Neural Plasticity

The Neurobiology of Time Processing

Guest Editors: Francesca Frassinetti, Marinella Cappelletti, Domenica Bueti, and Shahar Arzy

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 1706373, 2 pages
http://dx.doi.org/10.1155/2016/1706373

Editorial
The Neurobiology of Time Processing

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Received 5 May 2016; Accepted 5 May 2016

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Time is the most elusive dimension of everyday experiences; we cannot "see" or "touch" time; nevertheless we can sense and represent its passage over a wide range of temporal scales, from a few hundreds of milliseconds to years. For example, we are able to appreciate and reproduce time in the millisecond range while playing music and we can perceive the passage of a few minutes of time while waiting for our train to arrive. We can also remember how many years back we first met our best friend or estimate how many minutes are ahead of our next meeting.

However, time does not only span across different scales; it can also be used for different purposes. We can sense the passage of time either to judge how long it takes to commute from and to work (i.e., duration estimation) or to establish which runner reached first the finish line (i.e., temporal order judgments). We can also use time to predict when a traffic light is likely to turn from red to green (i.e., temporal expectations), and we can place ourselves in a temporal prospective by remembering our past and imagining our future (i.e., mental time travel).

In the last two decades, the majority of investigations in the field of temporal cognition focused on the identification and the role of brain regions associated with time representation and processing. All these neuropsychological, neuroimaging, and brain stimulation studies in humans together with electrophysiological works in animals show that several brain areas, including basal ganglia, cerebellum, and posterior parietal, premotor, prefrontal, and insular cortices, are engaged in temporal computations [1–3]. Although the role of each of these "putative" time regions is unknown, it is becoming increasingly clear that time in different scales and the use of time for different purposes are associated with different temporal networks and subserved by distinct temporal mechanisms.

In this special issue, we are very pleased to present a series of articles investigating distinct aspects of the perception of time. The first novelty of this issue is to collect papers exploring different duration ranges (from milliseconds to seconds to minutes) by using different methodological approaches (psychophysics, neuropsychology, brain stimulation, and neuroimaging) and different temporal tasks (temporal order judgments, temporal predictions, temporal reproduction and discrimination, and mental time travel). Specifically, two studies focus on temporal predictions, that is, the capacity of estimating time in order to predict and anticipate the occurrence of behaviorally relevant events. In the first of these studies, P. Filip et al. in "Neural Network of Predictive Motor Timing in the Context of Gender Differences" explore gender differences in the neural networks associated with millisecond time estimation used to perform a visually guided action. The results highlight the pivotal role of the cerebellum in temporal predictions and provide novel insights into our understanding of gender differences linked to time processing. In the second of these works, Y.-H Su and E. Salazar-López

in "Visual Timing of Structured Dance Movements Resembles Auditory Rhythm Perception" investigated whether similar perceptual mechanisms as for auditory rhythms were employed when observing temporally structured dance movements. In two experiments, using visual and auditory stimuli, respectively, parallel results emerged, suggesting similarities between auditory and visual rhythmic timing.

Investigations on temporal predictions were complemented by two other studies exploring the neural basis of temporal judgments in the seconds range. M. Riemer at al. in "Systematic Underreproduction of Time Is Independent of Judgment Certainty" show that the posterior parietal cortex (PPC) is involved in mediating temporal discrimination but not temporal reproduction judgments. Using stimuli of a similar duration range, I. Patanè et al. in "Prismatic Adaptation Induces Plastic Changes onto Spatial and Temporal Domains in Near and Far Space" explore the effect of prismatic adaptation on both spatial and temporal judgments and investigate how temporal judgments are influenced by spatial manipulations (i.e., estimating time in near and far space).

From millisecond to much longer temporal ranges, two articles concern metal time travel (MTT), namely, the human ability to travel mentally backwards and forwards in time in order to reexperience past events and preexperience future ones. These studies explored different aspects of MTT. F. Anelli et al. in "Age-Related Effects on Future Mental Time Travel" explored the potential changes of MTT in aging. By behaviorally testing young and aging adults, the authors explored two different components of MTT, self-projection, that is, the ability to project the self towards a past or a future location, and self-reference, that is, the ability to determine whether events are located in the past or in the future with respect to a self-location. The study by C. Ansuini et al. in "The Role of Perspective in Mental Time Travel" asks whether people can adopt the temporal perspective of another person when travelling through time. To elucidate similarities and differences between time travelling from one's own perspective or from the perspective of another person, participants are asked to mentally project themselves or someone else (i.e., a coexperimenter) to different time points. Following a similar rationale of time travelling, M. Bonato et al. in "Hemispatial Neglect Shows That "Before" Is "Left"" investigate the ability of right brain damaged patients, with and without hemispatial neglect, to categorize events of a story as occurring before or after a central event. The results show that the event occurring immediately before the reference leads to particularly slow responses in neglect patients.

In sum, this special issue presents several novel and previously unexplored issues related to time processing, such as the effect of gender and age, the multimodality of time processing, as in the context of space, and the role of perspective (self/other) in the mental travel of time. Together, these original issues provide a new and interesting overview on the advances in the field of temporal cognition.

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 1678390, 17 pages
http://dx.doi.org/10.1155/2016/1678390

Research Article

Visual Timing of Structured Dance Movements Resembles Auditory Rhythm Perception

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Received 2 September 2015; Revised 29 January 2016; Accepted 14 April 2016

Academic Editor: Francesca Frassinetti

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Temporal mechanisms for processing auditory musical rhythms are well established, in which a perceived beat is beneficial for timing purposes. It is yet unknown whether such beat-based timing would also underlie visual perception of temporally structured, ecological stimuli connected to music: dance. In this study, we investigated whether observers extracted a visual beat when watching dance movements to assist visual timing of these movements. Participants watched silent videos of dance sequences and reproduced the movement duration by mental recall. We found better visual timing for limb movements with regular patterns in the trajectories than without, similar to the beat advantage for auditory rhythms. When movements involved both the arms and the legs, the benefit of a visual beat relied only on the latter. The beat-based advantage persisted despite auditory interferences that were temporally incongruent with the visual beat, arguing for the visual nature of these mechanisms. Our results suggest that visual timing principles for dance parallel their auditory counterparts for music, which may be based on common sensorimotor coupling. These processes likely yield multimodal rhythm representations in the scenario of music and dance.

1. Introduction

To appreciate means of communication unique to humans, such as music, speech, or dance, the perceptual system needs to keep track of the dynamic information unfolding over time [1]. Beyond simple interval timing [2], current understanding of more complex temporal processes, such as rhythm and beat perception, is mainly derived from findings of music [3] and speech [4] in the auditory domain. This, however, overlooks the fact that amongst the abundant *visually* available information, human movements (e.g., walking) are also often rhythmic [5], for which there is little knowledge how their temporal structure is visually perceived. In this study, we investigated timing mechanisms employed in visual perception of dance movements, a class of movements most immediately linked to musical rhythms [6]. We aimed to establish whether mechanisms adopted for processing auditory rhythms would be similarly found for ecological visual stimuli.

Timing especially in the range of hundreds of milliseconds forms the basis for rhythm perception. In this range, purely perceptual timing without requiring a motor task implicates cortical motor systems [7], supporting the idea that sensory and motor timing share common mechanisms within the time scale that is relevant for movement execution [8, 9]. In the same range, two modes of auditory timing have been distinguished, each subserved by a different motor circuitry that may work as a unified system [10]: the *duration-based* mechanism, which times the absolute interval duration in a sequence without a perceivable beat, and the *beat-based* mechanism, which relies on a perceived beat in a sequence as reference for timing an interval.

Rhythm perception entails tracking the underlying periodicity, such as a beat or pulse, in a temporal pattern of (often auditory) events [3]. It represents a subset of perceptual timing that especially engages motor activities. The audio-motor link has been shown externally as body movements assisting pulse extraction [11] and event timing [12] in auditory rhythms. Internally, beat perception implicates motor areas of the brain and is modulated by their connection to the auditory area [3]. While beat-based mechanism is not superior to duration-based in timing a single auditory

interval [10], the presence of a beat facilitates perception of an auditory rhythm (consisting of successive intervals) as a whole [13, 14]: for example, the patterns of auditory rhythms with a perceivable beat can be more accurately reproduced or recalled than those without a clear beat. One explanation of the beat advantage is that beat-based rhythms effectively couple humans' internal motor system, which in turn enhances rhythm perception [15].

Most studies in timing and rhythm perception converge to show auditory superiority compared to its visual counterpart, which may be attributed to a stronger link to the motor system in the former [16]. However, recent findings point to possible visual rhythm and beat perception in moving stimuli [15, 17], particularly for periodic movements of a biological motion profile [18, 19]. The significance of biological motion in timing is also supported by the literature that there seems to be a specialized timing mode for movements of biological kinematics compared to nonbiological ones [20, 21]. Furthermore, human movement kinematics facilitates temporal prediction of an action, compared to motions of artificial, linear velocity [22, 23], which is consistent with the internal motor simulation account during movement observation [24], as well as embodied theories of temporal processing [25]. As such, questions arise as to whether the sensorimotor coupling underlying rhythmic timing can be strengthened by visual observation of temporally structured biological motion [19] and whether this leads to visual timing behaviors similar to those found for auditory rhythms. One type of human movements, dance, provides suitable visual stimuli for addressing this issue, as dance is often performed in time with musical rhythms and may thus communicate visual spatiotemporal rhythms by observation [26]. Moreover, as dance entails whole-body movements, dance observation may activate internal motor representations [27] more effectively than simple, artificial moving stimuli [15, 17], which can be useful for visual timing purposes.

We designed the present study as a novel investigation of visual timing mechanisms during observation of realistic dance movements, focusing on possible beat-based advantages in this process. As periodic biological motion (whole-body bouncing) has been proposed to serve a visual beat [18, 19], we extended the idea to various movements in three experiments, using a duration reproduction task [28]. This task was chosen for the reason that it has not been established whether and how rhythms are visually perceived when observing realistic human movements. As opposed to various perceptual tasks typically employed to measure auditory rhythmic timing, no visual paradigm involving complex movements has yet been developed for this purpose. We thus probed visual temporal perception of a movement sequence in which the feature in question, a potential beat, was embedded or not. The perceived sequence duration and how well it was encoded would likely reflect the movement information during the sequence [29]. We hypothesized that when observing movements involving one or more body parts, periodic limb trajectories, such as recurrent hand clapping or foot tapping, would serve a visual beat. We expected such a visual beat to afford a beat-based mechanism that would benefit visual timing of the whole movement sequence.

Experiment 1 examined movements of the upper and the lower limbs separately. Participants watched short silent videos of a dancer moving with the arms or with the legs. The movements consisted of periodic trajectories (clapping or stepping), continuous and nonperiodic trajectories (circular movements), or a mixture of both interspersed. Participants memorized each sequence and reproduced the duration by mental recall. We expected that movements with periodic trajectories would be better timed than those without. In Experiment 2, we presented movements performed by both the arms *and* the legs, each of which could contain periodic trajectories or not. We examined whether the arms, the legs, or both yielded the salient beat in visual timing of whole-body movements. In Experiment 3, we verified whether the beat advantage in visual timing was attributed to auditory imagery of the impact sounds, by presenting auditory interferences during the same visual task. If the beat advantage persisted, it would argue for visual beat-based timing that is *not* transformed into auditory representations.

2. Experiment 1

We examined whether the arm or the leg movements with periodic trajectories were better timed visually than those without and whether the effect varied across different tempi. For the purpose of cross-modal comparison, a similar auditory timing task was also included, in which an auditory sequence could either contain a beat or not. We expected similar patterns of results for the visual and the auditory tasks: namely, better temporal perception for sequences with a beat than those without, within each modality.

2.1. Method

Participants. Twenty-two healthy volunteers (eleven male, mean age 27 years, SD = 4) took part in this experiment. Participants in all the experiments in this study were naïve of the purpose, gave written informed consent prior to the experiment, and received an honorarium of 8£ per hour for their participation. Participants were not prescreened for musical or dance training, and the training duration ranged from zero to fifteen years for music and zero to six years for dance. Eight participants had received music training (all amateurs), and the learned instruments included piano/keyboard (4), guitar (3), and flute (1). Five participants had received dance lessons (all amateurs). The study had been approved by the ethic commission of Technical University of Munich and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

2.2. Stimuli and Materials

2.2.1. Visual Stimuli. The visual stimuli consisted of videos of six kinds of movement sequences derived from the Flamenco dance repertoire. Each movement sequence was performed in five different tempi, yielding thirty different videos. The movements were chosen based on the moving body part, the body positioning in space, and the direction of the

body motion, following criteria similar to those employed by Calvo-Merino et al. [30]. The rationale of employing specific Flamenco movements was that (1) the chosen movements were not too complex for nondancers to imagine performing, thus minimizing potential effects of different sensorimotor experiences across expertise [31], and (2), at the same time, the specific postures and kinematics performed by a trained dancer, preserving the characteristic movement "accent" (in Flamenco term), distinguished these movements from everyday actions, thus maintaining the ecological plausibility of a dance scenario.

We defined a "movement sequence" here as a set of movements that lasted a certain duration from the start to the end posture. To generate the stimuli, we first choreographed each movement sequence with the knowledge of the second author, who holds a degree in Flamenco dance. The sequences were choreographed based on the planned experimental variables, while keeping the movements as characteristic of Flamenco as possible. We then recorded a professional Flamenco dancer (15 years of training) performing each of the six movement sequences paced by metronomes of five different tempi, corresponding to an interbeat interval (IBI) of 375 ms, 425 ms, 500 ms, 575 ms, and 625 ms (i.e., 500 ms ±0, ±15%, and ±25%). Each complete movement sequence corresponded temporally to eight IBIs at the respective tempo, equaling eight beats in a 4/4 musical meter. The dancer practiced each movement sequence until she could perform it fluently to all the metronome tempi. For each movement at each tempo, we recorded the dancer performing at least four cycles of the sequence continuously, one of which was selected later as the visual stimulus. The recordings were made with a camcorder (Panasonic HC-V500) at 25 frames per second in a dance studio against a white background. A spatial reference of 2.5 m × 1.75 m was marked, creating a 6.5 m^2 space in which every sequence was performed.

The videos were later edited on a frame basis using the software iMovie (Apple, Inc.). For each movement sequence, we defined a starting posture and an end posture in the video as encompassing a complete movement cycle. We then selected one cycle (corresponding to the eight-beat count) at each tempo that yielded the highest consistency of start and end postures with the same movement at the other tempi, as well as the best match to the duration of eight IBIs. Given the natural variability in real human movements and the fact that the kinematics of the same movement varied slightly when performed in different tempi (or speed), for each sequence we allowed five additional frames (i.e., 200 ms) to the intended eight-beat duration to ensure that each selected movement cycle could be fully and consistently presented across all the tempi. The total duration of a sequence at each tempo, shown as video, was thus 3200 ms, 3600 ms, 4200 ms, 4800 ms, and 5200 ms, respectively. Each sequence was exported as an .m4v file for playback in Matlab (2012b).

The movements varied according to two variables of interest: the limbs used to perform the movement (arms or legs) and the type of movement (with or without periodic trajectories, or a mixture of both). In all the movements the dancer faced the front. In the arms-only movements, the dancer's legs stood still with the feet separated by around 30 cm (basic Flamenco posture). In the legs-only movements, the dancer placed her hands on each side of the hips so that the arms did not move. Regarding the movement type, movements containing periodic limb trajectories were marked by successive, brief contact points such as handclaps or foot taps. For labeling purpose, we termed this movement type *discrete* to reflect the brief moments of discrete contact. We termed movements that did not contain such recurrent contact points as *continuous*, as the limbs moved continuously in a circular manner. Movements that contained components from both *discrete* and *continuous* types were termed *mixed*. It should be noted that the dancer performed all types of movement paced by the metronome; while it is more self-evident that *discrete* movement trajectories could be temporally segmented by the metronome beats, the dancer applied the same principle of segmentation in *continuous* movements, such that the limbs reached a defined body position at each given beat, regardless of movement tempo. The critical difference between these two movement types thus lied in the recurrent patterns, the absence of which made a movement continuous in our scenario.

In the following sections, we describe each movement sequence with reference to the metronome beat count that was used to pace the dancer's movements. Nomenclature of the Flamenco repertoire was supplemented where necessary. See also Table 1 for an overview of the movement and the limb displacement (total traveled distance) in each sequence. Limb displacements were calculated for sequences at the middle tempo (IBI = 500 ms), which should be most representative of the kinematics of each movement type.

(1) Discrete Movements. Trajectories were recurrent and gave rise to successive contact points with an underlying periodicity. (1A) The arm movement sequence was based on "Toque de Palmas," where the dancer held her forearms in front of the face and clapped her hands on the left-frontal side of the body. The dancer started with the two hands in a closed position and clapped six times (on beats 1, 2, and 3 and 5, 6, and 7 of the eight-beat count). See Figure 1(a), 1st row. (1B) The leg movement sequence was derived from "Zapateado," in which the dancer started with the standing position and made alternating foot taps on the ground (without horizontal translational motion) on beats 1, 2, and 3 and 5, 6, and 7. The taps were made in the following order of the foot: right-right-left, left-left-right (Figure 1(b), 1st row). Note that, in these *discrete* movements, the sequence was defined to start at the beginning of the limb trajectory leading to the first contact point (beat 1), instead of at the first contact point per se.

(2) Continuous Movements. Trajectories were nonrecurrent and circular. (2A) The arm movements were derived from "Braceo." The dancer started with both hands held above the head and moved the right hand downward to the hip level in a circular manner (the arm trajectory similar to that of the arm of a clock) and then upwards in front of the trunk until the two hands were joined above the head in the end. The left hand remained above the head throughout the sequence. The downward and upward movement occupied four beats each.

Table 1: The movement sequences presented in Experiment 1. Limb displacements were calculated for movement sequences in the middle tempo (IBI = 500 ms).

Movement type	Description	Limb displacement (cm)
Arms discrete	Arms performed *Toque de Palmas* on beats 1, 2, 3, 5, 6, and 7 of the 8-beat count. Legs stood still in basic position.	117.12
Arms continuous	The right arm performed *Braceo* during the 8-beat count. Legs in basic position.	239.71
Arms mixed	Two claps (*Toque de Palmas*) on beats 1 and 2, followed by both arms performing *Braceo* from beats 3 to 6 and then two more claps on beats 7 and 8. Legs in basic position.	415.00
Legs discrete	Legs performed *Zapateado* on beats 1, 2, 3, 5, 6, and 7. Arms remained still in basic position.	538.28
Legs continuous	The right leg was lifted up and down (beats 1 to 4), followed by a circular movement of the left leg (beats 5 to 8). Arms in basic position.	305.32
Legs mixed	The left foot tapped on beats 1 and 2, followed by a circular movement of the same leg during beats 3 to 6, and then two more taps on beats 7 and 8. Arms in basic position.	350.92

The arm movements were accompanied by hand gestures through wrist rotation that was typical of Flamenco. See Figure 1(a), 2nd row. (2B) In the leg movement, the dancer started with both feet on the ground, lifted the right leg up and down to the ground again to the right side of the body while shifting the hip balance rightward (beats 1 to 4), and then drew a circle on the ground with the left leg in front of the body (beats 5 to 8) that ended by the left foot joining the right (Figure 1(b), 2nd row).

(3) Mixed Movements. Segments of *discrete* and *continuous* movements were combined within a sequence. (3A) The arm sequence started with two handclaps in front of the face ("Toque de Palmas," beats 1 and 2), followed by a continuous trajectory of both arms drawing a circle in parallel in the frontal-coronal plane, stretching above the head and back to the face level (bimanual variation of "Braceo," beats 3 to 6), and ended with another two claps (beats 7 and 8) in front of the face (Figure 1(a), 3rd row). (3B) The leg sequence started with two taps on the ground by the left foot (beats 1 and 2), followed by the left leg drawing a full circle above the ground in the transverse plan (beats 3 to 6) and back with two more taps on the ground (beats 7 and 8). See Figure 1(b), 3rd row.

2.2.2. Auditory Stimuli. The auditory stimuli consisted of two types of sound sequences, discrete or continuous, each lasting the same five durations as those of the visual stimuli. The *continuous* sequence was a tone lasting one of the five durations, made up of continuously frequency-modulated linear sine sweeps that went from 600 Hz to 200 Hz in the first half of the stimulus duration and from 200 Hz back to 600 Hz in the second half (resembling a siren sound). In the *discrete* sequence, six discrete tones (i.e., six beats) were embedded in the same continuous sequence as described above. The discrete tone was of a synthesized sound of the instrument "clave" with 43 ms tone duration. The beats followed the same temporal structure as the claps or the steps in the visual discrete movement, that is, occupying beats 1, 2, 3, 5, 6, and 7 of an eight-beat count, with an IBI of 375 ms, 425 ms, 500 ms, 575 ms, and 625 ms for the respective sequence duration. The first beat always appeared at 200 ms after the onset of the continuous pitch sweeps. It should be noted that the *discrete* auditory sequence consisted of both a continuous sound and the discrete beats in parallel, the reason for which was to present comparable visual and auditory stimuli: The visual *discrete* movements contained continuously varying spatiotemporal information (i.e., velocity) in the trajectory between successive contact points. We reasoned that this should be more closely mirrored in a continuous sound whose rate of frequency sweeps also scaled according to the sound duration, with discrete beats on top of it, instead of successive beats bordering empty temporal intervals.

2.3. Procedure and Design. The experimental program was controlled by a customized Matlab script using Psychophysics Toolbox version 3 [32] routines running on a Mac OSX environment. The visual stimuli were displayed on a 17-inch CRT monitor (Fujitsu X178 P117A) with a frame frequency of 100 Hz at a spatial resolution of 1024 × 768 pixels. The videos were displayed at 960 × 540 pixels. Participants sat with a viewing distance of 80 cm. Sounds were presented at a sampling rate of 44,100 Hz through closed studio headphones (AKG K271 MKII).

Two timing tasks were presented in a blocked manner: a visual task and an auditory task, with the former always preceding the latter. Participants self-initiated each trial when they were ready. In the visual task, participants observed on each trial a short silent video of a dancer performing a movement sequence as described in the visual stimuli. Participants were informed that there were different movement speeds across different trials. We used the term "speed," instead of "tempo," as participants more easily understood the former where human movements were concerned. Participants were

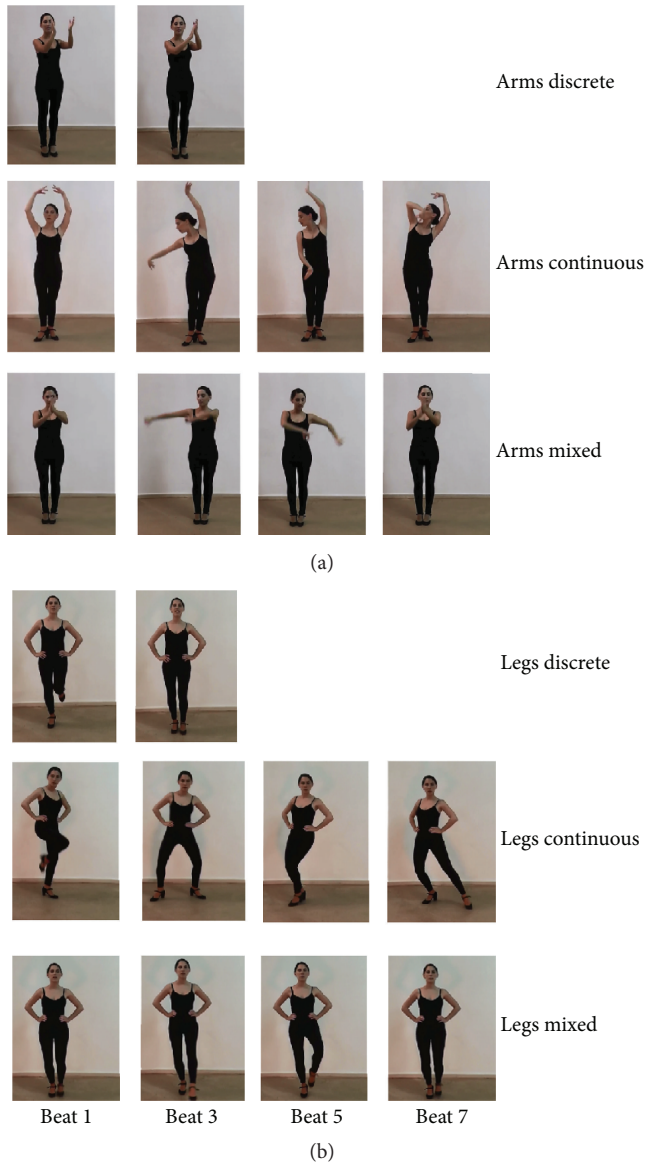

Figure 1: Illustrations of the visual stimuli for Experiment 1, shown as selected frames taken from the videos. (a) 1st row: *discrete* arm movement shown as one handclap. As this trajectory was repeated in the sequence, only one example is shown. 2nd row: *continuous* arm movement. 3rd row: *mixed* arm movement. (b) 1st row: *discrete* leg movement shown as one foot tap. As this trajectory was repeated in the sequence, only one example is shown. 2nd row: *continuous* leg movement. 3rd row: *mixed* leg movement. With the exception of the *discrete* arm and leg movements, the four frames for all the sequences correspond to beats 1, 3, 5, and 7 of the 8-beat count in the metronome that paced the dancer's movement.

required to attend to the sequence carefully and to memorize its entire duration. Immediately following the video a reminder text was briefly shown ("Please reproduce the duration now!"), after which an image of the dancer, taken from the first frame of the video, was displayed on the screen. As soon as this image was shown, participants were required to start reproducing the duration by mentally replaying the memorized movement sequence once. They were instructed to do so as closely to the movement speed of the video as possible. Participants indicated the end of duration reproduction by pressing a predefined key once. The image stayed on the screen during their mental recall until key-press.

In the auditory task, participants underwent a similar procedure of duration reproduction with the auditory stimuli as described above. During auditory stimulus presentation and the reproduction phase, only a fixation cross was shown in the middle of the screen, which participants should fixate. For both the visual and auditory tasks, participants were especially instructed not to use any explicit strategies such as counting or moving along [11] but should rather do so by

mere observation and listening, respectively. At the end of the entire experiment, each participant was briefly interviewed for any strategies they had adopted to perform each task.

The visual task followed a 2 (limb type) × 3 (movement type) × 5 (tempo) design, each with 10 repetitions (see [28]), and the total trials were presented in five blocks of about 15 minutes each. The auditory task followed a 2 (sound type) × 5 (tempo) design, each with 10 repetitions, presented in five blocks of around 5 minutes each. All the conditions were presented in a balanced manner across blocks, with the order of conditions randomized within a block. Participants underwent five practice trials prior to the visual and the auditory task, respectively. Every participant completed the visual blocks before starting the auditory ones, as we intended to avoid introducing the idea of auditory imagery for the visual task. The entire experiment was completed in about two hours, and a break was required after each block.

2.4. Analyses. No participant reported substantial difficulty in carrying out the tasks. In the rare occasions where a response was given by mistake before the duration reproduction was carried out (if a reproduced duration was shorter than 1500 ms, which exceeded three standard deviations from each within-participant mean), the trial was considered as errors and discarded from analyses. This constituted on average only 0.76% of the trials.

Three parameters were analyzed individually for each condition to index the performance of duration reproduction [33]: (1) Absolute Error (AE), calculated as the absolute deviation of the reproduced interval from the presented one, in percentage. A greater AE indicates a larger error in duration reproduction. (2) Ratio, calculated as the reproduced duration divided by the presented duration. A ratio of one signifies perfect reproduction, and a ratio smaller/larger than one represents underestimation/overestimation of the duration. (3) Coefficient of Variation (CV), calculated for a given condition as the within-participant standard deviation of the reproduced intervals divided by his/her mean reproduced interval, shown in percentage [34]. CV indexes the consistency of duration perception and reproduction; a greater CV signifies more variable reproduction and thus poorer performance. As the present task required timing the durations of movement sequences with varying embedded temporal structures, the perceptual mechanism was expected to resemble that for timing the pattern of an auditory rhythm (as opposed to timing a duration without content) [29]. While AE and ratio indexed how accurately a sequence was estimated in absolute terms, there could be systematic over- or underestimation due, for example, to Vierordt's law across sequence tempi [35, 36], or due to individual differences in the tendency to over- or underreproduce [13, 37], which is not necessarily associated with the presence or absence of a beat. In comparison, timing variability as indexed by CV may be more immune to these factors and able to reflect the rhythmicity of the movement [38]. As such, along with AE and ratio that describe timing behaviors, CV would be taken as the more indicative measurement of the present task.

Data from one participant were excluded from further analyses, as the intervals were overall substantially underreproduced (mean ratio = 0.63 and mean AE = 37%, which was the only case from the whole sample exceeding two standard deviations of the sample mean in both parameters). This suggests that the participant either did not fully understand the task or was hurrying through each trial without proper recall of the stimulus. The sample size for the reported results was therefore 21.

For all the repeated-measures ANOVAs and ANCOVAs reported in this study, Greenhouse-Geisser correction was applied to the p values of effects of variables with more than two levels. Tukey HSD was used as post hoc tests following a significant main effect.

2.5. Results

2.5.1. Visual Task. First we provide an overview of the strategies participants ($N = 21$) reported of adopting for the visual task: fourteen participants reported associating sounds along with visual imagery to aid mental replay, eight of whom used the auditory strategy only for the *discrete* movements (i.e., as if they could hear the impact sounds in their head). The others used only visual imagery for the visual task.

For each of the three parameters, we conducted a 2 (limb type) × 3 (movement type) × 5 (tempo) repeated-measures ANCOVA of the individual means, with individual music or dance training duration entered as covariate in each analysis. We pulled together training in music and dance as one general category of rhythm-related expertise that may influence performance in the present task.

AE. Only a significant main effect of movement type was found, $F(2, 38) = 3.95$, $p = 0.028$, and $\eta_p^2 = 0.20$, and the post hoc tests showed that AE was lower for *discrete* than for either *mixed*, $p = 0.02$, or (almost) *continuous*, $p = 0.058$, while the latter two did not differ from each other. The interaction between limb type and tempo was significant, $F(4, 76) = 3.73$, $p = 0.025$, and $\eta_p^2 = 0.16$, which was also modulated by the covariate of training duration, $F(4, 76) = 3.29$, $p = 0.038$, and $\eta_p^2 = 0.15$. Following this interaction, post hoc comparisons (Bonferroni corrected) for the arm movements did not identify any difference amongst different tempi, all ps > 0.5, while for the leg movements AE in the middle tempo (IBI = 500 ms) was lower than that in the two slowest tempi (IBI = 575 and 625 ms), $p = 0.028$ and $p = 0.014$, respectively. To examine how expertise modulated this effect, Pearson's correlations ($N = 21$) were computed between training duration and AE of leg movement for the three slower tempi, which revealed a significant negative correlation between AE and training duration at the slowest tempo (IBI = 625 ms), $r = -0.44$ and $p = 0.04$, and marginally so at the next slowest (IBI = 575 ms), $r = -0.41$ and $p = 0.06$. No other significant effects were found: limb type, $F(1, 19) = 1.60$, $p = 0.22$, and $\eta_p^2 = 0.078$, and tempo, $F(4, 76) = 1.06$, $p = 0.34$, and $\eta_p^2 = 0.053$ (Figure 2(a)). Training duration did not interact with any other effects, all ps > 0.2 and all $\eta_p^2 < 0.08$.

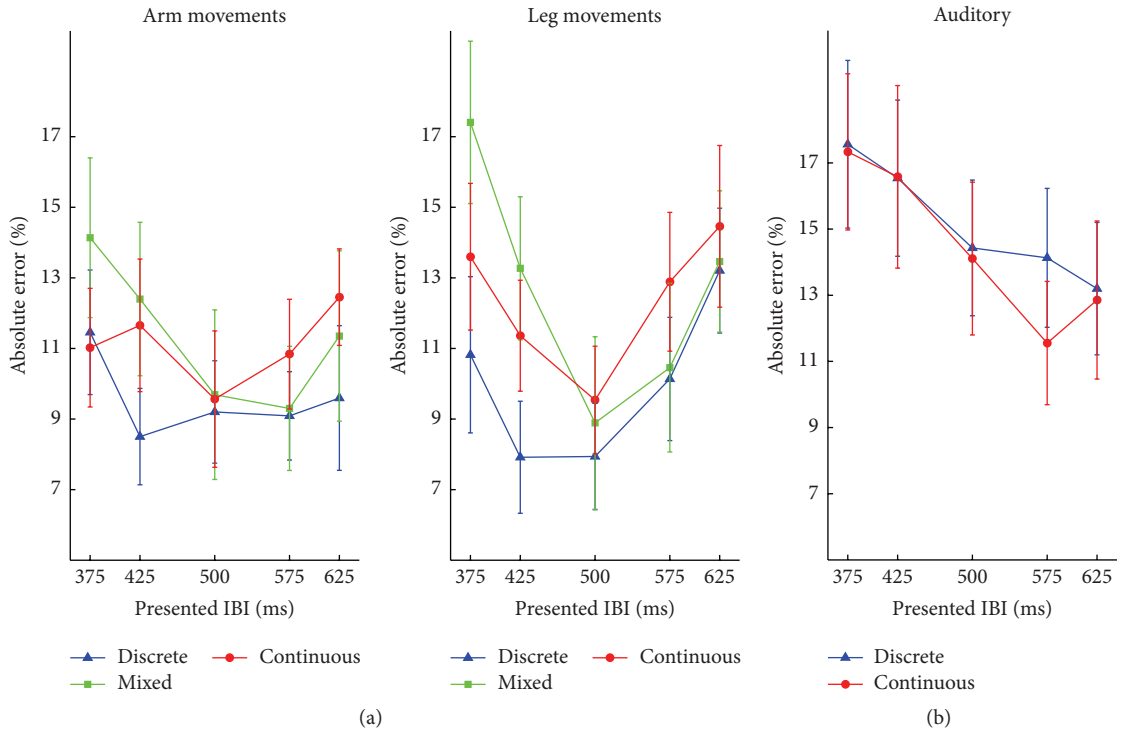

Figure 2: Mean Absolute Error (AE) of Experiment 1, for each experimental condition as a function of the movement tempo. Tempo is labeled as the metronome IBI (in ms) used to pace the dancer's movements. (a) Results of the visual task. (b) Results of the auditory task. Error bars represent standard error of the means.

