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Walking to a multisensory beat

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ABSTRACT

Living in a complex and multisensory environment demands constant interaction between perception and action. In everyday life it is common to combine efficiently simultaneous signals coming from different modalities. There is evidence of a multisensory benefit in a variety of laboratory tasks (temporal judgement, reaction time tasks). It is less clear if this effect extends to ecological tasks, such as walking. Furthermore, benefits of multimodal stimulation are linked to temporal properties such as the temporal window of integration and temporal recalibration. These properties have been examined in tasks involving single, non-repeating stimulus presentations. Here we investigate the same temporal properties in the context of a rhythmic task, namely audio-tactile stimulation during walking. The effect of audio-tactile rhythmic cues on gait variability and the ability to synchronize to the cues was studied in young adults. Participants walked with rhythmic cues presented at different stimulus-onset asynchronies. We observed a multisensory benefit by comparing audio-tactile to unimodal stimulation. Moreover, both the temporal window of integration and temporal recalibration mediated the response to multimodal stimulation. In sum, rhythmic behaviours obey the same principles as temporal discrimination and detection behaviours and thus can also benefit from multimodal stimulation.

1. Introduction

Living in a complex and multisensory environment demands constant interaction between perception and action. Our ability to merge information coming from several senses is crucial to produce and regulate our body movements.

1.1. Multisensory integration in time

Multisensory benefit refers to the improvement observed in tasks, such as sensorimotor synchronization, where presenting the stimulus via more than one sensory modality simultaneously leads to increased performance in comparison with unimodal stimulus presentation. Such benefit has been observed for audio-visual stimulation in terms of enhanced speech intelligibility (Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008), learning (Shams & Seitz, 2008) and reduced reaction times (Colonius & Diederich, 2004; Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994; Murray et al., 2005). These multisensory benefits have been linked to the activity of multisensory neurons, mostly located in the intraparietal sulcus, the ventrolateral prefrontal cortex and the superior temporal sulcus, capable of integrating into a unified percept the various signals received by different senses (Stein & Stanford, 2008). Certain specific conditions have to be fulfilled to achieve multisensory integration. A critical feature inherent in the stimulation is the temporal organization of multimodal stimuli, namely the "temporal principle" (Meredith, Nemitz, & Stein, 1987; Spence & Squire, 2003). This principle states that multimodal stimuli have to be presented approximately simultaneously, in order to be considered as having a unique source (object or event).

What exactly is the span of this simultaneity? The temporal principle was originally defined at the level of the single neuron (Stein & Meredith, 1993). It is not straightforward to determine the synchrony among different senses. For example, with respect to the physical medium carrying the sensory stimulation, sound travels at approximately 330 m/s whereas there is no travel time for tactile signals. Sensory systems also exhibit differences in terms of conduction speeds, response latencies and neural processing time (Fain, 2003; Lange & Röder, 2006; Lestienne, 2001; Nicolas,

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1997; Vroomen & Keetels, 2010). These differences between audition and touch have an effect on behaviour. In reaction time (RT) tasks participants respond 40–45 ms faster to auditory stimuli than to tactile stimuli (Diederich, 1995; Diederich & Colonius, 2004; Murray et al., 2005). This discrepancy between modalities is replicated in sensorimotor synchronization tasks when participants synchronize their fingers' movement to unimodal auditory or tactile rhythmic stimuli. In this condition, participants tap (Müller et al., 2008) or reach maximal flexion (when physical contact with a surface is absent; Lagarde & Kelso, 2006), preceding auditory stimuli but lagging behind tactile stimuli, with a difference between the two of approximately 40 ms. A similar temporal difference is reported in perceptual tasks with multimodal stimuli. During passive movement in the Temporal Order Judgment task (TOJ), tactile stimuli have to be presented 45 ms before the auditory stimuli in order to reach a point of subjective simultaneity (Frissen, Ziat, Campion, Hayward, & Guastavino, 2012). It is worth noting that there is no consensus about the temporal discrepancy leading to subjective simultaneity between auditory and tactile stimuli. Other studies reported values of 27 ms (Occelli, Spence, & Zampini, 2008) or 8 ms (Navarra, Soto-Faraco, & Spence, 2007). Finally, in forced-choice detection tasks with non-synchronous multimodal stimulation, performance improves when a tactile stimulus precedes an auditory stimulus (Wilson, Reed, & Braida, 2009). Altogether, the results obtained in a variety of tasks point to temporal differences between auditory and tactile sensory pathways and processing. This raises questions about the dynamical adaptation of the sensorimotor system necessary to achieve and maintain temporal synchrony.

The ability of the nervous system to deal with temporal lags between senses has been particularly investigated at the perceptual level (Vroomen & Keetels, 2010). The involved processes depend on the combination of modalities (audio-visual, audio-tactile or visuo-tactile) and on the direction of the asynchrony (e.g., auditory first vs. tactile first). For audio-tactile stimulation two properties are particularly relevant: the temporal window of integration (TWI) and temporal recalibration. Traditionally, a TWI implies that the nervous system is insensitive to small lags between the stimuli and that multisensory integration can occur despite those lags (Spence & Squire, 2003). The TWI hypothesis was tested in perceptual and RT tasks (Colonius, Diederich, & Steenken, 2009; Harris, Harrar, Jaekl, & Kopinska, 2009) as well as with complex stimuli such as speech (Navarra, Soto-Faraco, & Spence, 2014; Navarra et al., 2005). For example, the judgement of temporal order between two stimuli coming from different modalities (i.e., auditory and tactile) is at chance level when they occur within a small window of time. The size of this window, corresponding to the just noticeable difference, varies from 25 to 80 ms (Fujisaki & Nishida, 2009; Hanson, Heron, & Whitaker, 2008; Harrar & Harris, 2008; Kitagawa, Zampini, & Spence, 2005; Occelli et al., 2008; Zampini et al., 2005). The variability of the reported window size is probably due to task factors and methodological differences between the studies (Occelli, Spence, & Zampini, 2011). A time window (between 60 and 100 ms) is also reported in RT tasks but to our knowledge only for audio-visual stimuli (Diederich & Colonius, 2004; Mégevand, Molholm, Nayak, & Foxe, 2013).

Temporal recalibration is another process involved in the perceived temporal synchrony of multimodal stimuli. It refers to the tendency of the brain to minimize the inter-sensory discrepancies of events that normally belong together (Vroomen & Keetels, 2010). This capacity is tested by measuring participants' perception of synchrony before and after exposure to trains of multimodal stimuli with a constant temporal interval between modalities (i.e., Stimulus Onset Asynchrony, SOA). After exposure, the perceived stimulus synchrony is shifted (Hanson et al., 2008; Navarra et al., 2007). Recalibration is likely to be underpinned by various processes. It may result from a shift in the simultaneity criterion or from a change of the detection threshold in one of the modalities. An alternative is that the exposure to an isochronous sequence modifies the width of the TWI. The precise mechanism operating in different conditions is still an object of debate (Linares, Cos, & Roseboom, 2016; Parise & Ernst, 2016; Vroomen & Keetels, 2010). To the best of our knowledge, only two studies have investigated the effect of temporal recalibration on the timing of movement. One of them failed to observe temporal recalibration in an RT task (Harrar & Harris, 2008). However, evidence of temporal recalibration was found in a second study, using RT and visuomotor adaptation (Stetson, Cui, Montague, & Eagleman, 2006). Participants were asked to react to cues and after each response a delayed flash was presented. Following exposure to flashes occurring after a long delay (135 ms), if the visual flash occurred synchronously or at an unexpectedly short delay after the motor response, participants judged that the visual flash had preceded the motor response. Altogether, evidence is scant to conclude whether or not temporal recalibration affects motor performance.

