OPEN

Correspondence and
requests for materials
should be addressed to
A.C. (alessandro.
carlini@u-bourgogne.
fr)

Visual tracking combined with hand-tracking improves time perception of moving stimuli

Alessandro Carlini & Robert French

Laboratory for Research on Learning and Development (LEAD-CNRS), Université de Bourgogne, Dijon - France.

A number of studies have shown that performing a secondary task while executing a time-judgment task impairs performance on the latter task. However, this turns out not to be the case for certain motor secondary tasks. We show that concomitant secondary motor tasks involving pointing, when performed during a time-judgment task, can actually improve our time-judgment abilities. We compared adult participants' performance in a time-of-movement paradigm with visual pursuit-only and with visual pursuit plus hand pursuit. Rather than interfering with their estimation of stimulus movement duration, the addition of hand pursuit significantly improved their judgment. In addition, we considered the effect of three different movement profiles and four different movement speeds for the moving stimulus. As predicted by Vierordt's law, time judgments of shorter stimuli are overestimated and longer stimuli underestimated. Finally, timing performances appear to improve when the moving target follows a "biological" velocity profile.

Our effectiveness in everyday tasks depends on our ability to perform actions "on time". Action adjustment, multiple-task coordination or synchronization, and waiting, are examples in which the central nervous system evaluates and coordinates the flow of time and action production.

A considerable amount of work has been devoted to the study of timing abilities coupled to other temporal or non-temporal tasks[1]. In particular, researchers have looked at the deleterious effects of a variety of secondary tasks on the time perception. The fact that the performance of secondary tasks interferes with time perception has been called "one of the most consistent findings in the time- perception literature"[2].

Concomitant verbal functions, visual processing or spatial tasks tend to reduce the perceived time interval compared to a "no-secondary-task" control condition[3–5]. Cognitive tasks also cause shortening of perceived-time intervals and/or induce a larger error in time judgment[2,6,7]. This perceived shortening of time is mainly attributed to a reduction of mental resources (memory, attention, or processing capability)[2,3,5,6], or as the effect of contextual factors[4,6,7].

However, relatively little work has been done on the effect of motor tasks on time perception. Hawkins and Meyer[8] used a mechanical problem-solving task. Brown (1985)[6] adopted a mirror drawing and Brown (1997)[2] used a pursuit-and-tracking task. They found that the presence of a secondary motor task shortened perceived time. In other words, they demonstrate that concomitant motor tasks *interfere* with interval timing for the tasks performed by their participants.

In contrast, the goal of the present paper is to consider the extent to which a concomitant motor task could *improve* time-judgment performance. Based on the resource-economy principle of Navon and Gopher[9], Brown[2] has suggested that these results could be task-dependent. In other words, the appropriate choice of a concurrent secondary task could potentially make the principal time-perception task easier. We will use as a principal task the timing of an upward moving stimulus, and a visually guided hand tracking of the same target as the concurrent secondary task. In our first experiment, participants were asked to reproduce the time of movement of a target moving on a PC screen. After having seen the target move across the screen, they had to reproduce the duration of travel by pressing and holding a push-button positioned in front of the screen. In the second test they were asked to pursue the target during its motion with their dominant hand, and then to give their response in the same way of the first test. Because in the second test the focus of both tasks is on the same event, we expect better performance in the double-task condition compared to the "easier" simple visual pursuit of the moving stimulus.

Two other variables were manipulated in the present paper -- namely, the average speed of the target stimulus and its velocity profile. We examined three different velocity profiles ("Bio[logical]", "Tri[angular]" and
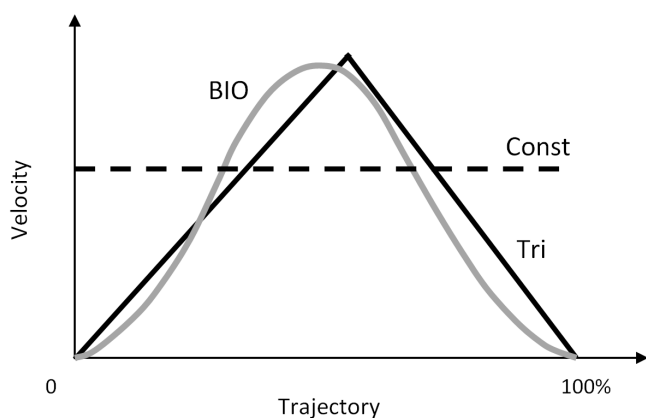
Figure 1 | Motion profiles. Three velocity profiles were used -- a "biological" (BIO, gray line), a "Triangular" (Tri, solid line) and a constant (Const, dotted line) profile. Four different average velocities were possible for each velocity profile: 5, 10, 15 or 30°/s.

