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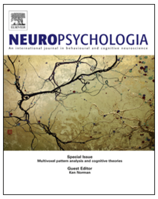

Poor synchronization to the beat may result from deficient auditory-motor mapping

Jakub Sowiński [a], Simone Dalla Bella [a,b,c,*]

[a] Department of Cognitive Psychology, WSFiZ in Warsaw, Poland
[b] EuroMov, Movement to Health Laboratory (M2H), University of Montpellier-1, Montpellier, France
[c] Institut Universitaire de France, Paris, France

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ABSTRACT

Moving to the beat of music is natural and spontaneous for humans. Yet some individuals, so-called 'beat deaf', may differ from the majority by being unable to synchronize their movements to musical beat. This condition was recently described in Mathieu (Phillips-Silver et al. (2011). *Neuropsychologia, 49*, 961–969), a beat-deaf individual, showing inaccurate motor synchronization to the beat accompanied by poor beat perception, with spared pitch processing. It has been suggested that beat deafness is the outcome of impoverished beat perception. Deficient synchronization to the beat, however, may also result from inaccurate mapping of the perceived beat to movement. To test this possibility, we asked 99 non-musicians to synchronize with musical and non-musical stimuli via hand tapping. Ten among them who revealed particularly poor synchronization were submitted to a thorough assessment of motor synchronization to various pacing stimuli and of beat perception. Four participants showed poor synchronization in absence of poor pitch perception; moreover, among them, two individuals were unable to synchronize to music, in spite of unimpaired detection of small durational deviations in musical and non-musical sequences, and normal rhythm discrimination. This mismatch of perception and action points toward disrupted auditory-motor mapping as the key impairment accounting for poor synchronization to the beat.

1. Introduction

Musical rhythm naturally engages our body. When we tap our foot or dance or sway along with the beat of our preferred song, we entrain to the regular pulse and rhythm of music. This phenomenon is universal. People across cultures synchronize to the beat of an auditory stimulus (e.g., Nettl, 2000). This ability is likely hard-wired. It appears spontaneously and precociously (e.g., Drake, Jones, & Baruch, 2000; Kirschner & Tomasello, 2009). Infants show sensitivity to violations in repetitive timing patterns (i.e., meter) (see Bergeson & Trehub, 2006; Hannon & Trehub, 2005; Trehub & Hannon, 2009; Winkler, Háden, Ladinig, Sziller, & Honing 2009), and can code rhythm via body movement (Phillips-Silver & Trainor, 2005), like adults do (Phillips-Silver & Trainor, 2007). Building on these perceptual abilities, two and half-year-old children can couple their movement to the beat of an auditory stimulus when interacting with a social partner (Kirschner & Tomasello, 2009; see also Provasi & Bobin-Bègue, 2003). Musical beat is indeed ideal to act as a coordinative device at a group level. Due to its communal character, moving to the beat is thought to foster social bonding (Benzon, 2001; Hove & Risen, 2009; Phillips-Silver, Aktipis, & Bryant, 2010; Wallin, Merker, & Brown, 2000; Wiltermuth & Heath, 2009). Finally, coupling movement to musical rhythm is likely exploiting the natural periodic property of brain activity, whereby neuronal oscillators (e.g., the Beta band) entrain to the periodicities of auditory stimuli (Fujioka, Trainor, Large, & Ross 2012; Nozaradan, Peretz, Missal, & Mouraux, 2011; see also Large, 2008; Large & Snyder, 2009). In summary, synchronization of movement to musical beat, an ability mastered by humans with unique flexibility, may be the outcome of an evolutionary pressure (McNeill, 1995; McDermott & Hauser, 2005; Merker, Madison, & Eckerdal, 2009).

In keeping with the idea that beat synchronization has biological relevance, it is expected that this ability is widespread, though, curiously, evidence is scant in this respect. In a recent study, Phillips-Silver et al. (2011) asked a group of 34 adults, most with a few years of musical practice, to bounce spontaneously to the beat of rhythmical songs (e.g., a Merengue song), and to a regular metronome. All participants except one, Mathieu, were successful in this task. Moreover, they could say whether the dancer in a movie clip was 'in time' with the auditory soundtrack.

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[*] Corresponding author at: University of Montpellier-1, EuroMov, Movement to Health Laboratory, 700 Avenue du Pic Saint Loup, 34090 Montpellier, France. Tel.: +33 411 759 065; fax: +33 467 415 704.

E-mail address: simone.dalla-bella@univ-montp1.fr (S. Dalla Bella).

