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Walking to a multisensory beat

Charlotte Roy [a,*], Julien Lagarde [a], Dobromir Dotov [b], Simone Dalla Bella [a,c,d,e]

[a] EuroMov Laboratory, Montpellier University, 700 Avenue du Pic Saint Loup, 34090 Montpellier, France
[b] Instituto de Neurobiología, Juriquilla, Universidad Nacional Autonoma de México, Mexico
[c] Institut Universitaire de France, Paris, France
[d] International Laboratory for Brain, Music, and Sound Research (BRAMS), Montreal, Canada
[e] Department of Cognitive Psychology, WSFiZ, Warsaw, Poland

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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,

* Corresponding author at: EuroMov Laboratory, University of Montpellier, 700 Avenue du Pic Saint Loup, 34090 Montpellier, France.
E-mail address: charlotte.roy@umontpellier.fr (C. Roy).

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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