly better (lower SD) than the one associated with NBio kinematics (all $p < 0.05$). Further, there is an interaction between Stimulus and Task ($F_{(1,7)} = 27.36$, $p < 0.0001$). The post-hoc Newman-Keuls comparisons indicate that the precision in Task A is significantly worse (higher SD) than the one in Task K for NBio conditions (all $p < 0.05$).

Notably, for both tasks the highest and the worst accuracy and precision (green range in Figure 2b,c) were obtained respectively after the observation of the biological or the non-biological stimulus moving at a velocity close to participants' natural pointing velocity ($80°/s$ -corresponding to a duration of 649 ms- a parameter measured in the preliminary experiment, see method).

To sum up, in the sub-second range of time the kinematics of the stimulus, regardless of the tasks, significantly affects accuracy and precision of participants' performance, with one exception for precision. In fact, although the accuracy does not differ significantly in both tasks, the precision in Task A is significantly worse than the one in Task K for NBio conditions. This is probably a side effect due to the musculoskeletal properties of the arm effector.

Time reproduction experiment: the compatibility between the internal models of action and the kinematics displayed calibrates time perception of visual motion. To validate our hypothesis (see introduction) we conducted another data analysis testing whether the temporal accuracy and precision recorded could depend on the compatibility between the motor representation of human actions (or internal models of action) and the kinematics displayed.

The musculoskeletal constraints of the arm imply an internal model that always produces for each potential movement a motor plan having an initial acceleration and a final deceleration phase (e.g. the Bio stimuli displayed). Consequently, the motor plan of the arm movements excludes the possibility that an arm could reproduce an observed constant velocity profile (e.g. the NBio stimuli displayed). For this reason, subjects' explicit task was not to mimic the observed velocity profile of the stimulus, but rather to reproduce its duration. Thus, if the motor plan of the arm movements (Task A) is not automatically and implicitly modulated by the stimuli's kinematics, the participants should only execute bell-shaped movements[13] for all the stimulus' durations presented.

On the contrary, in the sub-second interval of time (see Figure 3a, the typical subject) the arm velocity profiles' executed were not bell-shaped in the NBio conditions where several corrections appear (Figure 3a, blue traces), whereas they were bell-shaped in the Bio conditions (Figure 3a, red trace). These discrepancies suggest that in the Bio conditions the arm's motor plan was implicitly mimicking the velocity profile displayed with a good temporal accuracy. In contrast for the NBio conditions the several corrections in the motor plan could derive from some attempts (without any possible success) to mimic the kinematics displayed, maybe causing the subsequent bad temporal accuracy.

These qualitative observations could suggest that the compatibility between the kinematics observed and the internal models of action implicitly affect both the motor plan and the temporal accuracy.

To verify such a relationship, the degree of correspondence between the visualized and executed velocity profiles was quantified by the proportion of one shot movements (POS), computed as the number of movements without any correction divided by the total number of movements executed for each condition (from the Task A, see methods).

Inspecting Figure 3b,c it is visible that, across all stimulus durations, a negative linear relationship bridges over the POS with both the temporal accuracy ($|\Delta E|$) and the precision (Sd). This is supported by the following correlation indexes: $\rho(\Delta E_{Bio}, POS_{Bio}) = -0.97$; $\rho(\Delta E_{NBio}, POS_{NBio}) = -0.75$; $\rho(Sd_{Bio}, POS_{Bio}) = -0.94$; $\rho(Sd_{NBio}, POS_{NBio}) = -0.18$.

Indeed, there is a strong (Figure 3b,c) relationship of positive proportionality between the absolute difference of the POS associated to the 2 kinematics (Bio, NBio) at each duration of the stimuli observed and the absolute difference of the accuracy or precision respectively associated to the 2 kinematics (Bio, NBio). This relationship indicates that, more important than the type of kinematics observed, is the motor knowledge associated with it and possibly related to the temporal estimation.