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Mathieu, in contrast, was particularly inaccurate in bouncing to musical beat; synchronization was still possible, however, with the metronome. In addition, he showed poor beat perception on the Montreal Battery of Evaluation of Amusia (MBEA; Peretz, Champod, & Hyde, 2003) and when asked to match the movement of a dancer to music. Yet, he exhibited unimpaired pitch perception.

The case of Mathieu is particularly intriguing as it proves for the first time that a rhythm disorder can occur in isolation in untrained individuals. Beat deafness is thus distinct from the typical description of congenital amusia, a neurodevelopmental disorder in music perception (e.g., Ayotte, Peretz, & Hyde, 2002; Peretz, 2008). The core deficit in cases of congenital amusia (or tone deafness) described so far pertains to pitch perception and production (Ayotte et al., 2002; Dalla Bella, Giguère, & Peretz, 2009; Peretz, 2008; Peretz & Hyde, 2003). Poor rhythm perception and production can co-occur with poor pitch processing (Ayotte et al., 2002; Dalla Bella & Peretz, 2003; Hyde & Peretz, 2004). Yet such deficit is dependent on the presence of pitch variations in melodies. Once pitch variations are removed from melodies, congenital amusics can successfully discriminate rhythm differences between such melodies (Foxton, Nandy, & Griffiths, 2006).

How can we account for cases of beat deafness like that of Mathieu? A possibility is that poor synchronization to the beat is the outcome of poor beat perception. Impaired beat extraction from a complex auditory signal, like music, involving several periodicities at different embedded temporal scales (i.e., meter) (London, 2004) may hinder motor synchronization with music. Yet perceiving a single periodicity, as with a metronome, may still be possible thus allowing synchronization with an isochronous sequence. This account is a parsimonious explanation of Mathieu's deficits (Phillips-Silver et al., 2011), considering that he exhibited both poor synchronization and poor perception of synchronized movements to music.

The observation of concurrent perceptual and production disorders, however, does not entail that the former causes the latter. Other functional loci of impairment are possible. A failure of mapping the representation of the perceived beat to the appropriate synchronized action may be the key disorder hindering the coupling of movement timing to the beat (i.e., sensorimotor account). A similar explanation in particular is gaining increased interest as an account of deficient pitch processing in congenital amusia (e.g., Pfordresher & Brown, 2007; for reviews, see Dalla Bella, Berkowska, & Sowiński, 2011; Hutchins & Peretz, 2011). This account is supported by compelling evidence that perception and action can dissociate in pitch processing (for a review, see Dalla Bella et al., 2011). Disrupted pitch perception in congenital amusia can co-occur with normal singing (Dalla Bella et al., 2009; Loui, Guenther, Mathys, & Schlaug, 2008). Conversely, poor-pitch singing is compatible with normal pitch perception (in purely vocal tone deafness; see Dalla Bella, Giguère, & Peretz, 2007; Pfordresher & Brown, 2007; Wise & Sloboda, 2008). The sensorimotor account of pitch disorders is also biologically plausible. Tone deafness is associated with abnormally reduced connectivity of the fasciculus arcuatus (a pathway connecting temporal and frontal brain areas bridging perception and action) (Loui, Alsop, & Schlaug, 2009). Whether a sensorimotor account may similarly apply to explain poor synchronization to the beat is still unknown.

The main goal of this study is to examine whether poor synchronization to the beat can result from disrupted mapping of perception and synchronized action. This sensorimotor account would strongly be favoured by finding a mismatch between perception and action in the rhythm domain (i.e., poor beat synchronization concurrent with normal beat perception). Here we first screened a large sample from the general population for poor synchronization using a finger-tapping task. In Exp. 1, 99 participants completed a short test in which they synchronized (via finger tapping) to an isochronous sequence and to a rhythmical musical excerpt. Based on their synchronization accuracy and consistency, we expected to find a few participants showing difficulties in synchronizing either with music or with the metronome ('Poor synchronizers'). In Exp. 2, Poor synchronizers were submitted to a thorough assessment of their synchronization, as well as of their perceptual abilities with an anisochrony detection task (detecting a deviance from isochrony in an isochronous sequence or in a short musical excerpt), and with the Montreal Battery of Evaluation of Amusia (MBEA; Peretz et al., 2003). If deficient auditory-motor mapping is a potential cause of rhythm disorders, such as beat deafness, as we suspect, we should be able to uncover cases of poor synchronization with unimpaired beat perception.