Ratio. First, a main effect of tempo was found, $F(4, 76) = 39.73$, $p < 0.001$, and $\eta_p^2 = 0.68$, with the post hoc tests showing that the reproduced ratio for the two fastest tempi was greater than that for the two slowest ones, all ps < 0.001. The reproduced ratio for the middle tempo (IBI = 500 ms) also differed from those for the two fastest ones, both ps < 0.002, as well as from those for the two slowest ones, both ps < 0.05. On average, participants' reproduced ratio descended across decreasing tempo, with overestimation for the faster ones and underestimation for the slower ones. Main effects of limb type and movement type were not significant, $F(1, 19) = 2.81$, $p = 0.11$, and $\eta_p^2 = 0.13$ and $F(2, 38) = 0.91$, $p = 0.40$ and $\eta_p^2 = 0.046$.

Following a significant three-way interaction, $F(8, 152) = 4.42$, $p = 0.002$, and $\eta_p^2 = 0.19$, follow-up two-way ANOVAs were conducted for each limb type separately. For the arm movements, the movement type × tempo interaction was significant, $F(8, 160) = 5.95$, $p < 0.001$, and $\eta_p^2 = 0.23$, and the post hoc one-way ANOVAs for each tempo separately showed that only at the fastest tempo was the ratio different between *discrete* and *continuous* movements, $p = 0.008$ (Bonferroni corrected), while no effect of movement type was found in all the other tempi. For the leg movements, a main effect of movement type was found, $F(2, 40) = 3.61$, $p = 0.04$, and $\eta_p^2 = 0.15$, the post hoc test showing a trend of greater reproduced ratio for *mixed* than for *continuous* movements, $p = 0.08$. The movement type × tempo interaction was only marginally significant, $F(8, 160) = 2.32$, $p = 0.054$, and $\eta_p^2 = 0.10$ (Figure 3(a)). Training duration as covariate did not interact with any of the effects, all ps > 0.15 and all $\eta_p^2 < 0.08$.

CV. The main effect of movement type was significant, $F(2, 38) = 17.40$, $p < 0.001$, and $\eta_p^2 = 0.48$, with post hoc tests showing a lower CV for *discrete* than for either *continuous* or *mixed* movements, both ps < 0.005, while the latter two did not differ from each other. The main effect of tempo was marginally significant, $F(4, 76) = 2.66$, $p = 0.055$, and $\eta_p^2 = 0.12$. There was no effect of limb type, $F(1, 19) = 0.014$, $p = 0.908$, and $\eta_p^2 = 0.001$ (Figure 4(a)). Training duration as covariate did not interact with any of the effects, all ps > 0.16 and all $\eta_p^2 < 0.04$.

2.5.2. Auditory Task. For the auditory task, five participants reported visualizing the sounds, and two of them did so especially for continuous auditory sequences. The majority of the participants adopted only auditory imagery. Individual means of each of the three parameters were submitted to a 2 (sound type) × 5 (tempo) repeated-measures ANCOVA, with training duration as covariate.

AE. The analysis did not reveal any significant effect of the variables, sound type, $F(1, 19) = 0.01$, $p = 0.92$, and $\eta_p^2 = 0.001$, and tempo, $F(4, 76) = 1.36$, $p = 0.26$, and $\eta_p^2 = 0.067$, or interaction, $F(4, 76) = 1.34$, $p = 0.27$, and $\eta_p^2 = 0.066$.

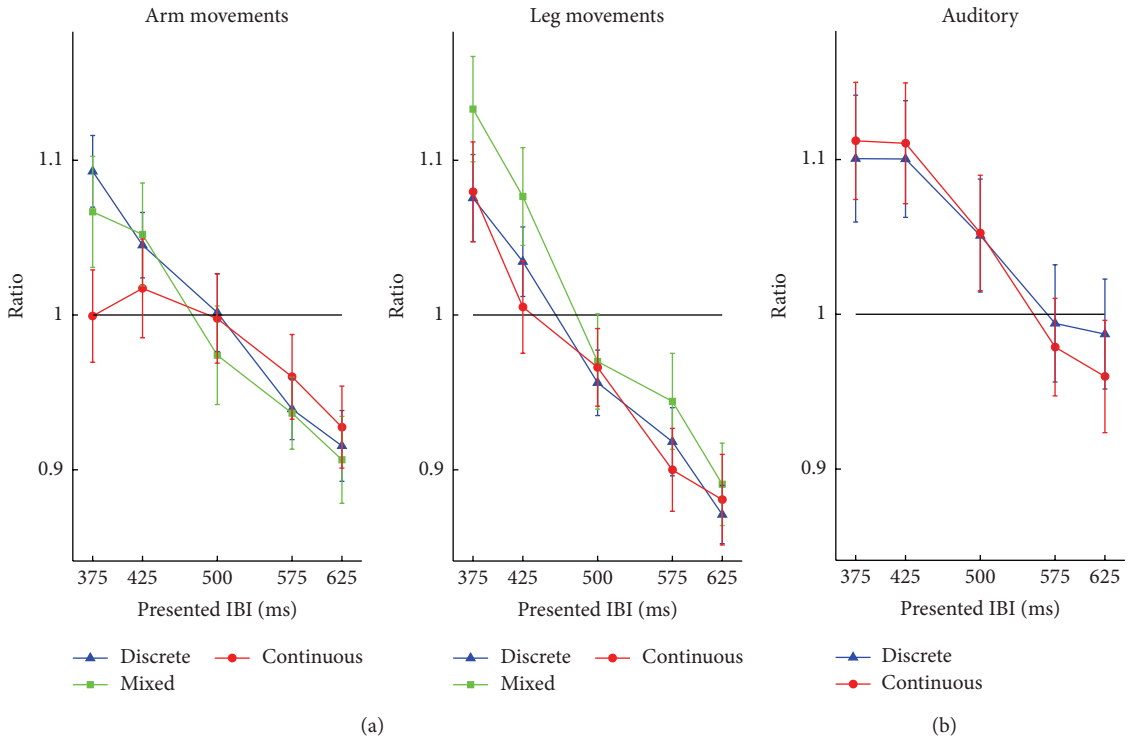

Figure 3: Mean ratio of Experiment 1, for each experimental condition as a function of the movement tempo. (a) Results of the visual task. (b) Results of the auditory task. Error bars represent standard error of the means. The black horizontal lines depict a ratio of 1, which would be perfect reproduction.

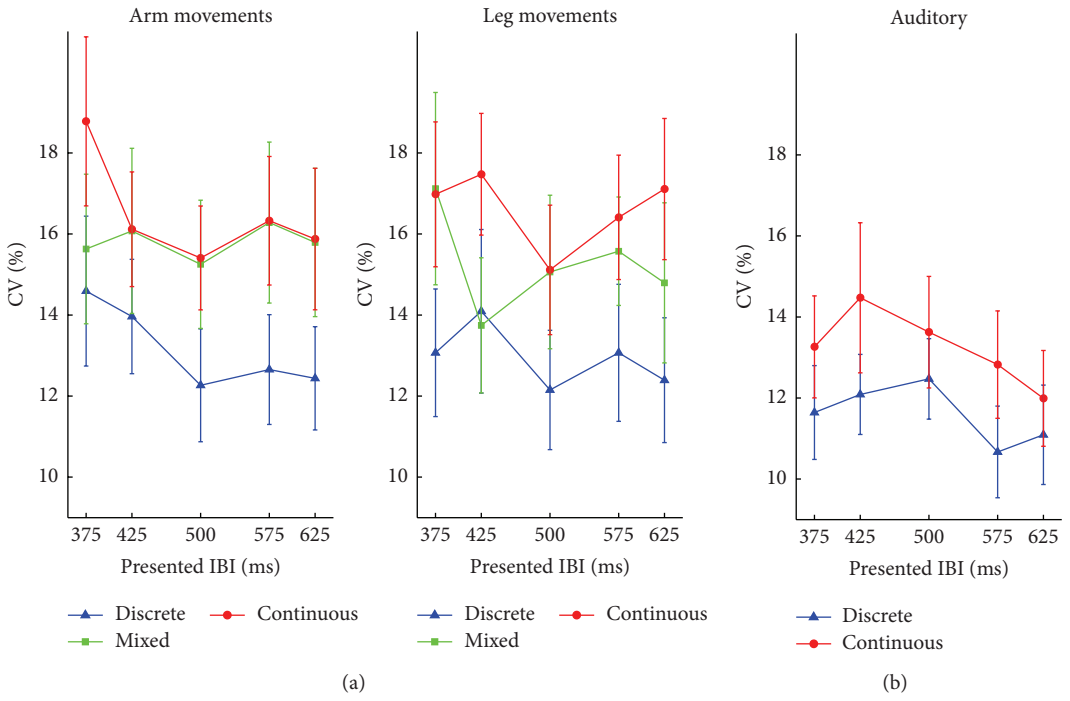

Figure 4: Mean Coefficient of Variation (CV) of Experiment 1, for each experimental condition as a function of the movement tempo. (a) Results of the visual task. (b) Results of the auditory task. Error bars represent standard error of the means.

Table 2: The movement sequences presented in Experiment 2.

Movement type	Description
Arms discrete + legs discrete	Left foot tapped on beat 1 followed by *Toque de Palmas* of the arms on beats 2, 3, and 4; right foot tapped on beat 5 followed by *Toque de* Palmas of the arms on beats 6, 7, and 8.
Arms discrete + legs continuous	The hands clapped on beats 1, 2, and 3 and 5, 6, and 7, with the arms moving from the right to the left diagonal. In parallel, the legs made a continuous movement as in Experiment 1.
Arms continuous + legs discrete	The left arm performed *Braceo* while the legs performed *Marcaje*, both covering 8 beats.
Arms continuous + legs continuous	The right arm performed *Braceo* from beats 1 to 4 while the right foot carried out a circular movement, and then the pattern was repeated with the left arm and the left foot from beats 5 to 8.

(Figure 2(b)). Training duration did not interact with any variable, all ps > 0.2 and all $\eta_p^2 < 0.1$.

Ratio. Only a significant main effect of tempo was found, $F(4, 76) = 21.09$, $p < 0.001$, and $\eta_p^2 = 0.53$. Post hoc comparisons showed that the reproduced ratio for the two fastest sequences was greater than that for the two slowest ones, all ps < 0.02 (Figure 3(b)). Effect of sound type was not significant, $F(1, 19) = 0.8$, $p = 0.38$, and $\eta_p^2 = 0.04$, nor was its interaction with tempo, $F(4, 76) = 2.07$, $p = 0.12$, and $\eta_p^2 = 0.098$. Training duration did not interact with any variable, all ps > 0.2 and all $\eta_p^2 < 0.1$. On average, as found in the visual task, shorter durations were overestimated while longer ones were underestimated, although the extent of underestimation appeared smaller than in the visual task.

CV. The effect of sound type was not significant in the ANCOVA analysis, $F(1, 19) = 1.76$, $p = 0.2$, and $\eta_p^2 = 0.09$, though it was in the ANOVA without covariate, $F(1, 20) = 6.0$, $p = 0.02$, and $\eta_p^2 = 0.23$ (the covariate did not interact with sound type, $F(1, 19) = 0.66$, $p = 0.43$, and $\eta_p^2 = 0.03$). No other effect was significant: tempo, $F(4, 76) = 1.75$, $p = 0.16$, and $\eta_p^2 = 0.084$, and interaction, $F(4, 76) = 0.71$, $p = 0.53$, and $\eta_p^2 = 0.036$. Training duration only interacted with tempo, $F(4, 76) = 2.84$, $p = 0.04$, and $\eta_p^2 = 0.13$ (Figure 4(b)).

In sum, results of the visual task showed that, regardless of the limbs performing the movements and the movement tempo, *discrete* movements led to more accurate (lower AE) and more consistent (lower CV) temporal reproduction than both the *continuous* and the *mixed* movements, while performance in the latter two did not differ from each other. Timing for the leg movements was more accurate (lower AE) in the middle tempo compared to the two slowest tempi; this effect was modulated by expertise, such that longer training duration was associated with lower AE in the two slowest tempi. Besides, faster movements tended to be overestimated and slower ones underestimated. For the auditory task, the pattern of ratio was similar to that in the visual task, with overestimation and underestimation for the faster and slower tempi. The effect of a discrete beat on auditory timing was not robust enough to survive the analysis with the covariate included.

3. Experiment 2

Following results of Experiment 1, we examined whether the arms, the legs, or both, in a multi-limb movement sequence accounted for the beat advantage in visual timing. Applying the same visual timing paradigm, we presented now movements performed by both the arms and the legs, each of which could be either discrete or continuous.

3.1. Method

Participants. Twenty healthy volunteers (seven male, mean age 25 years, SD = 3) took part. Thirteen participants had received music training ranging from three to seventeen years (all amateurs), and the instruments included piano/keyboard (6), guitar (4), trumpet (1), oboe (1), and cello (1). Three participants had received dance lessons between one and three years. Seven of the participants had participated in Experiment 1 two to four weeks earlier.

3.2. Stimuli and Materials. Only visual stimuli were presented in this experiment, and they consisted of videos of four kinds of movement sequences derived from the Flamenco repertoire. The sequences were performed by the same Flamenco dancer across the same five tempi as in Experiment 1. The same procedures of movement recording and video editing and formatting were applied, yielding the same five sequence durations. All the movement sequences here were performed with the arms *and* the legs. The sequences now varied according to two variables: the arm movement type (discrete or continuous) and the leg movement type (discrete or continuous). See also Table 2 for an overview.

3.2.1. Arms Discrete + Legs Discrete. The dancer made one tap on the ground with the left foot (beat 1), followed by three claps on the right-frontal side of the body ("Toque de Palmas," on beats 2, 3, and 4), and then another tap with the right foot (beat 5), followed by three more claps on the left-frontal side of the body (beats 6, 7, and 8). The start of the sequence followed the same rule as previously described for the *discrete* movements. See Figure 5(a).

3.2.2. Arms Discrete + Legs Continuous. Discrete claps were combined with the continuous leg movement as described in

Figure 5: Illustrations of the visual stimuli for Experiment 2, shown as selected frames taken from the videos. (a) Arms discrete and legs discrete. (b) Arms discrete and legs continuous. (c) Arms continuous and legs discrete. (d) Arms continuous and legs continuous. The eight frames for each sequence correspond to the 8 beats in the metronome that paced the dancer's movements.

Experiment 1. The dancer held her arms at the head level and clapped three times along the right-frontal plane of the body (beats 1, 2, and 3), during which the left leg was lifted and stretched above the ground and down on the left side (beats 1 to 4), followed by another three claps on the left side of the body (beats 5, 6, and 7), during which the right leg drew a circle on the ground in front of the body (beats 5 to 8) that ended by joining where the left foot was. See Figure 5(b).

3.2.3. Arms Continuous + Legs Discrete. The arm movement was similar to the *continuous* one in Experiment 1 ("Braceo"), where the left arm moved downward (beats 1 to 4) and

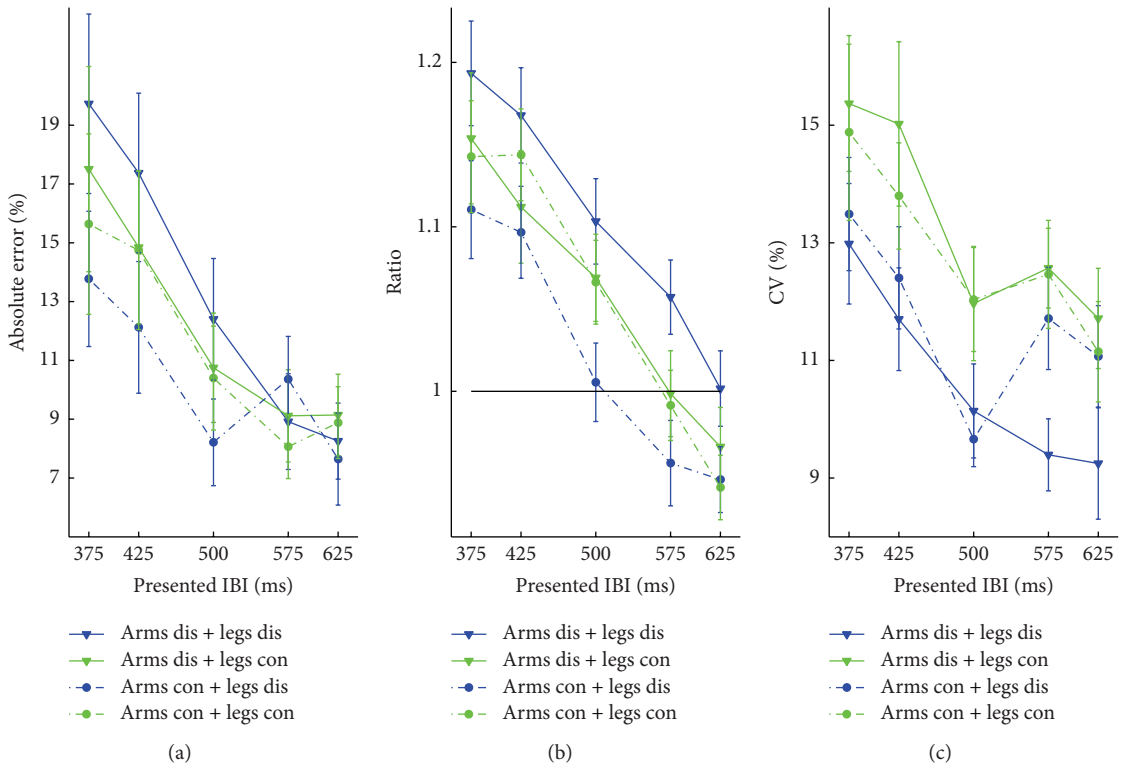

Figure 6: Results of Experiment 2, plotted for each experimental condition as a function of the movement tempo. (a) Mean AE. (b) Mean ratio. (c) Mean CV. Error bars represent standard error of the means. *dis*: discrete; *con*: continuous.

upward again (beats 5 to 8) in a circular manner to eventually join the right arm that was held above the head throughout. In parallel, the legs carried out discrete taps (without horizontal translational motion) derived from the movement "Marcaje," in which the first right tap (beat 1) was followed by the left foot doing a front kick by sliding the shoe forward (beat 2), one back kick by sliding the shoe backwards (beat 3), and then one down kick by tapping the ground with the toe cap (beat 4) and concluded by three successive left-right-left taps (beats 5 to 7). See Figure 5(c).

3.2.4. Arms Continuous + Legs Continuous. This movement combined similar continuous movements of the arms and the legs as in Experiment 1. The right arm carried out the circular movement ("Braceo") while the right leg drew a circle on the ground (beats 1 to 4), followed by the same movement pattern performed with the left arm and left leg (beats 5 to 8). See Figure 5(d).

3.3. Procedure and Design. The setup was the same as in Experiment 1. Participants performed the visual timing task following the same instruction and procedures as for the previous experiment, with special emphasis on observing the multi-limb movement as a whole instead of focusing on any specific body part. The experiment followed a 2 (arm movement type) × 2 (leg movement type) × 5 (tempo) design, each with 10 repetitions. The total trials were presented in five blocks of about 10 minutes each, with all the conditions presented in a balanced manner across blocks and the order of conditions randomized within a block. The whole experiment was completed within one hour, with a short break after each block.

3.4. Results. Erroneous trials with too short intervals (same criterion as in Experiment 1) were discarded, which constituted on average only 0.6% of the trials. Eight participants reported imagining the sounds along with visual imagery for the task, four of whom did so only when there were discrete movements. The majority of the participants reported adopting only a visual imagery strategy. The same three parameters as described in Experiment 1 were analyzed individually, and the individual means of each parameter were submitted to a 2 (arm movement type) × 2 (leg movement type) × 5 (tempo) repeated-measures ANCOVA, with training duration as covariate.

AE. No significant main effects or interactions were found, except for the marginally significant effect of arm movement, $F(1, 18) = 21.09$, $p = 0.077$, and $\eta_p^2 = 0.16$, and the marginally significant three-way interaction, $F(4, 72) = 2.76$, $p = 0.051$, and $\eta_p^2 = 0.13$. Training did not interact with any of the variables (Figure 6(a)).

Ratio. The main effect of arm movement was significant, $F(1, 18) = 19.22$, $p < 0.001$, and $\eta_p^2 = 0.52$, showing a greater

ratio in discrete than in continuous arm movements, but that of leg movement was not, $F(1, 18) = 0.024$, $p = 0.88$, and $\eta_p^2 = 0.001$. The main effect of tempo was also significant, $F(4, 72) = 35.56$, $p < 0.001$, and $\eta_p^2 = 0.66$, and the post hoc tests showed that while the ratio did not differ between the two fastest tempi or between the two slowest tempi, the two groups differed from each other, as well as from the ratio in the middle tempo, all ps < 0.02. As found in Experiment 1, sequences of the faster tempi were on average more overestimated than those of the slower tempi (Figure 6(b)). The arm × leg interaction was marginally significant, $F(1, 18) = 3.31$, $p = 0.086$, and $\eta_p^2 = 0.15$. Training duration did not interact with any variable.

CV. There was a main effect of leg movement type, $F(1, 18) = 5.83$, $p = 0.027$, and $\eta_p^2 = 0.25$, showing lower CV for discrete than for continuous leg movements, but not of arm movement type, $F(1, 18) = 1.16$, $p = 0.69$, and $\eta_p^2 = 0.009$. The main effect of tempo was also significant, $F(4, 72) = 8.59$, $p < 0.001$, and $\eta_p^2 = 0.32$; post hoc tests showed that CV for the two fastest tempi was higher than that for the other three slower ones, all ps < 0.01 (except for $p = 0.08$ between IBIs of 425 ms and 575 ms). No interaction was significant, all ps > 0.2 and all $\eta_p^2 < 0.1$ (Figure 6(c)). Training duration as covariate did not interact with any of the variables, all ps > 0.2 and all $\eta_p^2 < 0.1$.

To summarize, regardless of the movement tempo, discrete leg movements led to more consistent timing (lower CV) than continuous leg movements, while arm movements did not influence CV. Besides, movement tempo affected CV, which was not found in Experiment 1, such that faster movements led to lower consistency in timing than slower ones.

4. Experiment 3

The first two experiments showed better visual timing for (especially leg) periodic trajectories marked by discrete contact points, possibly due to a sense of visual beat arising from observing these movements. Here we verified whether this effect was attributed to internalized impact sounds, namely, whether the hypothesized visual beat was obligatorily encoded as auditory representation [39]. We presented the *discrete* and the *continuous* leg movements either in silence, or with task-irrelevant auditory sequences that were temporally congruent or incongruent with the foot taps. If the beat had been encoded auditorily, incongruent interferences would have eliminated the timing advantage of *discrete* movements. If the beat percept remained visual, then the result pattern should persist despite auditory interferences. We included both congruent and incongruent sounds so that, should an auditory interference effect be observed, it could be determined whether it was caused by the temporal structure or the mere presence of the sounds.

4.1. Method

Participants. Twenty healthy volunteers (nine female, mean age 28 years, SD = 4.6) took part in this experiment, whose musical training duration ranged from zero to twenty years (mean duration 4.9 years, SD = 5). Thirteen participants were musically trained (all amateurs), and the instruments included piano/keyboard (6), guitar (5), trumpet (1), and saxophone (1). No participant in this experiment had received formal dance lessons. Six and four participants had participated in Experiments 1 and 2, respectively, amongst whom two had participated in both.

4.2. Stimuli and Materials

4.2.1. Visual Stimuli. The visual stimuli here consisted of videos of two leg movement types as employed in Experiment 1: *discrete* and *continuous*. Two from the five previously displayed tempi, corresponding to an IBI of 425 ms and 575 ms (i.e., the second fastest and the second slowest), were used here.

4.2.2. Auditory Stimuli. The auditory interference in this task consisted of discrete tones of the same clave sound as used in Experiment 1. Two kinds of auditory sequences were presented that were temporally congruent or incongruent with the timing of the discrete leg movement. The *congruent* sequence consisted of four discrete tones, which, when presented concurrently to the discrete leg movement, would temporally coincide with four of the six foot taps (see the description of the *discrete* leg movement in Experiment 1). The four positions were randomly selected on a trial basis. The *incongruent* sequence was initially constructed in the same way as the *congruent* one, but each tone was then advanced or delayed for a magnitude of 20% to 40% of the respective IBI. Whether a tone was delayed or advanced, as well as the magnitude of this shift, was determined randomly for each tone on each trial.

4.3. Procedure and Design. The setup was the same, and participants performed the visual timing task following the same procedures as described before. In one-third of the trials, videos were presented in silence. In the other two-thirds, sounds were displayed through headphones during the video; half of them were the *congruent* sequences, and the other half were the *incongruent* ones. Participants received the same instruction as in Experiment 1 and were additionally informed that they would sometimes hear sounds during the video, which were task irrelevant and should be ignored.

The experiment followed a 2 (leg movement type) × 2 (tempo) × 3 (auditory interference) design, each condition with 10 repetitions. The total trials were presented in three blocks of around 10 minutes each. The whole experiment was completed in about half an hour, with a short break after each block.

4.4. Results. Erroneous trials were discarded in which a response was accidentally given too quickly (same criterion as

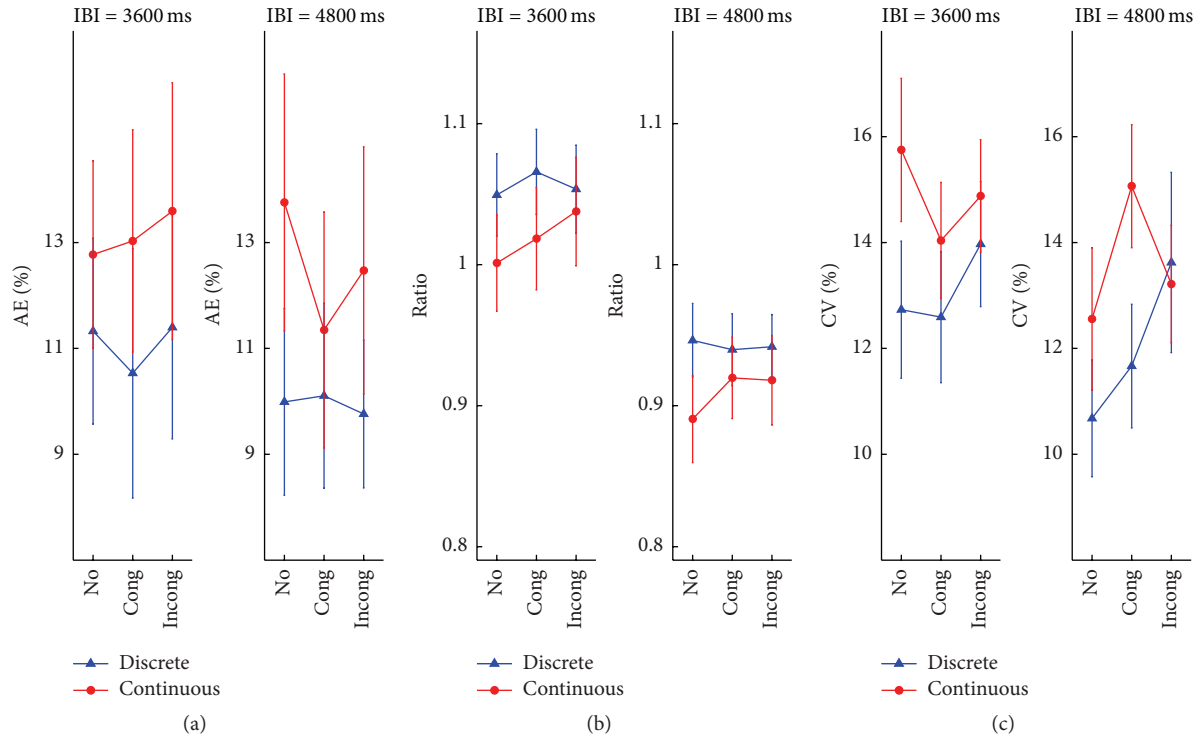

FIGURE 7: Results of Experiment 3, plotted for each movement type as a function of the auditory interference condition, for each tempo separately. (a) Mean AE. (b) Mean ratio. (c) Mean CV. Error bars represent standard error of the means. On the x-axis, *No*, *Cong*, and *Incong* represent no sound, congruent auditory sequence, and incongruent auditory sequence, respectively.

before), which occurred rarely (0.5% of the trials on average). Most participants reported having difficulty ignoring the sounds completely, despite the intention to comply with the instruction. As before, AE, ratio, and CV were analyzed individually and submitted to a 2 (movement type) × 2 (tempo) × 3 (auditory interference) repeated-measures ANCOVA, with training duration entered as covariate.

AE. No significant effect of any factor was found, movement type, $F(1, 18) = 1.92$, $p = 0.18$, and $\eta_p^2 = 0.097$; tempo, $F(1, 18) = 0.15$, $p = 0.70$, and $\eta_p^2 = 0.008$; auditory interference, $F(2, 36) = 0.63$, $p = 0.52$, and $\eta_p^2 = 0.034$, or any significant interaction (Figure 7(a)). Training duration did not interact with any variable.

Ratio. A significant effect of tempo was shown, $F(1, 18) = 39.86$, $p < 0.001$, and $\eta_p^2 = 0.69$. Similar to what was previously found, sequences of the faster tempo were overestimated (mean ratio > 1) while those of the slower tempo were underestimated (mean ratio < 1). Although there was a main effect of auditory interference, $F(2, 36) = 3.61$, $p = 0.041$, and $\eta_p^2 = 0.17$, post hoc comparisons did not identify any significant difference between conditions, all ps > 0.15 (Figure 7(b)). No other effects nor interactions were found significant, and training duration did not interact with any variable.

CV. There was a significant main effect of movement type, $F(1, 18) = 9.95$, $p = 0.005$, and $\eta_p^2 = 0.36$, showing a lower CV for discrete than for continuous movements. The effect of tempo was only marginally significant, $F(1, 18) = 3.48$, $p = 0.078$, and $\eta_p^2 = 0.16$, with a trend of higher CV for the faster tempo. The effect of auditory interference was again not significant, $F(2, 36) = 1.32$, $p = 0.28$, and $\eta_p^2 = 0.068$ (Figure 7(c)). No significant interaction was found, nor did training duration interact with any variable.

Compared to when the visual task was performed in silence, the presence of an auditory interference sequence, regardless of its temporal structure, had no influence on any of the measured parameters. The result of more consistent timing in discrete than in continuous movements, as found in Experiment 1, persisted despite the auditory interferences.

5. Discussion

We investigated whether perceptual mechanisms similar to those previously found for auditory rhythms, such as beat-based strategies [3], were employed when observing temporally structured dance movements. In all three experiments, we found that periodic limb trajectories benefitted visual timing of a movement sequence, which was most consistently reflected in timing variability (CV). When both the arms

and the legs moved, only periodicities in the leg movement accounted for the timing advantage. This advantage persisted despite auditory interferences, suggesting that it was *not* attributed to internal representation of the impact sounds.

We interpret the main result as evidence that observers extracted a visual beat from periodic trajectories [18], which facilitated temporal perception of the whole movement sequence. Notably, the periodic trajectories (handclaps or foot taps) did not necessarily occur on every beat. Their temporal structure resembled non-isochronous auditory rhythms that communicated an underlying beat [13, 40]. Our visual results are thus reminiscent of previous auditory findings that a *perceived* beat leads listeners to adopt a beat-based timing strategy [10] that enhances rhythm perception [13, 14], suggesting similarities between auditory and visual rhythmic timing. The lack of a robust beat effect on improving auditory timing in Experiment 1 might be due to several factors: For one, the auditory stimuli were not as rich and ecological as the visual ones. For another, in terms of contrasting conditions with and without a beat, the auditory stimuli might not have been optimally comparable to their visual counterpart. Perhaps a closer resemblance to the visual discrete condition would have been, for example, successive (shorter) filled intervals yielding the same beat structure. The auditory beat effect might also have been attenuated by the learning effect, as the auditory task was always performed after the visual one. Finally, whereas a picture of the dancer was presented to trigger participants' recall in the visual task, no such rich cues were given prior to the auditory recall, which might have compromised the auditory performance. Thus, different factors deserve consideration when comparing timing behaviors between dance movements and auditory rhythms: naturalistic content [41] or biological motion [18, 21, 23] of visual stimuli may enhance beat advantage in real dance movements, compared to artificial sounds simulating the temporal structure of these movements. In addition, the compatibility of the visual and auditory stimuli yielding the same temporal structure appears critical and needs further verifications.

The beat effect on timing was not modulated by music or dance expertise, suggesting the generality of this mechanism [17]. While it seems fitting to explain our visual results borrowing the framework of auditory timing [10], with beat-based mechanism for *discrete* movements and duration-based mechanism for *continuous* ones, given the differences in paradigms and stimuli, we do not imply that these auditory mechanisms can be directly mapped onto visual timing of realistic human movements. Whether these timing modes are indeed supramodal still warrants further investigations [2, 42]. Similarly, on the basis of shared perceptual and motor timing processes, our perceptual results (for *discrete* versus *continuous* movements) seem reminiscent of the dualistic motor timing in synchronization tasks: discrete movements (e.g., finger-tapping) employ event-based timing, whereas continuous movements (e.g., circle drawing) employ emergent timing [43]. The former carry motor timing advantages over the latter due to their perceivable discrete events (tap contact). It may be tentatively argued that the present timing advantages for beat-based movements arise from perceptual processes corresponding to, or even shared with, their motor counterparts. Furthermore, it has been proposed that these two motor timing modes cannot be combined [44], which seems consistent with our result that adding beat-based components to a non-beat-based movement (*mixed*) did not improve visual timing. Timing difficulty in this case likely arose from the continuous trajectory, which deterred the perceptual system from adopting a beat-based strategy.

One question may arise as to whether the observed advantage of a visual beat in timing was associated with possible counting strategies [45] for *discrete* movements. This explanation was, however, not supported by the result that *mixed* movements, despite the presence of regular trajectories and thus the possibility of counting, were not better timed than *continuous* ones. In addition, counting or segmenting would also have been possible in a *continuous* movement based on positional cues [18] and could thus not exclusively account for improved timing for *discrete* ones. Similarly, one might discuss whether visual timing could have been influenced by stimulus factors such as total traveled distance of the limbs. As shown in Experiment 1 (Table 1), while differences in limb displacement were admittedly hard to control for in real human movements, there was no systematic difference across different movement types or limbs that would correspond to the obtained results (e.g., more consistent timing for *discrete* movements was not associated with more or less limb displacement across limb types). Thus, performance in the present tasks was unlikely to be modulated by such stimulus features.