In order to quantify this direct proportionality a correlation coefficient related to Task A between $d\Delta E$ and $dPOS$ was computed.

$$\rho(d\Delta E, dPOS) = \frac{\sum_{i=1}^{n} Cov(d\Delta Ei, dPOSi)}{\sum_{i=1}^{n} Sd(d\Delta Ei) \sum_{i=1}^{n} Sd(dPOSi)} \quad (1)$$

where, n is the number of stimuli duration presented (all levels of factor time, that is $n = 6$), Cov and Sd are referred to covariance and standard deviation, respectively. The $d\Delta E$ was calculated as absolute value of the difference between the mean accuracy associated to the two types of kinematics for each level of time: $d\Delta Ei = |\Delta Ei_{Bio} - \Delta Ei_{NBio}|$. The $dPOS$ was computed as absolute values of the difference between the POS values associated to the two kinematics, consequently for each level of time: $dPOSi = |POSi_{Bio} - POSi_{NBio}|$. The result of the correlation shows a positive and high index: $\rho(d\Delta E, dPOS) = 0.98$, as expected from the visual inspection.

In the same way we have computed the precision correlation with the POS, which is between the dSd, and $dPOS$ ($\rho(dSd, dPOS)$; where $dSdi = |SDi_{Bio} - SDi_{NBio}|$). The result of the correlation analysis shows a positive and quite strong coefficient: $\rho(dSd, dPOS) = 0.76$.

According to the indexes presented above, the temporal accuracy and precision of the arm movements correlate with the implicit capacity of the motor system to correctly plan and replicate the stimulus' kinematics displayed.

Hence if it is true that the prior knowledge of the internal models of action is calibrating the time perception of visual motion, then the accuracy and the precision obtained from Task A should be replicated, at least as a trend, for a task totally different with respect to the motor plan required such as Task K.

In fact, Figure 3b,c (all participants) shows that the two tasks have the same trend of accuracy (ΔE) and precision (the size of the slopes). More precisely, Figure 3b illustrates that for both tasks (Key, the left column; Arm, right column), in all the six displayed motion durations (shorter in upper row, longer in lower row), the accuracy and the precision of the reproduced durations (the distribution of the answers) are equally modulated by the stimulus kinematics (Bio, red traces; NBio, blue traces).