"Const[ant]" imposed on the target motion: a biological type, a triangular shaped profile, and a constant velocity profile (Figure 1) Previous work by Pozzo and colleagues[10] and Carlini and colleagues[11] has demonstrated that performance on certain tracking tasks improves when the target follows a biologically plausible trajectory. Concerning the average velocity of the target stimulus, previous research has shown larger errors in determining the starting and the ending points of a moving stimulus as its velocity increases[12,13]. Thus, we can expect participants to demonstrate improved time-judgment accuracy for slower target velocities.

The key result of this paper is to show the benefit of motor function on timing for the type of task proposed. In the single-task condition participants tend to overestimate time durations[14]. The introduction of hand pursuit of the moving target as a secondary task significantly reduces the temporal estimation error. Four different durations were adopted for the stimulus motion; the analysis of the collected data shows a systematic overestimation of the shorter time intervals (in agreement with the Vierordt's law), and a systematic underestimation of longer intervals. Finally, in agreement with previous findings[15], the comparison between the three different velocity profiles shows that participants were more accurate in time perception when the moving stimulus followed a biological law of motion.

In summary, the present results demonstrate that the secondary motor task, rather than interfering with time-perception judgments, actually significantly improved them compared to a time judgment based on visual observation of the stimulus alone.

Results

To more easily identify the two main Tracking-Type conditions, we will designate them as follows: "Visual Pursuit Only" (VPO), and "Visual Pursuit + Hand Pursuit" (VPHP). Accuracy and precision of the participants' estimations in the VPO and VPHP conditions were evaluated in terms of Constant Error (CE) and Variable Error (VE)[16]. The CE was calculated as a difference between each subject response and the actual movement duration; negative values indicate underestimation of the time duration. The VE is calculated as a standard deviation of the responses of each participant, in each condition. We performed a multi-way ANOVA on CEs on the four within factors: Tracking-Type (VPO, VPHP), Movement-Type (BIO, Tri, Const), Velocity (Vel_1, Vel_2, Vel_3 and Vel_4) and Repetition (1 to 4). (We define the Movement-Types below.) The same four within factors are employed to perform the one-way ANOVAs on VEs.

An ANOVA showed the Tracking-Type main factor to be statistically significant $(F(1, 25) = 6.6033, p = 0.016527, \eta^2 = 0.2089)$.

Figure 2A presents the CE mean values for both conditions (mean Constant Error and SE - Standard Error, in seconds: VPO: CE = 0.1114 ± 0.09; VPHP : CE = -0.0098 ± 0.08). Figure 2A shows also the VE values for the same two conditions, for which a one-way ANOVA revealed significant statistical differences (mean Variable Error and SE, in seconds: VPO : VE = 0.5277 ± 0.04; VPHP : VE = 0.4811 ± 0.03; $F(1, 25) = 5.5602$, $p = 0.026$, $\eta^2 = 0.18$).

Figure 2B shows CE and VE for the three Movement-Types. The histogram shows in the Biological (BIO) condition a slight time underestimation (CE = -0.0575 ± 0.08), whereas in the two other "non-biological" conditions ("Tri" Triangular, and "Const" Constant velocity profiles), time judgments are generally overestimated by participants (CE = 0.0348 ± 0.08 and CE = 0.1751 ± 0.09, respectively for the Tri and the Const velocity profiles). A hierarchical repeated-measures ANOVA showed significant differences between motion types (i.e., between levels of the Motion-Type factor) $[F(2, 50) = 58.0631, p < 0.0001, \eta^2 = 0.70]$, and a Tukey HSD post-hoc confirmed significant differences among all conditions (between all conditions: $p < 0.001$). However, Variable Errors (VE) are similar for the three conditions (VE $\pm$ Standard Error: BIO = 0.5031 ± 0.04; Tri = 0.5188 ± 0.04; Const = 0.5019 ± 0.04) and a one-way ANOVA showed no significant difference between the conditions ($p = 0.570$).

Figure 2C shows the CE and the VE mean values for the four Velocity conditions. A four-way ANOVA analysis on CE showed Velocity to be a significant factor $[F(3, 75) = 121.3848, p < 0.0001, \eta^2 = 0.83]$. As evident by the diagram, the motion duration corresponding to the lower velocity appears to be systematically underestimated (vel_1: CE = -0.5448 ± 0.06), where in the other three conditions participants overestimated the time duration (CE = 0.0286 ± 0.08; CE = 0.2826 ± 0.11; CE = 0.4368 ± 0.10; respectively for vel_2, vel_3, and vel_4). The post-hoc test shows a remarkable difference among the four conditions (a Tukey HSD reported a $p < 0.001$ between each pair of conditions from Vel_1 to Vel_3, and $p = 0.0335$ between vel_3 and vel_4). Considering the VE values for the Velocity condition (VE: Vel_1 = 0.3027 ± 0.02; Vel_2 = 0.2954 ± 0.02; Vel_3 = 0.3765 ± 0.04; Vel_4 = 0.3558 ± 0.04) a one-way ANOVA shows this factor as significant $[F(3, 75) = 4.0076, p = 0.0106, \eta^2 = 0.13]$. A Tukey HSD indicates a statistically difference between Vel_2 and the Vel_3 ($p = 0.0256$). There is no significant difference for the Repetition factor.