2. Experiment 1

2.1. Method

2.1.1. Participants

Ninety-nine university students (86 females) from the University of Finance and Management in Warsaw participated in the experiment. They were aged between 19 and 43 (M=21.8 years, SD=4.4 years). Ninety-six had not received any musical training. Participants took part in the study in exchange of course credits.

2.1.2. Materials

Two pacing stimuli were used in the experiment: one isochronous sequence and one musical excerpt. The isochronous sequence was formed by 96 computer-generated tones (tone duration=30 ms). The musical excerpt was a computer-generated piano version of the beginning of the Radetzky march (opus 228) by Johann Strauss. The inter-onset-interval (IOI) between the tones in the isochronous sequence and between subsequent beats in the musical stimulus (inter-beat-interval, IBI; beat=quarter note) was 600 ms. Both stimuli were normalized at 75% of the maximum intensity level and recorded at a sampling rate of 44.1 kHz.

2.1.3. Procedure

Participants were submitted to three finger-tapping tasks: Synchronization with an isochronous sequence, Synchronization with music, and Spontaneous tapping. In the synchronization tasks, the participants tapped with their dominant hand in time with the tones of the isochronous sequence or of the musical beats, respectively. Each synchronization task was performed three times. In the Spontaneous tapping task, participants tapped with their hand for 1 min at their most natural pace in the absence of a pacing stimulus. The Spontaneous tapping task was performed once at the beginning of the experiment. Stimuli were delivered at a comfortable intensity level via Sennheiser EH2270 headphones with Presentation 9.90 software (Neurobehavioral Systems, Inc.) installed on an IBM-compatible computer. Participants' tapping was recorded with a tapping pad built for the purposes of the experiment (with 1-ms accuracy) and connected to the parallel port of the computer. The pad generated auditory feedback during tapping. The experiment lasted approximately 10 min.

2.1.4. Analyses

Synchronization data were analyzed with circular statistics (Fisher, 1993) using the Circular statistics Toolbox for Matlab (Berens, 2009). Circular statistics represent a good option for analyzing synchronization data (see Kirschner & Tomasello, 2009; Pecenka & Keller, 2011) and have an advantage in that they do not require a one-to-one correspondence between taps and pacing stimuli. This condition is rarely met in participants showing poor synchronization. For example, inexperienced adults, children, or individuals exhibiting inaccurate synchronization tend to omit taps or to produce more than one tap in correspondence of the same pacing stimulus (Kirschner & Tomasello, 2009). This fact is problematic, since it makes computing synchronization accuracy (i.e., the asynchrony between the tap and the pacing stimulus) impossible in many cases. Several taps are thereby typically discarded from the analyses. The number of discarded taps can amount to the majority of the collected data for individuals showing poor synchronization. Circular statistics are able to overcome this difficulty: by not requiring one-to-one correspondence between taps and pacing stimuli, all taps can be analyzed. In addition, this method is particularly well-suited to uncovering individual differences among participants (see Kirschner & Tomasello, 2009, for a thorough description of the advantages of circular statistics over standard linear statistics).

Data from a synchronized tapping trial (i.e., a sequence of taps in correspondence to a sequence of isochronous stimuli or musical beats) can be easily displayed applying circular statistics by representing the time interval between

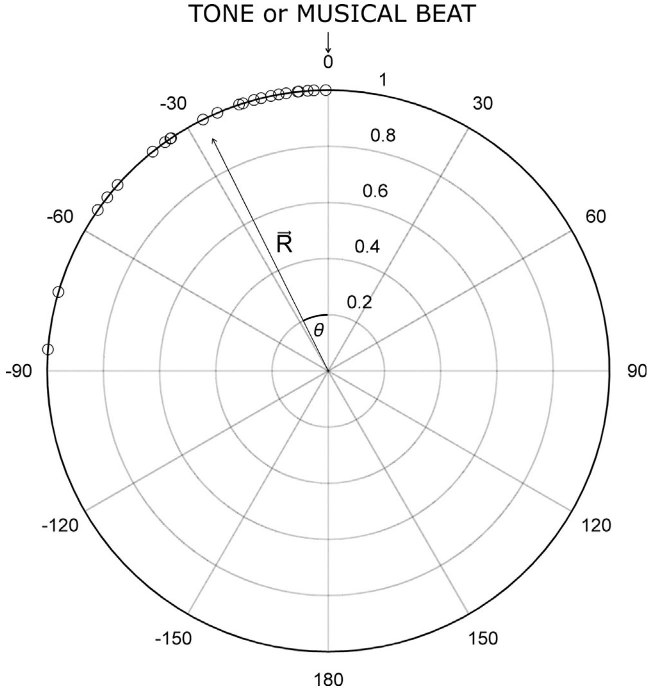

Fig. 1. Example of the distribution of taps from a trial taken from the synchronization task. The resultant vector R and its direction (angle theta, θ) are indicated. In the example, vector length$=$.95 and $\theta = -25^\circ$.