To critically test this hypothesis, we correlated the temporal accuracy and precision of Task A with the accuracy and precision in Task K, which has almost no physical constraint and a totally different motor plan:
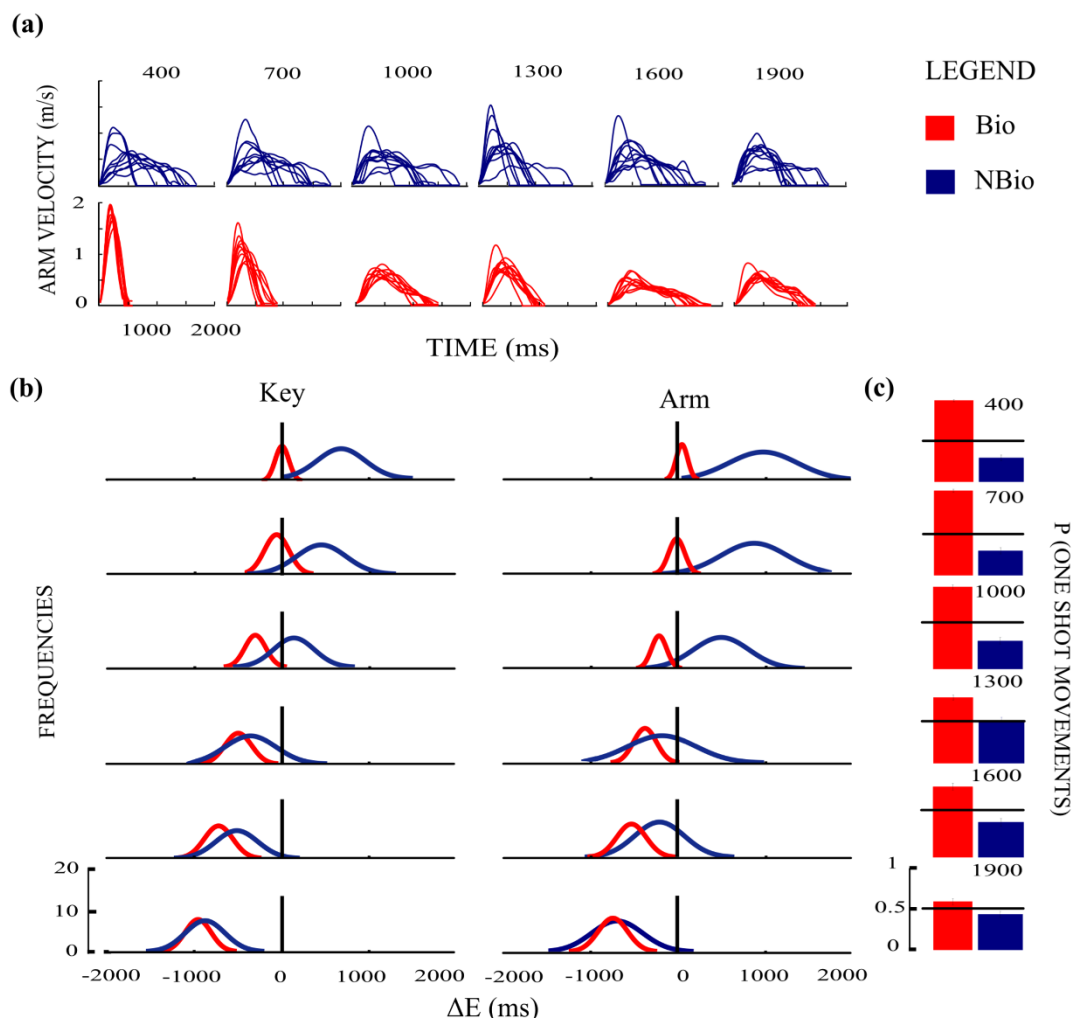
Figure 3 | The matching between the stimulus' kinematics and the internal models of action calibrates the temporal performance. The colors code the stimulus kinematics (red-Bio, blue-NBio). (a) Arm performance of a typical subject. Velocity (m/s, y-axis) as function of time (ms, x-axis). At the top of each row is reported the duration of the stimuli displayed. Each curve drawn represents a single trial. In both B and C panels each row corresponds to participants' responses accuracy to one stimulus duration (top 400 ms, bottom 1900 ms). (b) Distributions of the accuracy computed from participants' responses fitted with Gaussian functions. Left and right columns refer to the tasks K and A, respectively. The x-axis reports the accuracy of all the duration of participants' responses (Bins equal to 15) whereas the y-axis indicates how many times the response occurs (frequency). (c) Proportion of one-shot movements. Each histogram represents the proportion of one-shot movements in correspondence to each stimulus duration and kinematics.

$$\rho(Ad\Delta E, Kd\Delta E) = \frac{\sum_{i=1}^{n} Cov(Ad\Delta Ei, Kd\Delta Ei)}{\sum_{i=1}^{n} Sd(Ad\Delta Ei) \sum_{i=1}^{n} Sd(Kd\Delta Ei)} \quad (2)$$

Where, n is the number of stimuli duration presented, $Ad\Delta Ei$ and $Kd\Delta Ei$ are referred to the accuracy (i.e. $d\Delta E$ computed as previously described) obtained in both tasks (A,K). The result of the correlation shows a positive and very strong index: $\rho(Ad\Delta E, Kd\Delta E) = 0.98$. Applying the same equation we computed the precision correlation between $AdSd$ and $KdSd$ (i.e. dSd computed as previously described). The result of the correlation analysis shows a positive and very strong coefficient: $\rho(AdSd, KdSd) = 0.97$.

To sum up, the accuracy (ΔE) and precision (SD) of the arm movement are strongly correlated to the POS. Further, the accuracy and precision of the two tasks K and A strongly correlate together. Hence, such relationships exclude the possibility that the difference in temporal accuracy and precision obtained between the Bio and NBio conditions in the sub-second interval of time conditions would be due to the motor constraints or the specific motor plan required by the protocols. This result strongly reinforces an involvement of the internal models of action to the calibration of the time perception of visual motion.