So far we have been focusing on the temporal properties of multisensory integration in response to single, non-repeating multimodal stimuli. However, our everyday interaction with multisensory events very often goes beyond that. Our ability to integrate multimodal stimuli is crucial to produce and regulate our body movements. For instance, in conversation we need to coordinate our eye movements and integrate the auditory information with the visual information about the other speaker's lip movements. To date, only one study examined the role of temporal properties in coordinating rhythmic and continuous movements with audio-tactile stimuli. In a previous study (Roy, Dalla Bella, & Lagarde, 2017) we found evidence of a TWI in bimanual coordination with audio-tactile stimuli. Specifically, a widening of the TWI was observed in bimanual coordination (TWI of 160 ms) in comparison to perceptual tasks (maximal TWI of 80 ms, Zampini et al., 2005). Wider TWI may reflect the ability of the sensorimotor system to keep stable behaviour when movement is implied. In this previous study, we did not investigate the role of temporal recalibration. It is also unclear whether TWI and temporal recalibration are involved in gait just as they play a role in multisensory integration during perceptual, RT or bimanual coordination tasks. These questions are addressed in the present study in which we also test for the presence of a multisensory benefit in sensorimotor synchronization tasks.

1.2. Moving in a multisensory environment: multisensory benefit

There is evidence of a multisensory benefit when participants synchronize the movement of one limb, finger or step, to multimodal stimuli (Elliott, Wing, & Welchman, 2010; Wing, Doumas, & Welchman, 2010; Wright & Elliott, 2014). A benefit was also reported for bimanual coordination where participants coordinated two limbs and also while they synchronized to multimodal stimuli (Zelic, Mottet, & Lagarde, 2012, 2016). These studies indicate that multimodal stimuli can stabilize continuous movement. Here we address the hypothesis that audio-tactile stimuli can also stabilize overground walking which is a considerably more complex behaviour in that it is a full body task and also requires maintaining stability in addition to timing foot contact with the ground.

The effect of the multisensory integration observed in tapping or bimanual coordination has not been compared to multisensory integration in gait. Synchronization (Chen, Wing, & Pratt, 2006) and audio-visual integration (Wright & Elliott, 2014) have been studied in stepping without comparing that to traditional manual tasks. Synchronization variability in heel tapping was smaller while sitting than while stepping, presumably due to the reduction in biomechanical constraints (Chen et al., 2006). Concerning the effects of audio-visual integration in stepping, Wright and Elliott (2014) reported a pattern of results also observed in bimanual coordination (Blais, Albaret, & Tallet, 2015). An audio-visual benefit was found in synchronization variability (SD of relative phase for inter-manual coordination) but not in motor variability (SD of step-times). It appears that the ability to take advantage of multimodal stimuli applies equally to various behaviours but it is yet to be determined whether gait is among them. Note that sustained steady gait, as compared to making individual steps, involves additional constraints such as forward displacements of the body centre of mass, spatial navigation, monitoring for environmental changes and overcoming perturbations such as sharp turning that alter the structure of gait variability for multiple strides following each perturbation (Dotov, Bardy, & Dalla Bella, 2016). One study investigated multisensory integration including the tactile modality in the gait of healthy young adults and found no evidence of benefit with audio-visuo-tactile stimuli (Sejdić, Fu, Pak, Fairley, & Chau, 2012).

Despite this lack of multisensory benefit on gait in healthy young adults, clinical studies in patient populations such as Parkinson's disease and stroke show more promising results. Gait can become dysfunctional due to ageing and/or disease, causing loss of stability and falls (Malatesta et al., 2003; Morris, Huxham, McGinley, & Iansek, 2001). One way of compensating for gait disorders is to instruct older adults and/or patients to walk along with a sequence of isochronously presented sounds (e.g., a metronome). Auditory cues can drive immediate beneficial effects on spatiotemporal gait parameters and increase stride length and speed (Lim et al., 2005; Spaulding et al., 2013; Wittwer, Webster, & Hill, 2013). There are also preliminary indications that tactile stimulation may also improve gait and motor performance in patients with Parkinson's disease (Ivkovic, Fisher, & Paloski, 2016; van Wegen et al., 2006). Bimodal stimulation in the cueing of gait has been a subject of study. Cueing with audio-visual stimuli was found to improve gait velocity, cadence and stride length, more than unimodal stimulation (Suteerawattananon, Morris, Etnyre, Jankovic, & Protas, 2004). Yet, the effect of audio-tactile stimulation has not been fully investigated (Lim et al., 2005; Marchese, Diverio, Zucchi, Lentino, & Abbruzzese, 2000). In sum, clinical studies in patient populations point to effects of multisensory integration in gait with potential benefits for rehabilitation.

Additionally, auditory dominance is an oft-reported phenomenon which is likely to affect the synchronization of continuous movements with multimodal stimuli (Aschersleben, 2002; Kato & Konishi, 2006; Repp & Penel, 2002, 2004; Roy et al., 2017). The human sensorimotor system exhibits a strong preference to bind movement to the auditory sensory modality when visual and tactile rhythmic stimuli are also available in a synchronization task (tapping or bimanual coordination). Evidence for auditory dominance is typically provided in paradigms employing a parametric variation of the temporal discrepancy between multimodal stimuli such as a manipulation of the SOA. When participants synchronize with auditory stimuli, the presence of visual or tactile stimuli does not affect their performance. In contrast, synchronization to visual or tactile stimuli is disrupted by auditory stimuli which tend to attract participants' taps and increase performance variability (Aschersleben & Bertelson, 2003; Repp & Penel, 2004; Roy et al., 2017).

In the present study we first tested whether temporal properties underlying multisensory integration play a role in overground walking with audio-tactile stimulation. The widening of the TWI observed in bimanual coordination was expected to extend to gait as well. We also investigated temporal recalibration, a second property which is likely to be involved in multisensory integration (Vroomen & Keetels, 2010). Second, we examined whether audio-tactile stimulation during gait would lead to a multisensory benefit.

To these ends, the effect of audio-tactile stimulation on gait was examined in a cued walking task in which participants synchronized their gait to tactile stimulation. Young adults were asked to walk with unimodal or audio-tactile stimuli. We manipulated the SOA between tactile and auditory stimuli in multimodal conditions. We anticipated (1) a widening of the TWI in gait as compared to perceptual tasks and comparable to values reported for bimanual coordination movements (i.e., 160 ms); (2) an effect of temporal recalibration leading to a decrease of performance variability over time and (3) a benefit of multisensory integration in multimodal as compared to unimodal conditions.

2. Method

2.1. Participants

Nineteen students from Montpellier University (7 females, mean age = 29.25 years, *SD* = 4.10 years), with a mean height of 1.74 m (*SD* = 0.09 m), volunteered to take part in the experiment. All the participants reported normal audition and touch. The experiment was conducted in accordance with the guidelines of the Declaration of Helsinki (World Medical Association, 2008).

2.2. Material

The auditory stimuli were 60-ms square wave pulses with tone carrier frequency at 250 Hz and presented to participants at 65 dB. The tactile stimuli, which were provided by linear resonant actuator vibrators, were 60-ms square wave pulses with vibration carrier frequency at 235 Hz. The diameter of vibrators was 0.5 cm. The frequencies are within a region of optimal sensibility of the Pacinian receptors (200–300 Hz, Purves et al., 1997). At the beginning of the experiment participants were asked whether they felt like adjusting the volume of the sound to match the intensities between auditory and tactile stimuli. None of participants decided to reduce or increase it. The temporal gap between auditory and tactile stimuli was manipulated. Stimuli sequences with 9 SOAs between auditory and tactile stimuli were created: −160 ms, −120 ms, −80 ms, −40 ms, 0 ms, +40 ms, +80 ms, +120 ms, +160 ms.