subsequent stimuli/beats on the unit circle. This is possible because stimuli are perfectly isochronous and thanks to the natural periodicity of the circle. All IOIs/IBIs of the stimuli from a single trial were transformed onto a circular scale (from 0 to 360°). The time of occurrence of the stimulus/beat corresponds to 0° (see role plot in Fig. 1), and indicates the moment when participants were expected to synchronize to pacing stimuli. Response taps are represented as specific points on the circumference of the unit circle and mathematically defined by a direction (angle in degrees), indicating their phase relative to the pacing stimuli. For example, a tap occurring 150 ms after a tone when a participant was synchronizing with the isochronous sequence (with a 600-ms IOI), was represented as a point at $+90^\circ$ on the circle. In contrast, a tap preceding the tone by 150 ms was indicated with a point at -90°.

To obtain measures of synchronization accuracy and consistency for each trial, data on the circle were summarized by first transforming directions into unit vectors, then averaged so as to obtain the mean resultant vector R (for a detailed description of the procedure, see Berens, 2009; Fisher, 1993; Mardia & Jupp, 2000). The vector R is broken down into two components, that is its angle (θ or relative phase) and its length. The angle θ, relative to 0°, corresponds to *synchronization accuracy* (i.e., how far from the pacing stimulus participants tapped). To assess whether synchronization accuracy varied as a function of the pacing stimulus, angles obtained when participants tapped along with music and with the isochronous sequence were compared using the Watson–Williams test, the circular equivalent of a one-factor Analysis of Variance (ANOVA) (see Berens, 2009; for similar use of this test in motor control and in psychophysiology, see Bardy, Oullier, Bootsma, & Stoffregen 2002; Dimitrijevic et al., 2009; Faugloire, Bardy, & Stoffregen, 2006).

It is worth noting that θ can be interpreted if the distribution of taps around the circle is not random. This possibility is tested with the Rayleigh test (Wilkie, 1983), allowing to assess whether participants were performing above chance. The null hypothesis of this test is circular uniformity (i.e., random distribution of data points around the circle, which is indicative of at-chance performance). The alternative hypothesis is a unimodal distribution of circular data points centred on a given phase angle (see Fisher, 1993). In Rayleigh test the null hypothesis can be rejected if R vector length is large enough, thus indicating that participants were significantly tapping at a given phase relationship with respect to the pacing stimulus. In the present study, θ values were taken into account and submitted for further analyses exclusively for trials where the Rayleigh test yielded significant results.[1]

The length of vector R (i.e., from 0 to 1), indicates *synchronization consistency*. This measure reflects the variability of the timing discrepancy between the taps and the pacing stimuli. Consistency is 1 when all the taps occur at exactly the same time interval before or after the pacing stimuli; 0 when the taps are randomly distributed around the circle. Such differences between accuracy and consistency are illustrated in Fig. 2 by showing possible synchronization patterns – (a) accurate and consistent, (b) inaccurate but consistent, (c) inaccurate and inconsistent – when a participant synchronizes with a metronome with IOI$=$600 ms.

2.2. Results

2.2.1. Synchronization tasks

The synchronization tasks yielded 594 tapping time series overall (six per participant). The best synchronization performance of each participant among the three trials for each stimulus type (i.e., the one showing highest consistency) was submitted to the following analyses. Average accuracy and consistency yielded by participants in the synchronization tasks are presented in Table 1. Synchronization with an isochronous sequence and synchronization with music[2] were compared in terms of accuracy (i.e., angle θ) and consistency. Angle θ was more negative with the isochronous sequence than with music (Watson–Williams $F(1,192)=33.13$, $p<.001$), thus showing greater negative asynchrony with the former than with the latter. To compute consistency obtained in the two synchronization tasks, vector lengths were first submitted to an arcsine transformation as done in previous studies (e.g., Kirschner & Tomasello, 2009). Indeed, the distributions of vector lengths, ranging from 0 to 1 on a linear scale, were negatively skewed, as attested by the Kolmogorov-Smirnov test ($ps<.001$). Transformed data were submitted to a standard t test. The participants were more consistent when they synchronized with the isochronous sequence than with music ($t(98)=4.30$, $p<.001$).