The four-way ANOVA analysis revealed also a significant interaction between Movement-Type (BIO, Tri and Const) and Velocity $[F(6, 150) = 5.6908, p < 0.0001, \eta^2 = 0.18]$. Figure 3 shows the interaction between Movement-Type and Velocity. As indicated above there is underestimation of the movement duration for the slower velocity and an overestimation for faster velocity. A Tukey HSD post-hoc indicates all the pairs of conditions as statistically different, with the exception between BIO and Tri of the Vel_1 and Vel_2 conditions.

The interaction between Tracking-Type and Movement-Type is not-significant.

Discussion

The present work investigates the possibility that particular motor functions can improve our timing capabilities. We compared participants' timing performances in a single-task and a double-task paradigm, where the primary task involved visual pursuit of a visual target and the secondary task consisted of a concomitant hand pursuit (i.e. a motor task) of the same target. Rather than interfering with time-judgment performance, we found that the secondary motor task significantly improved it. This result could be explained by the availability of the efferent copy of the hand-pursuit motor control for the CNS[17–19] that enriches the perception of the temporal progression of motion.
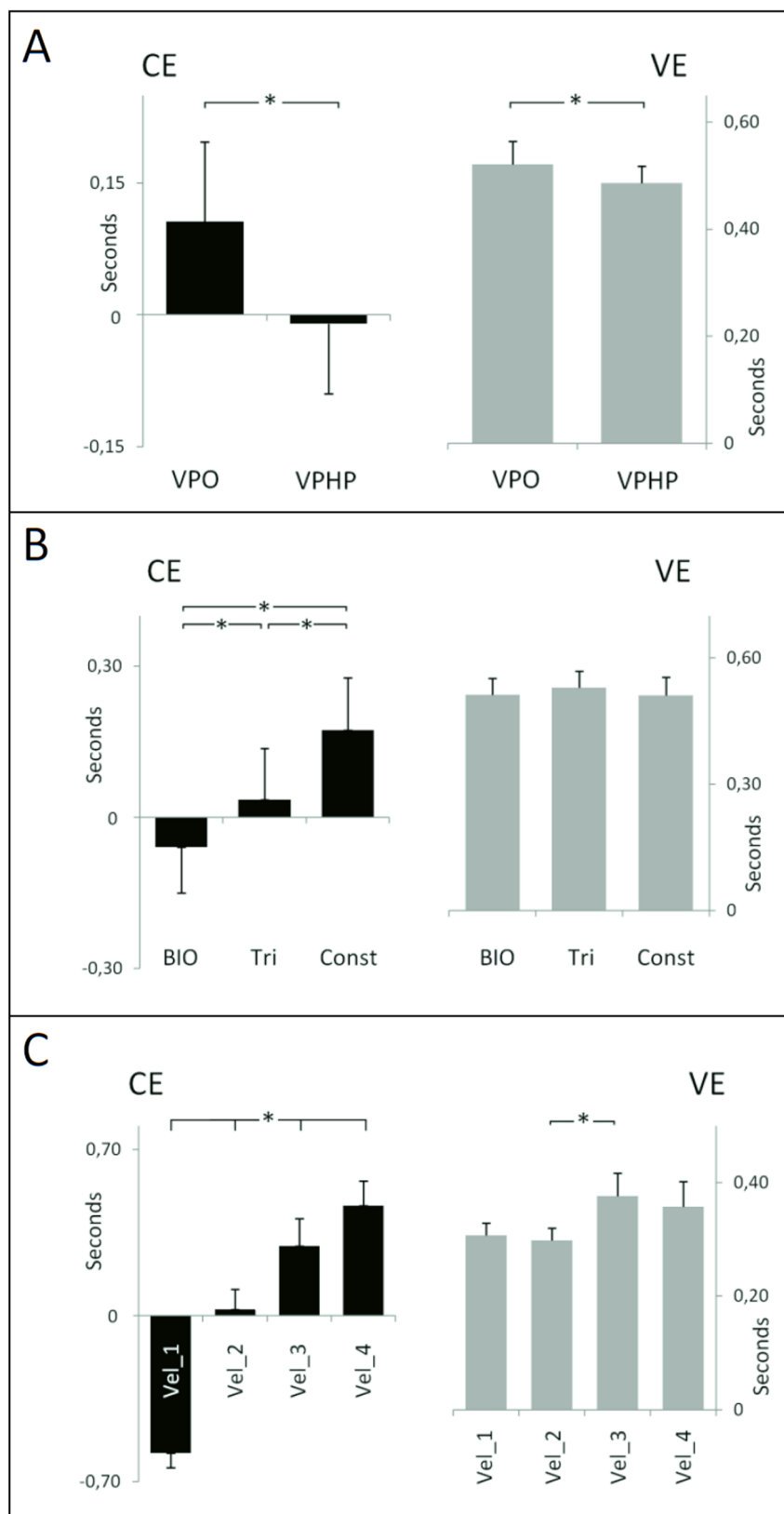
Figure 2 | Accuracy and precision. (A) - Constant Error (CE-black bars) and Variable Error (VE-gray bars) corresponding to the two Tracking-Type conditions: "Visual Pursuit Only" (VPO), and "Visual Pursuit + Hand Pursuit" (VPHP). (B) - Constant Error (CE-black