2.3. Equipment

The experiment was conducted using two computers. One computer was used for stimulus presentation. The equipment used to test participants is illustrated in Fig. 1. Auditory stimuli were delivered via earphones. In addition, participants wore silent headphones to reduce environmental noise. Tactile stimulation was provided with vibrators. To maximize tactile sensitivity (Johansson & Vallbo, 1979, 1983) and avoid gating effects from cutaneous reafferences of the active limb (Voss, Ingram, Haggard, & Wolpert, 2006), we positioned the vibrators on each index finger rather than on the legs. In addition, index fingers are the place where the mechanoreceptors are the most numerous (Weinstein, 1968). The second computer served to record simultaneously the temporal gait parameters using a wireless motion-capture system (APDM's Mobility Lab, Mancini et al., 2011) with four small body-worn inertial measurement units (IMU, 3D accelerometers, 3D gyroscopes, magnetometers), sampled at 128 Hz, which also have the capacity to record from an external analog input. All the stimuli were generated in Matlab and sent to a hardware system (Arduino 1.0.5) via the sound card of the computer and through an auditory wireless system (W3 Wireless Audio, Audioengine). The stimuli were sent simultaneously to both sides (to the two ears and/or

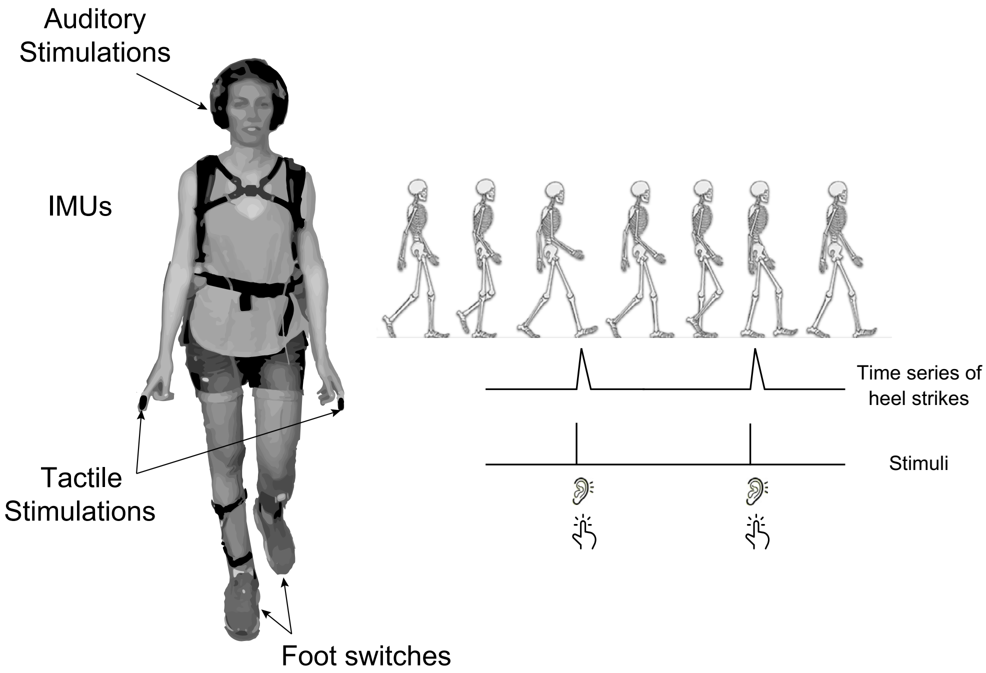

Fig. 1. Two tactile vibrators were positioned on participants' index fingers. Auditory stimuli were delivered via earphones. In addition, participants wore silent headphones to reduce environmental noise. In order to record steps intervals and asynchronies, participants were equipped with IMUs and foot-switches. On the right panel an illustration of the time series of the heel strikes and stimuli is provided.

two fingers). One IMU served to record the on-going auditory and tactile physical stimulation without any delay and with a clock synchronized with the three other IMUs used for the movement capture. The apparatus that received and transformed the physical signals into auditory or tactile stimulations and the IMU recording the stimulations were placed in a backpack worn by the participants. Two movement capture IMUs recorded footfalls via force sensing resistor foot switches positioned inside the shoe sole of the participants. The foot switches were connected to the IMUs which were attached 3 cm above each malleolus. The fourth IMU, attached on the upper trunk 2 cm below the sternal notch, recorded 3D linear accelerations and 3D angular velocities of the trunk with axes oriented along the anatomical antero-posterior, medio-lateral and vertical directions.

2.4. Procedure

The participants were submitted to an audio-tactile cued walking protocol. They were asked to synchronize their heel strikes to tactile stimuli. As observed in our previous bimanual coordination study (Roy et al., 2017), synchronization to tactile stimuli was the condition leading to beneficial effects of audio-tactile integration. In contrast, we did not find any effect of multisensory integration when participants were instructed to synchronize with the auditory stimuli. Lack of multisensory integration in this condition is likely to results from auditory dominance in sensorimotor synchronization task with audio-visual stimuli. There is compelling evidence that when participants synchronize with auditory stimuli, the presence of visual stimuli does not affect their performance (Aschersleben & Bertelson, 2003; Kato & Konishi, 2006; Repp & Penel, 2002, 2004). It is noteworthy that in the present study participants were not explicitly instructed to ignore the auditory stimuli. At the beginning of the experiment, participants were instructed to walk at their preferred walking speed around an indoor round path (walkway width = 3.50 m, length = 6.70 m) for 1 min. This first trial served to compute participants' preferred cadence (mean number of steps per minute). Preferred cadence was used to calculate the inter-stimuli interval (ISI) in the subsequent experimental trials. Cue frequency was decreased by 30% relative to preferred cadence by reducing ISI accordingly (mean ISI = 734.6 ms, *SD* ISI = 36.2, range = 684–780 ms). As the gait of healthy young adults is regular and stable (Kang & Dingwell, 2009), we presented stimuli at a lower than preferred cadence to create a condition in which gait was slightly more challenging (Terrier & Dériaz, 2012), thus potentially increasing sensitivity to the stimuli.

Each participant was submitted to 11 cued conditions. Two conditions were unimodal (tactile and auditory). The nine other multimodal conditions resulted from manipulating the temporal gap at the aforementioned SOAs between auditory and tactile stimuli from −160 to +160 ms in steps of 40. In each condition the SOA between auditory and tactile stimuli was constant. In each trial a sequence of 290 stimuli was presented.

Participants were asked to synchronize their steps to the tactile stimuli presented simultaneously to both sides of the body (tactile stimuli on right and left index fingers corresponding to right and left auditory stimuli). In both unimodal conditions participants were instructed to synchronize with tactile or auditory stimuli according to the presented modality. The order of the SOA conditions was counterbalanced across participants. The experiment took approximately 75 min, with breaks lasting approximately 1 min after each condition.

2.5. Pre-processing and data analysis

Data were pre-processed and analysed using custom scripts in Matlab and R (R core Team, 2013). The time series of footfalls and stimuli were obtained from IMU recordings as well as the trunk movements. Heel-strike times, stimulus presentation times and trunk kinematics were recorded by the IMUs. The automatic heel-strike detection in all trials was verified by visual inspection. The two first and the last eight steps of each trial were removed. Further analyses were carried out on the basis of 280 steps obtained in each trial.