Time reproduction experiment: The compatibility between the human motor repertoire and the kinematics displayed reduces the reaction times in both tasks. The reaction times are an index of the efficiency of the motor system to elaborate the motor plan associated to the kinematics presented. Hence, if our hypothesis is true, the compatibility of the participants' motor repertoire with the kinematics displayed should reduce the RT in Bio conditions for both tasks and not exclusively for Task A[22]. Nevertheless, the RT under Task A conditions could be faster for the spatial correspondence between the source of the stimulation and the effector response[23]. A three factors mixed-model analysis confirms our expectations showing a significant effect of the factor Stimulus on RT. In fact, RT was significantly shorter in Bio than in NBio conditions (see Figure 4a) in both tasks $(F(1,7) = 17.52, p < 0.01)$. Furthermore, the factor Task significantly affects the participant's responses: i.e. the motor response in Task A occurred significantly earlier than in Task K $(F(1,7) = 10.27, p < 0.05)$.

Control experiment: The evaluation of starting and ending positions of the visual motion are not affected by the different kinematics. To avoid that the different temporal accuracy following
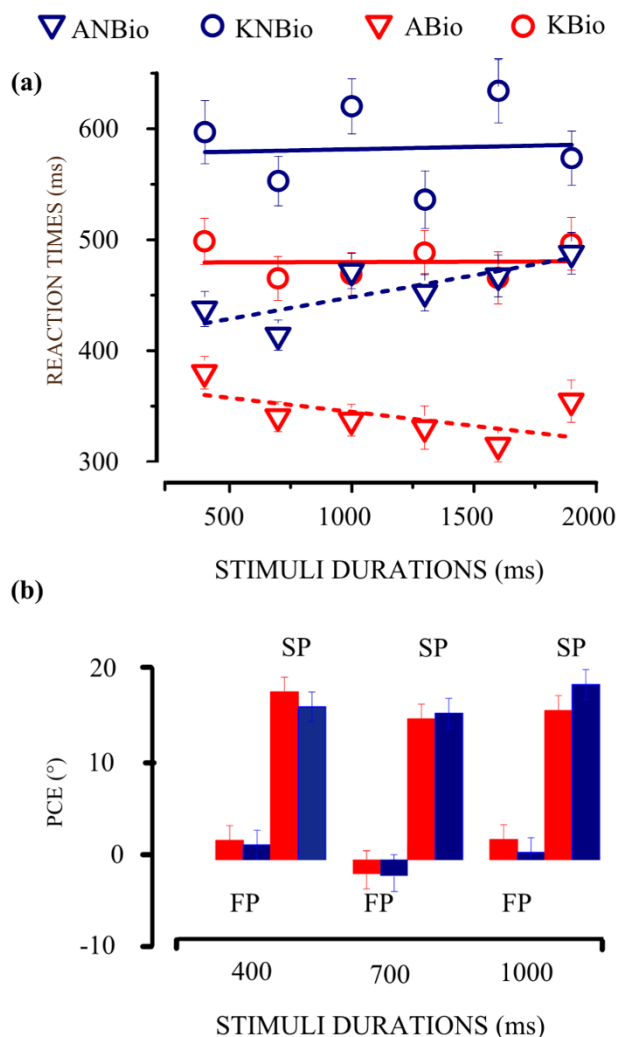
Figure 4 | Reaction Times and Spatial Accuracy. The colors code the Stimulus (red - Bio kinematics, blue - NBio constant motion), whereas the shape codes the Task (circle-key K, triangle–arm A). (a) Reaction times as a function of the -stimuli durations- Time. (b) PCE (±standard error) as a function of the stimuli durations. Positive values indicate errors in the direction of the stimuli motion. Each histogram is respectively named FP or SP in relation to the final or the starting position of the evaluation.