Our findings also reveal how different parts of a whole-body movement are timed in parallel. While a beat in either the arm or the leg movement assisted visual timing, in a multi-limb movement the beat-based benefit relied only on the legs. It would seem as if observers first oriented to the leg movement for a beat which, if found, enabled them to adopt beat-based timing. If not, however, observers did *not* resort to the arm movement either, even if a beat was available. This pattern suggests that temporal perception of multi-limb movements is somewhat different than can be explained by timing the upper or lower limbs alone, and a higher weight in timing is given to the lower limbs. The fact that the beat-based mechanism is driven by the leg movements seems to fit the action-perception coupling often proposed in rhythm perception: for example, preferred musical tempo corresponds to preferred frequency of locomotion, which concerns mainly the leg movements [5]. Thus, visual timing of dance movements may engage a common sensory-motor platform as for processing auditory rhythms, arguing for the multimodal nature of rhythm representations. It should be noted that the "leg dominance" in visual timing cannot be explained by a preference for the lower visual field alone, as such a preference has mainly been established in goal-directed actions involving tools, and only when viewers are actively engaged in object manipulation, not during passive viewing [46]. In addition, an upper visual field preference has also been found in a visual search task [47]. Thus, a general spatial bias regardless of the visual information does not seem to underlie our finding.

Contrary to earlier proposals that the temporal structures of simpler visual stimuli were obligatorily represented in

auditory terms [16, 39], where task-irrelevant sounds were shown to impair visual timing, the present lack of auditory interference effect argues for the visual nature of beat-based timing, at least for rich, ecological movement information, an idea that has received increasing support [19, 48]. The fact that also the congruent sounds had no effect on visual task performance suggests that either the auditory and visual streams were not integrated temporally, or the integration provided no additional assistance to the present task, as the sounds did not offer more beat-related information than the visual stimuli. It would be interesting for future studies to examine whether (task irrelevant) congruent and incongruent visual interferences would influence visual timing in this case. As several participants reported auditory imagery during the visual tasks, we cannot rule out possible auditory co-representations of visual movement rhythms. Although these co-representations may exist in parallel to the visual ones, they did not seem to replace the latter nor influence visual timing. In fact, when movements became more complex (as in Experiment 2), fewer participants reported using auditory strategies, indicating greater reliance on the visual representation. To what extent movement observation elicits auditory co-representations, how the tendency varies with movement complexity, and whether the two sensory representations interact remain interesting questions for follow-up research.

Movement tempo modulated visual timing of whole-body movements in Experiment 2, where slower movements were more consistently timed. As dance observation activates an internal motor program in the observers [27], greater difficulty in simulating these movements at faster tempi may increase difficulty in representing their temporal structures. This interpretation is supported by the fact that movement tempo did not affect visual timing consistency of simpler movements in Experiment 1, which could likely be simulated with equal ease across tempi. There might be a range of optimal tempi for each movement both in execution and in perception, such that movements considerably slower or faster than these tempi are less well represented and thus more difficult to time visually. Movement tempo did, however, influence absolute timing accuracy (AE) of the leg movements in Experiment 1, with more deviation in the two slowest tempi than in the middle one, whereby those with longer music or dance training were less subject to such errors. Thus, while beat-specific effects in visual timing were independent of expertise, training appeared to be beneficial for more general timing functions irrespective of beat, such as absolute duration estimation, in slower movements. Finally, the effect of tempo on ratio observed in both Experiments 1 and 2, namely, more over- and underestimation for faster and slower sequences, respectively, can be explained by Vierordt's law. The fact that shorter and longer intervals tend to be over- and underestimated when presented in the same experiment has been repeatedly reported in the timing literature, which also applies to tempo in a rhythmic context [35, 36, 49].

In conclusion, we presented evidence of visual timing mechanisms for dancelike movements, showing a beat-based advantage that relies especially on the leg trajectories. While they appear similar to mechanisms of auditory rhythm perception found in previous studies, we demonstrated the visual nature of movement timing. These results have implications in how we approach multisensory rhythms in an ecological scenario, which may lead to new research linking action perception and rhythm perception in music and dance.

Competing Interests

The authors declare that they have no competing interests.

Authors' Contributions

Both authors conceptualized and designed the study. Elvira Salazar-López choreographed and recorded the movements. Yi-Huang Su generated the stimuli and programmed the experiments. Both authors collected the data. Yi-Huang Su analyzed the data. Both authors discussed and interpreted the results. Yi-Huang Su wrote the paper; Elvira Salazar-López contributed to visual stimuli description and presentation. Both authors worked on improving the paper.

Acknowledgments

Yi-Huang Su was supported by the German Research Foundation (DFG), SU782/1–1 and SU782/1–2. The authors thank Noelia Urquiza Salvat for performing all the movements for their visual stimuli and Waltraud Stadler for helpful discussions on the paper. The publication of this work was supported by the German Research Foundation (DFG) and the Technische Universität München within the funding program Open Access Publishing.

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 2716036, 11 pages
http://dx.doi.org/10.1155/2016/2716036

Research Article

Hemispatial Neglect Shows That "Before" Is "Left"

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Received 28 October 2015; Revised 12 February 2016; Accepted 10 April 2016

Academic Editor: Marinella Cappeletti

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Recent research has led to the hypothesis that events which unfold in time might be spatially represented in a left-to-right fashion, resembling writing direction. Here we studied fourteen right-hemisphere damaged patients, with or without neglect, a disorder of spatial awareness affecting contralesional (here left) space processing and representation. We reasoned that if the processing of time-ordered events is spatial in nature, it should be impaired in the presence of neglect and spared in its absence. Patients categorized events of a story as occurring before or after a central event, which acted as a temporal reference. An asymmetric distance effect emerged in neglect patients, with slower responses to events that took place before the temporal reference. The event occurring immediately before the reference elicited particularly slow responses, closely mirroring the pattern found in neglect patients performing numerical comparison tasks. Moreover, the first item elicited significantly slower responses than the last one, suggesting a preference for a left-to-right scanning/representation of events in time. Patients without neglect showed a regular and symmetric distance effect. These findings further suggest that the representation of events order is spatial in nature and provide compelling evidence that ordinality is similarly represented within temporal and numerical domains.

1. Introduction

Mounting evidence suggests that time is represented in spatial terms [1]. Tversky and collaborators [2] were among the first to show that the spontaneous spatial positioning of temporally ordered events follows the direction of reading/writing. Also overlearned sequences of items, either temporally characterized (days of the week) or nontemporally characterized (letters of the alphabet), can interact with the spatial position of response keys [3, 4]. This interaction has often been described, within a given sequence, in terms of faster left-sided responses for earlier than for late items and, viceversa, in terms of faster right-sided responses for late than for earlier items. An association between ordinal value and lateralized responses can also be found for items whose order is newly and arbitrarily learned [5–7].

The method and the interpretation of these studies (all with healthy participants) have been however strongly criticized, among others, by Proctor and Cho [8]. According to their influential "polarity correspondence" theory, the space-order association in categorization tasks would be a byproduct of a structural, and not conceptual, overlap between the code used to categorize the item and the code used for providing responses. By testing the performance of patients who are affected by spatial processing disorders, it is possible to directly determine whether they show symmetric performance (as predicted by the polarity correspondence) or whether some distortions occur, therefore supporting the view that the representation of ordered items is truly spatial in nature. To this aim, the present study compared the performance of right hemisphere damaged (RHD) patients with and without a deficit in processing the contralesional space called hemispatial neglect or unilateral spatial neglect (henceforth: neglect). In neglect, the items which are present in the ipsilesional hemispace are not as efficiently processed (and sometimes completely ignored) as those presented in the ipsilesional hemispace [9–13]. Neglect patients offer the unique possibility to study the nature of order representation by contrasting a pathological performance for the contralesional hemispace with a less impaired (or close to normal) performance for the ipsilesional hemispace.

The idea of studying whether specific deficits for time processing are present in neglect is not new. Neglect patients have been already described to suffer from deficits in the processing of time-related aspects (for review, see [14]). Most of the previous reports, however, focused on slowed dynamics and on a number of collateral aspects that can be affected by several, heterogeneous and not necessarily spatial, factors. Only recently, some studies directly assessed whether the deficits neglect patients show in time processing support a functional analogy between impairments in the spatial and time domains [1, 15, 16]. One line of research in RHD patients focused on experienced time by presenting short duration stimuli (typically below two seconds) to be either reproduced/bisected or categorized with respect to a reference. For instance, in a temporal bisection task, neglect patients showed a severe underestimation for stimuli duration [17]. This study suggests a close analogy between the deficits they show in physical space and those they manifest in processing time durations [1]. The same group of neglect patients also showed a reduction of their underestimation following prismatic adaptation (PA) which generated a leftward compensatory aftereffect. This means that spatial attention, which is deficient in patients and modulated by PA, is probably the medium for spatially representing time. Moreover, in the same study, both RHD patients without neglect and healthy controls showed temporal underestimation following the same PA procedure, further suggesting a causal involvement of spatial attention when elapsing time has to be processed and quantified [18]. These findings suggest that the way time is processed is truly spatial in nature, leading to the proposal that time might be represented along a mental line [1]. The transient modulation induced by PA in time processing for RHD patients with neglect proves that their bias in time processing is not due to unspecific cognitive impairments [19] and points to their deficit in unilateral orienting of visuospatial attention as a key determinant for their performance.

Two studies have shown that neglect patients present selective deficits also when brief time durations have to be categorized with respect to a standard. In a first one [20], RHD patients with neglect performed significantly worse than RHD patients without neglect and healthy controls, irrespective of the duration of the standard tone and without any interval-specific deficit. In a second study [21], patients with more severe neglect showed a disrupted time-space association for short durations only, as if these were ignored because of a left-to-right ordering. In contrast, [22] showed, within a group of right brain damaged patients, a neglect-specific difficulty when the quantity of nonsymbolic items had to be compared to a reference quantity but not when the comparison had to be done with respect to a reference duration. All in all, previous studies on neglect and time durations have reported rather conflicting results [22].

Still other studies reported that, even in the absence of neglect on paper-and-pencil tasks, RHD patients may be particularly slow when detecting contralesional targets after having been exposed to future tenses, which are supposed to orient spatial attention rightward [23]. The presence of a spatiotemporal bias at a sensitive computer-based testing in the absence of neglect at (not so sensitive) paper-and-pencil tests is not surprising [24–26]. At the same time, however, it should be noted that, in the absence of neglect at paper-and-pencil tests, right hemisphere damage does not necessarily result in deficits when processing different time durations [15].

While converging evidence suggests a role for spatial attention in processing time durations, the possibility that neglect might also affect the processing and representation of more conceptual aspects of time is almost totally unknown. One recent study [16] showed that left hemispatial neglect results in distortions of the sequential ordering of time-related events/features. In that investigation [16], the crucial time aspect was not related to duration but to conceptual/order-related aspects. Right brain damaged patients memorized a list of events/features they were told occurred in the past or would occur in the future. Patients with neglect mislabeled items belonging to the past as being "future" items both in recall and in recognitions tasks significantly more than participants without neglect did. This spatial distortion closely mirrors spatial mislocalizations in the visual space whereby contralesional targets, under demanding tasks, are reported to appear in the ipsilesional space [27].

In the context of our current approach to these issues, it is important to mention that, also in the numerical domain, neglect patients often present some distortions resembling their deficit in contralesional space processing. They show, in magnitude comparison tasks, pathological slowing for the number immediately smaller than a reference (e.g., 4 if the reference is five; or 6 if the reference is 7); see [35]. This slowing only appears in magnitude comparison tasks and does not emerge in parity tasks [36, 37]. A principal component analysis [37] revealed that this asymmetric distance effect cooccurred with rightward shift in line bisection within one component and with numerical interval bisection/parity judgment within a different one.

This slowing is reduced by a cloud of dots showing leftward motion [38], extending, according to the authors, the effects of optokinetic stimulation (OKS) to representational numerical neglect (see also [39, 40]). All these findings converge in showing that attentional biases, due either to neglect or to an attentional manipulation, may affect representations of number and time.

In the present study, we designed a new task requiring a binary, lateralized left/right response to categorize items belonging to a sequence of temporally ordered newly learned events. This choice allowed us to avoid any confounding due to potentially interfering long term associations, while lowering processing load. The task we adopted was inspired by the methodology described in [35] to study numerical representations. We not only aim to demonstrate a causal role of spatial attention in serial order processing but are also willing to prove that the consequences of damage to the neural and cognitive circuits devoted to spatial processing can extend to the domain of online-ordinal/conceptual time.

2. Materials and Methods

2.1. Sample. The only criterion for inclusion in the study was the presence of a single stroke within the right hemisphere. Exclusion criteria were dementia, substance abuse, and presence of other neurological disorders. We tested in total fourteen right hemisphere damaged patients, all right-handed (Table 1). Two patients were admitted to the Rehabilitation Center of Conselve (Padova, Italy) and were Italian speaking. The remaining twelve patients were tested in the University Hospital of Geneva (Switzerland) and were French speaking.

2.2. Neuropsychological Testing. Patients from Italy ($n = 2$) were tested with a battery for neglect (Conventional Part, Behavioural Inattention Test, BIT) [34] including three cancellation tasks (Lines, Letters, and Stars) and four copying and three drawing from memory tasks, plus a line bisection subtest. The two patients tested were both considered as having neglect because of a total battery score below the cut-off (129).

Patients from Switzerland ($n = 14$) were considered to present neglect when their performance was pathological in at least two of the three following tests: line bisection [28] (cut-off score: rightward deviation > 11%), scene copying [31] (cut-off: 1 out of 4), and bell cancellation [30] (cut-off for left omissions: 2 out of 15).

According to these criteria, eight patients entered the neglect group (N+: mean age 61.1 ± 7.8 years) and six patients entered the nonneglect group (N−: 57.4 ± 14.8 years). Average time from stroke was 81.7 ± 53 days for N+ and 51.5 ± 39 days for N− patients.

The study protocol was approved by the Ethical Committee of the Department of General Psychology, University of Padova, and the Central Ethics Committee of the University Hospital of Geneva. Patients signed informed consent to take part in the study.

2.2.1. Lesion Neuroanatomy. For each patient, brain lesions were confirmed by brain scans (MRI or CT) and reconstructed on axial slices using MRIcro [41], according to previously described methods [42–44]. Lesioned areas were transformed to a three-dimensional region of interest (ROI) corresponding to the lesion volume and normalized to a standard brain template using MRIcro and SPM. The normalized lesion ROIs were then superimposed on a T1 MRI in order to determine the overlap of lesions across patients and define brain areas where damage was most commonly observed (Figure 1).

The mean lesion volume (the total number of lesioned voxels on the MRIcro brain template) did not significantly differ across the two groups ($p = 0.15$).

A direct contrast between these two groups using a voxel-wise subtraction analysis (Figure 1) indicates that damage to lateral frontal and temporal cortex was more commonly found in patients with spatial neglect (purple-yellow), whereas lesions in patients without neglect were centered on the pulvinar and the deep parietal white matter and medial temporal lobe (dark blue-turquoise).

2.3. Experimental Task. Patients were asked to pay attention to a story which was read aloud by the experimenter until the patient stated he/she succeeded in memorizing it.

The story (in Italian/French) was about a guy named "Giorgio." Its translation is as follows: "Giorgio was smiling while riding his bike. The sun was shining in the sky. Tired and sweated, Giorgio jumped down from his bike and started to push it while holding a bottle. He arrived over the top of the mountain and looked to the city below him. [This was later identified as the reference event]. Then Giorgio started a fast downhill among clouds of dust. Giorgio failed to control his bike and fell inside a bush. His fall ended over the hood of a car that was passing by."

Then the computer-based experiment was administered. Each trial started with a fixation cross (500 ms) followed by a blank screen (500 ms) and finally by an image representing one of the six events mentioned in the story (until response). Patients were informed that the reference event was the arrival of Giorgio at the top of the mountain and that they had to determine whether the image referred to an event that occurred before (images −3, −2, and −1) or after (images 1, 2, and 3) this reference event.

To overcome potential effects of neglect on visual perception, the image (92 mm wide and 45 mm high) was presented in the center of the screen. Since eye to screen distance was about 60 cm, image borders were relatively central (<5° of left/right eccentricity). The choice to present visual material was preferred after careful consideration of alternative possibilities: presenting target stimuli in auditory format would have strongly biased participants towards the use of verbal strategies for memorization. No image had critical information located on its extremities (neither left-sided nor right-sided).

To overcome left-side hemiplegia, responses were implemented by using a mouse (Figure 2) with the right hand (index finger/left and middle finger/right; see [35, 45]). Each response key was arbitrarily assigned one colour (left white versus right red). This was done to avoid the possibility that spatially characterized words in the instructions about key presses would have led to arbitrary spatial associations. An auditory feedback (low tone) was given in case of wrong response. There were 12 repetitions for each condition and for each mapping, for a total of 144 trials for each patient. The monitor was positioned at a viewing distance of about 60 cm.

There was a practice run of 12 trials which was repeated if needed. For performing the second experimental block, patients were asked to switch the response keys; a second practice was again performed before performing the experimental trials with the new mapping. The initial mapping ("before" response assigned to the left key and "after" assigned to the right key) or vice versa was counterbalanced between participants.

3. Results

3.1. Reaction Times. Before analysing RTs, we checked for overall accuracy (analysis on error rate is reported later). One neglect patient (N+ 3) failed to achieve with instructions and had to be excluded from the study. Neglect patient

Table 1

Group case	Age	Sex	Aetiology	Lesion vol	Days from onset	Bisection [28] % deviation	Bisect. [29] 5 cm	Bisect. [29] 20 cm	Total Om. [30]	L	C	R	Copy [31]	MoCa [32]	Delayed recall (/5)
N+ 1	60	M	H	271885	125	25.04	−0.5	21	22	15	4	3	3	23	4
N+ 2	50	M	H	461428	140	83.72	3	27	28	15	5	8	2	26	5
N+ 3	65	M	H	310108	23	57.20	−2	12	20	14	4	2	3	24	5
N+ 4	70	M	I	455633	45	32.45	9	30	9	9	0	0	1	28	4
N+ 5	52	M	H	15379	156	3 (max 16)*	na	na	75[b]	53[b]	nc	22[b]	na	24[MM]	na
N+ 6	59	F	I	45313	60	10 (max 16)*	na	na	66[b]	49[b]	nc	17[b]	na	27[MM]	na
N+ 7	72	M	I	56439	23	28.47	3	31	12	8	4	0	1	28	4
N+ 8	60	M	I	116513	65	57.20	8	54	20	14	4	2	1	28	5
N− 1	57	M	H	35377	41	8.65	1	2	0	0	0	0	0	30	5
N− 2	79	M	I	11755	12	7.10	0	3	0	0	0	0	0	27	4
N− 3	32	M	I	18379	18	3.40	2	4	2	1	1	0	0	30	5
N− 4	43	M	I	232185	74	7.10	1	6	4	1	2	1	0	29	4
N− 5	67	M	H	24366	130	4.20	2	1	1	0	0	1	0	29	5
N− 6	67	F	I	245984	34	−0.4	0.8	1	2	2	0	0	0	30	5

Line bisection 1 [28]: mean error in percentage of maximal possible error. A positive value indicates a rightward error.
Line bisection 2 [29]: mean left (−) or right (+) deviation in mm for 2 lines of 5 and 20 cm.
Omissions at bell cancellation task [30]: number of total omitted bells then separately reported for the left (L; /15), central (C; /5), and right (R; /15) parts of the test sheet.
MM: *MMSE* [33].
Delayed recall (MoCA): number of correctly recalled items.
na: not administered.
b: mean of all cancellation tasks from the BIT [34].
nc: not calculated.
*BIT [34] aggregated score (sum of bisection, copy, and drawing subtests).

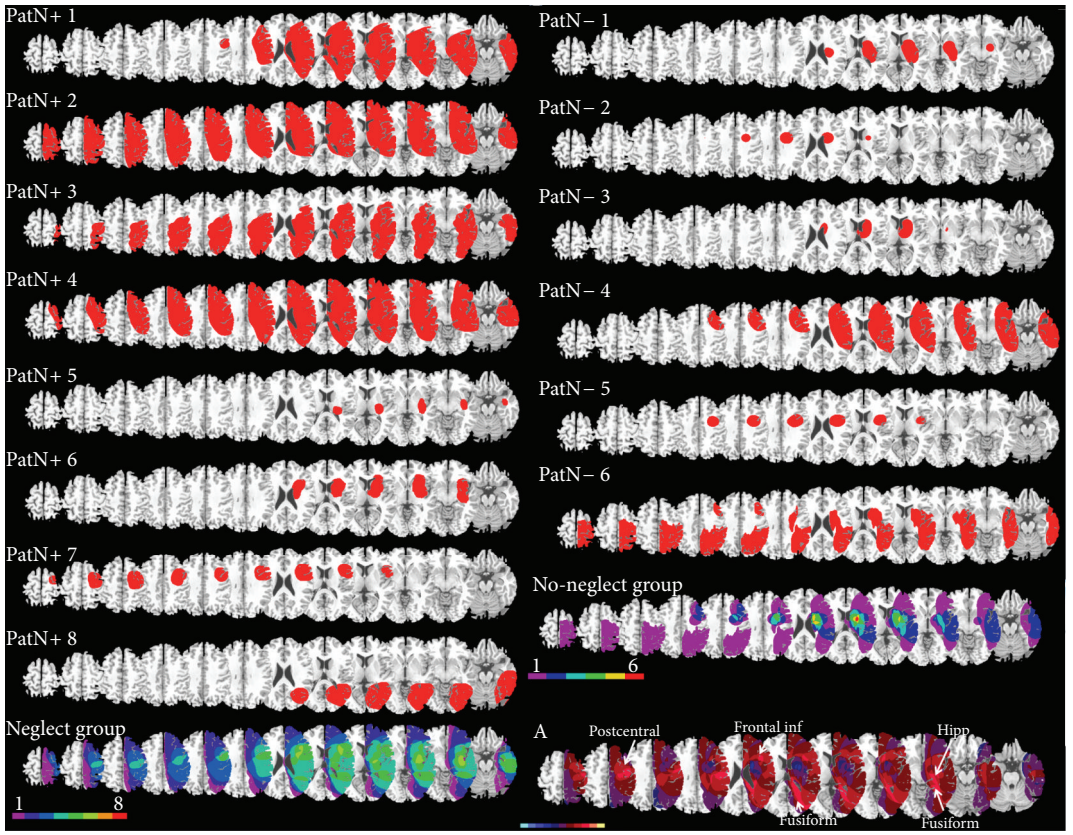

Figure 1: Individual lesion mapping (in red) and group overlap for neglect patients (N+, left) and no-neglect patients (N−, right). Lesion reconstruction was performed on axial slices of a normalized magnetic resonance imaging brain template. In the group overlap colors code for the number of patients with damage to a given area (from 1 = violet to 6 (N−) or 8 (N+) = red). (A) Median split subtraction analysis, comparing the lesion in patients with spatial neglect versus without. Each color in the scale bar codes for a 16.67% frequency of lesion in one or the other group, except for the central purple color that represents −16.67 to +16.67%.

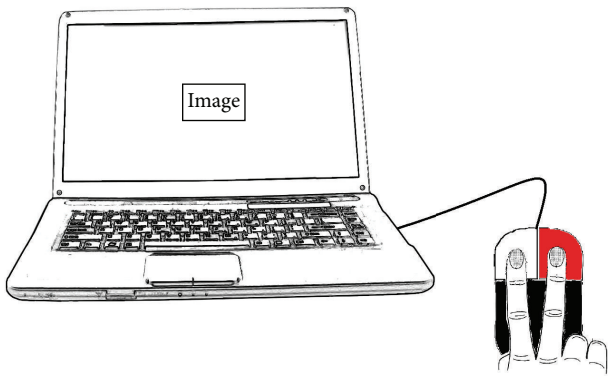

Figure 2: Experimental setup. Patients had to determine (index versus middle finger of the right hand) whether the presented image referred to an event occurring before or after the "central" event of the story, acting as temporal reference (adapted from http://jn.physiology.org/content/78/1/117 and from a drawing by Nita Jatar Kulkarni).

N+ 2 presented an error rate in the DP mapping too high (68%) to consider his reaction times reliable. We therefore analysed his median RTs from the PD mapping only, where his performance was better (less than 30% of errors). Reaction times for correct responses in 13 patients entered an ANOVA with Time (before versus after the reference) and Distance (1 versus 2 versus 3) as within-subject factors, plus Group (N+ neglect present versus N− neglect absent) as between-subjects factor (Figure 3). For each patient, condition, and mapping, medians were calculated and then averaged across mappings.

The main effects of Time, $F(1, 11) = 5.9$, $p < 0.05$, and $\eta^2 = .35$, and Distance, $F(2, 22) = 7.8$, $p < 0.01$, and $\eta^2 = .42$, were significant. The Group effect was also significant; neglect patients were overall slower: $F(1, 11) = 7.7$, $p < 0.05$, and $\eta^2 = .41$ (N+: 1433 ms versus N−: 751 ms).

These effects were qualified by the crucial Time × Group interaction, indexing slowing for items before the reference which occurred in neglect patients only: $F(1, 11) = 6.6$, $p < 0.05$, and $\eta^2 = .38$ (N+ before = 1659 ms; N+ after = 1208 ms; N− before: 752 ms; N− after: 751 ms). The Distance × Group interaction failed to reach significance: $F(2, 22) = 1.8$, $p = 0.18$, ns.

To better understand the pattern determining the interaction, two separate ANOVAs, one for N− and one for N+, were performed with the same within-subjects factors as above.

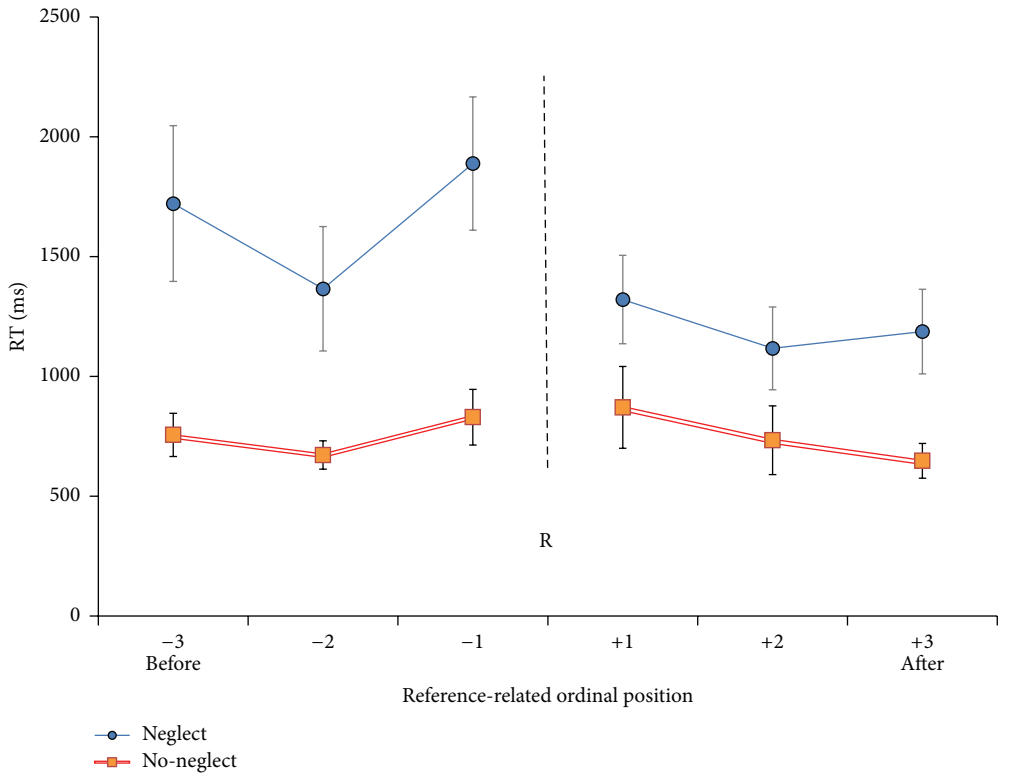

Figure 3: Distance effect. RTs as a function of the presented image are shown. In the N+ group (upper line, in blue) the Distance effect (slower RTs when closer to the reference) is asymmetric for items before versus after the reference whereas in N− (lower line, in red/orange) it is symmetric. The "position" of the reference event is represented by the letter "R." Bars index SEM.

In N− group, only the main effect of Distance was significant: $F(2, 10) = 4.6$, $p < 0.05$, and $\eta^2 = .5$. It reflected slower and symmetric (no interaction with "Time") responses for items closer to the reference ($d1 = 850$ ms; $d2 = 703$ ms; $d3 = 702$ ms).

In N+ group, the main effect of Distance was also significant: $F(2, 12) = 5.58$, $p < 0.05$, and $\eta^2 = .48$. In addition, as predicted, a main effect of Time emerged, $F(1, 6) = 7.9$, $p < 0.05$, and $\eta^2 = .57$, indicating an asymmetry for items presented before versus after the reference. The Time × Distance interaction was not significant: $F(2, 12) = 1.11$, $p = 0.36$, and $\eta^2 = .16$. Inspection of data revealed that the main effect of Time was due to slower responses to events occurring before the reference (average before = 1659 ms; average after = 1208 ms). The slowing was seemingly irregular across the different distances [d] (before items: $d1$ 1889 ms; $d2$ 1366 ms; $d3$ 1721 ms).

To investigate our specific hypothesis on the presence of a selective asymmetry in neglect involving items before versus after the reference, we performed, separately for N+ and N− patients, one t-test for each of the three temporal distances. A significant slowing emerged, in the N+ group only, for the item immediately before the reference versus the item immediately after [$t(6) = 4.2$, $p < 0.01$], as well as for the first versus the last item [$t(6) = 2.39$, $p < 0.05$ (one-tailed)]. Differences were particularly large (about half second) for both distances 1 (before 1889 ms; after: 1321 ms) and 3 (before 1721 ms; after: 1187 ms).

3.2. Different Mappings. Finally, an ANOVA with response Side as additional factor was performed. The main effects of Time and Distance and the Time × Group interaction were still present. Moreover a significant Time × Side interaction (SNARC-like [46]) emerged: $F(1, 10) = 10.96$, $p < 0.001$, and $\eta^2 = .52$. Average RTs for events occurring "before" the reference were 950 ms for left-sided and 1255 ms for right-sided responses; for events occurring "after" the reference, the average RTs were 796 ms for right-sided responses and 1090 ms for left-sided ones. The three-way interaction Time × Side × Group was not significant: $F = 1.44$ and $p = 0.26$, suggesting that the spatial coding of events order similarly interacted with the response side in both neglect and nonneglect patients. Overall, no significant effect of response side emerged: $F(1, 10) = .006$ and $p = 0.94$ (left 1020 ms versus right 1025 ms). When considering the two groups separately, the two-way Time × Side interaction turned out to be significant in neglect only (N+: $F(1, 5) = 7.23$, $p < 0.05$, $\eta^2 = .59$; N−: $F(1, 5) = 3.75$, $p = 0.11$, $\eta^2 = .43$). A pattern suggesting the presence of a Time (before/after) × Side (left-sided versus right-sided response) interaction was however clearly present in both groups (N+: left before 1233 ms; right before 1673 ms; left after 1325 ms; right after 946 ms; N−: left before 667 ms; right before 838 ms; left after 856 ms; right after 645 ms), as confirmed by the relatively high η^2 in both groups.

3.3. Accuracy. As done for RTs, correct response rates from 13 patients were analysed with a first ANOVA with Time (before versus after the reference) and Distance (1 versus 2 versus 3) as within-subject factors, plus Group (N+ versus N−) as between-subjects factor and mean accuracy as dependent variable. Data from neglect patient N2 were entered (for both mappings) only in this but not in the following ANOVA, as previously done for RTs.

The main effect of Distance was significant, $F(2, 22) = 3.89$, $p < 0.05$, and $\eta^2 = .26$, as well as the Time × Distance interaction: $F(2, 22) = 6.89$, $p < 0.01$, and $\eta^2 = .39$. Accuracy was similar, for both items before and after the reference, for $d1$ (84%) and $d2$ (90%). In contrast, at $d3$, accuracy was higher for the last (93%) than for the first (82%) item ($t(12) = 2.13$, $p < 0.05$, one-tailed). No other main effects or interactions emerged. A tendency for lower accuracy in N+ (80%) than in N− (94%) was present: $F(1, 11) = 4.57$, $p = 0.056$, and $\eta^2 = .29$. In N+ group, the lowest accuracy rates occurred for items 1, 3, and 4 (73%, 75%, and 77%, resp.).

When performing a second ANOVA considering response side (therefore excluding patient N+ 2) the interactions Side × Time, $F(1, 10) = 6.83$, $p < 0.05$, and $\eta^2 = .406$, and Time × Distance, $F(1, 10) = 5.46$, $p < 0.05$, and $\eta^2 = .35$, were significant. The first interaction was suggestive of a SNARC-like effect, with less errors for left-sided responses to items before the reference (93%) than after the reference (86%), while the opposite effects emerged for right-sided responses (85% accuracy for items before the reference and 95% of accuracy for items after the reference).

The second (Time × Distance) interaction was seemingly due to a difference in accuracy between the two $d3$ values, that is, for the first (88%) and the last item (94%), whereas across distances 1 and 2 the performance was rather similar.

The Side × Time × Group interaction just missed significance: $F(1, 10) = 3.68$, $p = 0.084$, and $\eta^2 = .27$. In N+, accuracy was strongly dependent on the mapping [mean accuracy "incompatible" left-after mapping = 78% (71% if including N+ 2); mean accuracy "compatible" left-before mapping = 93% (90% if including N+ 2)]. This finding mirrors previous studies of neglect within the numerical domain [35, 36] whereby the left-large versus right-small mapping, which is "incompatible" with a left-to-right ordering, leads to a number of errors remarkably higher than the opposite mapping, up to the level of being "impossible" to perform (as occurred for cases 2 and 3 here). In N− patients, this difference was much reduced (mean accuracy left-after mapping = 93%; mean accuracy left-before mapping 96%).

Thus, the analyses on accuracy generally resembled those on RTs, allowing us to rule out that the effects found for RTs were due to a speed-accuracy tradeoff.

4. Discussion

We tested a group of right-hemisphere damaged patients, with and without left hemispatial neglect, to study whether the processing of time-ordered events is spatial in nature. Patients were presented with an image depicting one event taken from a story they had memorized. They were asked to categorize this image as occurring before or after an event occurring in the middle of the story. An asymmetric distance effect emerged, in neglect patients only, with slower responses to the images/events that took place before the temporal reference. The first event of the sequence as well as the third one (occurring immediately before the reference) elicited significantly slower responses than their counterparts occurring after the reference. Patients without neglect showed, in contrast, a standard yet symmetric distance effect with respect to the temporal reference.