A measure of synchronization was obtained by computing the difference between the time of each heel-strike and stimulus onset. This difference, referred to as "asynchrony", is negative when the movement precedes the stimuli and positive when the movement lags after the stimulus. *Mean asynchrony* for each trial was computed as a measure of synchronization accuracy. The standard deviation of asynchrony (*SD asynchrony*) was calculated as a measure of synchronization variability. Two variables accounted for gait stability, by measuring variability in terms of the step-time coefficient of variation (*CoV step-time*) and local stability in terms of the *maximum Lyapunov exponent* λ. *CoV* step-time is the *SD* of the step-time divided by the mean step-time multiplied by 100 (see Footnote). Large *CoV* indicates high gait variability (low gait stability). Maximum Lyapunov exponent derives from stability theory of nonlinear dynamical systems. Note that the definition and use of Lyapunov exponents have been extended to stochastic dynamical systems (Osedelets, 1968). Since its first application to gait (Dingwell, Cusumano, Sternad, & Cavanagh, 2000), it has been applied repeatedly in the context of human gait. The local Lyapunov exponent is estimated in terms of the rate at which adjacent state trajectories diverge. The general idea is to locate the points in time where the system visits the same point in phase space that it also visits on other points in time and measure how quickly the trajectories depart from each other. Thus, the maximum local Lyapunov exponent λ, also called local logarithmic divergence, is the rate at which the system under consideration departs from its own baseline pattern. The methods for estimating local dynamic stability have been presented in detail elsewhere (Bruijn, Meijer, Beek, & Van Dieën, 2013). We applied the recommended Rosenstein algorithm (Rosenstein, Collins, & De Luca, 1993) on the data collected by the 3D accelerometers and gyroscopes located on the trunk (Bruijn et al., 2013). We limited the estimation to the so-called short-term λs where the window of estimation is equal to the average duration of one step. This is based on the fact that most of the compensation to centre-of-mass perturbations will happen within the span of a step. We employed recommended procedures for calculating λs consisting of phase-space reconstruction by time-delayed embedding each of the three acceleration and three angular velocity dimensions to form a 12-dimensional phase-space (Gates & Dingwell, 2009). The faster the trunk trajectory diverges in the reconstructed phases space, the less stable the system is. Thus, small values of the local Lyapunov exponent λ are indications of high stability.

The study of the multisensory benefit and of two temporal properties (TWI and temporal recalibration) in continuous rhythmic movement may imply novel methodology and criteria compared to perceptual and RT tasks. Measures of gait stability (*CoV* step-time and Lyapunov exponent) and synchronization variability (*SD* asynchrony) were obtained per trial from the entire trial time series. In perceptual tasks the TWI is determined by the just noticeable difference (Vroomen & Keetels, 2010). For example, in the TOJ task, the boundary of the TWI corresponds to the SOAs at which the participants cannot decide any more the order of arrival for two stimuli coming from different senses. A similar method applies to the Simultaneity Judgment Task. In RT tasks, the TWI is determined by the range of SOAs within which RTs show a multisensory benefit (Mégevand et al., 2013). Such methods cannot be applied in tasks comprising continuous stimulus presentation and continuous rhythmic motor performance. Previously a method has been proposed to identify the TWI in bimanual rhythmic movement (see Roy et al., 2017). The method consists in subtracting the performance in the unimodal conditions from performance in the multimodal conditions. Thus, the TWI corresponds to the SOAs where the aforementioned differences are below zero. As in our previous study, the TWI in the present study was determined from the variability of the synchronization (*SD* asynchrony). Even if the *SD* asynchrony determined the size of the TWI, in the present study we also choose to apply this method to gait performance, that is for *CoV* step-time and Lyapunov exponent.

To measure temporal recalibration, a statistical model of the evolution of key variables within a trial was built. To this end, each trial was divided in five temporal blocks to form the Block repeated measures factor. A block included 56 events and lasted approximately 40 s, depending on the preferential cadence of each participant. On average a trial lasted 3.40 min (range: 3.24 min–3.54 min). The *CoV* step-time, *SD* asynchrony and Mean asynchrony were computed for each block. Lyapunov exponent was not included in this analysis because it requires long time series and thus does not allow the trial to be divided into parts (Bruijn, van Dieën, Meijer, & Beek, 2009).

Finally, to assess the multisensory benefit we compared the performance in multimodal and unimodal conditions (Stein & Stanford, 2008). We considered only *SD* asynchrony, *CoV* step-time and Lyapunov exponent. The mean of asynchrony was not treated as an indicator of this benefit.

3. Results

The data of three out of 22 participants could not be analysed due to technical problems during the recording of gait performance or incorrect performance of the task. Data from the remaining 19 participants were submitted to the following analyses.

3.1. Effect of SOA

Summary statistics of *CoV* step-time, Lyapunov exponent, *SD* asynchrony, Mean asynchrony as a function of SOA are presented in Fig. 2. These were submitted to a repeated-measures Analysis of Variance (ANOVA) taking SOA (−160 ms, −120 ms, −80 ms, −40 ms, 0 ms, +40 ms, +80 ms, +120 ms, +160 ms) as the within-subject factor. The ANOVA yielded a significant effect of the SOAs on *CoV* step-time, ($F(1,18) = 8.34$, $p < .001$, $\eta^2 = .14$), Mean asynchrony ($F(1,18) = 20.45$, $p < .001$, $\eta^2 = .50$), *SD* asynchrony ($F(1,18) = 4.13$, $p < .001$, $\eta^2 = .17$) but not Lyapunov exponent ($F(1,18) = 1.44$, $p = .18$). Pairwise comparisons are reported in Section 3.4. Also, a more in-depth analysis of the effects of SOA magnitude and sign is reported in Section 3.3. With regard to synchronization accuracy (i.e., Mean asynchrony) the effect of SOA depends on the order of presentation of the auditory stimuli (whether they are presented before or after the tactile stimuli), as can be seen in Fig. 2D. Two additional ANOVAs were conducted, one on the SOAs when the auditory stimuli preceded the tactile stimuli (SOAs −160, −120, −80 and −40), and the other when the auditory stimuli occurred later (SOAs +40, +80, +120 and +160). Mean asynchrony increased when the auditory stimuli followed the tactile stimuli ($F(1,18) = 9.08$, $p < .001$, $\eta^2 = .27$). In contrast, we did not find an effect of SOA when auditory stimuli were presented first ($F(1,18) = .17$, $p = .91$).

It is worth noting that the three variables measuring gait stability and synchronization were highly correlated. An increase of the *CoV* of step-time was strongly associated with a larger Lyapunov exponent ($r = .90$, $p < .001$), and greater *SD* asynchrony ($r = .89$, $p < .001$). Moreover, the Lyapunov exponent and *SD* asynchrony were strongly positively correlated ($r = .89$, $p < .001$).

3.2. TWI

To assess the presence and width of a TWI we subtracted from *SD* asynchrony and *CoV* step time the respective average values of uni-auditory and uni-tactile conditions. For the Lyapunov exponent, the uni-auditory condition was subtracted from multimodal