bars) and Variable Error (VE-gray bars) for the three Movement-Type applied to the stimulus motion ("BIO" Biologic, "Tri" Triangular, and "Const" Constant velocity profile). (C) - Constant Error (CE-black bars) and Variable Error (VE-gray bars) for the four Velocities applied to the stimulus motion (5, 10, 15 and 30°/s, respectively for Vel_1, Vel_2, Vel_3, Vel_4). In all cases, Y-values are in seconds, error bars represent standard error of the mean (SEM) and stars indicate significant statistical differences. Positive values indicate overestimation of the motion duration.
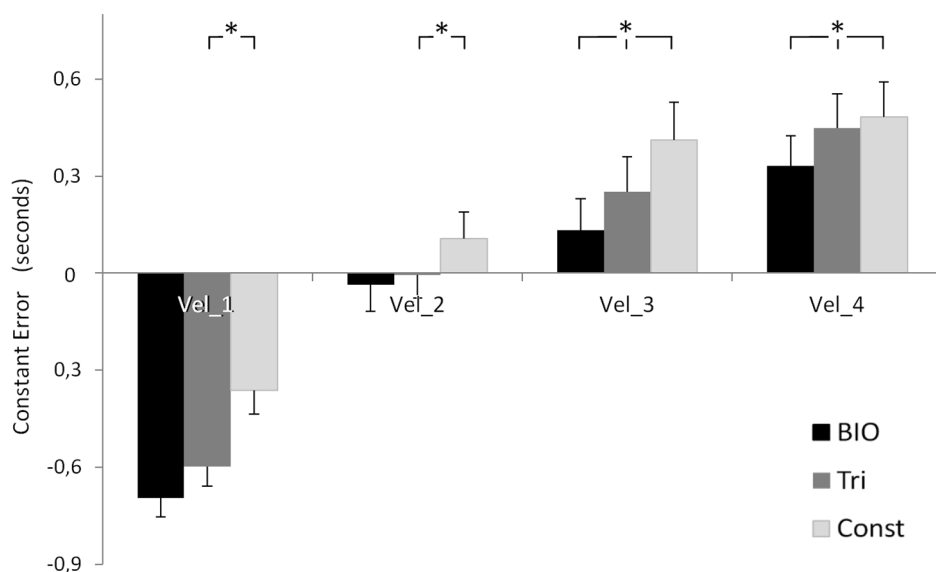
Figure 3 | Interaction between Motion-Type and Velocity. Constant Error for the three Motion-Types ("BIO" Biologic profile - black bars; "Tri" Triangular profile - dark gray bars; "Const" Constant velocity profile - light gray bars) and Velocity (5, 10, 15 and 30°/s, respectively for Vel_1, Vel_2, Vel_3, Vel_4). Positive values indicate overestimation of the motion duration. Y-values are in seconds, error bars represent standard error of the mean (SEM) and stars indicate significant statistical differences.

The experimental results in the single-task paradigm (i.e., the Visual Pursuit Only, VPO, condition) show that participants generally overestimate the duration of stimulus movement. A constant-error analysis shows that participants' time-judgment performance improved in the double-task condition compared to than in the single-task timing. The variable-error analysis indicates that, when the motor function was involved in timing, participants were more precise in their time estimates.