These findings demonstrate that the representation of events order is spatial in nature and provide strong evidence that ordinality is similarly processed in temporal and numerical sequences. They also confirm that, in left-to-right readers and in the absence of specific manipulations, the left-to-right direction is the preferred axis to spontaneously represent ordinal events in space. Whether the major determinants of this preference mainly are hemispheric asymmetries [47] or linguistic metaphors [48] or reading and writing habits [2] remains to be directly investigated altogether with the role of individual strategies/variability in responding to ordered items.

Within the numerical domain, studies on RHD patients with left neglect have provided crucial evidence supporting a key role for spatial attention in accessing numerical magnitude upon the MNL [36, 49]. Several authors ([37, 50]; see also [51]) have highlighted WM and its interplay with spatial attention as a major determinant of these effects. The effect of a brain damage on the already complex interplay between spatial attention and spatial representations unequivocally leads to a number of dissociations [52]. Strong support for the presence of a spatial representation for numbers comes from the numerical bisection task. When asked to verbally bisect a numerical interval (e.g., what number is halfway between "2" and "6"), patients with left neglect systematically misplace the midpoint of the numerical interval (e.g., responding with "5" instead of "4"). These errors closely resemble the typical pattern found in the bisection of visual lines: that is, patients show increased rightward shifts with increasing line length and a reverse leftward bias (crossover effect) with very short lines [53]. This bias is not directly related to neglect severity in peripersonal space [45, 50, 54] nor in the O'Clock Test [51]. This peculiar form of neglect, which seems to be neither visual nor representational, can be seen as a strong indication that numbers are represented in a way that is spatial in nature [53].

In the numerical cognition domain, the role of ordinality is seldom addressed (for discussion see [52]) and there are only few studies addressing ordinality as a common characteristic belonging to both temporal sequences and numerical quantities. Order processing in fish strikingly suggests that this ability is innate and does not rely on language [55]. The spatial effects characterizing number and time might have a common origin in a spatial representation of order (see [56]). It is, however, also known that order and numerical magnitude processing can dissociate. Turconi et al. [57] described a Gerstmann syndrome patient [58] who performed well in a number comparison task (which number

is larger?) but was markedly impaired in a numerical order task (which number comes first?).

With respect to our results, which mechanisms gave rise, in neglect patients, to specific impairments for the items occurring before the reference? Broadly speaking, temporal order responses were selectively slowed in neglect patients and for items occurring "before" the reference. It is important to note that the bias for "what happened before" occurred with significantly asymmetric slowing which emerged selectively for distances 1 and 3 (the first event in the sequence and the one immediately before the reference). Why were positions 1 and 3 disproportionally affected? An explanation might be related to the way the task was solved. It is possible that different representations were generated according to the ordinal position of the presented item. We speculate that when the first item had to be responded to, the whole sequence before the reference was also activated, in such a way that the item was spatially coded as being "left" relative to the whole sequence. On the other hand, when the item immediately before the reference was presented, it might have been spatially coded relative to the reference only. The second item in the sequence would not be double coded as "left" and would then be responded to more quickly. Another alternative explanation might be that item 1 was located to the "leftmost" position in past time and therefore most severely neglected. One might then question why the same slowing for the first item has not been described in the numerical domain for number 1 when the reference is 5 [35–37]. The answer may be that in the numerical domain the presentation of number 1 would not trigger an automatic activation of the numerical range because in that case number 1 only codes for a magnitude and not a "first of many" order. It might then be claimed that when the numerical range is not "canonical," the first item should lead to slower processing in left neglect because it indexes a "first of many" in the order representation. Surprisingly enough this last prediction is confirmed by previous data [35, Figure 1]; when the reference number was 7 rather than 5, apparently selective slowing for the digits 1 and 2 (versus 3) emerged. Regardless of its origin, the presence of selective slowing for the first item allows ruling out the idea that a spatially characterized slowing occurs only in interaction with the most difficult condition (e.g., distance 1). A final alternative explanation, although more complex, would be that this result reflects an abnormal primacy effect on top of the representational effect for the item immediately preceding the reference. This explanation would however not provide a reason as to why neglect should affect the primacy effect. On the contrary, in order to emerge, the slowing for the first item had to be strong enough to overcome primacy effect. Moreover, it suggests that no verbal labelling of items was implemented to remember the sequence. If not, an advantage rather than a disadvantage for first item(s) should have emerged.

Within the numerical domain, some authors [45] also maintained that the distortions due to neglect in numerical processing reflect impaired access rather than a distorted representation itself. Supporting evidence can be found in [36], whereby spationumerical deficits shown by neglect patients varied according to the task at hand (present in magnitude comparison but absent in parity judgement). Leaving terminological issues aside, it seems that these spatial effects are due to the active "handling" of stimuli. Whether these operations are related to spatial attention shifts and/or to WM processes (see also [7, 59]) will be object of future investigations, altogether with the role of different strategies implemented at individual level.

Our results suggest the presence of a particular representational domain, encompassing both spatial and temporal characteristics, which is affected by neglect. For the moment, it seems unclear whether there is any strict overlap between the spatiotemporal distortions and patients' performance in the physical space. This could not be tested due to the small sample size and variability of neglect tests. Also its relation with the clinical presence/degree of neglect seems puzzling. On the one hand, one could claim that if time is truly spatially represented, a strong quantitative correlation should be expected between neglect severity and time processing. On the other hand, it should be noted that, despite the strong analogies we found, space and time are distinct domains and that it might not be adequate to a priori expect a correlation in performance between the two. Moreover, performance of neglect patients at clinical tests is often the result of the implementation of compensatory strategies, whereas this seems to be less often the case in computer-based tests [26]. Larger-sample studies might shed further light on this issue. The potential absence of a clear correlation between neglect severity and magnitude of the slowing for items "before the reference" may however also suggest another close analogy with the numerical cognition domain, where there is little or no evidence of correlations between neglect severity and behavioural effects in numerical comparison and numerical interval bisection tasks [36, 50].

Also the absence of these spatiotemporal distortions from the standard clinical experience might be explained in analogy with the numerical cognition domain: neglect has little or no impact on "general" numerical abilities. When numerical magnitude has to be processed/ranked (magnitude comparison), dramatic impairments can emerge [36, 53] as opposed to when numerical magnitude is task-irrelevant (party judgment [36]; see also [60]). While the current sample is too small to suggest any reliable lesion to behaviour correlation, it seems worth noting that in most of the patients the parietal lobe was spared.

5. Conclusions

Performance of left neglect patients showed selective slowing for items appearing before a time-related reference. While this core finding demonstrates that serial order is spatially coded, four additional conclusions can be also drawn. The first is that while patients show spectacular spatiotemporal distortions, the processing of time as space does not involve neglect patients only. Indeed, healthy participants spontaneously associate early items of a sequence with a left-sided response and late items with a right-sided one [5–7]. In contrast, when the to-be-measured effect involves a shift of attention and single letters are used as sequential stimuli, the results are less clear-cut and

might depend on the meaning letters convey. For instance, letters are not associated with a strong ordinal meaning related to their position in the alphabet [61], although letters can interact with the appearance of a lateralized target when they convey order/position in a short-term sequence [62].

A second aspect is the presence, in patients as well as in healthy participants, of overlapping representations for both perceived and conceptual aspects of time. Despite the presumable difference in the cognitive processes involved, very similar effects (for instance, the association of short-before with left and of long-after with right) has been found with experienced as well as with conceptual time [63], again supporting a more general role of spatial attentional operations. At the same time, however, here we describe for the first time that neglect differently affects the processing of the items before a temporal/ordinal reference depending on the ordinal position these items occupy.

A third aspect is related to the demission of the polarity correspondence argument [8] as a viable explanation for order/space associations. Yet, as originally commented by Umiltà [64], the polarity coding can explain potential space-side arbitrary associations when the labelling is verbal. The strikingly different performance showed by neglect patients cannot be attributed to differences in verbal processes.

The last issue concerns the potential broader implications of our findings. By showing that order processing is affected by neglect, our study suggests that neurologically caused spatial deficits present in this syndrome might have widespread consequences, disrupting a number of cognitive aspects well beyond the domains of spatial attention and visual perception. Indeed, given the current evidence that ordinal processing is hampered in neglect, it is not implausible that this deficit might also influence other functions relying on sequential information such as the retrieval of episodic memory. Indeed, the knowledge of order is crucial in many domains and only partly implemented through verbal coding. Based on functional neuroimaging data, it has been proposed that the parietal lobes play a pivotal role in episodic memory [65]. It is tempting to speculate that a mechanism subtending parietal processes in memory would be implemented by spatial attention and shifts between sequential time points. Whereas some evidence of an interplay between spatial attention and episodic memory is already available [66], the two domains might be more closely intertwined than one might think. It might not be inappropriate to think that the loci method for memorizing arbitrary lists of items (cfr. memory palace or mind palace) might build upon a spontaneous tendency of representing order as space.

Competing Interests

The authors declare that they have no competing interests.

Authors' Contributions

Mario Bonato and Arnaud Saj equally contributed.

Acknowledgments

This study was supported by Swiss National Foundation (no. 3200B0-114014) to Patrik Vuilleumier. Mario Bonato was supported by a Marie Curie Intra European Fellowship within the 7th European Community Framework Program. Arnaud Saj is supported by Geneva Academic Society (Foremane Fund).

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 1867270, 8 pages
http://dx.doi.org/10.1155/2016/1867270

Research Article

Age-Related Effects on Future Mental Time Travel

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Received 29 October 2015; Revised 29 February 2016; Accepted 23 March 2016

Academic Editor: Aage R. Møller

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Mental time travel (MTT), the ability to travel mentally back and forward in time in order to reexperience past events and preexperience future events, is crucial in human cognition. As we move along life, MTT may be changed accordingly. However, the relation between re- and preexperiencing along the lifespan is still not clear. Here, young and older adults underwent a psychophysical paradigm assessing two different components of MTT: self-projection, which is the ability to project the self towards a past or a future location of the mental time line, and self-reference, which is the ability to determine whether events are located in the past or future in reference to that given self-location. Aged individuals performed worse in both self-projection to the future and self-reference to future events compared to young individuals. In addition, aging decreased older adults' preference for personal compared to nonpersonal events. These results demonstrate the impact of MTT and self-processing on subjective time processing in healthy aging. Changes in memory functions in aged people may therefore be related not only to memory per se, but also to the relations of memory and self.

1. Introduction

Healthy aging is associated with changes in autobiographical episodic memory, that is, the ability to recall one's past experiences in their spatial and temporal context [1, 2]. In a seminal study, Levine and colleagues tested memory for past experiences in younger and older adults using the Autobiographical Interview (AI), which allows quantifying separately the episodic (internal) and semantic (external) details constituting participants' autobiographical reports. While external details were comparable across groups, internal details were significantly fewer in older compared to younger adults, indicating that aging is associated with a loss in autobiographical memory specificity [3]. More recently, Addis and colleagues demonstrated that the loss in specificity characterizing older adults' autobiographical memory spreads to their ability to imagine future events ([4]; see also [5, 6]). Using a modified version of the AI, young and older adults were required to remember past events and imagine plausible future events. Older (compared to young) adults produced fewer internal details and more external details for both past and future events, suggesting a similar effect of aging on remembering the past and imaging the future (e.g., [4, 7]).

The parallel performance in remembering the past and imagining the future in older adults dovetails with functional neuroimaging (fMRI) evidence that imagining the future engages a distributed network of brain regions largely overlapping with those activated while remembering the past [8–10]. One way of conceptualizing the neural overlap between remembering the past and imagining the future rests on the "constructive episodic simulation hypothesis" [11], according to which the episodic memory system supports the construction of future events by extracting and recombining flexibly information stored in memory into a novel event. In light of this hypothesis, the problems in imagining the future observed in older adults may derive from their difficulties at remembering past events: if autobiographical memories

contribute to the construction of future events, then poor autobiographical memories will result in poor simulations of the future. This is confirmed by neuroimaging data showing a reduced activity in older compared to younger adults in both conditions [11].

Despite evidence that older adults performed worse in both remembering the past and imagining the future, more recently Gaesser and colleagues [12] found that they might show even more pronounced difficulties in imagining future events than in remembering past events. In this study, indeed, older adults' difficulties at imagining the future remained significant when controlling for memory (as well as narrative) performance. As for the anatomical bases of this age difference, a recent fMRI study by Addis and colleagues showed that whereas young adults engaged ventrolateral prefrontal and frontopolar cortex more strongly while imagining future events than when remembering past events, older adults did not show the same asymmetry. This may be due to an inability in modulating prefrontal cortex activity in response to the increased constructive demands of the future task [13]. Additionally, in recent studies, older adults had more difficulties at imagining future events than fictitious, atemporal events compared to younger adults [14], and were less capable of using future thinking adaptively [15]. Thus, older adults' difficulties with episodic future thinking are not completely explained by a general deficit with imagining complex experiences (such as fictitious, atemporal events) [16] or with travelling in time mentally (such as while remembering the past) [12].

There is great interest in revealing the component processes of future thinking that are especially susceptible to the effect of aging. In this respect, humans' ability to recall the past and anticipate the future has been conceptualized as "mental time travel" (MTT), that is, travelling mentally back and forward in time in order to reexperience past events and preexperience future events [6, 17–19] or "self-projection" [20]. Recently, it was proposed that humans spatially map events in real and imagined past and future on an imagined time line, the mental time line (MTL) ([21]; for a review see [22]). Self-projection, therefore, may be conceived as the ability to imagine oneself located in a specific point on the MTL. Arzy and colleagues have proposed that, "projecting" one's habitual self-location in time to the past or future, humans not only recall and predict events, but also change their mental egocentric perspective on life events [23, 24]. Indeed, when we assume a different location in time, life events are regarded differently with respect to their relations to past or future: if we project ourselves back to 15 years ago, for example, last year's events are future (i.e., relative future) events, whereas they were past events if seen from the present time.

Arzy and colleagues [23] developed a psychophysical MTT paradigm requiring young participants to "project" their self-location in time to the past, the present, or the future (i.e., self-projection). Then, participants were required to determine whether a given event happened before (relative past) or might happen after (relative future) the specific self-location they had assumed in time. This classification of events is called self-reference. Behaviorally, the main findings were that response times (RTs) and error rates (ERs) were (1) higher in past and future self-locations than in the present self-location, highlighting the costs of projecting one's self in time, (2) lower for relative future than for relative past events, suggesting that humans are "tuned" to the future as opposed to the past, and (3) lower for personal compared to nonpersonal events, indicating that self-relevant information is prioritized. At the neural level, these effects activated both regions traditionally involved in autobiographical memory and regions associated with space processing and self-representation, including the anteromedial temporal, inferior frontal, and temporoparietal cortices [23, 24].

To specify the potential changes of the mental time travel in aging, we tested young and older adults in a modified version of the MTT paradigm from Arzy et al. [23]. First, basic episodic/autobiographic memory abilities were assessed by asking young and older adults to classify events as past or future from the perspective of the present time, that is, the one that is typically adopted in laboratory studies. To assess self-projection, we asked subjects to make similar self-referencing judgments from a past or future self-location in time. We hypothesized that older adults may face difficulties in (1) classifying events as past or future (self-reference) or (2) adopting a past or future perspective (self-projection). Considering that prefrontal activity is downregulated during future mental time travel in older compared to young adults [13], we predicted older adults would especially face problems at projecting themselves in the future time.

2. Materials and Methods

2.1. Participants. Twenty-four healthy young adults (8 males, mean age ± sd: 24 ± 1.11 years old) and twenty-four healthy older adults (13 males, 67 ± 7.57 years old) participated in the experiment. There was no statistical difference between the two groups in the level of education (young group = 16.5 years; elderly group = 14.7 years; $p = 0.31$). All participants were right-handed and had normal or corrected-to-normal vision and no history of neurological or psychiatric diseases.

Participants were naive as to the purpose of the study and provided written consent to participate in the experiment, which was approved by the Ethical Committee of the University of Bologna, in agreement with the 2008 Helsinki Declaration. Additionally, older adults did not show any cognitive impairment as measured by the Mini Mental State Examination (MMSE score ≥ 29) [25] or an impairment of executive function as measured by the Time and Weight Estimation Test (STEP total score > 40) [26].

2.2. Stimuli and Procedure. Participants sat in front of a 15-inch color monitor, at a distance of about 60 cm. Brief descriptions of personal (e.g., car license and first child) or nonpersonal events (e.g., Obama's election and Middle East peace) were presented on the computer screen (for a complete list of stimuli, see Table 1). Most stimuli (events) we used have already been used and validated in previous studies [23, 24], whereas some other events have been adapted according to the elapsed time. In particular, nonpersonal events were the same for young and older adults. Past nonpersonal events

Table 1: List of events presented to young and older participants.

	Past self-location	Present self-location	Future self-location
Young participants: personal events (relative past)	First best friend	First time at the dentist	Graduate
	First school trip	10th birthday	30th birthday
	First time at the sea	First school day	Maturity examination
	Bicycle without wheels	First political vote	First political vote
	10th birthday	Maturity examination	First salary
	First day of school	Driving license	Driving license
Young participants: personal events (relative future)	30th birthday	30th birthday	Living on the moon
	First political vote	First son	Retirement
	First son	Silver wedding	Silver wedding
	Maturity examination	Son marriage	Son marriage
	Leave the hometown	Graduate	Son graduate
	Driving license	First salary	50th birthday
Older participants: personal events (relative past)	First boyfriend	Using glasses	Using glasses
	First car	40th birthday	80th birthday
	First salary	First son	Silver wedding
	Driving license	First car	First grandchild
	40th birthday	Retirement	First trip by train
	First day of school	First hospitalization	Golden wedding
Older participants: personal events (relative future)	80th birthday	80th birthday	Living on the moon
	Son retirement	First great grandchild	Son retirement
	First great grandchild	Grandchild marriage	Diamond marriage
	Grandchild marriage	Diamond wedding	Grandchild marriage
	Admission to the nursing home	Admission to the nursing home	Flying to Mars
	Golden wedding	Son retirement	100th birthday
Young and older participants: nonpersonal events (relative past)	Pertini's election	Obama's election	Obama's election
	Fall of Berlin wall	First use of euro	First use of euro
	Chernobyl disaster	Chernobyl disaster	Europe unites
	Man on the moon	Man on the moon	Gaddafi's death
	September 11th	September 11th	Pope Francesco's election
Young and older participants: nonpersonal events (relative future)	Pope Francesco's election	Peace in middle east	Flying car
	Gaddafi's death	Completely defeat illnesses	World peace
	Woman president in USA	Woman president in USA	Completely defeat mafia
	Rita Levi Montalcini's death	Completely defeat mafia	Completely defeat illness
	End of the world	End of the world	End of the world
	Completely defeat mafia	Completely defeat world hunger	Completely defeat world hunger

comprehended very famous events from the last 40/50 years of national and international history, and future nonpersonal events involved events that may happen in the future but whose timing cannot be predicted with certainty.

With respect to personal events, these were, in all cases, events characterizing important stages of one's lives, but the specific events were adapted to the two groups, with the main aim of having equally important and meaningful events for younger and older adults. Past personal events were referred to the last 20 and 50 years, for young and older people, respectively, in proportion to their past life duration. Future personal events comprehended for young as well as old people events that could happen in the next 30 years or whose timing cannot be predicted with certainty.

For each event, participants were required to indicate if the event had already happened (relative past event) or was yet to happen (relative future event). Participants performed the task in three different conditions, which corresponded to three different self-locations in time (Figure 1). In one condition, they were required to answer the questions while imagining themselves as being located in the present time (present self-location), in a second condition they had to answer while imagining themselves as being located in the past (10 years ago, past self-location), and in a third condition

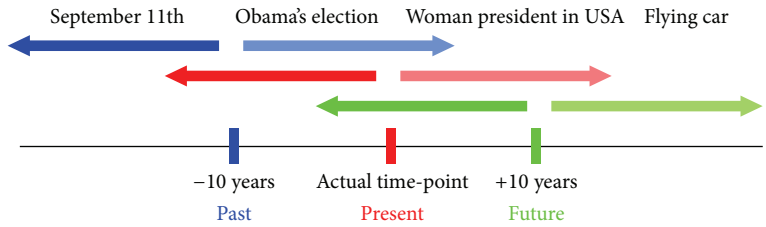

Figure 1: Stimuli and procedure. Participants were required to project themselves in three different self-locations in time (past, present, or future) and determine whether the event being presented was located in the past or the future relative to the current self-location.

they had to answer while imagining themselves as being located in the future (10 years from now, future self-location). Thus, in each self-location condition, participants had to determine whether the event being presented was located in the past or the future relative to the current location of the self in time.

Each self-location condition included 24 stimuli, half personal and half nonpersonal, equally distributed between relative past and relative future events, which were presented in random order for a total of 72 trials. Each event appeared in the center of the computer screen and remained visible until a response was given, with an interstimulus interval of 1000 ms. Judgments were given using the index finger of the left or right hand if the event was past or future, respectively (counterbalanced). E-Prime 2.0 software was used for stimulus presentation and response collection. Before the experimental task, subjects performed a brief practice session, with 8 stimuli randomly presented. Moreover, the experimenter encouraged participants to self-project in time, for example, focusing on their age in 10 years ago/in 10 years or on the exact year it was/will be 10 year ago/in 10 years.

While nonpersonal events were the same for young and older adults, personal events were adapted for the two groups and therefore differed between groups. An independent group of twenty-five young adults (3 males, mean age: 23 years, age range: 22–28) and twenty-five older adults (10 males, mean age: 66 years, age range: 53–80) rated the events in the main experiment for level of importance (with 1 = completely unimportant event and 5 = very important/life-changing event) and intensity of emotion (with 1 = event eliciting low levels of emotion and 5 = event eliciting high levels of emotion) on a Likert scale. Events presented to the young adults were evaluated by an independent group of young adults whereas events presented to the older adults were evaluated by an independent group of older adults. No statistical difference was found between the two groups ($p > 0.05$ for both comparisons). For each rating, response means were entered into a repeated-measures ANOVA with *Event* (personal and nonpersonal) and *Self-location* (past, present, and future) as within-subject factors and *Group* (young and older adults) as between-subject factor. The analysis on events' importance did not reveal a significant main effect or interaction (all $p > 0.43$). The analysis on intensity of emotion showed a significant main effect of *Event* [$F_{(1,44)} = 26.89$, $p < 0.001$, power = 0.99], since personal events received higher scores than nonpersonal events (3.84 versus 3.21, resp.). Importantly, neither the effect of *Group* nor that of *Self-location* was significant, suggesting that potential differences in mental time travel between young and older adults could not be attributed to differences in the quality of the events considered by different groups or at different self-locations in time.

The present self-location condition was always run first, because a pilot study revealed that this made the task more easily comprehended by older adults. The past and future self-location conditions were run second or third (order counterbalanced across participants). Participants' performance in the present condition, which did not require self-projection in subjective time, was considered as a pure measure of episodic/autobiographical memory, as it required locating in time (past versus future) autobiographical as well as nonpersonal events. Next, to examine age-related changes in self-projection, response times (RTs) and error rates (ERs) in the present self-location condition were subtracted from those in the past and future self-location conditions. At the end of the experiment, anamnestic data were collected to determine correct responses according to the responses provided separately by each participant.

2.3. Data Analysis. A first analysis was conducted to assess participants' general ability to locate autobiographic as well as nonpersonal events in time. To this aim, RTs and ERs (analyses were also conducted combining speed and accuracy by calculating the inverse efficiency score (i.e., IES) [27, 28] which consists of reaction time divided by 1 − proportion of errors. These results confirm those obtained using RTs.) relative to the present self-location condition were analyzed using a repeated-measures ANOVA with *Event* (personal and nonpersonal) and *Response* (relative past and relative future) as within-subject factors and *Group* (young and old) as between-subject factor. Then, a second analysis was carried out to investigate age-related changes in self-projection. For each participant, we calculated the difference between RTs and ERs (analyses were also conducted combining speed and accuracy by calculating the inverse efficiency score (i.e., IES) [27, 28] which consists of reaction time divided by 1 − proportion of errors. These results confirm those obtained using RTs.) obtained in the past and future self-location condition and in the present condition (ΔRTs and ΔERs, resp.). In both cases, a positive Δ indicated a disadvantage for the past/future self-location condition with respect to the present condition (more time needed or more errors occurring while answering questions from the past/future compared to the present self-location), whereas a negative

Δ indicated an advantage. These scores were submitted to a repeated-measures ANOVA with *Event* (personal and nonpersonal), *Self-location* (past and future), and *Response* (relative past and relative future) as within-subject factors and *Group* (young and old) as between-subject factor. Post hoc Duncan tests were performed on significant interactions.

3. Results

3.1. Older People Have Difficulty in Processing Personal Events. Analysis of RTs revealed a significant interaction between *Group* and *Event* [$F_{(1,46)} = 5.74$, $p < 0.01$, power = 0.76] (Figure 2). Duncan post hoc tests showed that young adults responded faster to personal than to nonpersonal events (1677 versus 1871 ms, resp., $p < 0.05$), whereas older adults showed comparable RTs for personal and nonpersonal events (2306 versus 2158 ms, resp., $p = 0.10$). Moreover, a difference between groups emerged only with personal events, since young adults responded faster than older adults ($p < 0.01$), whereas no difference between groups was found in nonpersonal events ($p = 0.16$).

Analysis of ERs did not show any significant main effect or interaction (all $p > 0.09$).

These results indicate that older adults are slower than young adults in determining whether personal/autobiographical events are past or future, whereas they perform normally while judging nonpersonal events, thus showing a difficulty in autobiographical memory.

3.2. Older People Have Difficulty in Projecting Themselves to the Future. The analysis on ΔRTs showed a significant main effect of *Group* [$F_{(1,46)} = 8.13$, $p < 0.01$, power = 0.80] and a significant *Group* × *Self-location* interaction [$F_{(1,46)} = 16.59$, $p < 0.001$, power = 0.98] (Figure 3): in the future self-location, older were disproportionately slower than young adults (532 versus −88 ms, resp., $p < 0.001$), whereas no difference in ΔRTs was recorded between older and young adults in the past self-location condition (110 versus 21 ms, resp., $p = 0.53$). Moreover, older adults showed a disadvantage (larger ΔRTs) in evaluating events from a future compared to a past self-location (532 versus 110 ms, resp., $p < 0.001$), whereas young adults reported comparable ΔRTs in both conditions (−88 versus 21 ms, $p = 0.24$). The three-way interaction among *Group* × *Self-location* × *Event* was also significant [$F_{(1,46)} = 14.24$, $p < 0.001$, power = 0.96]. Post hoc tests revealed that the disadvantage observed for older adults in the future (versus past) self-location condition was driven by personal events. Indeed, when judging personal events, older adults showed significantly larger ΔRTs from the future versus past self-location (750 versus −139 ms, resp., $p < 0.001$), whereas younger adults did not (future 9 versus past 2 ms, $p = 0.94$). In contrast, when considering nonpersonal events, older adults did not show the same disadvantage in the future versus past self-location (315 versus 360 ms, resp., $p = 0.63$), and young adults were even faster in the future self-location condition (future −185 versus past 40 ms, $p < 0.05$).

The analysis on ΔERs showed a significant interaction between *Group* and *Response* [$F_{(1,46)} = 7.42$, $p < 0.01$, power = 0.76], as ΔERs for future responses were higher in elderly than in young participants (6% versus −1%, resp., $p < 0.01$). No group difference was found for past-responses (young 2% versus older adults 2%, $p = 0.80$).

Taken together, these results indicate that after controlling for basic autobiographic/episodic memory performance (present self-location), older compared to younger adults were slower to judge personal events from the future self-location and made more errors while making relative future than relative past responses (in both the future and past self-location).

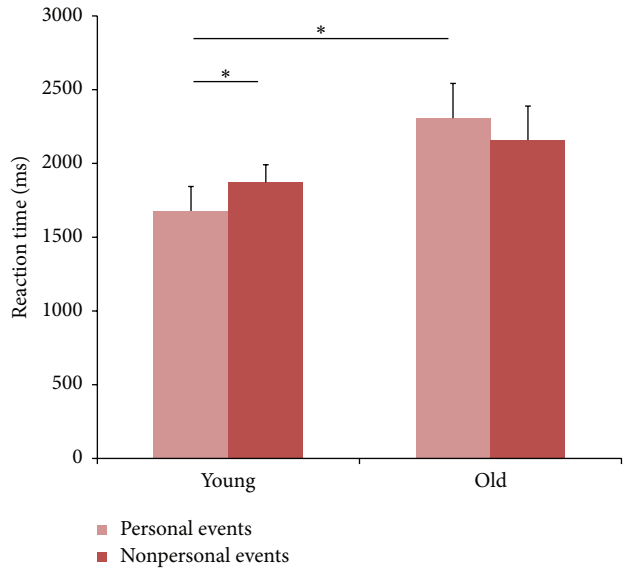

Figure 2: *Group* × *Event* interaction on RTs. Values are in ms and error bars depicted SEM. Asterisks indicate significant differences ($p < 0.05$).

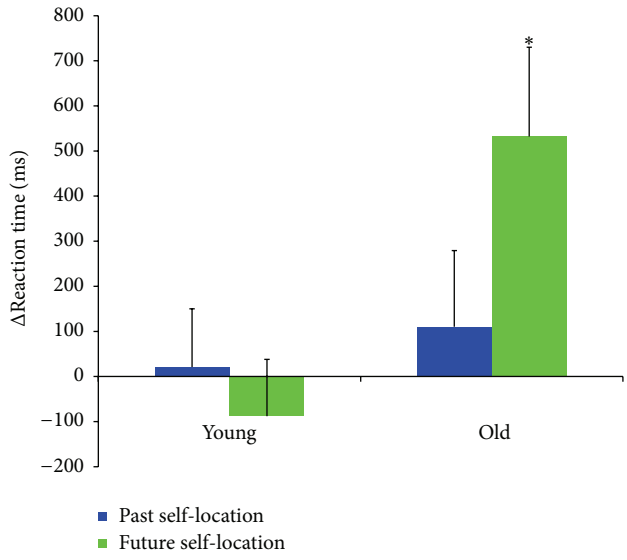

Figure 3: *Group* × *Self-location* interaction on ΔRTs. Values are in ms and error bars depicted SEM. Asterisk indicates significant differences ($p < 0.05$).

4. Discussion

This study revealed difficulty in future processing in older adults on various planes. Older adults were significantly slower compared to young adults in judging personal events while adopting a future self-location perspective. Since older participants did not perform worse than young adults while adopting a past self-location, our findings indicate that aging does not affect self-projection in time in general but, rather, projecting one's self to the future. Consistent with this, in a recent study Gaesser and colleagues [12] asked younger and older adults to remember past events, imagine future events, and describe a complex picture of a natural scene in as much detail as possible. In older compared to young adults, internal details were reduced across all conditions. However, older adults' performance at imagining the future remained significantly worse even after controlling for both description and memory performance. This finding suggests that older adults may face problems in processes necessary for future thinking that go beyond those involved in autobiographical memory and description of complex scenes.

It is important to emphasize that older adults' preserved self-projection towards the past suggests that age differences in self-projecting towards the future cannot be explained with poor comprehension of task demands. Nor can older adults' difficulties with future self-projection be attributed to future self-projection being inherently more difficult than past self-projection: in fact, young adults were faster at classifying events from the future compared to the present self-location (negative Δ), whereas the past self-location made them slower (positive Δ). Rather, the observed age-related effect may relate to differences in the cognitive processes underlying self-projection towards the future versus past time. First, more executive resources may be required for self-projection toward the future compared to the past, as while the past has already happened, the future is a mental construction [29]. Projecting the self 10 years to the future requires simulating how one's self, others, and the world will be in 10 years. Second, older adults' difficulties at projecting themselves in the future may be related to an inability to construct and use self-related information, which is required to conceive the personal future [30, 31]. D'Argembeau and Mathy [32], for example, have shown that self-knowledge, especially knowledge about one's own goals, is particularly important to frame search and integration of information for future thinking.

A selective difficulty in processing the future in older adults also emerged with respect to self-reference, which is the ability to determine whether events are located in the past or future in reference to a given self-location. In both the past and future self-location, older adults made more errors than younger adults in judging events belonging to the relative future, whereas no group differences emerged for relative past events. Similar effect of MTT with respect to past events in both groups despite differences in the presented stimuli suggests that this difference does not account for the identified effect with respect to future processing. It has been proposed that the primary role of MTT is the anticipation of future occurrences and decision-making related to the future (e.g., [33]), leading humans to perform better for future-related events [23]. One possibility, therefore, is that poorer performance measured in older participants in this task may be linked to a loss of such future-preference. This result may be related to a tendency with aging to be (adaptively) less motivated and less oriented towards the future (see also [15]). When people perceive time as limited, indeed, they shift priorities from acquisition-related goals to maintenance or loss-prevention (e.g., socioemotional selectivity theory) [34]. Notably, the loss of future-preference was also found in the past self-location condition, that is, when older adults were contemplating events that were not actually future (i.e., with respect to the present time) or necessarily yet to happen.

Finally, unlike young adults [23, 24], older adults did not show a "self-effect," that is, a faster performance with personal compared to nonpersonal events. The self-effect in young adults relates to several evidence that autobiographically relevant information boosts both memory encoding and retrieval (see also [35, 36]). Participants' ratings indicated that personal and nonpersonal events did not differ in importance, but they differed in the emotions they elicited, which were more intense for personal events. This was expected, given that personal events are strongly connected to one's self and identity, and connected to past desires and future goals [37]. Older adults, too, judged personal events as more emotionally laden than nonpersonal events, but they showed a reduced ability to locate them in time. This finding may be interpreted as an age-related decline in the access to contextual details of autobiographical memories (e.g., [3, 4]), due to changes in the efficiency of strategic retrieval processes with aging (e.g., [1, 38]).

While the present work does not include neuroimaging, neuroanatomical information may enrich the scope of our results. Previous work has suggested that both autobiographical memory and future thinking rely on a distributed network of brain regions, including medial temporal and frontal cortices, posterior cingulate cortex, retrosplenial cortex, and lateral parietal and temporal areas [4, 23, 24, 39, 40]. These regions grossly overlap with a "default network" of brain regions whose activity is enhanced by internally focused thought [39, 41–43]. Our study highlights a change in autobiographical memory in older adults, consistent with the observed decline with age in the functionality of the default network [44]. Considering that older adults especially face difficulties in self-projection towards the future and self-reference to future events and that prefrontal cortex is preferentially involved in imagining future events [13], it may be speculated that the results observed here are to be mainly ascribed to age-related changes in the structure and function of prefrontal cortex (e.g., [1, 45–48]). However, more posterior regions of the default network, affected, for example, in Alzheimer's disease [42], may also play a role in explaining future-thinking changes with aging.