2.2.2. Spontaneous tapping task

Ninety-nine tapping time series were submitted to the following analyses. The mean inter-tap-interval (ITI) and tapping variability, as indicated by the coefficient of variation of the ITIs (CV of the ITIs, that is the *SD* of the ITIs divided by the mean ITI) were computed. The first and last 15 taps in each performance were discarded. Mean ITI and CV of the ITIs are reported in Table 1. To assess whether accuracy and consistency in synchronization with an isochronous sequence were dependent on general abilities in rhythmic tapping as revealed in the Spontaneous tapping task, two regression analyses were performed. In one analysis, mean ITI and CV of the ITIs were used to predict synchronization accuracy; in the other, they were used to predict consistency. The regression models are significant for accuracy[3] ($R^2=.15$; $F(2,96)=8.63$, $p<.001$) and for consistency ($R^2=.08$; $F(2,96)=4.09$, $p<.05$). The CV of the ITIs significantly predicts accuracy (*Beta*$=-.36$, $p=.001$) and consistency (*Beta*$=-.28$, $p<.01$), thus indicating that lower accuracy and consistency in the synchronization task are generally linked to higher variability in spontaneous tapping. This relation was not observed when participants synchronized with music.

2.2.3. Individual differences

To examine differences among participants with regard to synchronization accuracy and consistency, individual data obtained in the synchronization tasks are presented in Fig. 3.[4] Participants

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[1] This condition was satisfied by all performances when participants synchronized with an isochronous sequence and by 95% of performances when they synchronized with music.

[2] When synchronizing with music, the participants could tap to eighth, quarter, or half notes (i.e., at different metrical levels). The chosen metrical level was the one at which the participant tapped more consistently (i.e., exhibiting the highest vector length). Participants mostly tapped in correspondence with the quarter note (71% of the cases), less often with the eighth note (25%), and with the half note (5%).

[3] Since the goal of this analysis was to examine the relation between the performance in the spontaneous tapping task and the degree of synchronization accuracy without considering direction (i.e., whether the taps anticipated or followed the pacing stimuli), the absolute value of θ was taken as the dependent variable.

[4] In Fig. 3(b) we reported only the values of θ for participants synchronizing above chance (as revealed by the Rayleigh test; Wilkie, 1983).