Bio and NBio motion observation could be attributed to the inaccuracy in stimulus position estimation, participants were asked to estimate the starting and the ending positions of the stimulus (i.e. factor Session, see methods). Figure 4b represents participants' spatial accuracy (PCE) as a function of the stimuli durations (i.e. factor Time), showing that participants' spatial accuracy was not affected by the displayed kinematics (red-Bio, blue-NBio, i.e. factor Stimulus). A three factors mixed-model analysis of variance was conducted on PCE (Stimulus, Time, Session) confirming that participants' spatial accuracy was not affected by the displayed kinematics. Instead, a main effect of Session appeared ($F(1,5)=27.4$, $p<0.005$), indicating that subjects were less accurate to evaluate the initial than the final position.

Discussion

This study tested the existence of a functional relationship between the time estimation process of visual motion and the motor system. Our data analyses show that both the temporal accuracy and precision recorded are associated with the congruence between internal models of action and the kinematics visualized. In fact, the performance's

accuracy and precision significantly improved for both tasks in the sub-second intervals depending on whether the visual stimulus moved or not (constant velocity profile) according to the human motor repertoire.

Importantly, our results are not in agreement with the findings that a stimulus with a higher density of events or complexity - changes such as successive accelerations and decelerations - lengthens the subjective experience of time[5,24]. More precisely, in the sub-second interval of time we found that the duration of the fast constant speed stimulus was overestimated, a result in agreement with previous discoveries showing that the perceived duration of visual object motion increases with speed (that is, the density of events visualized in a stimulation)[1–3]. However, participants' performance became significantly more accurate and precise for accelerated-decelerated motion (i.e. Bio stimulus), especially when the visual display reached the natural execution duration and for faster motions. Indeed, one could have expected the reverse since perceptual detection and discrimination of accelerating or decelerating movements are usually poorer than those of constant speed[25–27].

Considering the arm movement reproduction (Task A), one may argue that the movement of the rising dot may be perceived as much in terms of movement as in terms of time perception. This argument is based on idea that the influence of the perceived kinematics on the executed motion could contribute to a better temporal estimation of the motion compatible with the human motor repertoire[28]. Alternatively, one may hypothesize that observers would simply mimic the stimulus' kinematics instead of estimating its duration.

However, although participants were requested to reproduce only the duration of the moving dot and not its kinematics, the velocity profile's smoothness reproduced by the arm movement and its temporal correctness were implicitly affected both from the different kinematics visualized and their durations (Figure 3a,b,c). This observation is validated by the strong correlation found between the temporal accuracy and precision of the arm movements with the degree of correspondence between the visualized and executed velocity profiles of the arm movement reproduction [$\rho(d\Delta E, dPOS)=0.98$; $\rho(dSd, dPOS)=0.76$, see results and Figure 3b,c].

So, according to this correlation we could believe that the implicit capacity of the motor system to correctly plan and replicate the stimulus' displayed kinematics is strongly associated to the capacity to correctly time a visual motion.

This idea is sustained both by the lack of a significant difference in temporal judgment (between A and K Tasks) and by the tight correlation between the temporal accuracy and precision of the two tasks [$\rho(Ad\Delta E, Kd\Delta E)=0.98$; $\rho(AdSd, KdSd)=0.97$, see results and Figure 3b,c]. For this reason, the possibility that the difference in temporal accuracy and precision obtained between the Bio and NBio conditions is due to the motor constraints or the specific motor plan required by the protocols, can be excluded. Thus the alternative and potential explanation of a mimicking effect is invalidated as well.

Therefore, our results suggest that the prior knowledge of the internal models of action calibrates the time perception of visual motion belonging to the human motor repertoire.

Attentional processes, which are more involved when observing a moving dot that continuously change in velocity, could also explain the different participants' performances in timing the two kinds of visual stimuli. However, this possibility is contradicted by the fact that attentional effect is classically associated with time dilation[29–32], an effect here mainly recorded for stimuli following the NBio kinematic.