The overestimation of the duration of a moving stimulus that we observed is in agreement with previous findings demonstrating that the dilation of perceived time is a direct result of stimulus movement[14,20–22]. Brown (Brown, 1995[14], experiments 1 and 2) showed that static stimuli generally are not affected by this misperception. Poynter hypothesized the perceived time duration to be determined by the amount of changes experienced[23]. In a similar vein, Rovee-Collier[24] proposed that time perception varies according to a person's cognitive processing performed during a given interval. Brown[14] suggested that perceived "time dilatation" could be associated with the increase in changes experienced when the stimulus moves, because "… *moving stimuli occupy a sequence of different spatial positions, and thus provide to the observer a dynamic pattern of changing events*".

The effect on time-judgment of a secondary task associated with the primary task has generally been shown to be deleterious[1,2,7,25]. In contrast to these studies, the present study demonstrates that concomitant motor activity associated with the primary task can produce an improvement of timing performance, even though a combined motor pursuit task and a visual pursuit task is a more complex task than a visual pursuit task alone.

Gavazzi speculated about a potential positive effect of associating motor activity and visually based time perception[15]. However, their approach mainly focused on the benefit of biological motion perception and involved only a single-task paradigm. In the present paper, we investigated timing in two experimental conditions, with and without an associated secondary motor task. Our results show an improvement produced by motor functions on time perception, supporting the existence of a "concurrence benefit" theorized by Navon and Gopher[9] and applied specifically to time perception by Brown[2].

Numerous models have been proposed, to explain how the brain creates its internal representation of the time[1]. The principles underlying these models can be broadly classified into two categories: (1) those proposing the existence of dedicated functional structures for time perception (e.g. the pacemaker–accumulator model[26,27]; the multiple-oscillator model[28], etc.), and (2) those assuming that motor, sensory, memory and cognitive processes act to keep time during its activities[29–33].

The present results support the latter hypothesis. Research based on FMRI analysis of timing tasks and the study of focal brain lesions show the involvement of certain areas in time perception[34]. Spencer[35] and Bo[36] found decreased performance for motor timing when cerebellar lesions are present in the human brain. O'Reilly[37] observed cerebellum activation, as well as middle-parietal area activation, during spatio-temporal prediction tasks (see also Beudel[38]). Lewis & Miall speculated that the cerebellum was linked specifically to motor representations of sub-second durations[39]. Recordings of neuronal activity by Akkal showed activation related to the action timing in the pre-supplementary motor area[40]. These experimental results, taken as a whole, support the theory that the neuronal mechanisms to achieve timing are distributed across different brain areas and that internal motor representations associated with temporal activity can improve the perception of time and motion.

Participants saw a stimulus moving on a vertical trajectory on the screen at one of four possible average velocities. Their time-judgment responses showed (1) an underestimation of the motion duration at slower speeds, i.e., where the stimulus movement lasted 3 seconds, (2) a good accuracy with the motion lasting 1.5 seconds; and (3) a progressive overestimation of motion duration as the duration decreases from 1.5 up to 0.5 seconds (see Figure 2C).

These results are in agreement with the Vierordt's law that says, in a retrospective timing paradigm, shorter intervals of time are generally overestimated, and longer intervals are generally underestimated[41,42]. These errors have generally been explained as a memory effect and have been reported under a variety of different experimental conditions[14,43,44].

The work presented in the present paper supports this prior work on the influence of target velocity on time-duration judgments of moving stimuli.

The interaction between Tracking-Type and Movement-Type is not-significant, indicating that the support provided by the motricity improves performance irrespective of the type of motion.

The combined analysis of the Motion-Type and the Velocity (Figure 3) shows that time perception of a moving stimulus is better when the stimulus follows a "biological" law of motion[10,11] rather than other laws violating biological constraints, even if the latter appear less complex. This holds for all conditions except the slowest (3 seconds).

These findings are in agreement with previous work showing improved timing performance when the moving target follows a biological velocity profile. Carlini[11] and Pozzo[10] compared biological and non-biological kinematics by means of an investigation of the spatial localization of the starting and the ending points of a moving target. They found improved localization precision when the target followed the biological law of motion, demonstrating the availability and the benefit of the internal model of the biological kinematics. Recent work by Gavazzi[15] compared biological and non-biological motions in a single-task time-reproduction task. In the first condition participants had to reproduce the duration of a displayed straight-line motion by pressing a push-button; in the second condition they had to produce an arm-pointing movement whose duration matched the duration of a stimulus motion. Their results show the equivalence of the two conditions and the improved performance when the stimulus followed the biological law of motion.

Our results constitute the first confirmation of which we are aware – based on the task-accomplishment accuracy – of the improved capabilities in time perception when the stimulus follows a biological law of motion. Moreover, the constancy of the Variable Error over the three conditions indicates equal precision in participants' responses. This result strongly supports the hypothesis that internal models of action are used to calibrate the time perception of a visual motion.