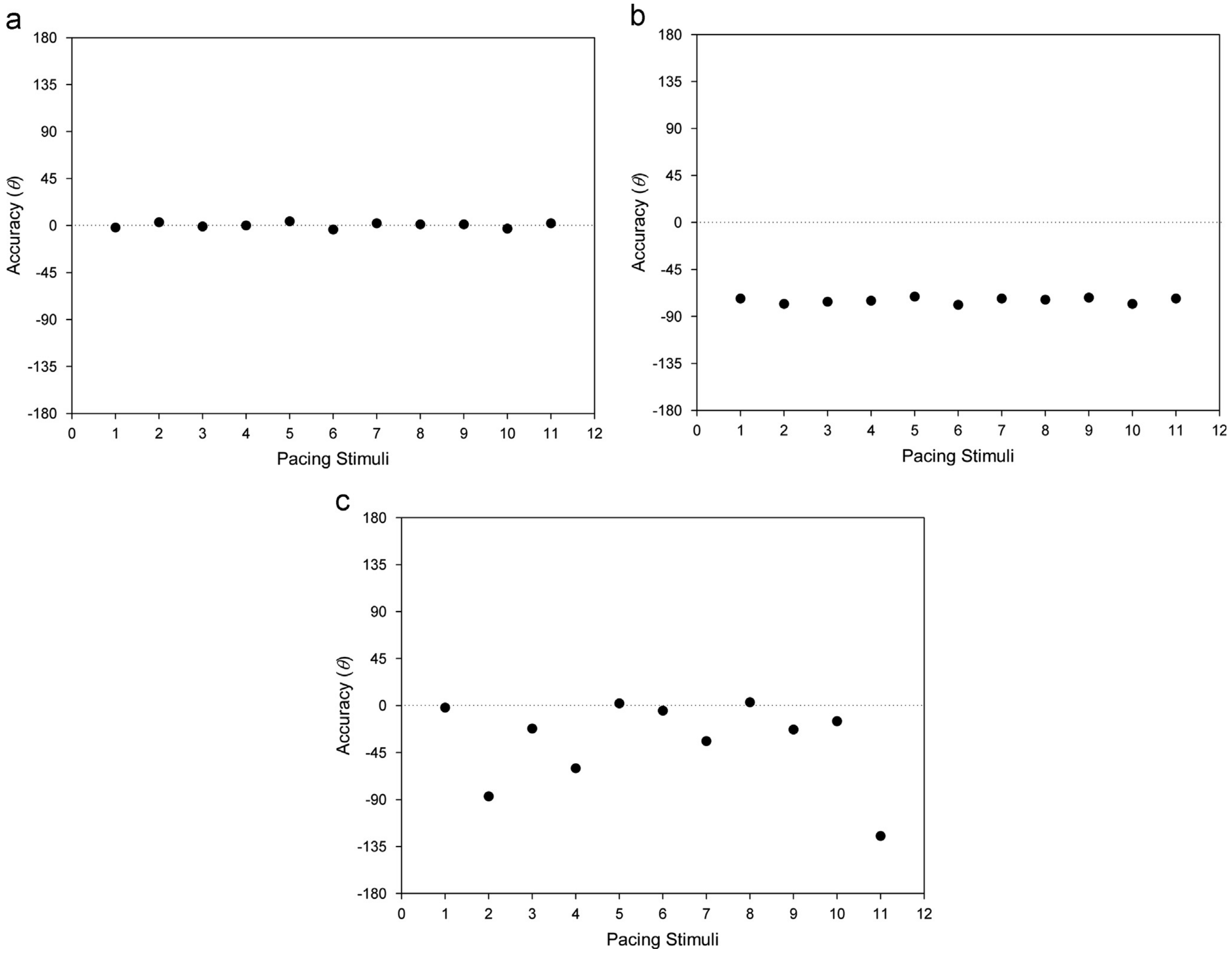

Fig. 2. Possible synchronization patterns based on measures of accuracy and consistency: (a) indicates a performance that is accurate and consistent, (b), inaccurate but consistent, and (c), inaccurate and inconsistent.

were referred to as ‘Poor’ or ‘Good’ synchronizers. Individuals exhibiting accuracy departing by more than 2 *SD* from the mean of the group, or showing consistency lower than 2 *SD* than the mean of the group were treated as Poor synchronizers (see Fig. 3). Two participants were Poor synchronizers when tapping along with the isochronous sequence (on both accuracy and consistency, $n=1$; only on accuracy, $n=1$), and 12 participants when tapping to music (on both accuracy and consistency, $n=2$; only on accuracy, $n=4$; only on consistency, $n=6$). Two participants showed very poor performance in both synchronization tasks, when considering either accuracy or consistency.[5] All Poor synchronizers were accurate in spontaneous tapping but one (CV of the ITIs=.10), departing from the group mean by more than 2 *SD*.

2.3. Discussion

In this first experiment, we screened a large sample of university students using two simple synchronization tasks to identify individuals with potential synchronization deficits. The majority was accurate and consistent in synchronizing to an isochronous sequence or to the beat of music. Synchronizing with

Table 1
Exp. 1: Average accuracy and consistency when participants synchronized with an isochronous sequence and with music, and in Spontaneous tapping. Average accuracy was computed based only on the values of θ for participants synchronizing above chance.

	M	*SE*	*Minimum*	*Maximum*
Synchronization				
Isochronous sequence				
Accuracy (θ)	−31.4	1.9	−117.6	2.6
Consistency (*vector length*)	.94	.01	.46	.98
Music				
Accuracy (θ)	−7.6	3.5	−141.7	179.7
Consistency (*vector length*)	.83	.03	.10	1.00
Spontaneous tapping				
Mean ITI (ms)	719	23	171	1393
CV of the ITI	.06	.002	.02	.13

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[5] Three of the Poor synchronizers with music exhibited accuracy with θ approximately around +180°. This indicates that they were synchronizing with the beat anti-phase, thus suggesting that their performance may not be completely inaccurate. Two of these participants showed good consistency (average vector length=.99). Yet one of them was inconsistent, with vector length=.24.

music was more difficult than with a metronome. People were less consistent with the former than with the latter. Moreover, five of them, albeit well synchronizing with the metronome, could not tap to the musical beat. Nevertheless, those participants who synchronized consistently above chance (i.e., as attested by a significant Rayleigh test) ($n=94$) were more accurate when they synchronized with music than with an isochronous sequence. This finding is in keeping with the observation that mean asynchrony (i.e., a linear measure for accuracy) is typically negative when synchronizing with an isochronous sequence (Aschersleben, 2002; Aschersleben & Prinz, 1995; for a review see Repp, 2005), whereas it is smaller or absent with more complex rhythmical stimuli (Wohlschläger & Koch, 2000).