To summarize, in this study the proposal that a higher density of events (or fast velocity[5]) and intrinsic complexity (resulting from continuous velocity variations) would generate systematic errors does not extend to visual kinematics belonging to the human motor repertoire. Rather, our finding is that dynamic stimuli are better reproduced than constant velocity stimuli, independently of the visual stimulation's velocity or complexity, suggesting that perceived

duration relies on a motor prior. The results of the Control experiment are in agreement with this proposal. Indeed, the fact that the difference among performances after Bio and NBio kinematics observations were not due to inaccurate onset and offset stimulus spatial location agrees with the idea that time perception of visual motion is not processed based on local retinal coordinates but relies on central representations that link space and time[33,34].

Biological events, as natural and predictable ones, produce stimuli with high probability, facilitating the decoding of the temporal structure of the visual scene[9,35]. Accordingly, old and more recent evidence has suggested that perception exploits implicit knowledge of the structure of the environment[9,36,37]. However, the present work makes a step forward in showing that encoding of visual event duration also uses the observer's knowledge of the internal models of action. This agrees with the proposal that the brain constantly calibrates its time estimation to take into account the physical laws of the outside world[11]. Accordingly, the position of an inanimate object (e.g. a falling ball) at a given time in the near future would be predicted by a forward internal model of Newtonian mechanics and compared with visual feedback to keep the perceived time calibrated[11,13]. Hence we propose here that in the case of body motions, the position of the stimulus would be predicted using the corresponding motor plan (here, the specific timing of acceleration and deceleration phases of arm movement[38]) whereas the temporal estimation would result from the matching between the internal models of action and the visual kinematics in the input. Following this idea, one can speculate that when the kinematic of the visual event matches the natural duration of the arm movement kinematic (Bio stimulus), the arm reproduction should agree with the optimality principle for natural pointing movements[39]. More specifically, when the stimulus moving upward reproduced the subject's nominal upward pointing movement kinematic, the corresponding motor output is optimal and the energetic cost minimized[40]. As our data suggest, temporal estimation significantly improved in both tasks when the stimulus velocity was in the range of participant's natural movement velocity and degraded when the kinematic displayed was far from participants' natural action pace. Further, when the temporal estimation relied on visual representation incompatible with motor optimality (e.g., for constant velocity stimulus or slow velocities), the resulting discrepancy altered participant response in both tasks.

Moreover, according to our outcomes one may speculate that the temporal processing of kinematics compatible with the human motor repertoire may rely on a common neural network that encodes both the kinematics of observed and executed movements. For instance, it is well accepted that the superior temporal sulcus area (STS) is responsible for recognizing biological kinematics[e.g.41]. Therefore, we hypothesize that this information could be sent from the STS to the fronto-parietal mirror neurons system as shown in the imitation circuit[42–46]. A circuit, which could be involved in a matching process between the kinematics visualized onto the motor repertoire in order to calibrate the temporal accuracy and precision of the estimation. Indeed some neurons in the parietal cortex and motor areas seem to reinforce this possibility being able to represent the elapsing of time[47,48].

To conclude, we propose that temporal processing of visual motion is constrained by visuomotor transformations that match the visual input with the motor competences that in turn would calibrate the temporal estimation. This possibility agrees with the idea that timing is distributed across many brain areas capable of temporal processing[49,50]. Therefore, the observer's motor repertoire would provide an egocentric frame of reference, in which the visual events moving status is referred to the observer frame of reference that has been suggested crucial for subjective temporal processing[35]. Lastly, because temporal scaling of visual events is rarely disconnected from subsequent execution of actions, we speculate that the motor system may represent a generic and integrative calibrator embedded in perception of time for efficient human-environment interactions.

Methods

This study was divided into three experiments called *Preliminary experiment*, *Time Reproduction experiment* and *Control experiment.*

Participants. A total of fourteen healthy young adults took part in the experiments. Eight participants (M=4, F=4, age mean= 24.5, sd= 3.6) performed both the *Preliminary experiment* and the *Time Reproduction experiment*. Six different participants (M=3, F=3, age mean= 28.1, sd= 1.7) performed the Control experiment. All participants were naive with regard to the purpose of the study, right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained from each participant in the study, which was approved by the local ethical committee ASL-3 ("Azienda Sanitaria Locale", local health unit), Genoa, and was in agreement with the Helsinki Declaration of 1975, as revised in 1983.