5. Conclusion

To conclude, our results show that aging impacts self-projection to the future as well as reference of the self to future events and occurrences. These findings suggest

that changes in mental time travel in healthy aging (and possibly even in pathology) may be related not only to memory functions per se, but also to the relations between self and memory. Considering that the ability to envisage the future has a strong adaptive value, for example, allowing considering the potential consequences of choices (e.g., [33]), losing the capability to travel in time towards the future may have important consequences for older adults' psychological well-being and decision-making. In this perspective, the present findings may be relevant to interpret the behavioral difficulties observed in aging as well as pathological states such as mild cognitive impairment, Alzheimer's disease, and other dementia states.

Competing Interests

The authors had no competing interests that could influence the research.

Authors' Contributions

All authors developed the study concept and contributed to the study design. Testing, data collection, and data analysis were performed by F. Anelli. F. Anelli drafted the paper, and E. Ciaramelli, S. Arzy, and F. Frassinetti provided critical revision. All authors approved the final version of the paper for submission.

Acknowledgments

The authors thank Marta Pisano for her help in collecting data and Associazione AMA Amarcord Onlus (San Pietro in Casale, Italy) and AIMA Associazione Italiana Malattia di Alzheimer Onlus (Reggio Emilia, Italy) for collaboration. This work was supported by Fondazione Del Monte of Bologna and Ravenna (Italy), by Fondazione Maugeri (Italy), and by RFO (Ricerca Fondamentale Orientata, Ministry of University and Research, Italy).

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 2073454, 9 pages
http://dx.doi.org/10.1155/2016/2073454

Research Article

Neural Network of Predictive Motor Timing in the Context of Gender Differences

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Received 27 August 2015; Revised 24 January 2016; Accepted 4 February 2016

Academic Editor: Marinella Cappeletti

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Time perception is an essential part of our everyday lives, in both the prospective and the retrospective domains. However, our knowledge of temporal processing is mainly limited to the networks responsible for comparing or maintaining specific intervals or frequencies. In the presented fMRI study, we sought to characterize the neural nodes engaged specifically in predictive temporal analysis, the estimation of the future position of an object with varying movement parameters, and the contingent neuroanatomical signature of differences in behavioral performance between genders. The established dominant cerebellar engagement offers novel evidence in favor of a pivotal role of this structure in predictive short-term timing, overshadowing the basal ganglia reported together with the frontal cortex as dominant in retrospective temporal processing in the subsecond spectrum. Furthermore, we discovered lower performance in this task and massively increased cerebellar activity in women compared to men, indicative of strategy differences between the genders. This promotes the view that predictive temporal computing utilizes comparable structures in the retrospective timing processes, but with a definite dominance of the cerebellum.

1. Introduction

Time perception is a critical element of both conscious and subconscious experience, providing synchrony and reliable representation of the surrounding environment. Despite the significance of the temporal dimension, our knowledge of the neuropsychological mechanisms underlying timing processes and computations remains relatively poor [1, 2]. Modern theories about internal time representation share the view that the processing of temporal information is mediated by a distributed network with varying engagement of its individual components depending on the task requirements [3]. However, there is substantial disagreement on the effects reported in various studies, providing no definitive anatomical or cognitive model [3–5]. Several regions, including the basal ganglia, cerebellum, posterior parietal cortex, and frontal cortex, have been implicated as relevant to interval timing; however, their precise role remains shrouded.

The traditional model describing the processing of time passage in the brain is the pacemaker-accumulator model, a straightforward solution that is surprisingly effective in explaining behavioral data [6, 7]. The pacemaker oscillates at a frequency subject to modulation by the temporal properties of sensory stimuli [8]; the pulse count is converted by the accumulator into a linear metric of time. However, recent advances point towards an alternative view offered by distributed timing models, deriving temporal information from the coincidental activation of different neural populations [1]. Although diverse, regarding the hypothesized specific neuropsychological mechanisms of time processing, this broad spectrum of models basically postulate the representation of time as ubiquitous in more networks that also encode other

stimulus properties [4, 9]. Thus, temporal information may be encoded in the entire activity pattern of a neuronal mechanism, as suggested in the state-dependent network model [9, 10]. At the same time, the majority of authors agree that, in the multisecond range, the linear integration of temporal signals is a plausible mechanism for temporal coding and considers it supplemental to the second class of models arising from the inherent temporal properties of the neural networks that provides automatic timing dealing with millisecond range durations [9, 11–13]. Nonetheless, the boundary and overlap between these two systems remain to be delineated.

Of particular relevance in this context is the observation that the processing of temporal information in the millisecond range involves a different network than multisecond operations [9, 12, 14]. Following this distinction, short duration processes would be predominantly evaluated within the motor and sensory-motor network (cerebellum, premotor cortex, and sensory cortex), whereas the timing analysis in longer intervals would be associated with the striatal-prefrontal circuit [15, 16]. The suggestion that correct cerebellar function may be essential for successful temporal processing is not new [17]; its prominence in facilitating performance in time analysis has been further underscored by both clinical studies of patients with cerebellar pathology [18–22] and neuroimaging studies [15, 23–25], mostly based on paced finger tapping or temporal discrimination with the retrospective character of temporal computing (for review see [3]). However, surprisingly few studies have investigated the cerebellar role in the complex processes necessary for predictive timing—the analysis of various environmental factors in the subsecond spectrum leading to a delineation of the probable future state of the surroundings which enables preemptive action in simple, routine activities and even in life-threatening situations. Possible variations in the composition of the timing network related to gender might be of significant interest as well, as reports are available, albeit scarce, of both structural [26] and functional dissimilarities [27] between men and women in the infratentorial area. Behavioral performance differences between males and females have been well known for decades [28], with the field of numeric operations, spatial processing, and probability and data analysis dominated by men [29] and language and social skills being the realm of women [30]. Interestingly, a similar disparity has been repeatedly confirmed in complex analyses of reaction time to various stimuli revealing a significant disadvantage for women [31–34] and a differential pattern of reaction times as a function of stimuli location and character [32] that might reflect different information processing strategies. Hence, understanding the underlying neural mechanisms associated with contingent performance and functional differences in specific processes in the context of gender may offer an important insight into neurological and psychiatric diseases with strong sex biases.

Hence, the aims of the present study were twofold. We wished to establish the neuroanatomical signature of complex predictive motor timing in a well-characterized sample of healthy individuals using the fMRI blood oxygen level dependent (BOLD) signal and to contrast the performance of men to that of women.

2. Materials and Methods

2.1. Subjects. Forty healthy volunteers, 24 men (mean age 40.15; SD 15.20) and 16 women (mean age 43.85; SD 14.76), with no symptoms of neurologic diseases participated in the study. All the subjects were right-handed according to the Edinburgh Handedness Inventory [35]. All of the subjects underwent a screening to ensure a safe MRI procedure, and their anatomical MRI scans did not show any structural pathology. All participants provided their written informed consent prior to the experiment in accordance with the guidelines of the local research ethics committee. The study was approved by the institutional review board of St. Anne's University Hospital (Brno, Czech Republic).

2.2. Experimental Task Design. The participants performed the same motor-timing computer task as employed in our earlier studies [20, 22, 36, 37]. The subjects were required to press a key with the dominant hand to launch a projectile that was intended to intercept a green circular target moving from the left side of the screen toward the upper right corner (Figure 1(a)). The target (diameter 1 cm) moved to the fixed interception zone at three possible speeds (slow, medium, and fast), at three possible angles relative to the horizontal plane (0, 15°, 30°), and in three different manners (constant speed, deceleration, and acceleration), reaching 27 distinct combinations of movement parameters with the intention of moderating the expected learning effect and providing varying levels of difficulty for further fMRI models and analyses. The projectile (diameter 0.3 cm) was launched from the lower right corner of the screen at a constant speed of 20.0 cm/s on a vertical, unchanging trajectory. The subjects were instructed to press the key only once at the optimal time for the projectile to intercept the moving circular target in the upper right corner of the screen. A successful interception was followed by a small explosion animation as feedback for the subject (Figure 1(b)). The participants were specifically asked to visually follow the target at all times and encouraged to use the same strategy throughout the experiment. Due to the varying, complex movement parameters of the target, simplified approaches such as fixating the gaze on a launching area consciously estimated based on the previous trials and waiting for the target to reach the area or mentally counting the time from the target's appearance to a preselected point would prove useless.

The experiment was organized into 6 blocks, each formed by 54 trials, with pseudorandomized combinations of the target movement parameters to provide 12 repetitions of each combination for a total of 324 trials. We employed a counterbalanced presentation of various stimuli types within each block to minimize the repetition of the same movement parameter combinations in consecutive trials. The duration of one trial was on average 3.5 s.

The entire paradigm consisted of a training session (performed while scanning, but not subject to analysis) and the main task. The duration of the whole session (including the acquisition of anatomical scans, the training session, and the main session with short breaks between the blocks to prevent motor or cognitive fatigue) was about 50 minutes. The task

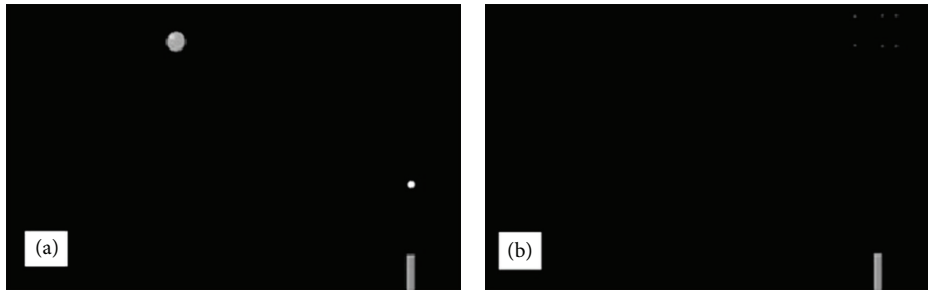

Figure 1: The experimental task. (a) The green ball flies from the left side of the screen to the upper right corner, the interception zone. The "gun" in the right lower corner has just fired a "projectile" travelling vertically at a constant speed to intercept the target. (b) Successful hit is associated with an "explosion" in the interception zone in the upper right corner. If the subject misses, no animation is displayed.

was presented using the LabVIEW 6.1 (National Instruments, Austin, TX, USA) interface.

2.3. fMRI Data Acquisition. Imaging was performed at the radiology department of St. Anne's University Hospital, Brno, on a 1.5 T Siemens Symphony scanner equipped with Numaris 4 System (MRease). High-resolution anatomical T1-weighted images were acquired using the magnetization-prepared rapid gradient-echo (MPRAGE) sequence (TR = 1.7 s, TE = 3.93 ms, TI = 1100 ms, in-plane voxel size 0.96 × 0.96 mm, 160 sagittal slices, slice thickness 1.17 mm, matrix 256 × 256 × 160). A total of 850 volumes of functional images were acquired during the entire run (TR = 2.3 s, TE = 35 ms, FA = 90°, FOV = 220 × 180 mm, in-plane voxel size = 3.44 × 3.44 mm, 28 axial slices, slice thickness 4.40 mm), but only 490 volumes corresponding to the main task were used for further analyses (the remaining volumes scanned during the training part were discarded). Two dummy scans, acquired before each fMRI run in order for the fMRI signal to reach a steady state, were discarded from the analysis as well.

2.4. Analysis of Behavioral Data. The main variable of interest was the success rate (i.e., the hit ratio) across the different types of movements (stable speed, acceleration, and deceleration) and speed types. The angle was excluded from the analyses, since it was proven to have no effect on the hit ratio [20, 38]. We computed the average success rate in each subject for every movement type in order to be able to use parametric statistical analysis. The effects of the movement parameters on the main variable were assessed using ANOVA analysis, with the hit ratio as a dependent variable and the speed and the movement type as independent factors. The analyses were performed using the Statistica 12 software (Statsoft Inc., Oklahoma, USA).

2.5. Analysis of fMRI Data. The fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab R2013 (Mathworks Inc., Sherborn, MA, USA). The images were realigned to correct for head movement effects. No subject's movements exceeded 3 mm in each spatial direction or 3° of rotation. Afterwards, the coregistration of functional and anatomical images, interpolation in time to correct for volume acquisition phase progression, spatial normalization into the stereotactic Montreal Neurological Institute (MNI) space, and spatial smoothing using an isotropic Gaussian kernel of 8 mm full-width at half-maximum were performed. To minimize low frequency artifacts possibly associated with the block length, the data were high-pass filtered with a Gaussian kernel filter of 128 s.

At the first level, the general linear model of BOLD activations consisted of bidirectional comparisons of successful hits and errors in each subject separately. The individual design matrix for every participant also included the speed, as interpreting the results of this parameter was more straightforward than with the complicated scheme of the movement type (acceleration, deceleration, and stable speed). The onset was modelled as the moment the green circular target appeared on the left side of the screen and the end was the moment when the subject pressed the key to launch the projectile.

In the analysis of the main hypothesis, six contrast maps were created at the first level (two possible results [hit or miss] × three speeds) and a second level factorial design (2 × 3) was implemented with the following factors: success (two levels: hit and miss) and speed (three levels: slow, medium, and high). The analysis of our secondary aim, the gender distinctions, was based on a first level model (3 speeds × 3 movement types (stable, acceleration, deceleration)) and the successive second level model with gender, speed, and the movement type as factors (i.e., 2 × 3 × 3) and the respective hit ratios for the individual target movement parameters as a nuisance variable to control for the effect associated primarily with the individual success rate differences.

The results were considered significant at $p < 0.05$; family-wise error (FWE) corrected for multiple comparisons at the whole brain level with a cluster threshold of 35 contiguous voxels in all the comparisons.

3. Results

3.1. Behavioral Results. The analysis of pooled data provided a mean hit ratio of 0.4281 (SD = 0.1534), with a significant effect of movement type ($F_{2,354} = 24.75$; $p < 0.001$) (Figure 2(a)) and a borderline trend in the effect of speed ($F_{2,354} = 2.054$; $p = 0.11$) (Figure 2(b)). Overall, acceleration was associated with a lower success rate than either deceleration or stable

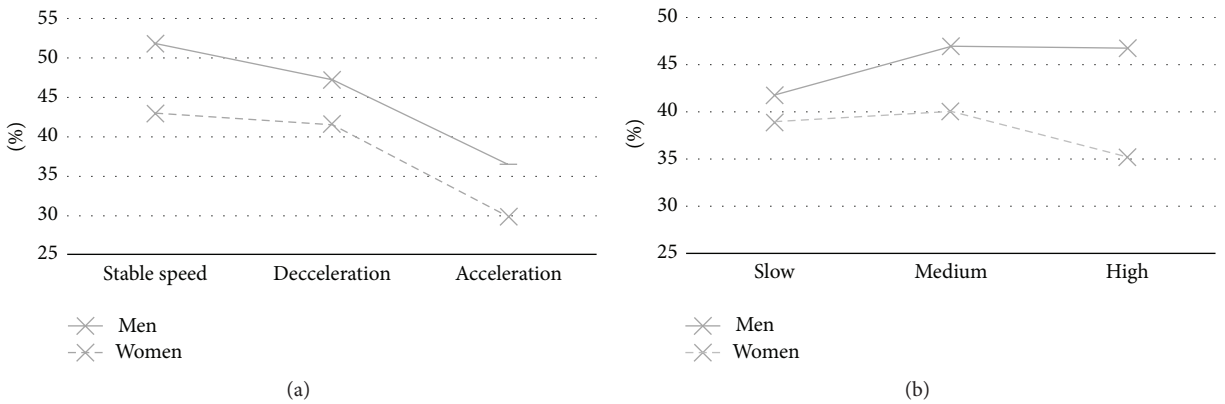

Figure 2: Graphical representation of performance in both genders and the influence of the movement parameters. (a) Mean success rate as a function of acceleration in males and females. (b) Mean success rate as a function of speed in males and females.

speed. Furthermore, the character and timing of errors were put to test, distinguishing between early errors (i.e., errors when the subject pressed the button too early) and late errors (the subject pressed the button too late). There was no difference between the occurrence of early and late errors; early errors constituted 51.6% and the late errors, 48.4% of all the errors ($p > 0.05$). Due to this even distribution of errors, the average response time (period between the onset of the stimulus and the motor response—key press) did not differ between successful trials, "hits" (1.301 s), and unsuccessful trials, "misses" (1.265 s) ($p > 0.05$).

Interestingly, significant gender differences were found, with a mean hit ratio of 0.4589 (SD = 0.1552) in men and 0.3803 (SD = 0.1383) in women ($p < 0.001$). Sex did not interact significantly with acceleration ($F_{2,354} = 0.2864$; $p = 0.75$) (Figure 2(a)) or speed (only a borderline trend of performance decrease in women with higher speeds than men—$F_{2,354} = 2.235$; $p = 0.11$) (Figure 2(b)).

3.2. Activation Maps. The results of the 2 × 3 ANOVA (hit/miss × speed) were as follows:

(1) Main effect of hit versus miss: The areas significantly more activated in successful trials included the basal ganglia (specifically the putamen and caudate bilaterally) and a larger cluster comprising the posterior cerebellum (lobule VI and crus 1 on the right side) and the inferior part of the occipital lobe (Figure 3(a), Table 1). The reverse contrast (miss > hit) did not provide any results surviving the threshold of $p < 0.05$, FWE-corrected.

(2) The effect of speed: Speed changes of the target were closely associated with cerebellar activity in the posterior cerebellum (specifically vermis 6 and vermis 7, bilateral lobules VI, and crura 1, with the predominance of the right cerebellar hemisphere) and, furthermore, with the right middle temporal lobe, the middle occipital lobe on the left side, and smaller clusters of activity in the putamen bilaterally and in the left precentral gyrus (Figure 3(b), Table 1).

(3) Interaction of hit versus miss and speed: No clusters survived at the level of $p < 0.05$ with FWE-correction at the whole brain level.

The analysis of the effect of gender, with the hit ratio as a nuisance variable due to performance differences (see the behavioral results), yielded the following activation maps:

(1) Women > men: Figure 3(c) demonstrates the patterns of hyperactivation in women when compared to men, comprising primarily of the posterior cerebellum (specifically the left lobules IV-V, VIII, IX, and the right VIII, VII, and VI with left-sided predominance). Further regions found in this contrast included two clusters in the left temporal gyrus (Brodmann area 39) (Figure 3(c), Table 1).

(2) Men > women: The reverse contrast revealed differences of lesser magnitude than the ones reported above, including the cingulum and Brodmann areas 45 and 21.

(3) The interaction between gender and speed or movement type did not yield any results surviving the threshold of $p > 0.0$, FWE-corrected at the level of whole brain.

4. Discussion

Research efforts have been increasingly directed towards understanding the neuroanatomical substrates of time perception by studying the characteristic patterns of neuronal activity and behavioral correlates in both healthy individuals and specific patient populations. Although a large corpus of research has implicated complex, overlapping networks bringing together information from multiple modalities, including the basal ganglia, cerebellum, posterior parietal cortex, and frontal cortex, substantial disagreement persists regarding the relevance of these structures and the specific computing models used to delineate temporal parameters from various inputs [1, 6, 7, 9, 10]. Functional neuroimaging studies have consistently used tasks based on paced finger tapping and temporal discrimination [3]. Building upon

Table 1: Anatomical localization of clusters in the activation analysis (threshold of $p < 0.05$, FEW-corrected). Data provided for the main effect of hit versus miss, the effect of speed, and the gender differences.

Anatomical regions	Brodmann area/lobules in cerebellum	Side	Volume (in voxels)	p value (FWE)	T-score of local max	MNI coordinates of local maxima		
Hit > miss								
Occipital lobe	BA 18-19	R	433	<0.001	8.75	27	−91	−8
	BA 18-19	L	174	<0.001	6.68	−39	−76	−11
Putamen, caudate		R	63	<0.001	6.05	21	11	−5
Putamen, caudate		L	80	<0.001	5.81	−24	8	−2
Cerebellum	Lobule VI, crus 1	R	48	<0.001	5.55	36	−76	−20
Anatomical regions	Brodmann area/lobules in cerebellum	Side	Volume (in voxels)	p value (FWE)	F-score of local max	MNI coordinates of local maxima		
Main effect of speed								
Cerebellum	Vermis 6, vermis 7 Lobule VI, crus 1	C BIL	597	<0.001	38.73	6	−70	−20
Middle temporal gyrus	BA 37	R	94	<0.001	36.82	45	−67	1
	BA 37	L	161	<0.001	34.73	−48	−70	4
Occipital lobe	BA 18-19	L	536	<0.001	35.02	−12	−100	1
Putamen		R	144	<0.001	28.72	24	8	−5
Putamen		L	149	<0.001	25.97	−30	5	1
Precentral gyrus	BA 6	L	36	<0.001	24.35	−30	−10	58
Anatomical regions	Brodmann area/lobules in cerebellum	Side	Volume (in voxels)	p value (FWE)	T-score of local max	MNI coordinates of local maxima		
Female > male								
Middle temporal gyrus	BA 39	L	35	<0.001	7.48	−48	−79	22
Cerebellum	Lobule IV-V	L	47	<0.001	7.36	−9	−49	−2
	Lobule VIII, IX, IV-V	L	430	<0.001	7.36	−21	−43	−44
	Lobule VIII, VII, VI	R	227	<0.001	6.76	15	−70	−38
Middle temporal gyrus		L	35	0.001	5.59	−36	−52	−2
Male > female								
Middle temporal gyrus	BA 21	L	40	<0.001	7.17	−66	−25	−2
Cingulum		C	83	<0.001	6.95	−6	−40	22
Inferior frontal gyrus	BA 45	L	48	<0.001	5.94	−51	26	−8

BA = Brodmann area, L = left, R = right, C = central, and BIL = bilateral.

the previous research, but with a substantial step forwards, the current study is not concerned with the simple ability to maintain certain intervals or to assess and compare the length of various stimuli, that is, with retrospective temporal processing. It is designed to analyze the neural networks involved in predictive timing processes in the subsecond spectrum that enable preemptive action on the basis of the estimated future state of our environment, an essential ability whose absence would virtually preclude even simply catching a ball.

Our results highlight the specific functional role of several areas, including the putamen and caudate, the temporal cortex, and primarily the cerebellum, an area previously commonly associated with temporal tasks, although probably of an underspecified level of contribution [11]. Our finding of high activation in the cerebellum associated with increasing speed, and hence also with the difficulty of the task, is well in accordance with previous studies of subsecond spectrum retrospective temporal processing utilizing transcranial magnetic stimulation of the cerebellum [39–41] and imaging methods [25, 42–46], and also with the hypothesis that this neural node acts as a timing system for brief intervals [47]. Even if reported as the most commonly engaged structure in retrospective subsecond temporal computing [5], the extent of the volume of activated cerebellar tissue and the dominance of the cerebellar cluster in the current study far exceeds the volumes and the rank among the other neural nodes reported in retrospective timing tasks [3]. In contrast to the prevailing retrospective tasks, only a few studies have focused primarily on temporal predictions; the anterior-inferior parietal cortex and ventral premotor cortex in the Posner paradigm [48] and the anterior-inferior parietal cortex in trajectory prediction [49] have been suggested. The findings presented here are also very much in keeping with the analysis of perceptual prediction change and trajectory extrapolation

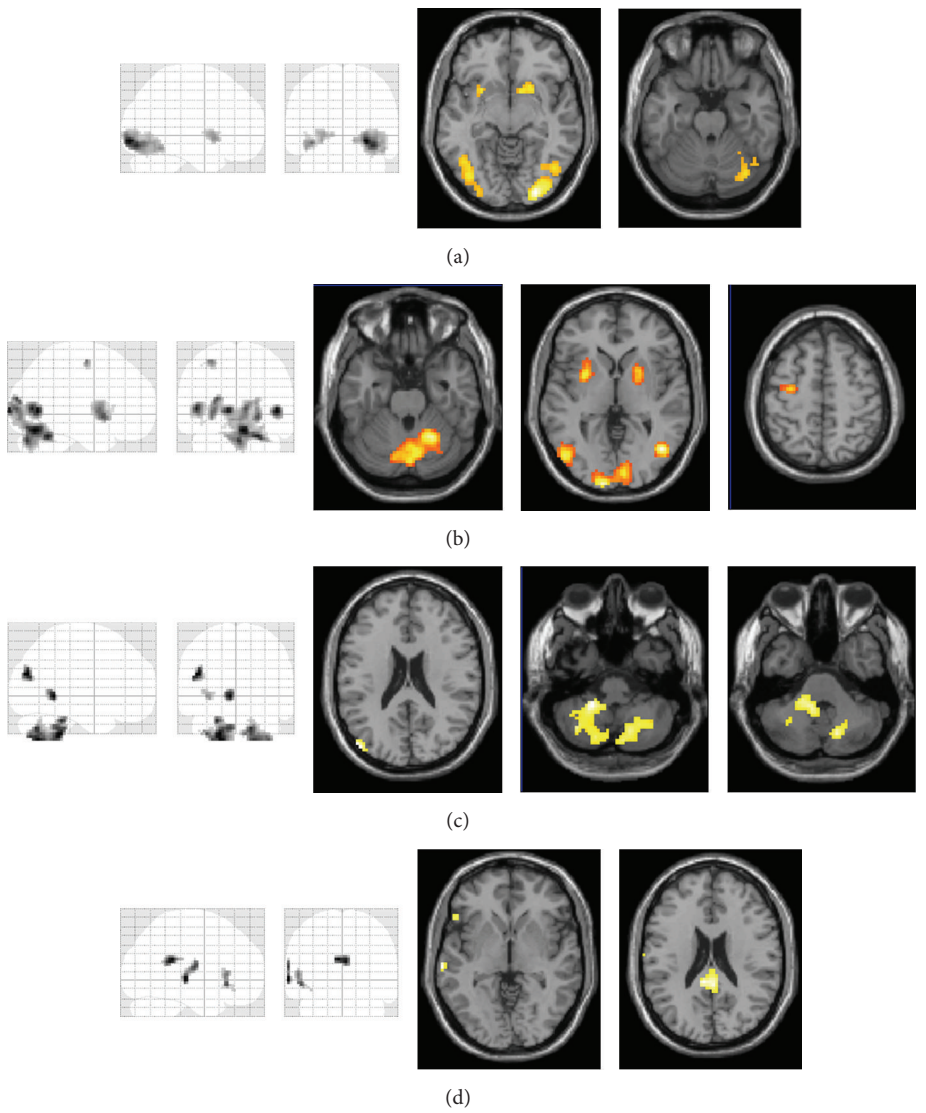

Figure 3: Results of the 3 × 2 ANOVA ($p < 0.05$, FWE-corrected at the whole brain level): (a) main effect hit versus miss (hit-miss) (threshold $T = 4.56$). (b) Main effect of speed (F-contrast) (threshold $F = 13.36$). (c) Female > male (threshold $T = 4.56$). (d) Male > female (threshold $T = 4.56$). Radiological conventions for the laterality were used where the right side in the figure corresponds to the right side in the scanned area and vice versa.

associated with the notable engagement of the posterior cerebellum [50].

Turning to the other regions implied in the current study, the putamen, clearly revealed here in both the speed and success versus failure analysis, is extensively documented in temporal processing in the subsecond and multisecond range in both animals and humans (for review see [5]). It was highlighted in tasks requiring the comparison of durations with a probe stimulus [51, 52] and even proposed as a core timer across the whole temporal spectrum [5], responsible for the early stages of temporal computation [51], temporary storage [52], or as a functional center in stimulus encoding, integrating the temporal signals and generating a subjective perception [11]. Our findings of a significant relation of putaminal activity to the hit ratio in predictive temporal computing not only resonate with the previous hypotheses, but also go beyond these and underscore its function as a neural node engaged in the evaluation of success and precision of the undergoing prospective temporal analysis. Furthermore, although often not commented upon, the activity in the middle temporal lobe during timing tasks has also been implicated before [15, 51–53]. This supramodal involvement of the auditory cortex was demonstrated both in auditory [54] and visual timing [55].

Our secondary aim, delineating gender differences in predictive timing, was already partly addressed in the analysis of behavioral data revealing a significantly lower success rate in women. The emergence of the cerebellum as the main hyperactivity cluster in women in the neuroimaging analysis, even when corrected for the hit ratio difference, may seem rather surprising, as the cerebellum is traditionally considered to be a fairly monomorphic structure with minimal sex

dissimilarities. Neuroimaging studies seem to provide contradictory results, and a higher volume of cerebellar hemispheres in men [26, 56], analogous to observations of the cerebral cortex [57], was reported, although other analyses, volumetric assessments based on MRI [58] and examination of fixed human tissue [59], failed to reveal a significant relationship between gender and cerebellar structure. The situation is similar in the field of functional studies. PET confusingly revealed increased metabolism in women in the cerebellum [27], corresponding to the findings of our study, decreased metabolism in women in the cerebellum [60], or no gender differences at all in the infratentorial area [61]. The lack of association with gender, though not completely surprising given the character of the stimulation task, was also reported in fMRI studies [62, 63]. On the other hand, strong cerebellar hyperactivity in women during simple silent counting, markedly similar to our results, provided a foundation for the hypothesis of distinct cognitive and executive strategies in response to various stimuli between the genders [64]. Moreover, behavioral performance differences between the genders have been well known for decades, for example, in language, dominated by women, and visuospatial tasks, where men show superior results [28]. Due to the versatile nature of cerebellar functions, this neural node has been implicated in many of those areas [65–67]. Hence, even the extent and character of cerebellar engagement may be of different magnitude in men and women. Future studies incorporating complex analyses will be helpful in expanding upon our current results and confirming the disputable dissimilarities in activity patterns in the infratentorial area. The mechanisms underlying the increased cerebellar activity in women may have the character of a compensatory hyperactivation of one node of a complex neural network commonly responsible for temporal analysis, but without further support from other studies using various methods, this hypothesis is far from elucidating this poorly understood issue.

A number of points need to be considered with our results. First, given the temporal constraints of fMRI, the plausibility of disambiguation of individual components and their specific functional signature in the process of prospective temporal timing in intervals of short duration used in our task may be considered borderline at best. Ergo, no further hypotheses about the probable temporal processing model utilized in predictive timing may be provided, except for the obvious statement of multiple neural nodes engaged, with cerebellar dominance. Second, the emergence of occipital cortical areas in the analysis of hit versus miss and, to a lesser extent, even in the analysis of the speed effect may not be surprising given the increased demands for both primary and secondary image processing necessary for the successful interception of the moving target. However, in the light of this distinction, the interpretation of other significant clusters as core structures for predictive temporal processing might be challenged. Moreover, the notion of variable analyzed time interval with the offset of the regressor corresponding to the motor response may point to possible contamination with the signal associated with motor processing due to the temporal proximity of early motor responses (early errors). However, due to the even distribution of errors between too early and too late responses, this convolution seems unlikely. Nonetheless, our results are well in accord with the previous body of research on retrospective timing, thus allowing us confidence in our findings. The final issue worth reiterating in the context of gender distinctions is the complexity of the task; it consists of series of component processes, and the neural activity in males and females may show differences for only specific segments, unfortunately outside the temporal resolution of fMRI. Further work will be necessary to tease apart the extent to which cerebellar activation varies between genders and to develop experimental tasks optimized to probe specific hypotheses about the gender differences.

Taken together, our findings underscore the pivotal role of the cerebellum in predictive temporal processing, with considerably higher engagement than in retrospective timing tasks, and provide novel insights for understanding different neural mechanisms in men and women. Moreover, our results offer a more nuanced perspective on the contribution of the putamen in analyzing predictive temporal processing precision and success as a possible node in a feedback loop activated more in successful trials than in errors. Despite the increasing amount of research, the complex function of the cerebellum in predictive timing remains notably underexplored. It will be important for future studies to expand upon the current results in other domains of complex prospective timing.

Conflict of Interests

There are no potential conflict of interests and no financial or personal relationships that might bias the authors' work.

Acknowledgments

The authors are grateful to the participants and their families for their support of this research. This work was supported by the "CEITEC (Central European Institute of Technology)" Project (CZ.1.05/1.1.00/02.0068), from the European Regional Development Fund, and by the Ministry of Health of the Czech Republic/Ministry of Health's Departmental Research and Development Program III (2010–2015).

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 3495075, 13 pages
http://dx.doi.org/10.1155/2016/3495075

Research Article

Prismatic Adaptation Induces Plastic Changes onto Spatial and Temporal Domains in Near and Far Space

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Received 30 October 2015; Revised 8 January 2016; Accepted 13 January 2016

Academic Editor: Stuart C. Mangel

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A large literature has documented interactions between space and time suggesting that the two experiential domains may share a common format in a generalized magnitude system (ATOM theory). To further explore this hypothesis, here we measured the extent to which time and space are sensitive to the same sensorimotor plasticity processes, as induced by classical prismatic adaptation procedures (PA). We also exanimated whether spatial-attention shifts on time and space processing, produced through PA, extend to stimuli presented beyond the immediate near space. Results indicated that PA affected both temporal and spatial representations not only in the near space (i.e., the region within which the adaptation occurred), but also in the far space. In addition, both rightward and leftward PA directions caused opposite and symmetrical modulations on time processing, whereas only leftward PA biased space processing rightward. We discuss these findings within the ATOM framework and models that account for PA effects on space and time processing. We propose that the differential and asymmetrical effects following PA may suggest that temporal and spatial representations are not perfectly aligned.

1. Introduction

The constructs of time and space saturate our discourses, as the two experiential domains are, of course, fundamental to how we interact with and organize our environment. Considerable empirical evidence has revealed interactions between time and space in both brain and behavior, from low-level perception to high-level linguistic processes. In this respect, Walsh's prominent theory (well known as A Theory of Magnitude, ATOM) [1] has tried to account for these systematic interdomain influences. As posited by this theory, time and space, along with other forms of magnitude, may share a single cross-domain metric system in the brain, in particular within regions of the parietal cortex [1, 2]. A distributed and integrated network of other areas, such as the prefrontal cortex, are presumably involved in the magnitude system, even if the cross-domain magnitude representations seem to be specially coded by the parietal regions [2]. Thus, temporal events and spatial extents may share a representational and neural format, such that two events are separated by a particular duration in the same way as two locations are separated by a particular distance.

In addition to this neural model, at the behavioral level one of the most well-established interactions between space and time is captured by the Spatial Temporal Association of Response Codes effect (STEARC effect): temporal concepts, such as "before" versus "after," are spatially associated with horizontal locations [3–7]. Converging evidence of time-space interactions has therefore supported the proposal that time is represented spatially along a horizontal mental time line ("MTL") [8, 9]. Hence, it has been suggested that humans experience time as flowing along a mental horizontal line,

so that smaller magnitudes (intervals) of time are associated with the left part of the line and larger magnitudes (intervals) are associated with the right part of the line. Accordingly, the duration of stimuli presented in the left space is underestimated relative to that of stimuli presented in the right space, which tends to be overestimated [10, 11].