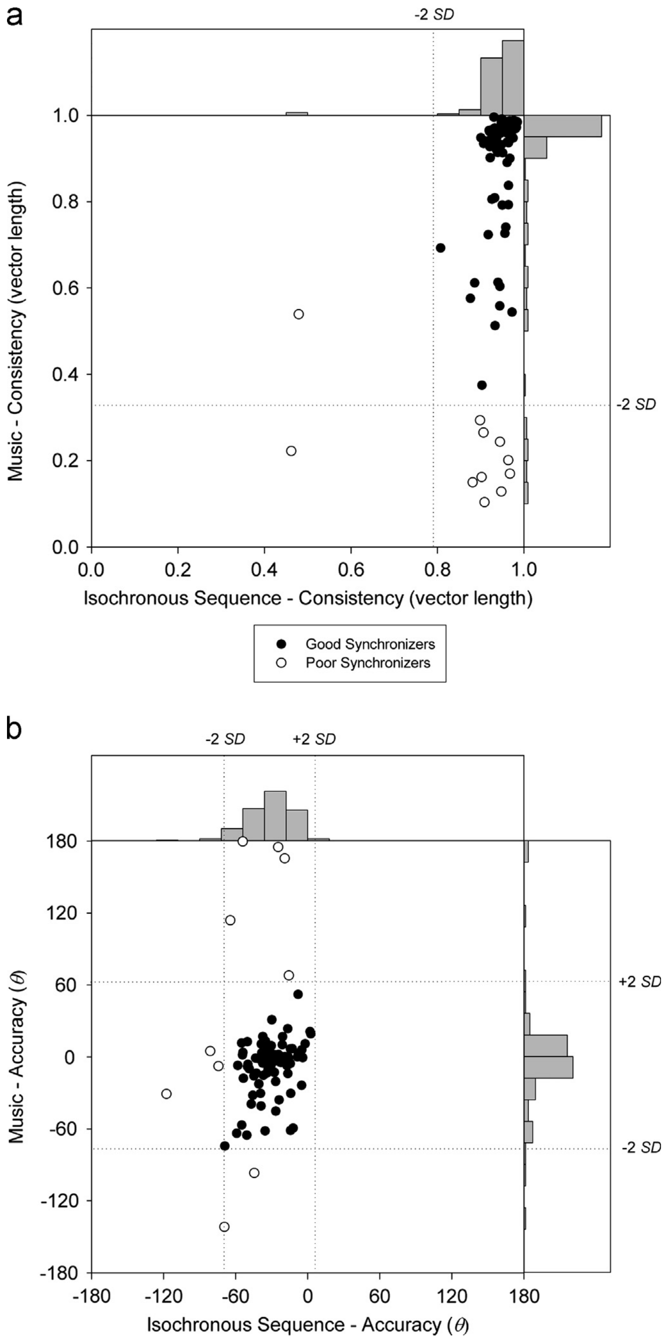

Fig. 3. Exp. 1: Individual data for synchronization accuracy (a) and consistency (b) with music and the isochronous sequence. Participants departing by more than 2 *SD* from the average of the entire group were identified as Poor synchronizers.

In this screening phase, 16 out of 99 participants (about 16%) were categorized as Poor synchronizers (i.e., they exhibited inaccurate and/or inconsistent synchronization). Most of them ($n=12$) were inaccurate/inconsistent in tapping along with music, without showing poor synchronization with the isochronous sequence. Two participants showed the opposite pattern. Note that poor synchronization cannot be ascribed merely to poor motor performance. Indeed, most Poor synchronizers ($n=14$) could normally tap at a spontaneous tempo in absence of a pacing stimulus.

In summary, synchronization to auditory rhythms is widespread in the general population, yet some individuals manifest difficulties in coupling movement to the beat. Similar disturbances were reported in the case of Mathieu (Phillips-Silver et al., 2011), and in congenital amusia (Ayotte et al., 2002; Dalla Bella & Peretz, 2003). In both these cases poor synchronization was systematically associated to deficient beat perception. Impoverished perception may similarly account for the performance of Poor synchronizers in the present study. This possibility was systematically assessed in Exp. 2. Ten Poor synchronizers identified in Exp. 1 underwent a battery of synchronization tasks, to confirm the results obtained in Exp. 1. In addition, perception was assessed with an anisochrony detection task and with the MBEA (Peretz et al., 2003). If poor synchronization in some cases is caused by faulty auditory-motor mapping, we should observe a dissociation between synchronization abilities and beat perception in Poor synchronizers.