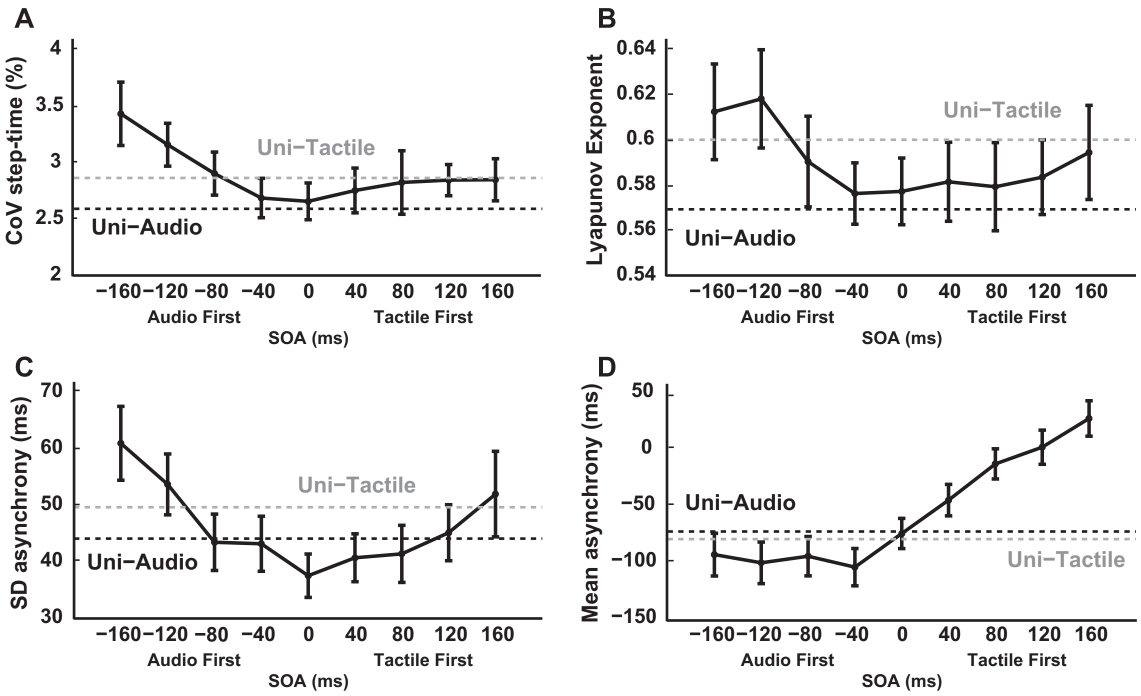

Fig. 2. (A) *CoV* of step-time, (B) Lyapunov exponents, (C) *SD* asynchrony and (D) Mean asynchrony as a function of SOAs. Black dashed lines indicate the mean value obtained in the unimodal auditory condition; grey dashed lines the mean value for the unimodal tactile condition. Error bars indicate *SE* of the mean.

conditions due to the differences between unimodal conditions. As illustrated in Fig. 3, the TWI is represented by the conditions which were below 0 (i.e., black bars). For *CoV* step-time a TWI of 80 ms was identified between −40 and +40 ms (see Fig. 3A). For *SD* asynchrony a TWI of 200 ms between −80 and +120 ms was found (see Fig. 3C). Finally, no TWI was found for Lyapunov exponent (see Fig. 3B).

3.3. Effect of time course

In subsequent analyses, we investigated the time course of *CoV* step-time, *SD* asynchrony and Mean asynchrony. To do so, trials were divided into five “temporal” blocks, as seen in Fig. 4. The results did not vary as a function of Block in the unimodal condition.

The time course of selected dependent variables within trial was fitted using a statistical model. In order to simultaneously account for the association among selected performance variables while also controlling for the possible learning effect of time course and individual baseline levels of performance, we applied a linear mixed-effects modelling technique developed for the statistical analysis of longitudinal studies with so-called multilevel designs (Singer & Willet, 2003). Conceptually, it resembles the regression of an outcome variable against multiple predictors but can deal simultaneously with predictors at different levels of grouping, i.e. time-varying predictors such as SOA, |SOA|, and Block, and constant randomly assigned grouping factors such as participant.

The outcome variables of *SD* asynchrony, Mean asynchrony and *CoV* step-time were fitted independently to the time-varying predictors SOA, |SOA|, and Block. The analysis was performed using the dedicated statistical package *lme4* (Bates, Mächler, Bolker, & Walker, 2014) for R (R core Team, 2013) and a recommended model development procedure (Singer & Willet, 2003). In particular, the procedure consisted of incrementally including the predictors in a hierarchical sequence of models (see Table 1: models A, B, C, D, E) and evaluating the increase in goodness-of-fit associated with each expanded model (see Table 1: AIC, BIC, Log-Likelihood, X^2). The order of inclusion is theoretically motivated in order to evaluate a null hypothesis. A minimal model consisting of a constant intercept (Model A) is expanded by including the predictors in succession (see Table 1 for details). The final models are specified in Table 1 and can all be expressed by the equation:

$$Y_{ij} = \beta_{00} + \sigma_{0i} + \beta_{01}|SOA|_{ij} + \beta_{02}SOA_{ij} + \beta_{03}BLOCK_{ij} + \beta_{04}SOA_{ij}BLOCK_{ij} + \sigma_{ij},$$

where *i* stands for participant number, *j* for measurement number, β for estimated coefficients (comparable to regression coefficients) and σ are the random-effects components of the model (i.e., see Table 1: Variance Components). To interpret the parameters, consider first that the model intercept corresponds to the first measurement in a trial (Block = 0) and no stimulus onset asynchrony (SOA = 0). SOA and |SOA| indicate how much the given outcome variable increases as SOA increases and as the absolute distance from the zero SOA increases, respectively, whereas the interaction of SOA with Block indicates an effect of Block conditional on SOA. Both SOA and |SOA| had to be included as predictors due to an observed small asymmetry in the association of performance measures with positive and negative SOAs. The results of the linear-mixed effects models as well as the entire procedure for modelling *SD* asynchrony are summarized in Table 1.

The statistical model fitted for each performance variable indicated that increases in absolute asynchrony |SOA| were associated with increases in variability of synchronization and gait (*SD* asynchrony, Mean asynchrony and *CoV* step-time). No effect of time course (Block) neither an interaction between Block and SOA was observed for Mean asynchrony ($p = .87$). For *SD* asynchrony and *CoV* step-time, the significant negative parameter for the signed SOA (*SD* asynchrony: $\beta = -.05$; *CoV* step-time: $\beta = -.001$), in combination with the absolute SOA implies an asymmetry of the effect of SOA whereby negative SOA increases variability more than positive SOA. The effect of Block on performance was conditioned by signed SOA (interaction Block∗SOA). The negative coefficient for Block (*SD*

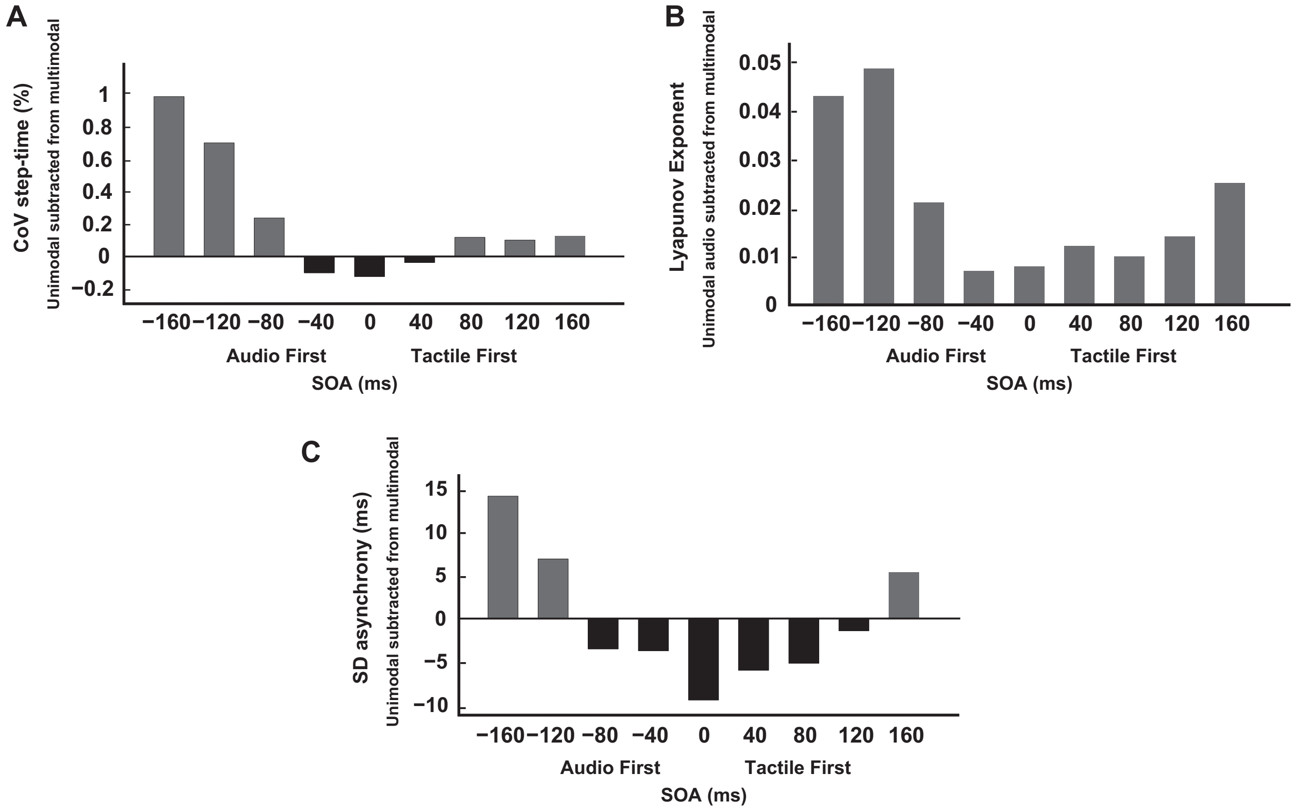

Fig. 3. Differences between the average of unimodal (A, C) or uni-audio (B) conditions and multimodal conditions for *CoV* step-time (A), Lyapunov Exponent (B), and *SD* asynchrony (C). The black bars represent the estimated TWI.