Apparatus. All the experiments were performed in a darkened room. Participants sat on a chair, in front of a large rear projection screen (190×140 cm). A video-projector, with a refresh rate of 75 Hz, placed behind the screen and connected to a PC, back-projected the visual stimuli onto the display screen.

Preliminary experiment. This experiment aimed to measure the natural upward arm movement duration. Two vertically aligned light blue dots (2° in diameter) were displayed on a black screen for 2000 ms and placed at a distance of 52° from each other. The lower dot showed the starting position of the participant's arm, and the higher one was the target for the movement. When both dots disappeared participants were requested to perform single upward arm movement at a spontaneous and natural velocity toward the target dot. Each participant executed 20 repetitions preceded by a training phase of 5 trials. Movements were analyzed as described in *Time Reproduction experiment* (*Data analysis* paragraph). The mean subjects' natural arm movement duration was 649±91 ms.

Time Reproduction experiment. Visual stimuli. Participants observed single upward motions of a dot (2° of visual angle in diameter) at the viewing distance of 60 cm. The dot motion (Figure 1A) was included in a sequence of visual stimuli generated using MatLab Psychtoolbox 3[16]. The appearance of a green cross at the center of the screen cued the participants for the beginning of a new trial, which always started with a 100 ms mask in order to avoid retinal adaptation process. The mask was composed of two-dimensional randomly distributed small discs, randomly variable in luminance and colors (with diameters between 2° and 20° of visual angle), and covered an area of about 100° of visual angle in diameter. When the mask disappeared, a blue cross was displayed to indicate the movement starting position. Such initial position varied randomly across trials. After 150 ms, the cross was replaced by a blue dot that moved along a vertical, upward trajectory. The dot covered in all conditions a space of 52° of visual angle with six different durations (400-700-1000-1300-1600-1900 ms), and vanished at the end of its motion. The kinematics of the visual stimuli (Figure 1B) either corresponded to that of an upward arm movement (called biological motion/Bio, Figure 1B red line) or not replicable by the motor system (called non biological motion/NBio, Figure 1B blue line). In the Bio condition the stimulus velocity profile traced a bell-shaped curve: zero velocity at start, acceleration phase, deceleration phase, and stop[17,18]. In the NBio condition the stimulus velocity was constant along the entire trajectory (i.e. constant velocity profile), and corresponded to the mean velocity of the biological kinematics (for each stimulus duration).

Experimental procedure and design. Participants were asked to reproduce the duration of the visual stimulus in two different ways called: Task A (Arm) and Task K (Key). During the Task A, participants moved the right arm between the initial and the final position of the stimulus. They were instructed to point to the cross preceding the appearance of the dot with their right arm, to keep the arm in this position while observing the dot motion, and to perform an upward arm movement of the same duration as soon as the stimulus vanished. The participants' shoulder level was roughly at the middle of the dot displacement. One passive infrared reflective marker was applied onto the fingertip of each participant's right index finger, and a VICON motion capture system with seven cameras (sampling frequency of 100 Hz) recorded the movements. The Task K was a typical perceptual task of time reproduction[2,3,5]. So, participants had to watch the dot motion, and, when it disappeared, to hold down a keyboard button as long as they had perceived the duration of its motion.

Data analysis. The kinematic data recorded in Task A were low-pass filtered at 5 Hz using a 2nd order Butterworth filter. To define the onset and the offset of the movement, a threshold corresponding to 5% of the maximum velocity was applied. In both tasks the variables used to evaluate the performance of the participants were: time estimation error (ΔE), reaction times (RT), variability in the time estimation (SD) and proportion of one shot movements (POS, extracted from Task A). ΔE–or accuracy-was computed as the mean difference between the duration of the participants' performance and the duration of the displayed stimulus. ΔE=0 indicates a perfect estimation of the stimulus duration (evaluated by either holding down a key or producing an arm movement). SD-or precision-indicates the variability of the performance, and it is calculated as the standard deviation of the mean participants' time

reproduction. RT represented the time elapsed between the end of dot motion and the onset of participants' answers in both tasks. The POS was calculated as the proportion of one shot movements (i.e. movement with a bell-shaped velocity profile with no more than one peak) at each stimulus duration and for both stimulus kinematics. More precisely, a one shot movement has no corrections to the initially planned motion. Thus, in the sub-second range of time, if no problems occur during the motion planning phase, participants' movements had to be one-shot when performing an upward movement. Therefore, in this range, the POS gives information concerning the effect of the observed kinematics onto the motor planning.