In conclusion, the experimental results presented in this paper suggest an advantageous contribution of the motor system to visual perception when doing interval time judgments of moving stimuli.

Methods

Participants. Twenty-nine students/employees of the University of Burgundy took part in the experiment (10 m, 19 f, age: M = 26.21, SD = 5.13). All reported having normal or corrected-to-normal visual acuity. All participants were naive with regard to the purpose of the study; all participants performed both the single-task (a motion timing) and the double-task (a motion timing with a concurrent hand pursuit) tests. The protocol was in agreement with the Helsinki Declaration (1964 and subsequent revisions), the CNRS's guidelines (French National Center for Scientific Research), and the French Psychology Society Code of Conduct. The protocol was non-invasive and posed no risks for participants. French legislation for this type of research does not require approval by an ethics review board; a qualified person supervised the research. Written informed consent was obtained from each participant in the study.

Three participants gave responses more than twice the standard deviation from the mean of the group, and their data were removed from the analyses.

Apparatus and stimuli. The stimuli were displayed on a 17-inch color flat monitor (1280 × 1024). All stimuli were handled and displayed using the Psychophysics Toolbox for Matlab (Brainard 1997[45]; Pelli 1997[46]). Each stimulus was a light-gray disk (fifteen pixels in diameter, about 0.38° of visual angle) moving on a black background.

A push-button was situated in front of the screen at a comfortable distance (about 30 cm from the participant) to allow participants to give their responses.

The stimulus moved vertically in a straight line, as described below, within a presentation window of 1000 × 740 pixels centered on the screen. Each trial was randomly displayed in a different position within the presentation window.

The length of trajectory of the moving stimulus was 600 pixels in all trials (about 15 degrees in the participant's visual field). The stimulus always moved upward in a straight, vertical line. One of three different laws of motion was applied to the stimulus motion: one biological and two non-biological (Figure 1). The biological velocity profile (BIO) was obtained as the average velocity profile of several arm pointing movements, with straight arm and upward oriented, previously recorded in frontal view (Papaxanthis 1998[44]). The two non-biological laws consisted in a constant velocity profile (Const) and a triangular velocity profile (Tri), characterized by a linear acceleration and deceleration of the stimulus.

Each velocity profile was presented with one four possible average velocities: 5, 10, 15 and 30 degrees/second (corresponding to 3.0, 1.5, 1.0 and 0.5 seconds of motion duration). Each Velocity Profile with each Velocity was presented 4 times to each participant. The 48 trials (3 Velocity profile × 4 Velocity × 4 Repetitions) were presented in a random order. There were two conditions and a two-part familiarization phase as described below. The two conditions were i) Visual Pursuit Only (VPO), where the participants were told to follow the moving stimulus with their eyes only, and ii) the Visual Pursuit + Hand Pursuit (VPHP), in which they were told to follow the moving stimulus with their eyes and to follow the stimulus by pointing to it as it moved with their dominant arm.

Procedure. Each participant sat at a comfortable viewing distance from the screen (about 60 cm) in a dimly light room. Participants were informed that the experiment was composed of a familiarization phase and a trial phase. They were asked to make an informed guess about the duration in time of each displayed stimulus. Participants were also asked to push the button with their dominant hand only.

Each participant performed the three phases in the same order: (1) familiarization, (2) visual-pursuit-only condition (VPO), and (3) visual pursuit + hand pursuit condition (VPHP).

Familiarization. The familiarization phase consisted of two parts. It was very important for participants to be familiar with maintaining a button-press to reproduce a previously observed time interval. In addition, they needed to be familiar with using a button-press procedure to reproduce a dynamically evolving stimulus. Consequently, the familiarization phase was divided into two short sections, each lasting slightly less than 3 minutes.

In the first, participants were familiarized with button-pressing to reproduce a static stimulus that appeared on the screen. After reading the screen page with the written instructions, the participant was invited to start the test by pressing the pushbutton. This phase of the familiarization procedure was composed of thirty-two trials in which the participant was asked to reproduce the display duration of a static stimulus. Each trial began with a blank interval lasting 1.0–2.2 seconds, and then a green disk (about 40 mm in diameter) was presented in the center of the screen for a pre-determined duration. Sixteen different durations were possible, randomly selected between 0.4 and 3.4 seconds where each possible duration recurred two times. After the disk disappearance, the participant was asked to reproduce the perceived display duration by holding down the push-button for an equivalent time interval. The release of the push-button started the next trial. The new display occurred 0.2 seconds after the release of the push-button. This "static" familiarization phase lasted approximately 3 minutes. After completion of the first phase of familiarization, the second phase began. The task for the second phase of familiarization was equivalent to the first phase, except that the stimulus was not static, but moved upward on a straight trajectory. In this phase participants were explicitly asked not to visually pursue the moving stimulus. This familiarization phase was necessary to ensure that participants could apply the button-press procedure to reproduce the duration of a moving stimulus. The requirement that participants continue to fixate the fixation cross (rather than the moving stimulus) was necessary to avoid learning during familiarization.