asynchrony: $\beta = -.39$; *CoV* step-time: $\beta = -.04$) indicates a positive effect of time on variability: as a trial progresses the *SD* asynchrony decreases, suggesting also an increase in multisensory advantage. To illustrate this, consider the slope at SOA of 160 ms (auditory first) in Fig. 4A which indicates that the multisensory benefit expressed by *CoV* step-time increased over time. The slope is also slightly negative for *SD* asynchrony, even though the Block effect did not reach significance in this case ($p = .9$).

3.4. Multisensory benefit

To assess whether multimodal stimulation led to a multisensory benefit, pairwise comparisons among unimodal and SOA conditions were performed using multiple *t*-tests (Bonferroni correction, $p = .0056$) independently on *SD* asynchrony, *CoV* step-time, and Lyapunov exponent. In *SD* asynchrony, SOA = 0 ms showed an advantage as compared to uni-tactile ($t\ (df = 18) = -4.13$, $p < .001$) and uni-auditory conditions ($t\ (df = 18) = -3.57$, $p = .002$). Thus, the synchronous presentation of auditory and tactile stimuli led to a multisensory benefit in terms of lower synchronization variability. No differences were observed in the step-intervals variability (*CoV* step-time) and local stability of gait (Lyapunov exponent). An advantage of uni-auditory stimulation as compared to uni-tactile was found ($t\ (df = 18) = -3.32$, $p = .003$) in Lyapunov exponent. No such difference was observed in *CoV* step-time (uni-tactile = 2.60; uni-auditory = 2.84), *SD* asynchrony (uni-tactile = 43.79; uni-auditory = 49.32) and Mean asynchrony (uni-tactile = −81 ms; uni-auditory = −74 ms).

4. Discussion

In the present study we investigated the effect of multisensory integration on gait by asking young adults to walk with audio-tactile stimuli. Variability of gait and the ability to synchronize steps to the stimuli were examined as a function of the SOAs between the stimuli. A multisensory benefit was observed. Participants showed lower variability in the synchronization to audio-tactile stimuli as compared to unimodal stimulation (tactile or auditory). In addition, as predicted, the temporal properties of multisensory integration (i.e., TWI and temporal recalibration) influenced gait performance. Variability between step-times and stimuli onset was unchanged between −80 and +120 ms SOAs between auditory and tactile stimuli. These findings provide first evidence about the existence of a TWI in gait (width around 200 ms) when participants walk to audio-tactile stimuli. Note that synchronization accuracy varied within the TWI depending on whether auditory stimuli led or lagged relative to the tactile stimuli. Moreover, we found that temporal recalibration influenced the variability of step intervals and of synchronization exclusively at large SOAs when auditory stimulation preceded tactile stimulation. Thus, temporal recalibration is influenced by the amount of temporal gap and the order between the sensory modalities.

4.1. Temporal properties in gait

4.1.1. Temporal window of integration

We found that a TWI can be identified in multisensory integration constrained by performance in ecological conditions rather than isolated perceptual judgements or single-joint movements. The stability of synchronization was similar within a window of 200 ms (from −80 to +120 ms). The width of the TWI is comparable to the value previously found in bimanual tapping (160 ms; Roy et al., 2017). Interestingly, we confirmed that the TWI found in a rhythmic whole-body task is larger than the values reported in perceptual judgement tasks. In fact, it was more than twice larger than the maximum value reported in perceptual tasks (80 ms;

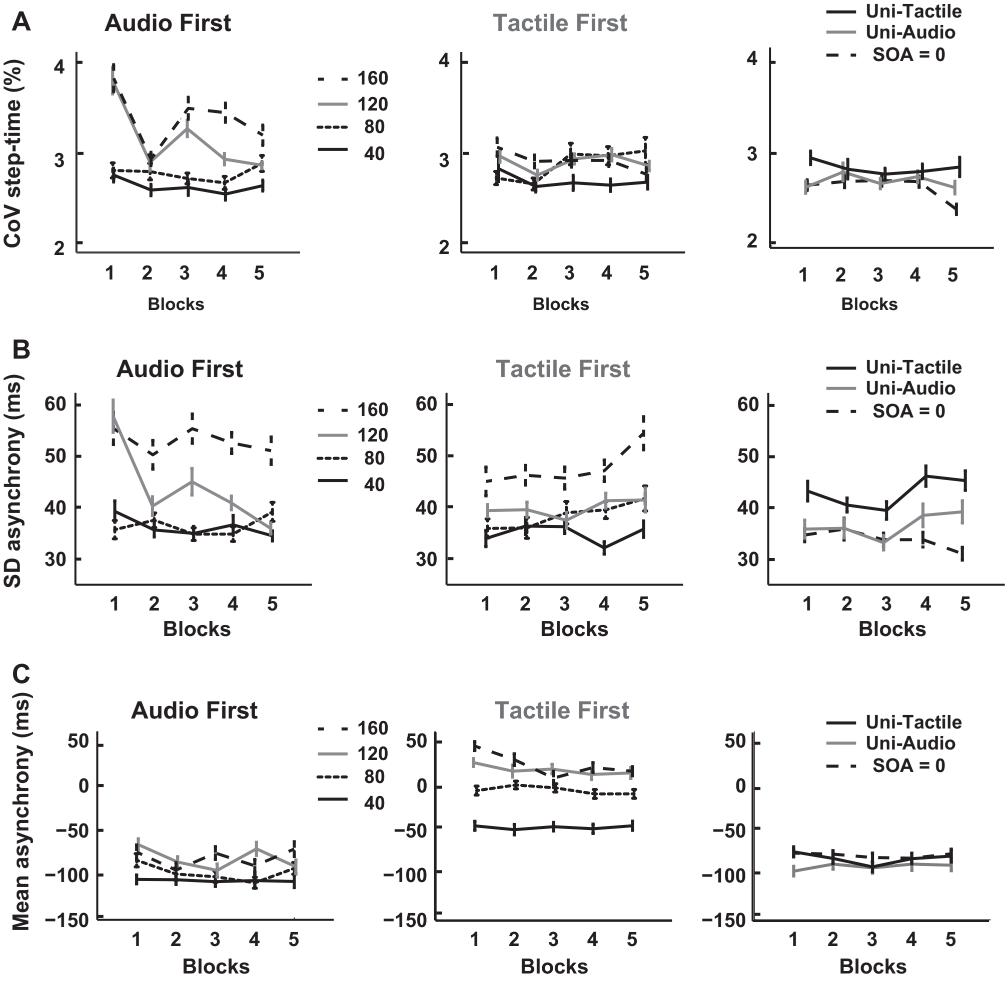

Fig. 4. (A) *CoV* step-time, (B) *SD* asynchrony and (C) Mean asynchrony as a function of the Block for each SOA and in unimodal conditions. Each curve represents for each condition the evolution of the step-intervals variability, of synchronization variability and accuracy over time.