Statistical methods. Three factors were considered as sources of variability: Task (A and K), Stimulus (Bio, NBio), and Time (6 durations), resulting in a total of 240 trials for each participant. In order to avoid any possible effect of learning or cognitive strategies, the order of Task was counterbalanced across participants, whereas Stimulus and Time were presented in a randomized order. Task A and K were separated by a resting of 20 min and they had a duration of 1 hour and of 40 minutes, respectively. A training phase of 10 trials preceded each task. During the experiment, a pause of 2 minutes occurred at the end of each block of 30 trials. Outliers values (more than twice the standard deviation from the mean) were removed from the analyses. A three factors mixed-model analysis of variance (Task, Stimulus and Time) was conducted on ΔE, SD and RT. This analysis was chosen for its flexibility to designs that are not perfectly balanced (as in this case), taking into account of the intrinsic (and uncontrolled) variability among the participants, everywhere treated as a random factor. Post-Hoc Newman-Keuls comparisons were applied to interpret significant interactions.

Control experiment. The purpose of the control experiment was to evaluate if the two kinematics were perceived with the same spatial length. In fact, according to the literature[19–21], time and space seem to be coupled and represented within a common metric, so that, the alteration of one dimension would impact on the other one. Hence, to discard the possibility that the temporal estimation associated to Bio and NBio observed kinematics was due to a different spatial accuracy (and consequently a different representation of the motion's length) we tested if subjects perceived equally the initial and the ending positions of the stimuli observed.

Visual stimuli. The same stimuli sequence (Figure 1A–B) applied in *Time Reproduction experiment* were used. However, because participants' ability to reproduce the observed biological movement durations were optimal in the sub-second range (see Results), only three stimulus duration were tested (400, 700, 1000 ms).

Experimental procedure and design. This experiment was divided into two sessions where participants were requested to indicate the starting or the ending position of the dot when it disappeared. In particular, the subjects were asked to move the mouse with their right hand in order to place the cursor where the displayed motion started or stopped, depending on the session. Subjects confirmed their choice by pressing the right mouse button. To prevent any cognitive bias, the initial position of the cursor was randomized among trials (from 3° to 10° with respect to the location opposite to that requested in the specific session).

Data analysis. Spatial accuracy (renamed position constant error, PCE) in estimating the starting (SP) and the final position (FP) of the stimulus motion was defined as the average difference between the estimated position and the true position.

Statistical methods. Three factors were considered as sources of variability: Session (Start, Stop), Stimulus (Bio, NBio), and Time (3 durations), resulting in a total of 120 trials for each participant. In order to avoid any possible effect of learning or cognitive strategies, the order of the sessions were counterbalanced across participants, whereas Stimuli and Time were presented in a randomized order within each Session. The total duration of the experiment was about 50 minutes. A three factors mixed-model analysis of variance (Stimulus, Time, Session) was conducted on PCE. This analysis was chosen for its flexibility to designs that are not perfectly balanced (as in this case), taking into account of the intrinsic (and uncontrolled) variability among the participants, everywhere treated as a random factor. Post-Hoc Newman-Keuls comparisons were applied to interpret significant interactions. No analysis was conducted on the variability because the value was almost the same in all the conditions.

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Author contributions

G.G., A.B., T.P. had the idea and design the experiments; G.G., A.B. prepared the experimental setup; G.G., A.B. collected the data; G.G. analyzed all the data; G.G., A.B., T.P. designed together the control experiment and wrote the paper.

Additional information

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