Test 1: visual-pursuit-only (VPO) condition. In the first test, participants were asked to visually pursue the moving target (a light-gray disk) moving upward on the screen on a straight trajectory. The target moved according to one of the four velocity profiles presented in Figure 1, as previously described. Each of the 48 trials began with the presentation of an initial blank interval lasting 1.0–2.2 seconds; next the target appeared immediately began moving, and disappeared at the end of its motion. 0.6–1.2 seconds before the moving target appeared, a white dot flashed once for 150 ms, at the point where the moving stimulus would appear and start moving. After the moving disk disappeared the participant attempted to reproduce the duration of the moving stimulus by pushing and holding down a button in front of the screen with their dominant hand. The release of the push-button starts the new trial.

Test 2: visual-pursuit + hand-pursuit (VPHP) condition. Identical to the previous tests, except for the presence of the secondary task. During the motion of the stimulus, the participant was asked to perform a hand pursuit of the moving target, with the index of the dominant hand, from the beginning to the end of the stimulus movement. Because the disk was covered by the participant's finger during the pursuit, two thin lines (70 pixels in width and 2 pixels in height) were presented alongside of the disk.

Participants performed the experiment in less than 30 minutes. All participants were tested between 10.00 p.m. and 6.30 p.m.

1. Grondin, S. Timing and time perception: a review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, Psychophys.* **72**, 561–582 (2010).
2. Brown, S. W. Attentional resources in timing: interference effects in concurrent temporal and nontemporal working memory tasks. *Percept. Psychophys.* **59**, 1118–40 (1997).
3. Gautier, T. & Droit-Volet, S. Attention and time estimation in 5- and 8-year-old children: a dual-task procedure. *Behav. Processes* **58**, 57–66 (2002).
4. Sawyer, T. F., Meyers, P. J. & Huser, S. J. Contrasting task demands alter the perceived duration of brief time intervals. *Percept. Psychophys.* **56**, 649–57 (1994).
5. Zakay, D. The roles of non-temporal information processing load and temporal expectations in children's prospective time estimation. *Acta Psychol. (Amst).* **84**, 271–280 (1993).
6. Brown, S. W. Time perception and attention: The effects of prospective versus retrospective paradigms. **38**, 115–124 (1985).