Zampini et al., 2005). However, synchronization accuracy varied within the TWI and, in addition, was influenced by stimulus order. Thus according to the conditions of discrepancies between senses (SOAs), participants can put their foot down either close or far to the stimuli and conjointly presented the same regularity of synchronization in these same conditions. For some discrepancies between senses, the sensorimotor system can be both sensitive and stable (i.e., within the 200 ms of the TWI). This finding can be related with caution to previous results obtained in the audio-visual modalities showing no link between the TWI in RT task and TOJ tasks (Mégevand et al., 2013). In Mégevand et al. study (2013) one sub-group of participants presented a narrowing of the TWI in the RT task (RT task = 50 ms, TOJ task = 200 ms), while a second one showed approximately a similar size of the TWI but for different SOAs (RT task = from −80 to 0 ms, TOJ task = from −20 to 50 ms, negative indicated auditory preceded visual). These results indicate that perceived synchrony is not directly related to the best performance in a RT task. In the present experiment synchronization accuracy is not directly related to synchronization variability. We did not consider the synchronization accuracy as a measure of the perception of synchrony. Participants, however, were instructed to synchronize their steps with the stimuli. Thus, the mean asynchrony reflects the moment for which the participants had perceived the synchrony between their movements and the stimuli. A plausible interpretation is as follows: despite the sensitivity to discrepancies between stimuli the sensorimotor system managed to maintain a stable performance. For rhythmic movement, such as bimanual coordination and gait, the sensorimotor system exhibits considerable capacity to keep stability in a perturbed multisensory environment. In sum, the TWI for continuous coordination with rhythmic events in the environment is not defined solely by the relative sensitivity of the brain to lags between senses but by its capacity to maintain stable dynamic performance despite the lags between senses.

We defined TWI on the basis of synchronization performance. However, it can also be estimated by taking into account the variability of step intervals irrespective of the synchronization to the stimuli (i.e., considering *CoV* of step time). This alternative measure provides an estimate of the TWI (i.e., 80 ms) that is narrower than the one based on synchronization variability. Thus the ability to keep stable behaviour despite discrepancies between senses may be more constrained. Gait stability in multimodal conditions with discrepancies is reduced for smaller SOAs as compared to the synchronization stability. This finding can be related to the pacing frequency. We decreased the spontaneous gait frequency by 30% in order to challenge the gait of healthy young adult which is already very regular and stable. This manipulation increases gait variability (Terrier & Dériaz, 2012) and could potentially impact the stability of gait more than the stability of synchronization. Further studies are required to investigate gait and synchronization behaviour at different pacing frequencies, spontaneous versus decreased by 30%, for example. This also could indicate that stability afforded locally by synchronizing a limb to external events is not systematically transmitted to interlimb coordination.

Table 1
Linear mixed-effects models for three outcome variables: *SD* asynchrony, Mean asynchrony and *CoV* step-time normalized per participant. For brevity, only the final Model E (indicated in bold) for the latter two outcome variables is considered. An identical procedure was used in all three cases. The models are specified in terms of the fitted predictor parameters and random effects (Variance components). Parameter SE is shown in brackets. Participant acts as a grouping factor.

	SD asynchrony					Mean asynchrony	*CoV* step-time
	Model A	Model B	Model C	Model D	Model E	Model E	Model E
Fixed effects							
β_{00}: Intercept (Block = 0, SOA = 0)	39.51 (2.16)***	35.28 (2.27)***	33.08 (2.28)***	33.15 (2.37)***	**33.87 (2.37)*****	**−44.14 (8.76)*****	**−2.67 (.11)*****
β_{01}: |SOA|		.04 (.001)***	.07 (.01)***	.07 (.01)***	**.07 (.01)*****	**−.21 (.03)*****	**.00 (.01)*****
β_{02}: SOA			−0.03 (.01)***	−0.03 (.01)***	**−.05 (.01)*****	**.23 (.02)*****	**−.00 (.01)*****
β_{03}: Block				−0.04 (.32)	**−.39 (.33)**	**−1.45 (1.26)**	**−.04 (.01)****
$\beta 04$: SOA*Block					**.01 (.01)*****	**.00 (.01)**	**.00 (.01)***
Variance components							
σ_{ij}: Level-1: within-person (residual)	233.54	224.94	212.84	212.83	**210.49**	**2977.81**	**.27**
σ_{0i}: Level-2: Individual intercept (at Block = 0, SOA = 0)	84.70	84.85	85.07	85.08	**85.12**	**1116.70**	**.20**
Goodness-of-fit							
AIC	8728.13	8691.64	8636.89	8638.88	**8629.53**	**11396.88**	**1697.38**
BIC	8742.99	8711.44	8661.65	8668.59	**8664.19**	**11431.54**	**1732.04**
Log-Likelihood	−4361.07	−4341.82	−4313.44	−4313.44	**−4307.76**	**−5691.44**	**−841.69**
$^{\dagger}\chi^2$		38.50	56.75	.01	**11.35**	**.03**	**4.48**
$^{\dagger}p$		<.001	<.001	.90	**<.001**	**.87**	**<.05**

For parameters, $^{**}p < .001$, $^{**}p < .01$, $^{*}p < .05$. Observations in each model = 1045. Groups (Participants) = 19.

† The goodness-of-fit test is with respect to the model standing previous in the series of models for the given outcome variable, i.e. Model B with respect to Model A for *SD* async.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

To sum up, we found evidence of a TWI of 200 ms when participants walked to audio-tactile stimuli, apparent for synchronization variability. Although the size of the TWI is wider than observed in perceptual tasks, its width is smaller when estimated based on step-time variability.

4.1.2. Temporal recalibration

A second temporal process examined in the present study was temporal recalibration. This phenomenon has been mainly described for perceptual tasks, by exposing participants to asynchronous stimuli and measuring the effects of repeated perceptual exposure (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Hanson et al., 2008; Harrar & Harris, 2008; Navarra et al., 2007). In the present study we did not use this method but we expected that some form of temporal recalibration may occur and influence performance. Results showed that both variability of step intervals and of synchronization varied with time for the largest SOAs (120 and 160 ms) when auditory stimuli occurred first. Yet, synchronization accuracy did not vary. This effect of temporal recalibration is unlikely to result from mere learning or adaptation because the performance in unimodal and synchronous conditions did not change over time. Thus, the effect of temporal recalibration is rather likely to be linked to multisensory integration.

That temporal recalibration occurred when there was large physical separation between the stimuli (SOA = 120 and 160 ms) is particularly interesting. In perceptual tasks, temporal recalibration during the exposure phase can also occur at large SOAs. For example, two studies examining temporal recalibration in TOJ task for audio-tactile pairs (Harrar & Harris, 2008; Navarra et al., 2007), used SOAs in the exposure phase of 75 and 100 ms, with stimulus durations of 20 and 50 ms, respectively. We posit that for large SOAs the discrepancy between multimodal stimuli is clearly perceived at the beginning of a trial, thus leading to a strong perturbation effect. This would trigger temporal recalibration, which in turn will reduce the perception of the discrepancy between the stimuli over the trial. This explanation, albeit it is appealing, will need to be corroborated by further experiments. In addition, temporal recalibration was conditional on a given order of presentation of the stimuli (Occelli et al., 2011). In Navarra et al.'s study (Navarra et al., 2007) temporal recalibration was found when auditory stimuli were presented before tactile stimuli. With the reverse order, the effect was not replicated (Harrar & Harris, 2008). Our results are consistent with previous studies by showing that temporal recalibration influences the performance only when auditory stimuli precede tactile stimuli. This finding is akin to other effects of the order of presentation often observed in both TOJ and detection tasks (Bresciani et al., 2005; Fujisaki & Nishida, 2009; Mégevand et al., 2013; Powers, Hillock, & Wallace, 2009; Wilson et al., 2009). Results are consistent in showing that when the auditory stimulus occurs before tactile or visual stimuli the performance is worse than when the stimuli occur in the reverse order. This effect of order will be discussed more extensively below.