In line with the finding of a spatial representation of time intervals in ascending order from left to right, a "distortion" of time perception is observed following leftward or rightward attentional shifts created through prismatic adaptation (PA) procedure. Broadly speaking, PA is a well-known sensorimotor technique for investigating cerebral plasticity in neurologically healthy individuals by inducing a relatively transient shift of spatial attention [12–16]. In addition, leftward- and rightward-deviating prisms affect performance on a variety of temporal tasks. Previous research has indeed reported that PA is able to modulate systematically the spatial representation of time in healthy individuals [11, 17, 18]. In these studies, participants performed a time (duration) reproduction task and/or a time (duration) bisection task, before and after leftward (LPA) and rightward (RPA) prismatic adaptation. According to the above-recalled left-to-right organization of the spatial representation of time, PA caused an opposite and symmetrical modulation on time processing: LPA produced an overestimation of time durations, whereas RPA produced an underestimation of time durations. These findings have thus demonstrated that manipulating spatial representations can shape biases in the estimation of time durations.

Somewhat similarly, biasing attention orientation by means of PA alters performance, not only in temporal, but also in visuospatial tasks. So, for instance, in a distinctive visuospatial task, the line bisection, young individuals typically show pseudoneglect: they judge the middle of the horizontal line to the left of the true center [19–23]. More interestingly, following adaptation to leftward prism (LPA) participants shift their midline judgments to the right, thus reducing or cancelling their leftward bias at baseline [16, 24–27]. It is worth noting that most studies have demonstrated a significant modulation after LPA, but no effect following RPA on visuospatial processing [16, 24–29].

In the bine bisection task, however, such a pseudoneglect phenomenon appears to be limited to stimuli presented close to the body, with bias shifting to the right of the true center as viewing distance increases [23, 30–34]. Specifically, individuals show a leftward bias (i.e., pseudoneglect) within near space and a rightward bias in far space, and the point of transition from the left-to-right bias can be manipulated by extending or contracting the participant's reach [32, 34]. This pattern, systematically related to reach capabilities, has been interpreted as evidence of distinct representations of space, which are encoded on the basis of action potentiality [35–37]. This interpretation is in line with the proposal that pseudoneglect is usually found in the space near the body where individuals can act upon directly by the use of the arm, whereas rightward bias is observed where the line to be bisected is presented in the space far from the body, beyond the space with immediate action potential [32–34]. Indeed, the results of neurophysiological [23, 38–41], neuropsychological [42–44], and neuroimaging studies [45–48] converge suggesting that, on the basis of the potential actions that can be performed, the space close to the body (i.e., near space) and the space that lies just beyond reach (i.e., far space) are represented differently by the brain (for reviews, see [48–51]).

Based on the abovementioned evidence indicating tight relationships between attentional mechanisms and representations of space and time, our study was designed to explore, for the first time within the same experimental design, the effect of PA in both near and far space on both spatial and temporal tasks. So far indeed, previous research has investigated the effect of the shift of spatial attention on time processing in the near, but not in the far space.

For the purpose of the study, the landmark task, which is a nonmanual, perceptual variant of line bisection, was used to measure the visuospatial bias caused by PA. We chose this paradigm in order to minimize the influence of motor factors on bisection judgments and to slow down the deadaptation process after PA procedure [16, 22, 24, 52–54]. In this task, participants are required to make forced-choice responses according to whether they perceive a vertical transector to be closer to the left or right end of a horizontally displayed line.

The time bisection task was instead used to measure the modulation on the spatial representation of time caused by PA. The paradigm is a well-established task in which participants classify whether a series of stimuli are closer in duration to a "short" reference or to a "long" reference duration [55–57]. In order to compare the temporal and spatial changes induced by PA, we needed similar stimuli to be employed in the two tasks. To this end, in the landmark paradigm stimuli were lines pretransected at one of different locations and were presented for 2000 ms. Similarly, in the time bisection paradigm stimuli were lines pretransected at veridical center and had one of different durations. Finally, to answer the question of whether PA aftereffects measured by the landmark and time bisection tasks would extend to stimuli presented in the far space, all subjects were submitted to the two tasks at two different distances: 60 cm (within arm's reach, i.e., in near space) and 120 cm (outside arm's reach, i.e., in far space).

2. Materials and Methods

2.1. Participants. Sixty-four healthy volunteers (46 females, mean age = 23.78; SD = 2.13 years) participated in the study (mean education = 16.27; SD = 1.61 years). The participants had no self-reported history of neurological or psychiatric diseases, had normal or corrected-to-normal vision, and were right-handed according to self-report and as assessed by administration of the Edinburgh Handedness Inventory (mean = 78.29; SD = 17.51) [58]. They were naïve as to the experimental hypotheses being tested and gave informed consent to take part in this study, which was approved by the local ethics committee and conducted in accordance with the ethical standards of the 2008 Declaration of Helsinki.

2.2. Design. All data were collected in a noise-attenuated room. The experiment consisted of two blocks: one before

and one after a PA session. The preadaptation block included the landmark and the time bisection tasks; then participants performed a single session of PA. In the postadaptation block they repeated the landmark and the time bisection tasks five minutes after prisms removal. Within each block, the landmark and time bisection tasks were performed at two viewing distances: near space (60 cm, i.e., monitor screen placed within arm's reach) and far space (120 cm, i.e., monitor screen placed beyond reaching). The order of the tasks and the two viewing distances was counterbalanced across participants. Participants were asked to keep their eyes closed between the tasks and to rest their hands on their thighs during the whole experiment, except during the PA session. The experimenter ensured that the subject's body position remained constant throughout the experiment. All phases of the experimental session are described in details in the following paragraphs.

2.3. Landmark Task. The paradigm represented a computerized version of the landmark task. Participants were comfortably seated directly in front of the monitor screen, with lights extinguished to reduce external visual cues. Their midsagittal planes were aligned with the monitor screen. Viewing distance was also held constant using a chin-rest.

2.3.1. Stimuli. Stimuli were presented using the E-Prime software package (Psychology Software Tools, USA) on a LDC monitor (17 inches, 1280 × 1024 pixel resolution and 75 Hz refresh rate) controlled by a MacBook Pro laptop. Stimuli were white pretransected lines of 100% contrast displayed on a black screen positioned 60 cm (near space) or 120 cm (far space) from the participant's eyes. The size of horizontal line stimuli was adjusted across viewing distances to ensure the retinal angle subtended remained constant at 19.03° of VA (visual angle) in width by 3.23° of VA in height. Horizontal lines stimuli were centered with respect to both the midsagittal plane of each subject and the computer screen. Lines were pretransected at the true center (i.e., 0.00°) and at ±0.1°, ±0.2°, ±0.3°, ±0.4°, and ±0.5° of VA toward the left and right of the true center. Transectors were 1.53° in vertical length and 0.08° thick. Each of the 11 different pretransected lines was presented eight times in a random order, yielding a total of 176 trials, 88 in the near space, and 88 in the far space. The order of presentation in near and far space was counterbalanced across participants.

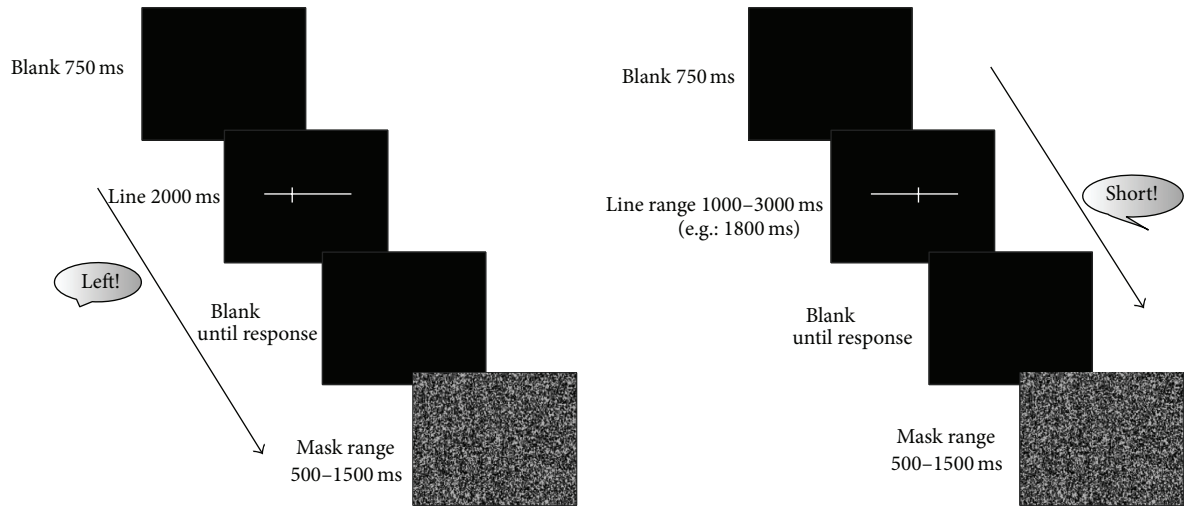
Trials began with the presentation of a blank (black background) for 750 ms, after which the line stimulus was presented. Each pretransected line was displayed for 2000 ms and then replaced by a blank (black background), which remained visible until a response was made. After the response, a black-and-white patterned mask stayed on the screen for a random duration (range 500–1500 ms) before the subsequent trial was presented (see Figure 1).

2.3.2. Procedure. The task was a two-alternative forced-choice paradigm and consisted of the verbal classification of pretransected lines that appeared centrally displayed on the monitor screen. On each trial, participants were asked to fully inspect each pretransected line and to judge which end of the line the transector was closer to. Thus, participants were instructed to verbally classify each prebisected line as "left" if the transector was perceived as being closer to the left end of the line and as "right" if they perceived it to be closer to the right end. To ensure that participants understood the task instructions, a practice session was administered before the experimental task. In this practice session participants had to classify five lines pretransected at −0.5° as "left" and five lines pretransected at +0.5° as "right," all presented in a random order. Participants received feedback only in these ten practice trials, which was repeated until they had reached at least 80% of accuracy. All participants reached such level of accuracy with the first practice session. Then, they were submitted to the experimental task in which all the possible eleven prebisected lines were displayed in random order. Participants were required to make a left/right-forced-choice and were told to make their best guess if they were unsure. They were also instructed to respond as accurately and as quickly as possible, without receiving any feedback. The experimenter seated behind participants (at least 1 m) and recorded participants' verbal responses by pressing one of two keys on a keyboard ("Q" for left and "P" for right). The landmark task took approximately twelve minutes to complete.

2.3.3. Data Analysis. In order to obtain an objective measure of perceived line midpoint in each condition for each participant, cumulative Gaussian functions were fitted to the proportion of "right" responses (i.e., when subjects judged the transector as being at the right of the true center) given by each participant as a function of the position of the 11 transector positions. The estimate of the point at which the psychometric function cuts the 50% of "right" responses indicates the point of subjective equality (PSE). An increase of "right" responses after PA, as compared to baseline, induces a decreased PSE, reflecting a relative shift toward the left of the perceived midline. On the contrary, an increase of "left" responses after PA, as compared with performance at baseline, induces an increased PSE, reflecting a relative shift to toward the right. So, the PSE allows us to detect any rightward (leftward) spatial shifts induced by PA on midpoint judgments in near and far spaces.

2.4. Time Bisection Task. The experimental procedure of the time bisection task was similar to the landmark paradigm, with the following exceptions.

2.4.1. Stimuli. Stimuli were lines, presented on the monitor, always pretransected at the true center (i.e., 0.00° of VA). Lines had different durations that were linearly spaced from 1000 to 3000 ms at 200 ms intervals (i.e., 1000, 1200, 1400, 1600, 1800, 2000, 2200, 2400, 2600, 2800, and 3000 ms). The size of the pretransacted lines and the monitor distance were the same of the landmark task in order to keep constant the visual angle at the two viewing distances (60 cm and 120 cm). Eight trials for each of the 11 different intervals were randomly presented, yielding a total of 176 trials, 88 in



(a) Landmark task (b) Time bisection task

Figure 1: Graphical representation of sequence of events in each trial for the two tasks. (a) Landmark task. Following 750 ms presentation of a blank, pretransected lines were presented for 2000 ms before reappearance of the blank on the screen until the subject responded. Lines were pretransected at 1 of 11 locations ranging symmetrically from -0.5° to $+0.5^{\circ}$ of visual angle (distance between transector locations = 0.1°) and including veridical center. After the participant's response (the transector is closer to the "right" or to the "left"), a black-and-white patterned mask was presented at random duration (range 500–1500 ms) before the next trial was presented. (b) Time bisection task. Following 750 ms presentation of a blank, pretransected lines were presented before reappearance of the blank until the subject responded. Lines were pretransected at veridical center and had 1 of 11 different duration ranging from 1000 to 3000 ms at 200 ms intervals. After the participant's response (the duration of the line is "short" or "long"), a black-and-white patterned mask was presented for a random duration (range 500–1500 ms) before the next trial.

the near space and 88 in the far space. Trials began with the presentation of a blank (black background) for 750 ms, after which the line stimuli were presented. One of 11 lines with different durations (range 1000–3000 ms) was displayed and then replaced by a blank (black background), which remained visible until a response was made. After the response, a black-and-white patterned mask stayed on the screen for a random duration (range 500–1500 ms) before the subsequent trial was presented (see Figure 1).

2.4.2. Procedure. The time bisection task consisted of the verbal classification of a series of pretransected lines that were displayed for different durations at the center of the computer screen. Participants were instructed to verbally judge (forced-choice) whether the duration of each line was "short" or "long" with respect to previously acquired pair of reference durations (1000 ms and 3000 ms). Before administering the experimental task, the practice session served to familiarize participants with the two reference durations presented in random order. In this session ten practice trials were displayed and participants had to classify five intervals of 1000 ms as "short" and five intervals of 3000 ms as "long." Feedback was given on accuracy only for these ten practice trials. All participants reached at least 80% of accuracy with no more than two practice sessions. After the experimenter had ensured participants were confident with the practice session, all the eleven lines with different durations were presented in random order during the experimental task. Participants were required to classify each line duration as "short" or "long" and to make their best guess if they were unsure. The experimenter was seated behind the participants (at least 1 m) and recorded participants' verbal responses by pressing one of two keys on a keyboard ("Q" for "short" and "P" for "long"). The task in the near and in the far space took approximately fourteen minutes to complete.

2.4.3. Data Analysis. A psychophysical response function was created for each participant by calculating the proportion of "long" responses for each of the 11 line durations. The data were fit with cumulative Gaussian function, whose mean (50% point) indicated the "Point of Subjective Equality" (PSE). The PSE is the duration at which a participant is equally likely to classify the stimuli as short or long. For each participant, the PSEs were separately calculated in each condition.

An increase of "long" responses after PA, as compared to baseline performance, induces a decreased PSE, reflecting a relative shift towards overestimation of temporal midpoint (i.e., durations are perceived being longer with respect to before PA). Conversely, an increase of "short" responses after PA, as compared with performance at baseline, induces an increased PSE, reflecting a relative shift towards underestimation of temporal midpoint (i.e., durations are perceived shorter).

Accordingly, the PSE allows us to observe whether PA caused a bias in their temporal judgment towards either an

underestimation or an overestimation of durations in near and far spaces.

2.5. Prism Adaptation. The procedure, stimuli, and material conformed to well-established PA described in Frassinetti et al.' study [11]. Subjects were submitted to either the rightward prismatic goggles inducing a leftward aftereffect (RPA group, n = 32, 23 females; mean age = 23.66; SD = 1.91) or the leftward prismatic goggles inducing a rightward aftereffect (LPA group, n = 32; 23 females; mean age = 23.91; SD = 2.35). During PA subjects were seated at a table in front of a box (height = 30 cm, depth = 34 cm at the center and 18 cm at the periphery, width = 72 cm) that was open on the side facing the participants and on the opposite side, facing the experimenter. The box consisted in a Plexiglas panel erected in a vertical and semicircular position and graduated by vertical lines spaced by 1° of VA. The experimenter placed a visual target (a pen) at the distal edge of the top surface of the box, in one of three possible positions (randomly determined on each trial): a central position (0°), 21° to the left of the center, and 21° to the right of the center. Subjects were asked to keep their right hand at the level of the sternum and to point toward the pen using the index finger of the same hand as quickly and as accurately as possible. Participants were also instructed to make a ballistic movement and to correct any errors on the successive movement. Participants could not see their hand when it was at the starting position and during the first third of the pointing movement to ensure effective adaptation. The experimenter recorded the end position of the subject's pointing direction. The pointing task was performed in three experimental conditions: preadaptation, adaptation, and postadaptation. In the preadaptation condition, the subjects performed two types of trials (total of 60 trials). On half of the trials, their pointing was visible to them (as in the adaptation condition). On the other half, the subjects were required to look at the target and then to point at it with their eyes closed, so that the pointing was not visible at any stage of the movement (i.e., invisible pointing as in the postadaptation condition, open-loop pointing). In the adaptation condition (total of 90 trials), the subjects performed the task while wearing prismatic lenses that induced a 10° shift of the visual field to the left (LPA) or to the right (RPA). Participants could see the trajectory of their arm (i.e., visible pointing). In the postadaptation condition, immediately after prisms removal, the subjects were required to look at the target and make their pointing movements with their eyes closed as in the preadaptation condition (i.e., open-loop pointing; 30 trials). The adaptation procedure took approximately 15–20 min to complete.

3. Results

3.1. Landmark and Time Bisection Tasks. We focused our results exclusively on the mean PSEs yielded by these tasks. Therefore, for each participant the PSEs in the temporal and spatial tasks were separately calculated for each condition.

Kolmogorov-Smirnov tests separately conducted for each group and experimental condition revealed that data were normally distributed (i.e., the tests of normality gave non-significant results).

In order to explore PA effects on temporal and spatial judgments in the near and the far space, we ran a multivariate analysis of variance for repeated measures. MANOVA would supposedly reduce the experiment-wise level of Type I error compared to several separate analyses and allows for taking into account potential correlations among the dependent variables of different nature (here expressed in milliseconds and degrees of visual angle).

The MANOVA was performed on the average PSEs measured in the landmark and the time bisection tasks, considering as within-subject factors *space* (near, far) and *session* (pre-PA, post-PA), and as between-subject factors *prisms* (LPA, RPA). *Post hoc* paired t-tests with the appropriate Bonferroni correction were conducted, where necessary, unless otherwise specified. Partial eta squared and Cohen's d are used to report effect size. As preliminary analyses failed to find any significant effect of age, education, or Edinburgh scoring, these factors are not considered further here.

The multivariate analysis revealed a significant multivariate main effect for *space*, Wilks' $\lambda = .823$, $F(2, 61) = 6.55$, $p = .003$, and $\eta^2_p = .18$. Overall in the landmark task, *post hoc* analysis showed a negative PSE value in the near space, indicating that participants perceived the middle of the line towards the left of the true center (−0.026°), and a positive PSE value in the far space, indicating that participants perceived the middle of the line towards the right (0.016°, $p < .001$, $d = 0.42$). However, in the time bisection task, it must be pointed out that the difference between the mean PSE in near (1891 ms) and far space (1926 ms) was not significant ($p > .05$).

More important for the aim of the study, the MANOVA found a significant multivariate interaction effect *session* by *prisms*, Wilks' $\lambda = .667$, $F(2, 61) = 15.21$, $p < .001$, $\eta^2_p = .33$ (see Figure 2). In the landmark task, there was a significant rightward shift of the mean PSE after leftward-displacing prismatic adaptation with respect to before (post-LPA 0.028°; pre-LPA −0.005°, $p = .008$, Bonferroni corrected $p = .047$, and $d = 0.45$). On the contrary, prismatic adaption with rightward visual displacement did not affect the spatial judgments, as measured by the PSE (post-RPA = −0.016°; pre-RPA = −0.026°, $p > .05$).

By contrast, both right- and left-deviating prisms biased symmetrically the PSEs in the time bisection task. Indeed, LPA produced an overestimation of time durations as compared to a pre-adaptation baseline (post-LPA = 1860 ms; pre-LPA = 1946 ms, $p = .001$, Bonferroni corrected $p = .006$, and $d = 0.6$), whereas RPA produced an underestimation of time durations (post-RPA = 1964 ms; pre-RPA = 1866 ms, $p < .001$, Bonferroni corrected $p = .001$, and $d = 0.74$). Importantly, the symmetrical effect of LPA and RPA did not seem to be driven by a difference between the two prism groups at the baseline in the time bisection task, since the PSE measures before prismatic adaptation did not differ (Bonferroni corrected $p = .773$, $d = .28$, and power = .88).

Since the multivariate three-way interaction was not significant, Wilks' $\lambda = .952$, $F(2, 61) = 1.55$, $p = .221$,

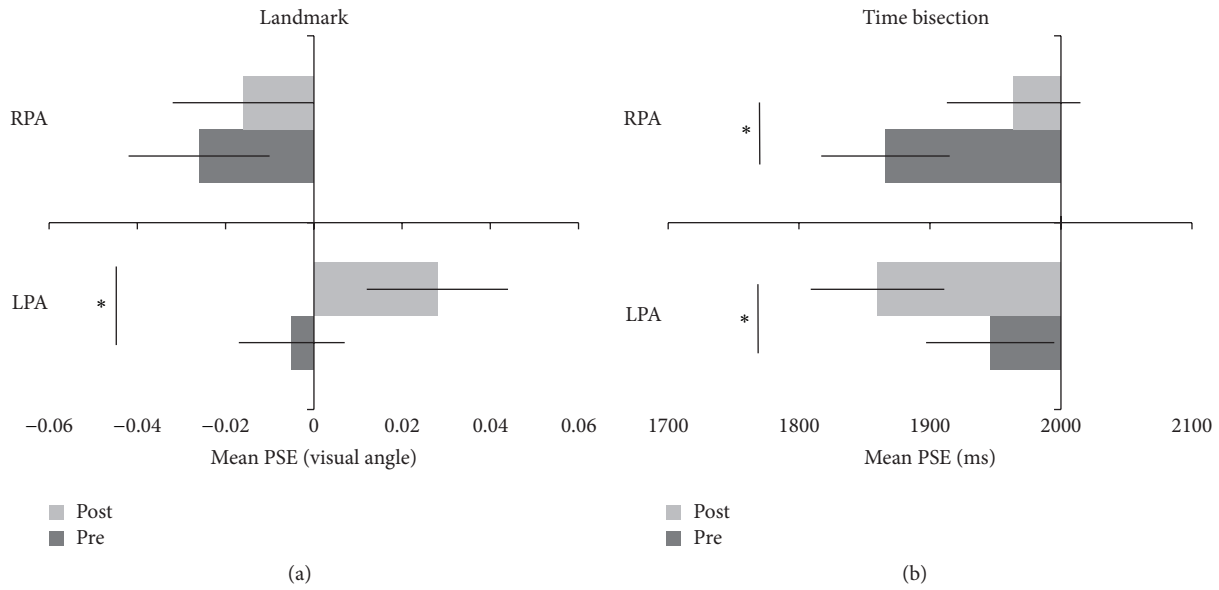


Figure 2: Point of subjective equality judgments (PSE) as a function of prism group (LPA and RPA) and session before (dark gray) and after PA (light gray). Landmark task (a): the line transector is judged (in visual angle) as nearer to the left (negative values) or to the right (positive values). After LPA the line transector is judged as nearer to the right compared to before PA (positive values). Time bisection task (b): interval duration (in millisecond) is classified as short (<2000 ms) or as long (>2000 ms). After LPA the time interval is classified as longer compared to before, whereas after RPA the time interval is classified as shorter compared to before PA. Bars represent the average point of subjective equality for spatial and temporal judgments, respectively, ± standard error (SEM). $^{*}p < .05$.

and $\eta^2_p = .05$, in the landmark task the spatial modulation following adaption procedure was present in both near (pre-LPA = −0.028°; post-LPA = 0.017°) and far space conditions (pre-LPA = 0.017°; post-LPA = 0.038°) for the leftward-deviating prism group. In contrast, no significant change emerged either in near (pre-RPA = −0.042°; post-RPA = −0.051°), or in far spaces (pre-RPA = −0.009°; post-RPA = 0.018°) for the rightward-deviating prism group. Remarkably, given that the symmetrical effects of PA on the time bisection task did not vary depending on the location of stimuli, temporal modulation caused by prisms was evident for the LPA group, in both near (pre-LPA = 1947 ms; post-LPA = 1844 ms) and far space conditions (pre-LPA = 1944 ms; post-LPA = 1876 ms), and for RPA group, in near (pre-RPA = 1837 ms; post-LPA = 1937 ms) and well as in far space conditions (pre-RPA = 1895 ms; post-RPA = 1991 ms).

Besides this, as suggested by the anonymous reviewers, we checked whether the MANOVA results described above might have been determined by differences in baseline values. We computed unpaired t-tests (both uncorrected and Bonferroni corrected for multiple comparisons) in each experimental task, comparing the mean baseline PSEs between the two prism groups in the near and far conditions. No significant difference emerged, either in landmark or in temporal judgments, prior to the adaptation procedure for the two PA groups (all ps > .05).

Finally, a series of Pearson's correlation analyses was performed to assess for possible relationships between the PSEs at baseline in the landmark and time bisection task for either prisms direction. Additionally, a series of correlations was conducted to assess the relationship between the effects of PA on temporal and spatial PSEs by comparing the measures in the two tasks before and after RPA and LPA session. No significant correlation was found (all ps > .05).

Taken together these data indicate that, first, spatial judgments were influenced by the space wherein the stimulus to be bisected had been presented (near or far space). More interestingly, the midpoint judgments in the spatial and temporal bisections were affected in a different fashion by PA, regardless of the space where the stimuli had been displayed. Namely, only LPA induced a rightward shift in the perceived midpoint of the line, whereas both RPA and LPA biased spatial representation of time toward an underestimation and overestimation, respectively. The absence of any interaction involving the *space* factor shows that the two different spatial representations (near and far space) did not enforce any differences in the shifts produced by PA, as indexed by the PSEs measured in the temporal and landmark tasks. That is, the effects of prismatic adaptation procedures on time and spatial processing occurred in both near and far spaces in a similar manner.

3.2. Prismatic Adaptation. To make sure that any potential differences in time and space estimation before and after prism session were due to PA, we assessed the presence of both error reduction (i.e., the tendency to compensate for prism-induced error in pointing during PA) and aftereffects (i.e., the subsequent tendency to point in the direction opposite to the visual displacement induced by prisms, after goggles removal). Pointing displacement measures (expressed as

degrees of visual angle, VA) carry a negative sign (−) when directed to the left and a positive sign (+) when directed to the right with respect to the target actual location.

To demonstrate the presence of pointing errors, in the first trials, and of error reduction, in the last trials of PA condition, participant's pointing performance during preadaptation and adaptation condition was compared. If prism adaptation procedures were effective, a difference should be found between the first trials of the adaptation condition and the preadaptation condition, but no difference should be found between the last trials of the adaptation condition and the preadaptation condition (error reduction).

In order to verify if participants showed an error reduction as they adapted to the prisms, an ANOVA was performed on the mean pointing measures, with *prims* (LPA, RPA) as a between-subject factor and *condition* (preadaptation measures, first three trials of the adaptation measures, and last three trials of the adaptation measures) as a within-subject factor. The ANOVA was followed by *post hoc* (two-tailed) *t*-tests for which the appropriate Bonferroni correction was applied for each prism group. Effect size is indicated as partial eta square or Cohen's *d*.

The ANOVA revealed a significant main effect of the between-subject factor *prisms,* $F(1, 62) = 572.92$, $p < .001$, and $\eta^2_p = 0.90$ (LPA = −2.163°; RPA = 2.174°). More interestingly, the interaction between *prisms* and *condition* was significant, $F(2, 124) = 604.83$, $p < .001$, and $\eta^2_p = 0.91$. Pointing error was significantly greater in the first three trials of the adaptation (LPA = −5.872°; RPA = 6.274°) than in the preadaptation (LPA = −0.207°, $p < .001$, Bonferroni corrected $p < .001$, and $d = 3.41$; RPA = 0.049°, $p < .001$, Bonferroni corrected $p < .001$, and $d = 3.16$) but did not differ between the last three trials of the adaptation and the preadaptation values (LPA = −0.410°, RPA = 0.198°, both *p*s > .05). This provided a profile of the direct effects of prismatic displacement, which reflects trial-by-trial error reduction.

To test for the presence of aftereffect, open-loop pointing measures were compared between the postadaptation and the preadaptation conditions. If PA produced a visuomotor bias opposed to deviation induced by prism, a leftward (rightward) error during open-loop pointing should be found when right (left) prismatic goggles have been removed. We conducted an ANOVA with *prisms* (LPA, RPA) as the between-subject factor and *condition* (preadaptation and postadaptation) as the within-subject factor, in order to test this prediction.

The main effect of *prisms,* $F(1, 62) = 321.81$; $p < .001$; $\eta^2_p = 0.84$, and its interaction with *condition,* $F(1, 62) = 599.28$; $p < .001$; $\eta^2_p = 0.90$, were significant. The open-loop pointing measures in the postadaptation condition differed from the open-loop pointing measures in the preadaptation in RPA (pre-RPA = −0.025°, post-RPA = −4.509°, $p < .001$, and Bonferroni corrected $p < .001$) as well as in LPA (pre-LPA = −0.396°, post-LPA = 4.517°, $p < .001$, and Bonferroni corrected $p < .001$).

Since the sign of the sensorimotor aftereffects depends upon the direction of the prisms, we also assessed whether the amount of sensorimotor adaptation was similar for the two groups by submitting the absolute value of the shift to a repeated-measures mixed ANOVA with *prisms* (LPA, RPA) as a between-subject factor and condition (pre- and post-PA) as a within-subject factor. In this ANOVA only a main effect of condition emerged, $F(1, 62) = 334.91$; $p < .001$; $\eta^2_p = 0.84$ (pre-PA = 0.732, post-PA = 4.513). This analysis revealed no interaction *prisms* by *condition*, suggesting that both PA groups were equally adapted and that the amount of sensorimotor adaptation was comparable in the two prism groups.

Finally, to assess whether there was any correlation between an individual participant's shift in PSE and the amount of sensorimotor aftereffects or error reduction in pointing, we computed separate Pearson correlation analyses between the absolute value of aftereffect or error reduction and subject's performance in the time bisection and the landmark task for each prism direction. None of these correlations was significant (all *p*s > .05).

In sum, data analysis on PA procedure demonstrated that both groups compensated, during prism adaptation, for prism-induced spatial errors in pointing (error reduction) and that, after prisms removal, they pointed in the direction opposite to the visual displacement induced by prism (aftereffect).

4. Discussion

The main purpose of this investigation was to examine whether the plastic effects on spatial and temporal processing following rightward and leftward prismatic adaptation are generalizable across near and far space. Given a considerable body of evidence suggesting, at least, two independent representations of space based on action potentiality, here we went on to ask whether temporal and spatial modulations induced by PA extend beyond the space near the body. Accordingly, two are the main results of the present study. The first main finding is that manipulation of PA-induced effects influences temporal and spatial judgments not only in the immediate spatial region within which the adaptation occurs (near space), but also in the sector of the space farther away and beyond arm's reach (far space). The second one is that LPA induces a significant modulation on spatial and temporal task, whereas RPA only acts on the temporal, but not on the spatial task. This pattern of results suggests that the effects induced by PA on representations of space and time are the same along the sagittal near-far axis, but different along the horizontal left-to-right axis. Therefore, we shall first discuss the results of PA modulation found in near and far space and then the asymmetrical effect of orienting spatial attention leftwards and rightward on space and time representations, and we shall finally try to understand the reason of such differences.

The finding that the attentional shift after adaptation, which occurred within the near space, may alter spatial-time representations in the two sectors of space in a similar fashion is the novelty of the study. Indeed, examining literature on prismatic adaptation, the visuospatial effects of this procedure in far space were investigated by Frassinetti

and colleagues [59] in neglect patients and by Berberovic and Mattingley [60] in neurologically healthy individuals. As regards clinical population, the efficacy of RPA in alleviating spatial attentional symptoms in neglect patients who, following a lesion of the right hemisphere, showing a deficit in orienting attention to the contralesional hemispace, has been already demonstrated [61–64]. Frassinetti and coworkers [59] revealed that a training of two weeks with RPA induced a long-lasting amelioration of neglect symptoms both in the near and in the far spaces, as assessed by two different behavioral and ecological tasks. Specifically, to explore the presence of neglect in the far space a room description task was used, in which patients were asked to name the items (e.g., window and chair) displayed symmetrically on the left and on the right wall of a room (3.6×2.2 m). As a consequence of the beneficial effects of PA procedure, the number of omissions on the left side was reduced after the two weeks of training with RPA. As far as healthy individuals, Berberovic and Mattingley [60] found that left-shifting prisms induced a post-PA rightward shift on estimates of visual center for stimuli appearing in far space in the landmark task. Relevant to the present study, the same authors also showed a surprising rightward, instead of leftward modulation, as it would have been expected, in the far space only. Our data appear to be at odds with this previous finding. However, there are several substantial dissimilarities between the study by Berberovic and Mattingley [60] and our own that could potetially explain such a discordant result. One important difference concerns the experimental procedure and methods adopted. At odds with our study, in Berberovic and Mattingley's work both participants and screen were moved between blocks, line stimuli appeared displayed centrally on the screen, or displaced slightly to the left or right, and all the participants used bimanual responses in the landmark task. Moreover, half of the sample used the left hand, and half used the right hand in the adaptation session. We cannot therefore exclude that these procedural differences might have brought discrepant results. From a statistical point of view, and still contrary to our study, the data obtained from the landmark task in the Berberovic and Mattingley's study were analysed separately for the LPA and RPA groups through two one-way repeated-measures ANOVAs. More importantly, our sample is twice as large as that of Berberovic and Mattingley and this further allowed us to perform an omnibus MANOVA that we believe more powerful and suitable analysis for our study. Albeit differences in experimental procedures could have contributed to this different statistical result, we wish to emphasize that in a larger sample we did not replicate this finding. By visual inspection, in our sample there is a tendency towards a rightward shift in the far space, which does not reach significance.

Furthermore, as in Berberovic and Mattingley's study and previous studies [16, 28, 60], we found no linear correlation between the sensorimotor and cognitive aftereffects following adaptation. Indeed, it has already been established that the two aftereffects were uncorrelated in magnitude (i.e., the amount of sensorimotor aftereffect does not predict the amount of spatial modulation or its magnitude), and this finding is reminiscent of the lack of correlation between pointing errors and line bisection performance in neglect patients following prisms adaptation [28]. The lack of any significant relationship supports the idea that the changes found on the landmark and time bisection tasks are not directly related to the sensorimotor aftereffect. PA might indeed act at both sensorimotor and cognitive levels, but the link between the two different measures might not be a linear association and might imply more complex relationships.