7. Block, R. A., Hancock, P. A. & Zakay, D. How cognitive load affects duration judgments: A meta-analytic review. *Acta Psychol. (Amst).* **134**, 330–43 (2010).
8. Hawkins, N. E. & Meyer, M. E. Time perception of short intervals during finished, unfinished and empty task situations. *Psychon. Sci.* **3**, 473 (1965).
9. Navon, D. & Gopher, D. On the economy of the human-processing system. *Psychol. Rev.* **86**, 214–255 (1979).
10. Pozzo, T., Papaxanthis, C., Petit, J. L., Schweighofer, N. & Stucchi, N. Kinematic features of movement tunes perception and action coupling. *Behav. Brain Res.* **169**, 75–82 (2006).
11. Carlini, A., Actis-Grosso, R., Stucchi, N. & Pozzo, T. Forward to the past. *Front. Hum. Neurosci.* **6**, (2012).
12. Hubbard, T. L. & Bharucha, J. J. Judged displacement in apparent vertical and horizontal motion. *Percept. Psychophys.* **44**, 211–21 (1988).
13. Actis-Grosso, R. & Stucchi, N. Shifting the start: Backward mislocation of the initial position of a motion. *J. Exp. Psychol. Hum. Percept. Perform.* **29**, 675–691 (2003).
14. Brown, S. W. Time, change, and motion: the effects of stimulus movement on temporal perception. *Percept. Psychophys.* **57**, 105–16 (1995).
15. Gavazzi, G., Bisio, A. & Pozzo, T. Time perception of visual motion is tuned by the motor representation of human actions. *Sci. Rep.* **3**, 1168 (2013).
16. Schutz, R. W. & Roy, E. A. Absolute error: The devil in disguise. *J. Mot. Behav.* **5**, 141–153 (1973).
17. Von Holst, E. Relations between the central Nervous System and the peripheral organs. *Br. J. Anim. Behav.* **2**, 89–94 (1954).
18. Wolpert, D. M., Ghahramani, Z. & Jordan, M. I. An internal model for sensorimotor integration. *Science (80-.).* **269**, 1880–1882 (1995).
19. Miall, R. C. The cerebellum, predictive control and motor coordination. *Novartis Found. Symp.* **218**, 272–284; discussion 284–290 (1998).
20. Brown, J. F. Motion expands perceived time. On time perception in visual movement fields. *Psychol Forsch* **14**, 233–248 (1931).
21. Bonnet, C. Influence de la vitesse du mouvement et de l'espace parcouru sur l'estimation du temps. *Annee. Psychol.* **65**, 357–363 (1965).
22. Kanai, R., Paffen, C., Hogendoorn, H. & Verstraten, F. A. J. Time dilation in dynamic visual display. *J. …* **6**, 1421–1430 (2006).
23. Poynter, D. Judging the Duration of Time Intervals: A Process of Remembering Segments of Experience. *Adv. Psychol.* **59**, 305–331 (1989).
24. Rovee-Collier, C. Time windows in cognitive development. *Dev. Psychol.* **31**, 147 (1995).
25. Smith Jr, N. C. The effect on time estimation of increasing the complexity of a cognitive task. *J. Gen. Psychol.* **81**, 231–235 (1969).
26. Gibbon, J., Church, R. M. & Meck, W. H. Scalar timing in memory. *Ann. N. Y. Acad. Sci.* **423**, 52–77 (1984).
27. Ivry, R. B. & Schlerf, J. E. Dedicated and intrinsic models of time perception. *Trends Cogn. Sci.* **12**, 273–80 (2008).
28. Church, R. M. & Broadbent, H. A. Alternative representations of time, number, and rate. *Cognition* **37**, 55–81 (1990).
29. Staddon, J. E. R. Interval timing: memory, not a clock. *Trends Cogn. Sci.* **9**, 312–4 (2005).
30. Zentall, T. R. Support for a theory of memory for event duration must distinguish between test-trial ambiguity and actual memory loss. *J. Exp. Anal. Behav.* **72**, 467–72 (1999).
31. Lewis, P. A. & Miall, R. C. Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Curr. Opin. Neurobiol.* **13**, 250–255 (2003).
32. Reutimann, J., Yakovlev, V., Fusi, S. & Senn, W. Climbing neuronal activity as an event-based cortical representation of time. *J. Neurosci.* **24**, 3295–303 (2004).
33. Buonomano, D. V. Decoding temporal information: A model based on short-term synaptic plasticity. *J. Neurosci.* **20**, 1129–41 (2000).
34. Coull, J. T., Cheng, R.-K. & Meck, W. H. Neuroanatomical and neurochemical substrates of timing. *Neuropsychopharmacology* **36**, 3–25 (2011).
35. Spencer, R. M. C., Zelaznik, H. N., Diedrichsen, J. & Ivry, R. B. Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. *Science* **300**, 1437–9 (2003).
36. Bo, J. *et al.* A Cerebellar Deficit in Sensorimotor Prediction Explains Movement Timing Variability. 2825–2832 (2008). doi:10.1152/jn.90221.2008.
37. O'Reilly, J. X., Mesulam, M. M. & Nobre, A. C. The cerebellum predicts the timing of perceptual events. *J. Neurosci.* **28**, 2252–60 (2008).
38. Beudel, M., Renken, R., Leenders, K. L. & de Jong, B. M. Cerebral representations of space and time. *Neuroimage* **44**, 1032–40 (2009).
39. Lewis, P. & Miall, R. Brain activation patterns during measurement of sub- and supra-second intervals. *Neuropsychologia* **41**, 1583–1592 (2003).
40. Akkal, D., Escola, L., Bioulac, B. & Burbaud, P. Time predictability modulates pre-supplementary motor area neuronal activity. *Neuroreport* **15**, 1283–1286 (2004).
41. Vierordt, C. *Der Zeitsinn nach Versuchen.* (1968).
42. Lejeune, H. & Wearden, J. H. Vierordt's The Experimental Study of the Time Sense (1868) and its legacy. *Eur. J. Cogn. Psychol.* **21**, 941–960 (2009).
43. Woodrow, H. in *Handb. Exp. Psychol.* (1951).
44. Bausenhart, K. M., Dyjas, O. & Ulrich, R. Temporal reproductions are influenced by an internal reference: Explaining the Vierordt effect. *Acta Psychol. (Amst).* 1–8 (2013). doi:10.1016/j.actpsy.2013.06.011.
45. Brainard, D. H. The Psychophysics Toolbox. *Spat. Vis.* **10**, 433–436 (1997).
46. Pelli, D. G. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* **10**, 437–442 (1997).

Author contributions

A.C., R.F. conceived of and designed the experiments; A.C. prepared the experimental setup and collected the data; A.C., R.F. analyzed the data and wrote the paper.

Additional information