To sum up, the temporal properties of multisensory integration (i.e., TWI and temporal recalibration) influence gait performance. The second aim of this study was to examine whether audio-tactile cueing of gait leads to a multisensory benefit.

4.2. Multisensory integration

The results showed a multisensory benefit, as indicated by synchronization variability, suggesting that audio-tactile stimuli stabilize gait behaviour more than unimodal stimuli do. However, this effect does not extend to gait stability, as indicated by *CoV* step-time and by the Lyapunov exponent. We examine the relation between synchronization accuracy and stability. Then we will discuss the effect of the order of presentation.

As expected, maximum benefit is reported when auditory and tactile stimuli were synchronous (SOA = 0 ms). This finding is generally in keeping with the majority of experimental studies testing synchronous multimodal stimuli (Elliott et al., 2010; Lagarde, Zelic, & Mottet, 2012; Wing et al., 2010; Wright & Elliott, 2014; Zelic et al., 2016). However, this result is particularly interesting if considered in light of participants' synchronization accuracy. A difference of approximately 40 ms between unimodal auditory and unimodal tactile was observed in previous studies (Lagarde & Kelso, 2006; Müller et al., 2008; Roy et al., 2017). This difference was not replicated here. With both auditory and tactile unimodal stimuli the participants' steps anticipated the stimuli by about 80 ms. This was the case also when they walked with synchronous audio-tactile stimulation. Note that in our previous bimanual coordination study conducted using similar multimodal stimuli at different SOAs, a difference of 46 ms between auditory and tactile unimodal conditions was found, with best performance in the multimodal condition achieved when tactile preceded auditory stimuli by 40–80 ms (Roy et al., 2017). Even though the relation between synchronization accuracy and variability is not well understood, it is possible that when there is a difference in mean asynchrony between unimodal conditions, the most stable behaviour in bimanual coordination is afforded by an SOA corresponding to this difference. In keeping with the same logic, lack of difference in synchronization accuracy between unimodal conditions in gait performance suggests that the most stable behaviour with multimodal stimulation can be achieved when stimuli are presented simultaneously. This relation between synchronization accuracy and variability in unimodal and multimodal conditions is consistent with the Physiological Synchronicity Hypothesis (Diederich, 1995; Diederich & Colonius, 2004; Hershenson, 1962; Raab, 1962). The hypothesis indicates that physiological synchrony is more important than stimulus synchrony *per se*, thus the temporal gap is dictated by neurophysiological sensory transduction and condition processes in different modalities. In line with this hypothesis, another hypothesis was put forward long ago to account for delays in rhythmic movement by Fraisse (1980) and Paillard (1949). This hypothesis was proposed to account for mean negative asynchrony, typically observed in finger tapping experiments. When asked to tap to sequences of isochronous sounds, participants tend to anticipate the sound by 20–80 ms, a phenomenon termed "mean negative asynchrony". According to the Paillard-Fraisse hypothesis, this phenomenon is due to the constant time differences between the perception of sound and the cutaneous and proprioceptive reafferences produced by movement, in order to ensure an alignment at some central level in the CNS. This explanation at the physiological level has been extended to the cognitive level more recently (for reviews see Aschersleben, 2002; Repp, 2005). The results of the present experiment suggest a link between synchronization accuracy and variability mediated by the processing time needed by each sensory modality. After having presented this relation between synchronization variables, we will discuss the effect of order.

The effect of the temporal intervals between auditory and tactile stimuli on gait performance and on synchronization accuracy and variability is related to the order of presentation of the stimuli. Larger variability of synchronization and gait performances is found when auditory stimuli are presented first. This effect may partly result from auditory capture of synchronization movements (i.e., auditory dominance). Dominance entails greater perturbation when auditory stimuli are presented first. One of the explanations of this effect could be the privileged link between auditory modality and movement (Chen, Penhune, & Zatorre, 2008; Chen, Zatorre, & Penhune, 2006; Zatorre, Chen, & Penhune, 2007). However, an effect of order was also observed in both TOJ and detection tasks (Bresciani et al., 2005; Fujisaki & Nishida, 2009; Mégevand et al., 2013; Powers et al., 2009; Wilson et al., 2009). In most studies, improved performance (i.e., shorter RTs or better discrimination) is found when tactile stimuli precede auditory stimuli. A possible explanation of this effect is linked to the specific characteristic of different modalities. Typically, the auditory modality is efficient when temporal properties are critical for the execution of a task, while the visual modality is more appropriate for spatial properties and the tactile modality for surface discrimination (Welch & Warren, 1980). This specificity may be responsible for the aforementioned effect of order. Note that for all tasks the instructions are explicitly temporal. In reaction-time tasks participants are asked to respond as quickly as possible, in TOJ, to tell which stimuli came first and in the sensorimotor synchronization task, to move at the same time as the stimuli. This effect which is modality-specificity is related to a model and hypothesis described at the perceptual level. The Modality Appropriateness hypothesis formulated by Welch and Warren (1986) states that perception gives the priority to the most appropriate modality based on the task to perform. For temporal tasks the auditory modality tends to dominate visual or tactile modalities. This hypothesis is confirmed by recent studies showing that in synchronization tasks when the visual stimuli are continuous rather than discrete, such as flashes, the performance in a visual continuous condition is better than in a visual discrete condition (Armstrong & Issartel, 2014; Gan, Huang, Zhou, Qian, & Wu, 2015; Hove, Fairhurst, Kotz, & Keller, 2013; Iversen, Patel, Nicodemus, & Emmorey, 2015; Varlet, Marin, Issartel, Schmidt, & Bardy, 2012). It is worth noting that it is possible to limit this effect by reducing the reliability of the dominant modality (Maximum Likelihood Model, MLE; Elliott et al., 2010; Ernst & Bülthoff, 2004).

In synchronization tasks, reducing the reliability of the auditory modality, for example by using a jittered metronome, fosters multisensory integration. In contrast, when auditory stimuli are reliable, the effect of multisensory integration is not found (Elliott et al., 2010). It is likely that the MLE model and the Modality Appropriateness hypothesis can coexist depending on the situation. For example, when perception is reliable, the appropriate modality is associated to the task to perform. In contrast, in situations of ambiguous or unreliable perception, the non-appropriate modalities can supplement the ambiguous modality (Lunghi, Binda, & Morrone, 2010; Lunghi & Morrone, 2013; van Ee, van Bowtel, Parker, & Alais, 2009). Our tasks corresponds to the first situation, thereby the auditory modality appears to act as the appropriate modality. Note that even if the instruction of synchronization with the tactile stimuli counteracted the auditory capture, the effect of auditory dominance could not be completely erased, as indicated by the order effect.

5. Conclusion

In this study we report for the first time a multisensory benefit due to audio-tactile stimulation on gait in healthy young adults. In addition, we show that temporal properties engaged during multisensory integration as shown in perceptual studies, namely the TWI and temporal recalibration, generalize to continuous and rhythmic movement. This experiment suggests that the brain is constantly seeking to achieve temporal synchrony. If the environment does not afford this, then the brain will seek an alternative solution, within a temporal window of integration and using temporal recalibration. These properties are influenced by the order of presentation of multimodal stimuli.

Declaration of interest

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Footnote

We observed a difference in the *SD* of the time between the heel-strikes for the right and the left feet and of the time between the heel-strikes of the left and the right feet. This is probably the consequence of having participants walk on an ellipsoidal track. As a result, the *SD* in each case was computed separately and finally averaged.

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