Nevertheless, the finding that temporal and spatial changes following the procedure of adaptation are similar across representational spaces is in agreement with the hypothesis that PA-induced effects may be mediated by the oculomotor systems [65–67]. Indeed, during prismatic procedure participants perform a series of pointing movements, which relies on a form of visuomotor coordination between the hand and eye. Since movements are deviated toward the side of prismatic lenses, to compensate for the visual field displacement participants implicitly deviate their motor programs toward the left or right, thereby implementing a leftward or rightward recalibration into their sensorimotor systems. Due to the eye-hand coordination during pointing task, a deviation of eye movements in the direction opposite to the prismatic shift is expected. Provided that the areas involved in eye movements (area 8) and in eye movement programming (LIP) might contribute to far space representation [68, 69], the effects of PA in far space is compatible with a potential shift of the oculomotor system following the procedure of adaptation. Since the direction of eye movements can influence spatial representation [70], shifting oculomotor system can also impact the exploration on the horizontal mental time line, thus resulting in a modulation produced by PA on time representations, too, in near space as well as far space.

The second interesting result of the current study is that PA differently affects spatial and time processing, as indexed by comparing the landmark and the time bisection tasks. More in detail, LPA effects were found in landmark as well as in time bisection tasks, whereas RPA effects were limited to time bisection task. Indeed, in the spatial domain the effectiveness of PA in modulating spatial cognition has also been proven to be unidirectional in both pathological and neurologically healthy populations. Only RPA has been demonstrated to act on neglect symptoms [71] and, by contrast, only LPA has been so far reported to be effective in healthy individuals miming a neglect-like behavior. Accordingly, most of the studies investigating PA in healthy subjects did not find any significant plastic effects of RPA on spatial processing. Because of the lack of a significant leftward spatial modulation after rightward prism adaptation in nonclinical population, RPA has become the standard "control" procedure for studies examining LPA-induced effects on spatial processing. Moving on to a possible explanation of such a null effect, some authors [24] considered the null result regarding the effects of RPA in terms of a simulation of neglect in neurologically healthy individuals. Given that neglect syndrome is more likely to occur after right rather than left lesions, inducing a rightward bias of spatial attentional orientation, it has been put forward the hypothesis that the asymmetrical effects of LPA and RPA on spatial processing might reflect

an inherent bias of the brain's structural organization in directing attention to the right [72]. Thus, some reports hint that neglect and pseudoneglect may share common cognitive and neural mechanisms, as they appear to be two sides of the same coin [19]. In other words, spatial performances of healthy participants after leftward prismatic adaptation could be considered as correct approximation of a neglect-like behavior, with common main characteristics (e.g., directional bias and directional specificity of PA [25]).

Moreover, regarding PA effects on time processing, our results are in line with previous findings in healthy subjects [11]. In fact, both PA directions symmetrically alter time processing and the directional bias observed after PA depends on the direction of the prismatic deviation. After rightward optical deviation inducing a leftward aftereffect, participants show a significant underestimation of perceived time, relative to before PA. Furthermore, after leftward optical deviation inducing a rightward aftereffect, participants report a significant overestimation of perceived time. Thus, results from time bisection task are consistent with the predictions of the anatomofunctional model of PA by Pisella and coworkers [73], but the results from the line bisection task are not. This model hypothesizes that PA may act by hypoactivating the posterior parietal cortex contralateral to the direction of the prismatic deviation and this, in turn, is able to modify the interhemispheric balance involved in orienting spatial attention. The model provides a solid theoretical framework for understanding the functioning of adaptation procedures because it evokes the same mechanism to explain both RPA's therapeutic effects in neglect (e.g., [59, 61]) and the induction of rightward (neglect-like) biases following LPA in healthy individuals (e.g., [16, 24]). According to this model, both prism directions are expected to modulate the contralateral posterior parietal cortex, and therefore both LPA and RPA should affect spatial processing in nonclinical population. In line with this account, here we stress the point that, although this symmetrical predicted modulation has not been demonstrated for the space domain yet, the expected effects are here found in the time domain, since we observed that leftward and rightward prism adaptation induced opposite plastic effects on time representations. Indeed, the finding that leftward- and rightward-deviating prisms had a different impact on intact spatial cognition was not an unexpected result. As mentioned above, it has been largely demonstrated that PA procedures have an asymmetric action on visuospatial cognition in both patients and healthy individuals. The same studies showing that LPA affects spatial processing in healthy participants have reported no effect of RPA [16, 24–27], even though the sensorimotor aftereffects (the hallmark of PA) induced by both LPA and RPA have comparable magnitudes and opposite directions. This negative evidence in the literature concerning the absence of RPA effects on intact spatial processing contrasts with the prediction of the anatomofunctional model proposed by Pisella and colleagues [73]. Here, we concur with the results of the previous studies, in that the model is not supported for the spatial domain. In spite of this, the prediction of the model is confirmed in temporal cognition, which has been shown to be directionally modulated by both PA directions, thus providing partial support to Pisella et al.'s model at least in the time domain.

Remarkably, these findings are also in accordance with the proposed PA's mechanism of action on time processing [74]. As posited by Oliveri et al.'s model, in the absence of manipulation of spatial attention, in healthy individuals real time and perceived time are aligned at the beginning of a temporal duration. The leftward shift of spatial attention via RPA, by shifting the spatial representation of the mental time line leftwards, produces a backward perception of elapsing time. Because of this bias, participants underestimate time durations: the passage of time flow of the perceived duration beats more slowly than the real duration. The same mechanism is proposed for the rightward shift of spatial attention after LPA. Because of the rightward shift of attention following LPA, time seems to speed up and participants overestimated time durations (see Figure 3).

Hence, we wonder why we did not find a similar symmetric modulation caused by the same attention manipulation on two so well-interrelated domains that are space and time. Although the exact nature of PA aftereffects is unclear, in order to explain the asymmetrical effects induced by PA procedure, we propose that temporal and spatial representations are not perfectly aligned, and thereby the attentional plastic changes caused by PA could enforce this different alignment between the two representations.

A simple approach for testing for the hypothesis of misalignment between spatial and temporal processing is provided by correlation analyses. It does not indeed appear to exist any consistent correlation between the spatial and temporal measures of the landmark and time bisection tasks. Note that correlation only looks at linear relationships, as Pearson's correlation is a measure of a linear association between two variables, whereas the nature of this cross-domain association may be much more complicated than a linear one. There may be a need for further and more focused research on this open issue.

Within this ever-growing interest for the understanding of these phenomenological dimensions, we directly assessed the plastic changes induced by a very well-known spatial attentional manipulation onto representations of time and space. Despite the lack of previous evidence in literatures comparing PA modulation in temporal and spatial processes, the reading of research from space-time interactions seems to suggest that, although tightly intertwined, the two domains may also differ in several respects. For instance, while most physical quantities can be represented in an ascending and a descending manner, perceived time always runs in the same direction (the anisotropy of time). Along the same lines, whereas time is therefore one-dimensional, space is instead three-dimensional. Admittedly, when talking about time, one should take into account that our understanding of this domain could go far beyond simple spatially based concepts of duration according to a specific direction being ascending from left to right [75]. Time encompasses many different aspects, including, for example, ordinality (e.g., what comes before versus after) and sequentiality (e.g., first versus second) or historical aspects (e.g., 1960s versus 1980s) [76].

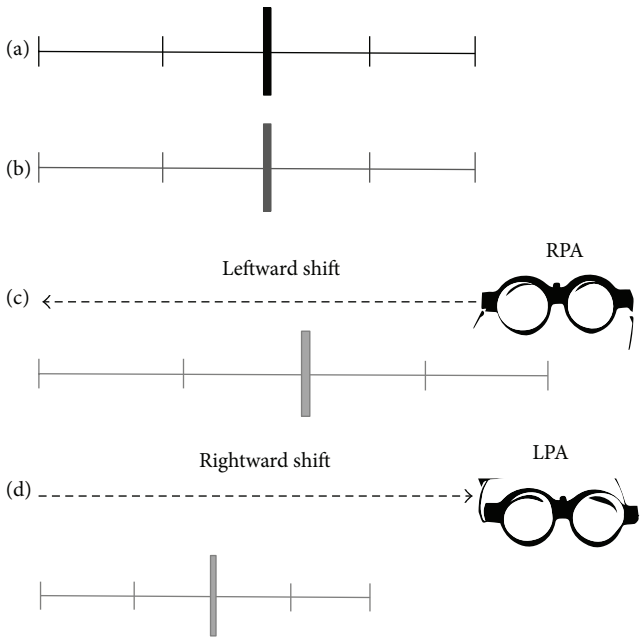


Figure 3: Theoretical model of the plastic prismatic adaptation effects on spatial representation of time processing. (a) The horizontal black line represents a putative duration to be bisected. The central vertical marker represents the real midpoint of the temporal duration. The little vertical lines represent time beats indicating the velocity of time flow passage: the greater the distance between the lines, the slower the passage of time flow. (b) The horizontal dark gray line represents time duration perceived by participants before PA. The central vertical marker represents the temporal bisection judgment of participants before PA. The real time duration and the perceived duration by participants are aligned: the passage of time flow of the perceived duration has the same velocity of the real duration. (c) Leftward shift of spatial attention following RPA induces an underestimation of time. The horizontal dashed black arrow represents the leftward shift of spatial attention induced by RPA. The horizontal light gray line represents the time duration perceived by participants after RPA. The central vertical marker represents the temporal bisection judgment of participants after RPA. The real time interval and the perceived interval are not aligned because of the rightward bias of spatial attention: the passage of time flow of the perceived duration beats more slowly than the real duration. (d) Rightward shift of spatial attention following LPA induces an overestimation of time. The horizontal dashed black arrow represents the leftward shift of spatial attention induced by LPA. The horizontal light gray line represents the time duration perceived by participants after LPA. The central vertical marker represents the temporal bisection judgment of participants after LPA. The real time interval and the perceived interval are not aligned because of the rightward bias of spatial attention: the passage of time flow of the perceived duration beats more quickly than the real duration.

Some of these proprieties of time might rely on a left-to-right horizontally oriented spatial representation [9, 77–79], but other aspects might not. Some scholars have also found evidence for the cognitive reality of front-back spatial representation of time with the past mapping to the back and the future mapping to the front [80]. Furthermore, the iteration of day and night and yearly seasons is not captured by the mental time line, so that some cultures around the world have developed "cyclic" time models. Additionally, we can use complementary, multiple spatial metaphors to understand the elapsed time and temporal relations, considering that time is not a monolith, but rather a mosaic of constructs (for a review [81]). Consistent with this view, even though the domains of space and time are closely interconnected and rely on shared neural resources, they also involve distinct structures and circuits. ATOM does indeed propose a shared neural substrate for representing and manipulating magnitudes but also acknowledges that the representation of all magnitudes may involve additional domain-specific neural substrates [2]. Along the same line of reasoning, ATOM's supporters proposed that "all magnitudes are not created equal" [2]. Indeed, interactions between space and time may be asymmetrical, such that, for instance, spatial cues may have a larger effect on temporal judgments than temporal cues do on spatial judgments [82]. There is considerable research demonstrating selective influences of the domain of space on the domain of time, but not corresponding influences in the other direction [75, 81, 83, 84]. So, although the ATOM framework does not explicitly predict spatial-temporal asymmetrical interactions, the model is in principle compatible with asymmetries that derive from differences in the domains themselves [2]. For all these reasons, at the moment, it is premature to provide a definitive account of the cross-domain temporal-spatial interactions given the complexity of each phenomenology of space and time.

5. Conclusions

Coming back to the purpose of the present study that is to directly compare spatial and temporal alterations after PA in the near and the far space, here we underline the two main findings. The first one is that PA acts in a similar fashion on spatial and temporal processing of stimuli on the sagittal axis (near/far). The second one is that the shift of attention along the horizontal axis (left/right) differently affects space and time. In this respect, it is important to note a difference when we consider sagittal near/far axis and horizontal left/right axis. Indeed, near and far are referred to as a *physical* distance from the body, whereas left and right are referred to as a *mental* spatial-temporal representation. Once prismatic adaptation has acted on this spatial-temporal representation, thus inducing different effects on space and time dimensions according to leftward/rightward attentional shift, the changes due to this manipulation may be extended to all the physical distances.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

This work was supported by grants from RFO (Ministry of University and Research) to Francesca Frassinetti and from

IHU CeSaMe ANR-10-IBHU-0003, FRC (Fédération pour la Recherche sur le Cerveau, Neurodon), and the James S. McDonnell Scholar Award to Alessandro Farnè and was performed within the framework of the LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon. The authors thank Michele Marzocchi for his technical assistance and Irene Veneziani for her help in collecting data.

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 6890674, 8 pages
http://dx.doi.org/10.1155/2016/6890674

Research Article

Systematic Underreproduction of Time Is Independent of Judgment Certainty

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Received 26 August 2015; Revised 26 November 2015; Accepted 6 December 2015

Academic Editor: Domenica Bueti

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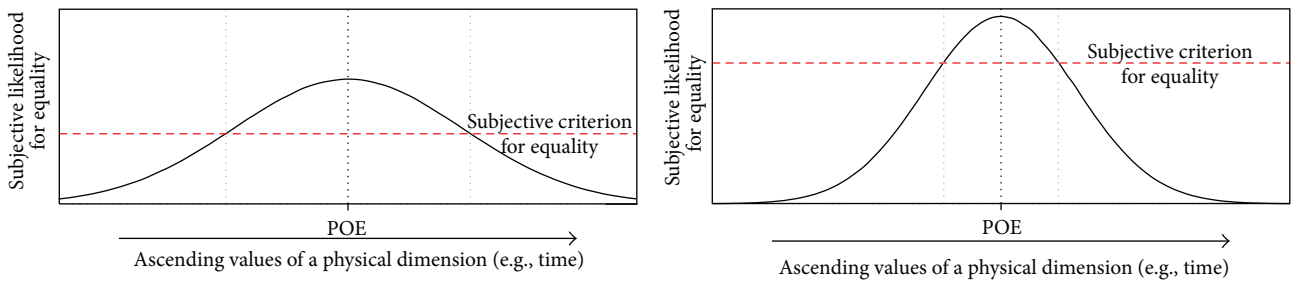
We recently proposed that systematic underreproduction of time is caused by a general judgment bias towards earlier responses, instead of reflecting a genuine misperception of temporal intervals. Here we tested whether this bias can be explained by the uncertainty associated with temporal judgments. We applied transcranial magnetic stimulation (TMS) to inhibit neuronal processes in the right posterior parietal cortex (PPC) and tested its effects on time discrimination and reproduction tasks. The results show increased certainty for discriminative time judgments after PPC inhibition. They suggest that the right PPC plays an inhibitory role for time perception, possibly by mediating the multisensory integration between temporal stimuli and other quantities. Importantly, this increased judgment certainty had no influence on the degree of temporal underreproduction. We conclude that the systematic underreproduction of time is not caused by uncertainty for temporal judgments.

1. Introduction

The goal of psychophysics is to describe the relation between physical and psychological realms [1], and, to this end, researchers should possess complete control over the physical stimuli used in their experiments [2]. This important principle is violated for the dimension of time [3]. While most physical qualities can be presented in an ascending and a descending manner (e.g., weights can increase and decrease), perceived time always runs in the same direction. This peculiarity is referred to as the anisotropy of time and it can explain some well-known phenomena in timing research, for example, the underreproduction of temporal intervals [4].

In time reproduction, participants are presented with a stimulus of a specific duration (i.e., the standard interval) and afterwards they have to terminate a second stimulus as soon as it has reached the same duration as the standard (i.e., the reproduced interval). Numerous applications of this task have consistently revealed that the reproduced intervals are shorter than the standards [5]. This phenomenon has often been interpreted as an erroneous perception of time, in the sense that the second duration is perceived as longer than the standard, and therefore it is terminated too early (e.g., [6]). This interpretation was questioned in a recent study [4], in which we proposed that the negative errors in time reproduction tasks might also be caused by the asymmetric flow of perceived time. Reproduction tasks are based on the method of limits [2], in which a target value on a specific dimension (e.g., loudness) is approached from smaller or larger values and for which it is pertinent to alter the direction of this dimensional change [3]. In other words, the correct value on a physical continuum (i.e., the presented standard) must be approached alternately from smaller and larger values. However, this important manipulation is not possible with respect to the time dimension. The probability for a correct response changes continuously during the reproduction phase. In the examples depicted in Figure 1, the duration with the highest probability of being judged as equal to the standard would coincide with the point of objective equality (indicating perfect mean accuracy), but



(a) Low certainty (b) High certainty

Figure 1: Probability curve for a correct response depending on the elapsed time during the reproduction phase. Increased certainty (b) should result in a sharpening of the curve and in a more restrictive criterion level, thereby attenuating the degree of underreproduction.

all other durations above the criterion level would also cause a termination of the reproduction phase. Due to the anisotropy of perceived time, this criterion level is necessarily reached at smaller values. Taken together, we proposed that the underreproduction of temporal intervals does not occur because shorter durations are more likely to be confounded with the standard than longer durations but rather occurs because shorter durations have to be presented previous to longer ones [3, 4].

One potential cause for the general bias towards earlier responses consists in the uncertainty involved in reproduction tasks. Increasing the certainty of temporal judgments should result in a sharpening of the probability curve for a correct response and in a more restrictive criterion level. As can be inferred from Figure 1, this would give rise to an attenuation of negative reproduction errors. Thus, if the bias towards earlier responses is due to uncertainty, then a reduction of this uncertainty should be accompanied by an attenuation of negative reproduction errors.

A promising method to manipulate uncertainty in timing tasks is provided by transcranial magnetic stimulation (TMS) [7]. Applied over the right posterior parietal cortex (PPC), repetitive TMS selectively influenced the precision in time discrimination tasks, reflecting altered certainty, whilst the mean accuracy of temporal judgments was unaffected [8]. An involvement of the right PPC in the perception of time has also been demonstrated by electrophysiological recordings in monkeys and by functional neuroimaging studies in humans [9–13].

In the present study, we examined judgment certainty as a potential cause for the general bias towards earlier responses in time reproduction and ultimately its role for the systematic underreproduction of temporal intervals. Specifically, we tested whether altered certainty regarding temporal judgments results in an attenuation of negative errors in a time reproduction task. To this end, the right PPC was inhibited via continuous theta-burst stimulation (cTBS; [14–16]). Under TMS and sham stimulation, participants performed a time discrimination and a time reproduction task. Time discrimination data served as a manipulation check, verifying that judgment precision (as an indicator of certainty) was affected by inhibition of the right PPC. Regarding time reproduction, it was hypothesized that the systematic underreproduction of time was attenuated when temporal certainty is high.

2. Methods

2.1. Participants. Twenty-four participants (9 males, mean age of 26.3 years) were recruited from the local community. All but one were right-handed. Exclusion criteria were metallic objects in the body (due to T1 image acquisition), auditory impairments, or previous occurrences of epileptic seizures. Participants received monetary compensation and gave written informed consent to the experimental protocol, which was approved by the local ethics committee.

2.2. Tasks and Stimuli. Participants performed a time discrimination and a time reproduction task (order counterbalanced across participants), each of which lasted about six minutes. In both tasks, durations were signalized by acoustic stimuli (sine wave sounds of 300 Hz) in filled intervals. Durations were in the suprasecond range, because temporal underreproduction has frequently been reported for intervals within this range [5]. Sounds were delivered via noise-cancelling in-ear headphones (Sennheiser CX 300 II) and controlled with Vizard (v4.0).

In the discrimination task, a standard duration of 3 s was presented, and, after an interstimulus interval of 1 s, one of six comparison durations (2.5, 2.7, 2.9, 3.1, 3.3, and 3.5 s). Each comparison was presented five times in a randomized order, accumulating to 30 trials. Participants had to decide in a two-alternative forced-choice task, whether the comparison duration was shorter (button C on a standard keyboard) or longer (button M) than the standard.

In the reproduction task, one of five standard durations (1, 2, 3, 4, and 5 s) was presented, and, after a 1 s ISI, the reproduction interval was started, which was also signalized by a 300 Hz sine wave sound. Participants were instructed to terminate the reproduction interval (button B), once it had reached the same duration as the standard. Participants responded always with their dominant hand. Standards were presented six times each, resulting in 30 trials.

During both tasks, participants were instructed to close their eyes and to refrain from mental counting strategies.

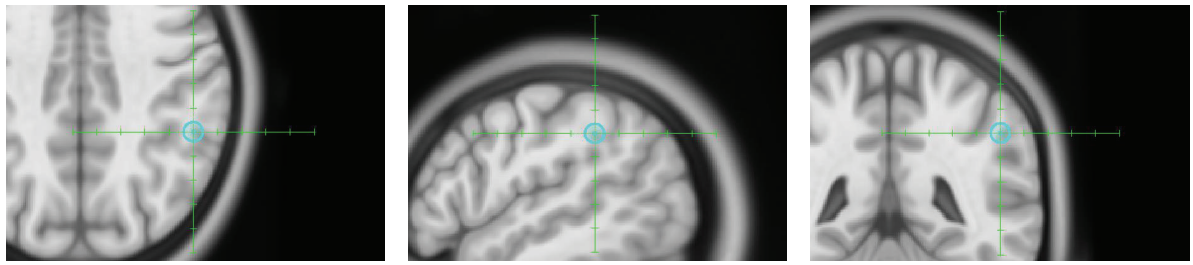


Figure 2: Target stimulation site in the right posterior parietal cortex.

Postexperimental interviews revealed no difficulties to adhere to these instructions.

2.3. TMS Protocol. The tasks were performed during two experimental sessions. In the TMS session, continuous theta-burst stimulation (cTBS) was applied over the right PPC. In the sham session, the coil was turned upside down and no TMS was applied. Due to this procedure, acoustic disturbance and vibrations of the coil were comparable during TMS and sham sessions. Each session contained either TMS or sham stimulation and was performed on a different day, with the order being counterbalanced across participants.

Stimulation site was determined on the basis of individual T1-weighted MRI scans. In each image, we identified the intersection point of Brodmann areas 39, 40, and 7 at the right intraparietal sulcus (IPS; Figure 2). Mean Talairach coordinates across subjects were (51.0, −41.1, 38.8). Navigation of the coil was supported by Localite TMS Navigator (version 2.1.18). As the focus of the present study was not to compare effects between two different stimulation sites but instead to test whether time discrimination and time reproduction tasks are differentially affected by PPC inhibition, we did not include a control stimulation site.

TMS was controlled by a MagPro stimulator (X100+MagOption, MagVenture) and pulses were delivered by a water-cooled figure-of-eight coil with an outer diameter of 75 mm (Cool B-65, MagVenture). We applied continuous theta-burst stimulation (cTBS) according to the protocol described in Nyffeler et al. [16] and in Chaves et al. [14]. Bursts containing three biphasic pulses (repeated at 30 Hz) were applied for 44 s at 6 Hz. Thus, TMS consisted of 267 bursts (801 single pulses). During stimulation, participants wore noise-cancelling in-ear headphones.

Pulse intensity was individually set to 100% of the resting motor threshold (MT), which was defined as the lowest intensity capable of inducing a motor evoked potential of 100 μV (recorded from the right abductor pollicis brevis) in at least 50% of a series of ten single pulses applied to the left motor cortex. MT was assessed for both experimental sessions separately. Mean pulse intensity for all subjects was 47.4% (ranging from 32% to 60%) of the maximal stimulator intensity.

2.4. Statistical Analysis. Regarding the discrimination data, psychometric functions were calculated for each subject and each session. Logistic functions were fitted using R package "modelfree," representing the probability of the response "comparison was longer than standard" depending on the comparison duration. Guessing and lapsing rates were set to .001. In order to quantify mean accuracy and precision of temporal judgments, we extracted the point of subjective equality (PSE) and the difference limen (DL). The data of four participants had to be excluded from this analysis, because the PSE was outside the range of the tested comparison durations (all were perceived as longer than the standard).

Regarding the reproduction data, we calculated the ratios between reproduced and standard durations. Values exceeding three times the standard deviation of the respective participant in the respective condition (0.4% of trials) were discarded as outliers. Median reproductions were calculated for each standard duration, and power functions of the form

$$f(x) = k \times x^{e} \tag{1}$$

were fitted for each subject and each session. The constant k determines the scale unit, x denotes the standard, and e is the power exponent. To quantify individual reproduction accuracy, we extracted the power exponent e and the median of reproduction/standard ratios (aggregated for all standards). Individual precision was quantified by the variability of reproductions, defined by the interquartile range of reproduction/standard ratios. Statistical analysis was performed using t-tests for paired samples (two-tailed) and correlation analyses.

3. Results

Results for the discrimination task are depicted in Figure 3. Inhibition of the right PPC significantly reduced the DL, indicating increased precision of temporal judgments ($t_{19} = -2.4$, $p = .03$), but had no influence on the PSE, indicating stable mean accuracy ($t_{19} = -0.1$, $p > .5$). These results validate the experimental manipulation used here. We were able to manipulate judgment certainty for temporal intervals independent of a shift of the psychometric function, which would denote a bias towards either "shorter" or "longer" judgments and thus a change in mean accuracy. No differences in overall reaction times were observed between TMS and sham stimulation ($t_{19} = 0.2$, $p > .5$).

Reproduction performance is depicted in Figure 4. PPC inhibition had no effect on accuracy, reflected neither by the power exponent ($t_{23} = -0.1$, $p > .5$) nor by the ratio between reproduced and standard durations ($t_{23} = 0.8$, $p = .42$).

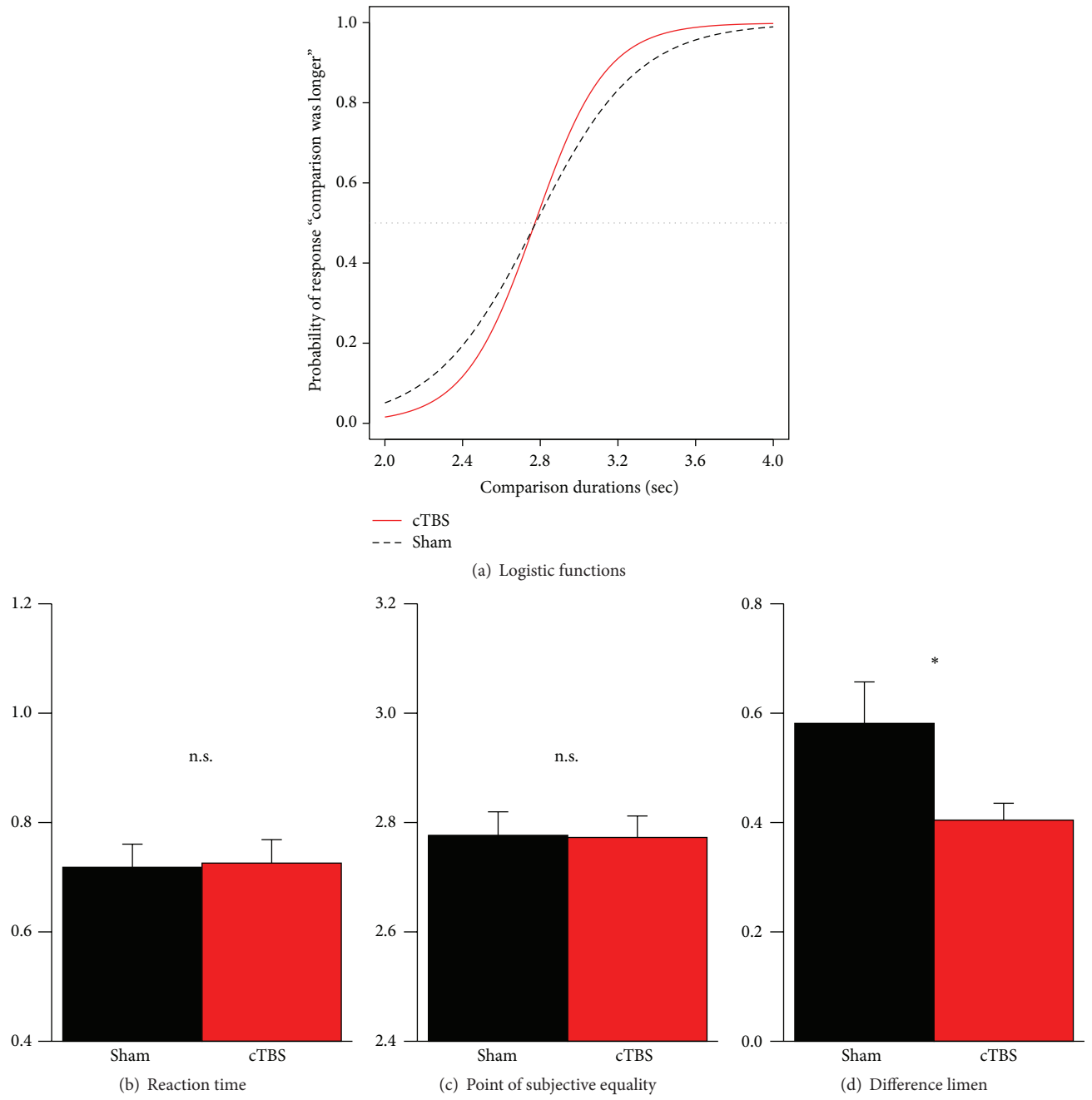


FIGURE 3: (a) Averaged logistic functions according to the discrimination data. No differences between cTBS (red bars) and sham stimulation (black bars) were found for reaction times (b) and the point of subjective equality (c). In contrast, reduction of the difference limen (d) indicates increased precision and thus a higher judgment certainty after cTBS. Error bars show standard errors of the mean across subjects.

Furthermore, cTBS did not influence precision, that is, the variability of responses in the reproduction task ($t_{23} = -0.6$, $p > .5$). Analysis of the coefficient of variation (CV) revealed the same results ($t_{23} = -1.5$, $p = .14$). Average CV was .17 after sham stimulation and .15 after cTBS.

Another test for our initial hypothesis that increased precision in discrimination tasks would coincide with an attenuation of reproduction errors is provided by correlation analyses. According to the hypothesis, individuals showing the highest TMS-induced precision increase in time discrimination should concurrently show a more pronounced attenuation of reproduction errors. However, this prediction was not confirmed by the data. TMS-induced changes in discrimination precision did correlate neither with respective

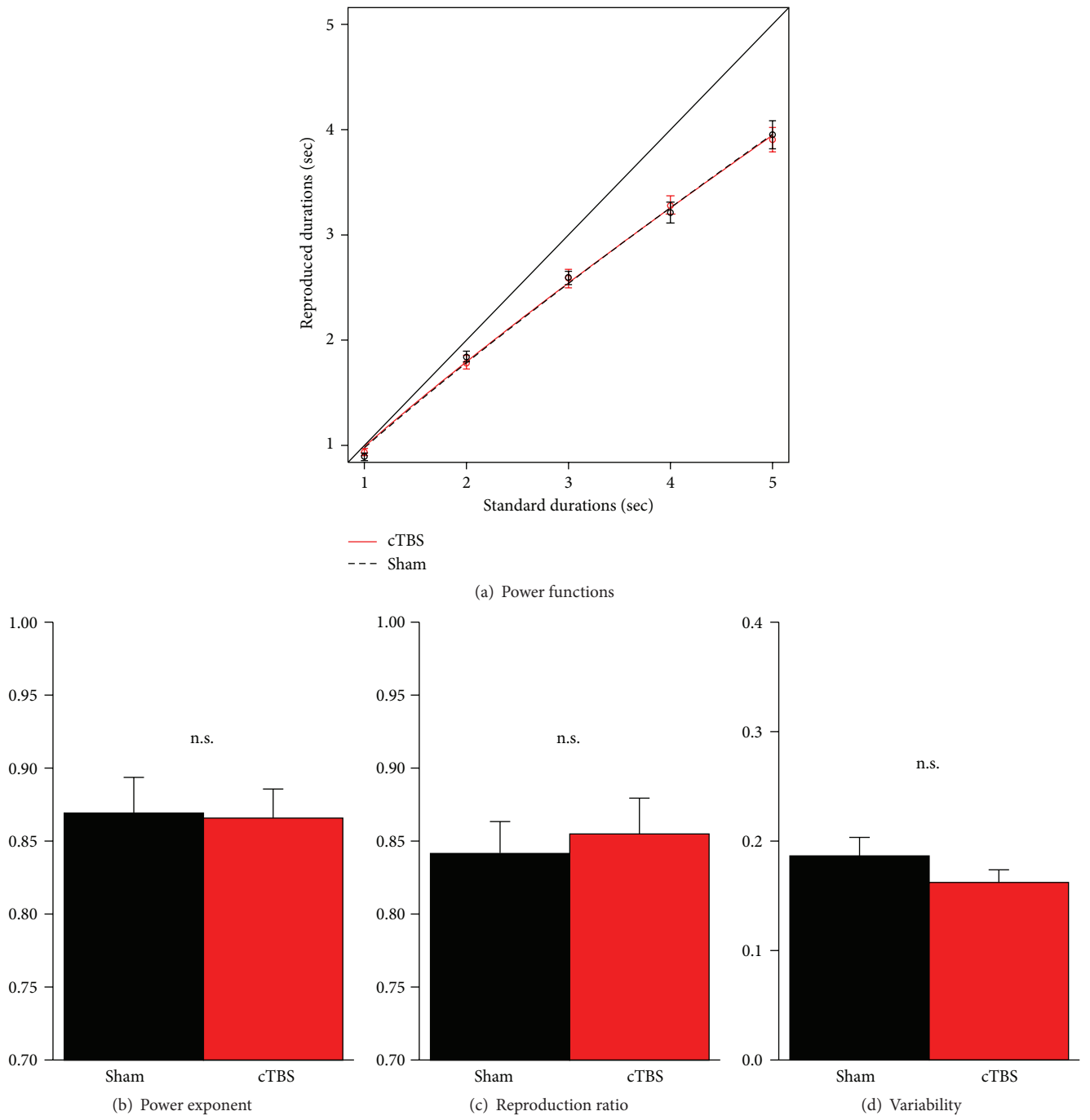


FIGURE 4: (a) Averaged power functions according to the reproduction data. No differences between cTBS (red bars) and sham stimulation (black bars) were found for the power exponent (b), the ratio between reproduced and standard durations, (c) and response variability (d). Error bars show standard errors of the mean across subjects.

changes in the power exponent for reproduction ($t_{18} = 0.6$, $p > .5$, $r = .14$) nor with changes in reproduction errors ($t_{18} = -0.8$, $p = .45$, $r = -.18$).

Given that time discrimination and time reproduction tasks were differentially affected by inhibition of the right PPC, it might be speculated whether both tasks are based on different processes. Therefore, we analyzed the correlation between accuracy and precision within the reproduction task, asking whether TMS-induced changes in response variability are related to an attenuation of underreproduction errors. No significant correlation was found ($t_{22} = -0.8$, $p = .4$, $r = -.18$).

4. Discussion

We proposed that systematic negative errors in time reproduction tasks are caused by a general judgment bias towards earlier responses, instead of reflecting a genuine misperception of temporal intervals [3, 4]. Here we tested whether different levels of uncertainty regarding temporal judgments can influence such a bias. Temporal certainty was manipulated by application of continuous theta-burst stimulation (cTBS) over the intraparietal sulcus (IPS) in the right posterior parietal cortex (PPC), an area involved in timing judgments [7, 8, 11–13, 17, 18].

Changes in certainty were reflected in increased precision in a time discrimination task after application of TMS, while the mean accuracy of discriminative judgments remained stable. In spite of this successful manipulation check, TMS had no effect on the performance in a time reproduction task. Both the precision and the accuracy of reproduced time intervals, quantified by response variability and mean errors, respectively, were not affected by the conditions. Accordingly, we can conclude that the certainty of temporal judgments is unrelated to errors in time reproduction. In line with this interpretation, we found no correlation between increased precision in the discrimination task and attenuated errors in the reproduction task, which would be expected if judgment certainty was a principal cause for the underreproduction of temporal intervals.

There are several reasons which potentially can explain the judgment bias towards earlier responses in reproduction tasks. First, uncertainty regarding temporal judgments can reduce the criterion level for the termination of the reproduction interval (as illustrated in Figure 1). Second, adaptation to previously presented stimuli (adaptation-level effects, [19]) can cause a systematic shift towards shorter durations, because the presentation of each interval is necessarily preceded by the immediate experience of shorter intervals [3]. Third, the awareness that we cannot go back in time and that the correct moment will be irretrievably missed when waiting too long can induce the urge to terminate the reproduction interval rather too early than too late. The first of these potential explanations is ruled out by the present study. The underreproduction of temporal intervals is independent of judgment uncertainty. The other possibilities need to be considered in future studies. For example, the third point might be addressed by analyzing the correlation between parameters of individual risk tolerance and individual underreproduction bias.

The results of the present study reveal a difference between the psychophysical methods of time discrimination and time reproduction and suggest that the two tasks are based on different neuronal mechanisms. Specifically, the reproduction performance seems to be independent of the certainty regarding temporal judgments, which we were able to manipulate by applying cTBS over the IPS within the right PPC, an area which is well known for its involvement in the processing of temporal intervals [8, 11, 13, 18]. However, the role of the PPC for the perception of time has mainly been investigated using discrimination tasks, while the application of other psychophysical methods in this regard is rather scarce. In recent years, it was increasingly acknowledged that many findings in time perception research depend on the nature of the psychophysical method used [3, 20, 21]. For example, patients suffering from attention-deficit/hyperactivity disorder and autism spectrum disorders show impairments in the reproduction of temporal intervals [22–24], but they perform equal to healthy controls when measured with other methods [25–27]. Our results are in line with this argument, as they demonstrate that time reproduction and time discrimination tasks are differentially affected by a transient inhibition of the right PPC.

Several previous studies have investigated the role of parietal areas for time discrimination and reproduction (e.g., [8, 28–30]). For example, Hayashi et al. [29] reported that application of cTBS over the right intraparietal cortex affected performance in a time reproduction but not in a time discrimination task. Harrington et al. [28] even reported a decreased precision in time discrimination in a patient group with right-hemispheric lesions. These findings seem to contrast with our result of increased precision in time discrimination and unaltered reproduction performance after inhibition of the right PPC.

A possible explanation for these different results is provided by the different range of intervals used [7]. In the present study, we implemented suprasecond intervals, while subsecond intervals were tested in Harrington et al. ([28]; 300–600 ms) and Hayashi et al. ([29]; 450–900 ms). There is much evidence for the existence of different neuronal mechanisms underlying the processing of subsecond and suprasecond intervals [7, 31, 32], and Lewis and Miall [31] found parietal areas to be especially recruited during discrimination of suprasecond intervals (3 s). The present study extends previous research by showing that cTBS-induced inhibition of the right PPC affects the precision for time discrimination in the suprasecond range, while the reproduction of suprasecond durations is unaltered. In this regard, it is interesting to note that Oliveri et al. [30] reported no effect of right PPC inhibition on the reproduction of relatively long intervals (1.6 to 2.4 seconds), while performance was affected when subjects were asked to stop the interval after half of the standard duration had elapsed (i.e., 800–1200 ms).

In accordance with a previous study, we found an effect of TMS on the precision in a time discrimination task [8]. However, our results deviate from this study in the fact that we show a precision increase, while Bueti et al. reported a precision decrease. This difference can be explained by the different TMS protocols used. Instead of online stimulation during the experimental task, we applied continuous theta-burst stimulation (cTBS), an offline protocol generally known for its transient inhibitory effects [14–16]. Bueti et al. applied a train of seven pulses at a frequency of 12 Hz, a protocol commonly associated with excitatory effects [33]. Thus, together with Bueti et al. [8], our results demonstrate that TMS over the right PPC not only can disrupt but also improve the precision in time discrimination tasks. This observation illuminates the role the right PPC plays for time perception. Parietal areas are known as key structures for the integration of sensory inputs from different modalities [9, 18, 34–39]. Interactions between the perceptions of temporal, spatial, and

numerical stimuli are mediated by neuronal structures within the PPC [18, 29, 30, 40]. Thus, PPC inhibition might suppress these multisensory interferences, leaving more resources for the processing of pure temporal stimuli. On the contrary, PPC excitation might stimulate the processing of combined stimuli, thereby reducing the precision for pure time judgments.

5. Conclusions

The psychophysical method of time reproduction has consistently revealed a systematic underreproduction of temporal intervals, that is, a judgment bias towards earlier rather than later responses [5]. The present study shows that these negative errors are not caused by temporal uncertainty. Increased certainty regarding temporal judgments had no effect on the magnitude of time underreproduction.

Ethical Approval

The study was approved by the local ethical committee and conducted according to the ethical standards laid down in the 6th Revision of the Declaration of Helsinki (Version Seoul 2008).

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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Hindawi Publishing Corporation
Neural Plasticity
Volume 2016, Article ID 3052741, 8 pages
http://dx.doi.org/10.1155/2016/3052741

Research Article

The Role of Perspective in Mental Time Travel

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Received 28 August 2015; Revised 22 October 2015; Accepted 2 November 2015

Academic Editor: Domenica Bueti

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Recent years have seen accumulating evidence for the proposition that people process time by mapping it onto a linear spatial representation and automatically "project" themselves on an imagined *mental time line*. Here, we ask whether people can adopt the temporal perspective of another person when travelling through time. To elucidate similarities and differences between time travelling from one's own perspective or from the perspective of another person, we asked participants to mentally project themselves or someone else (i.e., a coexperimenter) to different time points. Three basic properties of mental time travel were manipulated: temporal location (i.e., where in time the travel originates: past, present, and future), motion direction (either backwards or forwards), and temporal duration (i.e., the distance to travel: one, three, or five years). We found that time travels originating in the present lasted longer in the self- than in the other-perspective. Moreover, for self-perspective, but not for other-perspective, time was differently scaled depending on where in time the travel originated. In contrast, when considering the direction and the duration of time travelling, no dissimilarities between the self- and the other-perspective emerged. These results suggest that self- and other-projection, despite some differences, share important similarities in structure.

1. Introduction

When imagining time and their own life events, humans do not only retrieve or predict when events have occurred or will occur, but also automatically "project" themselves on an imagined *mental time line* [1]. Self-time travelling can thus be regarded as the ability to transpose one's habitual self-location in time to different temporal "locations" in the past or the future [2]. Emphasizing the role of perspective taking, this ability to change one's own temporal egocentric perspective has been proposed to share a common mechanism with the ability to change one's own spatial egocentric perspective [3]. In both domains, people would use existing representations as templates for processing and understanding new information, in order to plan their short- and long-term behaviors. On this account, the same processes that subserve simulation of the self at a different location *in space* would also subserve simulation of the self at a different point *in time* [4].

An interesting question, inspired by this parallel, is whether, similarly to taking another person's spatial perspective, people can also adopt the temporal perspective of another person when travelling through time. Studies investigating spatial perspective taking indicate that people can overcome their own position in space to adopt another person's spatial perspective (e.g., [5]). When the scene includes another person, for instance, people may spontaneously describe spatial relations from that person's perspective despite the very real presence of their own [5, 6]. These and other findings suggest that spatial perspective taking may induce an alterocentric remapping, that is, remapping of objects and locations to an alterocentric frame of reference [7].

To our best knowledge, no study has so far investigated whether a similar remapping may take place in the temporal domain. In other words, whether similarly to taking another

person's spatial perspective, people can take another person's temporal perspective when travelling through time. To address this issue, in the present study we directly compared self- and other-perspective time travelling with the goal of testing whether/how the representation of time varies as a function of perspective taking.

The psychological ability to traverse temporal distances is dependent upon a cognitive representation of time that has been suggested to be spatial in nature (e.g., [2, 8–12]; for an overview see [13]). In this conceptualization, time travel is characterized by three basic components: (a) *temporal location*, that is, the point in (space-) time from where the travel originates [8, 14, 15]; (b) *motion direction*, that is, the direction along which projection takes place (either backwards or forwards with respect to the temporal location) [8, 14]; and (c) *temporal duration*, that is, the temporal interval to be travelled (for a description of similar concepts, see also [16]). Within this framework, it has been demonstrated that rather than being mapped to space in a uniform manner, spatiotemporal representation presents areas of different granularity. For instance, Christian and colleagues [17] found that when asked to temporally locate events on a time line, participants used more space (-time) to represent one year in the present than in the past or the future. In a similar vein, Arzy and colleagues [14] showed that, irrespective of the temporal location, participants were faster and more accurate when asked to retrieve an event or a face located forwards rather than backwards (relative future effects in [14]; see also [8]). In addition, the speed of self-projection in time has been shown to depend logarithmically on the temporal distance between the imagined self-location in time and the location of the imagined event/face to retrieve [1].

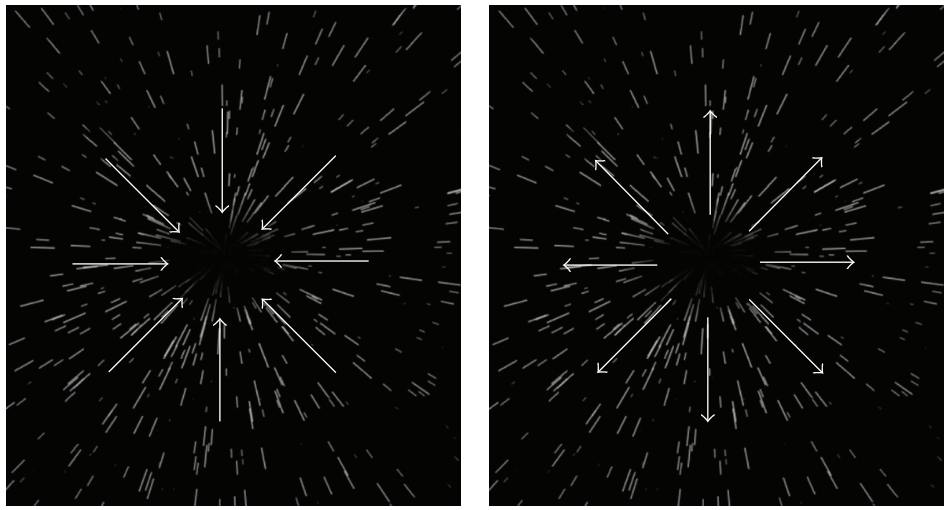
These patterns relate to the self-referenced topography of space-time mapping. To investigate whether similar patterns also apply to other-projection in time, here, we asked participants to imagine themselves or someone else at a specific point in time (i.e., past, present, or future) and "to operate" a notional time machine for travelling either backwards or forwards as to reach a target destination (i.e., one, three, or five years back/ahead). We used the travel duration as a proxy for how space-time representation depended on the perspective taking (self- versus other-perspective). Based on previous evidence that the amount of space used to represent time varies as a function of self-relevance [17], we expected that travelling in the self-perspective would take longer than travelling in the other-perspective. Moreover, we hypothesized that this effect of perspective would be greater when the travel originated in the present than in the past or future. In spite of these differences, however, we also expected similarities between self- and other-perspective time travelling. In particular, we predicted that, for both self- and other-perspective, travel duration would increase as a function of the temporal distance to be travelled. Finally, we expected that, in both perspectives and regardless of temporal location, travelling would be facilitated for the forwards motion direction (see relative future effect [14]).

2. Methods

2.1. Participants. Twenty-five participants (15 females, aged between 20 and 26 years, mean ± SD 23 ± 1.7 years) from the University of Turin took part in the study. All participants were right-handed and had normal or corrected to normal vision and no history of neurological or psychiatric disorders. All participants gave written informed consent before inclusion in the study, which was conducted in accordance with the principles of the revised Helsinki Declaration [18] and approved by the Ethical Committee of the University of Turin.

2.2. Design and Procedure. Participants were seated at a desk approximately 50 cm away from a 17″ computer screen (refresh rate = 60 Hz). At the beginning of the experiment, they were told that their task was to operate a notional "time machine" to travel through time. Next, they were given instructions about the temporal perspective (self versus other) and the time "locations" at which to imagine themselves. On other-perspective trials, a female coexperimenter was seated at a desk placed perpendicularly with respect to participant's desk (at a distance of ~1.5 m), in front of a computer monitor connected to participant's monitor. While sitting at their desk, participants could not see what was displayed onto the monitor in front of the coexperimenter. To control for possible effects related to age difference, participants were recruited as to be similar in age to the coexperimenter. At the beginning of the experiment, they were informed about coexperimenter's age (i.e., 24 years old).

Each trial began with the instruction to imagine oneself (for self-perspective trials) or the other person (for other-perspective trials) at specific past (i.e., the day of your/coexperimenter's 10th birthday), present (i.e., today), or future location in time (i.e., the day of your/coexperimenter's 50th birthday). As participants were in their late adolescence/early adulthood, past and future locations corresponded to two stages of development markedly distinct from their own (i.e., a point in middle childhood and a point in middle adulthood, resp.). From these locations, participants were instructed to move one, three, or five years, either backwards or forwards. To support the experience of "travelling" through time, an animated star-field display was projected onto the screen in front of the participant [17, 19, 20]. The display consisted of approximately 1000 randomly positioned white dots on a black background (see Figure 1). The dots (i.e., stars) were animated (25 fps) so as to appear to move, on a linear trajectory, either toward (i.e., centripetally) or away from (i.e., centrifugally) the center of the display, corresponding to the experience of backwards and forwards self-motion (Figure 1). Journeys in the past were accompanied by backwards optic flow, while those in future were accompanied by forwards flow (for a similar paradigm see [17]). On other-perspective trials, the same star-field display was projected onto the screen in front of participant and onto the screen in front of the coexperimenter. In both self- and other-perspective trials, the participant was instructed to look at the screen in front of him/her for the entire duration of the experiment. At a self-paced interval, participants were



(a) (b)

Figure 1: Illustrations of the direction of centripetal (a) and centrifugal (b) optic flow stimuli in trials with backwards and forwards motion direction, respectively.

requested to press a button (i.e., space bar) to begin the time travel (i.e., initiate the optic flow) and press it again once they felt they had reached the target (i.e., stop the optic flow). The "time travel" duration was calculated as the interval between these two events. Finally, to ensure participants' compliance with the task requests, in 20% of the experimental trials (a total of 72 trials per each participant, with 18 trials per each block), we asked participants to estimate the actual duration of their last "time travel" (in ms).

Self- and other-perspective trials were administered in different blocks. The order of presentation was either ABBA or BAAB. Each of the four blocks comprised 90 trials for a total of 360 trials. For each perspective condition (self, other), ten trials for each temporal location (past, present, and future) by motion direction (backwards, forwards) by temporal duration (one, three, and five years) combination were administered. Within each block, temporal location presentation was fully randomized and administered in miniblock of 6 trials (i.e., one trial for each temporal duration by motion direction combination). To familiarize participants with the procedure, at the beginning of the experiment a practice session was administered (6 self-perspective and 6 other-perspective-trials, one trial for each motion direction by temporal duration combination).

E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC was used to present trials and record the duration of the "time travel" (i.e., the time elapsed between starting and stopping the "time machine"). The experiment lasted about 60 minutes.

2.3. Statistical Analyses. To cope with the high variability within the range of travel duration (394–21304 ms), we converted individual temporal intervals data into z-scores, based on means and standard deviations computed over all trials per each participant. Since each standardized coefficient scales appropriately to adjust for the disparity in the variable sizes, this procedure makes it possible to bring all of the variables into proportion with one another without losing the possibility to directly compare participants' performance across conditions. The mean z-scores were then averaged separately for each trial type (i.e., temporal location by each motion direction by temporal duration in both perspectives). The investigation of standardized data distribution using one-sample *Kolmogorov-Smirnov goodness-of-fit* tests did not show any significant difference, suggesting that data distribution within the sample was Gaussian ($0.196 < p_s > 0.998$). Travel duration z-scores were then submitted to a repeated measures ANOVA with *temporal location* (past, present, and future), *motion direction* (backwards, forwards), *temporal duration* (1, 3, and 5 years), and *perspective* (self, other) as within subjects factors. Main effects were used to explore the means of interest (post hoc t-test), and Bonferroni's corrections (α level of $p < 0.05$) were applied.

In addition, to obtain an indirect measure of participants' compliance with the task requests over the experimental session, we analyzed the data from the control task to test whether participants' ability to reproduce time intervals decreased/increased over the four blocks. To this aim, we first computed a *temporal accuracy estimation index*, defined as the difference between the actual duration of the travel and the corresponding temporal estimation given by the participant at the control task trial (i.e., 20% of the total amount of trials: 18 trials per each block for a total of 72 trials by each participant). Then, we submitted this index to a repeated measures ANOVA with *block* (i.e., first, second, third, and fourth) as within subjects factor.

3. Results

Mental Travel Task. Participants' travel duration varied as a function of temporal location so that travels originating in

the present moment were longer than travels originating in the past or in the future (main effect of *temporal location*: $F_{(2,48)} = 3.621$; $p = 0.034$; partial eta square = 0.131; mean z-scores = 0.078, 0.004, and −0.082, resp.; $p_s < 0.05$). Moreover, temporal duration of journeys was longer for travelling forwards than backwards (main effect of *motion direction*: $F_{(1,24)} = 7.305$; $p = 0.012$; partial eta square = 0.233; mean z-scores = 0.038 versus −0.038, resp.; $p_s < 0.05$). Regardless of the temporal origin of the journey and its direction, the travel duration increased as a function of the number of years to travel (main effect of *temporal duration*: $F_{(2,48)} = 277.747$; $p < 0.001$; partial eta square = 0.920; mean z scores = −0.86 for 1 year; −0.01 for 3 years; 0.86 for 5 years; see Figure 2, $p_s < 0.05$). As predicted, neither *motion direction* nor *temporal duration* main effect were further qualified by significant interactions by *perspective*. In contrast, the effect of *temporal location* varied between self- and other-perspective (*perspective* by *temporal location* interaction: $F_{(2,48)} = 6.014$; $p = 0.005$; partial eta square = 0.200). For self-perspective trials, indeed, travel duration was longer when the travel started either in the past or in the present rather than in the future (0.034 and 0.163 versus −0.101, resp.; see Figure 2; $p_s < 0.05$). For other-perspective trials, in contrast, no similar modulation of travel duration by temporal location was reported (−0.007, −0.025, and −0.062 for present, past, and future location; Figure 2; $p_s > 0.05$). Moreover, travel duration was on average longer for the self-perspective than for the other-perspective when the travel started in the present, but not when it started in the past or in the future (self/present versus other/present = 0.163 versus −0.007, resp.; $p < 0.05$; self/past versus other/past = 0.034 versus −0.025 and self/future versus other/future = −0.101 versus −0.062, resp.; $p_s > 0.05$). Finally, the exploration of the significant *temporal location* by *temporal duration* interaction ($F_{(4,96)} = 3.780$; $p = 0.007$; partial eta square = 0.136) revealed that there was no difference across temporal locations when travels lasted either 1 year or 3 years (1 year: past = −0.897; present = −0.793; future = −0.912 and 3 years: past = −0.016; present = 0.057; future = −0.075; $p_s > 0.05$). In contrast, when participants were requested to cover a 5-year distance, the trip took longer when it started in the past or present rather than in the future (5 years: past = 0.926 and present = 0.968 versus future = 0.74; $p_s < 0.5$). Neither the main effect of *perspective* ($F_{(1,24)} = 1.588$; $p > 0.05$; partial eta square = 0.062) nor the remaining two-, three-, or four-way interactions were found to be significant (all $F_s < 1.484$; $0.213 < p_s > 0.942$; all partial eta squares < 0.058).

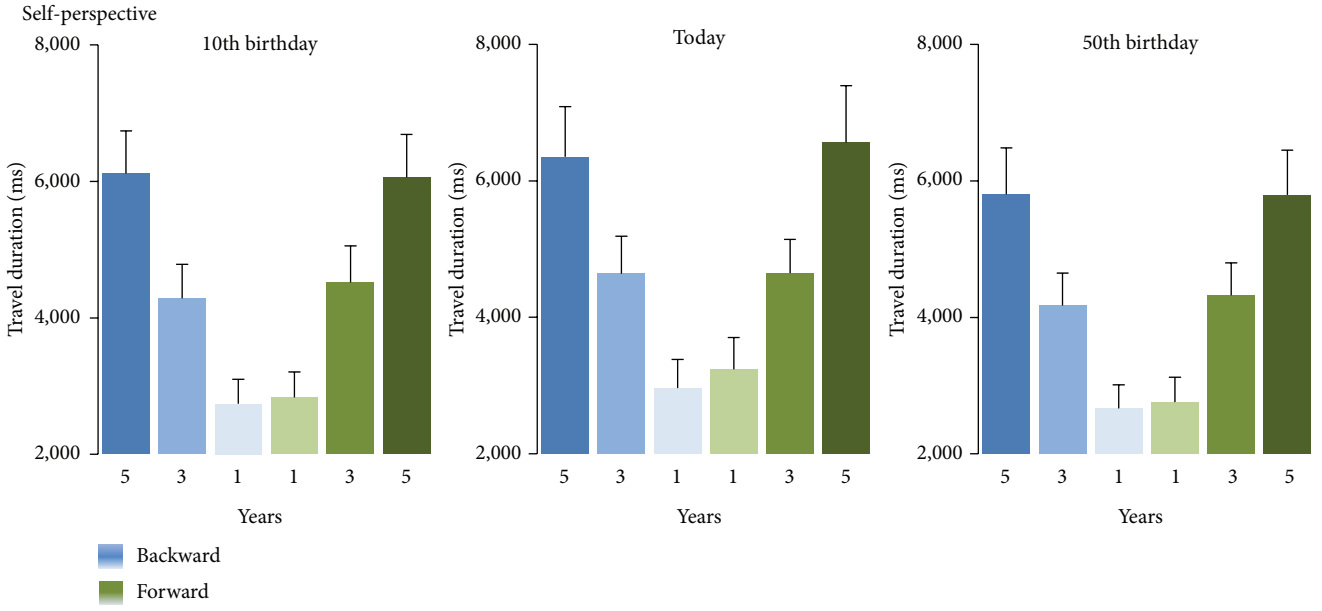
Control Task. ANOVA revealed no significant effect of *block* ($F_{3,72} = 2.212$; $p > 0.05$; partial eta square = 0.084) on temporal accuracy estimation index, suggesting that participants' compliance to the task request remained stable throughout the experiment.

4. Discussion

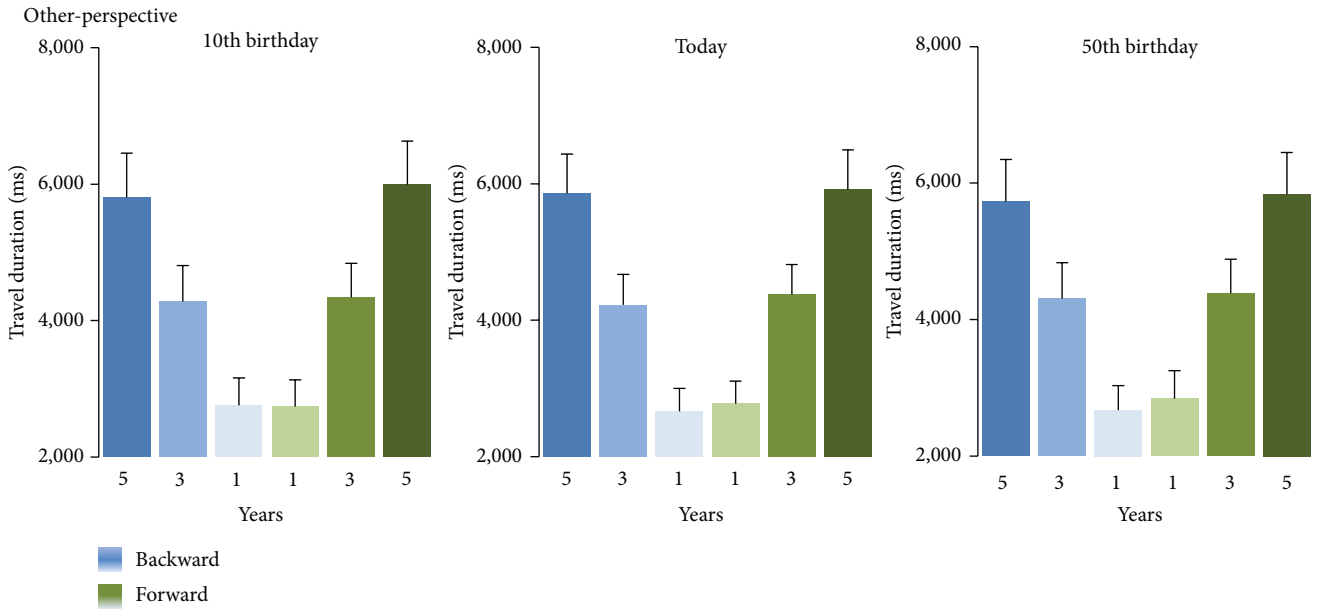
In this study, we assessed whether and how self- and other-projections in time map onto similar or different spatiotemporal representations. For the properties of this underlying representation to emerge, we used as a proxy the time taken to move through time (i.e., travel duration) and manipulated three basic properties of time journeys: temporal location (past, present, or future), motion direction (backwards or forwards), and temporal duration (one, three, or five years).

Our results suggest that self- and other-projections hinge on different temporal representations depending on the temporal location, that is, on where in time the mental travel originates. Specifically, for self-perspective, participants took longer to cover identical distances when the travel started in the past or in present compared as to when it started in the future. For other-perspective, in contrast, travel duration was not modulated by temporal location. This effect may reflect the tendency to form higher-level construals of information about remote future event [21]. In this respect, Trope and Liberman [21] suggest that "the greater the temporal distance from a future event, the more likely is the event to be represented abstractly in terms of a few general features that convey the perceived essence of events rather than in terms of more concrete and incidental details of the event." In the same vein, D'Argembeau and Van der Linden [22] provided evidence that projecting oneself in a specific positive or negative experience results in a richer representation when the event is expected to be experienced in the near future rather than in a more distant future. On this account, participants would travel more rapidly from a remote future location because they would simulate future events in more abstract and general terms. This is further supported by the consideration that, in contrast with remembering of past events whose features are already integrated, simulating remote future events requires the combination of disparate details gleaned from a variety of episodic sources [23]. Forming abstract representations of remote future event may thus serve a specific adaptive role in reducing the costs required to integrate unrelated details into a coherent future representation.

Over and above this, self- and other-projection also scaled differently for mental travels taking place in the proximity of the present moment. For the present location, regardless of motion direction, one year was indeed longer in the self-time rather than in the other-time. This was not the case for one-year travels originating from a past or future location. This pattern is in agreement with the finding that participants represent self-time as occupying a greater amount of space than an equivalent period related to others [17]. Of direct relevance to the present study, Christian and colleagues [17] asked three different groups of participants to "time-travel" from the present moment to their own birthdays or to the birthdays of either a close friend or a hypothetical stranger of a similar age as theirs. It was found that, irrespective of motion direction (either in the past or in the future), time relevant to self was represented as occupying more space than time relevant to others (i.e., best friend or unfamiliar other). On a closer examination, however, this effect of self-relevance was only evident for temporally close events (i.e., 10 years before or after the present moment), but not more distant events (i.e., the day of 8th or 58th birthday). Taken together with our results, this suggests that a distinctive relationship bounds the "self" to the "now." As observed by Núñez and



(a)



(b)

Figure 2: Durations (ms) for time travelling one, three, or five years backwards (blue tone bars) or forwards (green tone bars) from the past (10th birthday), the present (i.e., today), or the future (i.e., 50th birthday) in self-perspective (a) and other-perspective (b). Error bars depict standard error of mean.

Cooperrider [16], indeed, within an "internal" perspective, the ego is always and inherently colocated within the "now." It is perhaps therefore not surprising that self-projection is more "embedded" in the representation of the present time compared to other-projection. On a related note, this could explain why recent autobiographical memories tend to be recalled from the first-person perspective, while more remote memories, particularly early childhood memories, are more likely to be recalled from a third-person perspective [24–27].

Despite these differences, however, self- and other-projections also shared many similarities in structure. First, for both self- and other-perspectives, travel durations increased as a function of temporal duration (one year < three years < five years). With only one exception (i.e., five years from past and present lasts longer than five years from future), this effect was not modulated by the temporal location (i.e., past, present, and future). This is consistent with the idea that computation of temporal quantities rests on a common

system for magnitude processing [28], which is (at least in part) independent of self-relevant content specificity and episodic memory processes. The finding that 5-year travel duration lasted less when it originated in remote future might be taken to suggest that, as far as remote future is concerned, the spatial representation of time is compressed towards the anchoring point. Experiments using multiple temporal locations in remote past and future might help to address this issue.

Second, in both self- and other-perspectives, independent of temporal location, travelling forwards took longer than travelling backwards. The neural system subserving mental time travel has been proposed to have evolved to anticipate and pilot our behavior rather than primarily encoding the past [8, 29, 30]. In line with this, processing of events has been shown to be future oriented across present, past, and future self-location [8, 14]. For example, when asked to judge whether an event takes place before (relative past) or after (relative future) an imagined self-location in time, participants are typically faster and more accurate for relative future than for relative past events [8].

At first sight, the finding that travelling forwards took longer than travelling backwards may seem contradictory to response facilitation for future events. However, both phenomena may be parsimoniously interpreted as resulting from an anisometric pattern of internal spatial representation of relative past and future events, such that the representational medium is compressed towards the relative past and dilated towards the relative future. Compression towards the relative past would explain why travelling backwards lasts less, but also why judgements are more difficult (i.e., slower and less accurate) to the relative past. Along the same lines, dilation towards the relative future may account for both the increase in travel duration for travelling forwards and the relative future response facilitation.

An alternative, not mutually exclusive, explanation of the motion direction effect refers to discrepancy between external time direction (i.e., roughly, the time of the calendar) and subjective time direction (i.e., the personal time which is measured by the traveler's wristwatch; [31]) potentially experienced when travelling backwards. When participants are requested to time-travel towards relative future, the external time and their subjective time move towards the same direction (see also [32], for similar concepts). The subjective time may therefore be expected to add to the external time, extending the travel duration. In contrast, when participants travel towards relative past, the external time goes backwards, while their subjective time moves forwards [32]. The time traveler may therefore experience a shrinking of travel duration. On this account, the effect of motion direction would reflect the relative (forward) motion of the traveler making journeys end later in the future and earlier in the past. At this stage, both these hypotheses remain speculative and require further study for elaboration and validation.

5. Conclusions

A growing body of evidence indicates that self-projection in space and in time might rest on a common neural network and share similar cognitive processes and representations [3]. In the visuospatial domain, it has been documented that people can transpose their own actual point of view and "navigate" space from the perspective of someone else [5]. The current findings suggest that a similar ability might also exist in temporal domain, supporting the notion of temporal perspective taking.

By contrasting time travelling from self- and other-perspective, we found evidence that temporal representation underlying one's own projection shares many of the same characteristics of the temporal representation underlying another person's projection. Despite the fact that a greater "sensitivity" to temporal location for representing time in self- rather than in other-perspective emerges, when considering more abstract properties as direction and magnitude, self- and other-time exhibit a similar structure. Further research is warranted to clarify whether and to what extent these effects are sensitive to the degree of similarity between the self and the other person. For example, it will be important for future research to determine how travelling in time from the perspective of a younger or older person impacts on travel duration (depending, e.g., on whether the past/future of the participant overlaps with the present of the other person).

A second issue to be addressed in future studies relates to the neural underpinnings of self- and other-projection. Self-projection in time has shown to recruit a network of brain areas in distinct time periods including the occipitotemporal, temporoparietal, and anteromedial temporal cortices [4, 8]. For example, it has been reported that during mental time travel the left lateral parietal cortex is differentially activated by nonpresent subjective times compared with present (past and future > present) [33]. Capitalizing on the finding that left parietal cortex supports first-person perspective simulation [34], these results have been interpreted to suggest that the parietal cortex is specifically related to transformations in subjective time. Moreover it has been demonstrated that temporal self-projection into the personal past recruits greater ventral medial prefrontal cortex (mPCF) whereas self-projection into another person's perspective recruits greater dorsal mPCF [35]. Asking participants to simulate mentally past, present, and future time from their own versus another person's perspective might help to clarify how transformations in subjective and nonsubjective time are represented in left parietal cortex and to elucidate the exact contribution of the ventral and dorsal subregions of mPCF to self- versus other-projection. Finally, the hypothesis of a partial overlap between self- and other-mechanisms for projection in time could be tested in neuropsychiatric patients with temporal orientation failures [36]. To the extent that self- and other-projection rely on a common neural mechanism, self-referenced and other-referenced disorientation may be expected to share common fundamental characteristics.

Conflict of Interests

The authors declare there is no conflict of interests regarding the publication of this paper.

Acknowledgments

The authors thank Delia Sanmartino and Manuela Vignolo for their help with data acquisition. They also wish to thank Laura Taverna for her help in preparing optic flow stimuli.

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