3. Experiment 2

3.1. Method

3.1.1. Participants

Thirty-three university students participated in the experiment. Ten students (eight females; mean age=20.0 years, *SD*=1.0 year) were selected based on availability among the 16 participants characterized as Poor synchronizers in Exp. 1. A second group (i.e., Controls) was formed by 23 students (18 females; mean age=21.8 years; *SD*=5.5 years) randomly selected among the 83 Good synchronizers identified in Exp. 1. Participants took part in the study in exchange of course credits.

3.1.2. Materials and procedure

Participants were submitted to a battery of tapping tasks including Synchronization with auditory rhythms and Spontaneous tapping, to one Rhythm perception task (i.e., anisochrony detection), and to the MBEA (Peretz et al., 2003). The testing was performed over two separate days. In the first day, the tapping tasks and the anisochrony detection task were performed. The second day was devoted to the administration of the MBEA. Participants were tested for approximately an hour and a half on each day.

3.1.2.1. Tapping tasks. The participants were submitted to Synchronization and Spontaneous tapping tasks. In the Synchronization tasks, they synchronized to the same isochronous sequence and to the same musical excerpt as in Exp. 1. Moreover, in an additional task, the participants tapped along with an amplitude-modulated white noise stimulus having the same amplitude envelope of the musical stimulus. The amplitude-modulated stimulus shared the same rhythmical complexity with music (at least as conveyed by the amplitude envelope), but lacked all other musical features, such as pitch variation and harmony. All the stimuli were presented at three different tempos, with 450, 600, and 750-ms IOI/IBI. The Spontaneous tapping task is the same as in Exp. 1.

All stimuli were prepared and presented as described in Exp. 1 and the responses collected with the same equipment. The Synchronization tasks were performed twice, at the beginning and at the end of the first day of testing. The stimuli were presented in a blocked fashion: the three tempo versions of the same stimulus were presented prior to moving to the next stimulus. Amplitude-modulated noise stimuli were always presented at the end. The order of the other stimulus types (i.e., isochronous sequences and music) was counterbalanced across participants. Moreover, the order of the three IOIs/IBIs was counterbalanced across the two repetitions of the tasks. The Spontaneous tapping task was also performed twice, before the two repetitions of the entire set of Synchronization tasks. The tapping tasks (one repetition) lasted approximately 7 min.

3.1.2.2. Rhythm perception task (anisochrony detection). An isochronous sequence and two short musical fragments were used in an anisochrony detection task (see

Hyde & Peretz, 2004; Ehrlé & Samson, 2005). The isochronous sequence was formed by eight computer-generated tones (tone duration=30 ms). Each of the two musical fragments, corresponding to the beginning of two musical phrases of the same excerpt used in the synchronization tasks, contained eight musical beats. Both the isochronous sequence and the musical stimuli were presented at three different tempos (with 450, 600, and 750-ms IOI/IBI). For each stimulus type, a 'no-change' version (50% of the trials, $n=24$) and a 'change' version (50% of the trials, $n=24$) were prepared. In the no-change stimulus, the IOIs/IBIs remained unchanged within the sequence. In the change stimuli, the penultimate sound/musical beat occurred earlier or later than expected based on the previous IOIs/IBIs as done in previous studies (e.g., Hyde & Peretz, 2004). The magnitude of the change was 8, 12, or 16% of the sequence IOI/IBI. The participants were asked to pay attention to the entire sequence. After the presentation of the stimulus, they judged whether a change (i.e., departure from isochrony) was present or not. To discourage participants to respond by merely paying attention to the last two IOIs/IBIs of the sequence, six foil trails were also used, with a change (16% of the IOI/IBI) occurring after the second sound/musical beat. Data obtained in the foil trials were discarded from subsequent analyses. The answer was provided using the computer keyboard. The types of stimuli (isochronous sequence and music) were presented in a blocked fashion. In addition, the stimuli corresponding to the three tempos were also blocked. Within each block, the change and no-change stimuli were presented in random order. Stimulus type and the order of the IOIs/IBIs were counterbalanced across participants. The rhythm perception task lasted approximately 50 min.

3.1.2.3. Montreal battery of the evaluation of amusia (MBEA). Poor synchronizers and 22 out of 23 Controls were submitted to the MBEA (Peretz et al., 2003) to assess their pitch and rhythm perception. The first three tests of the MBEA assess pitch perception. In each test, 30 pairs of melodies are presented; in half of the pairs, the second melody includes a modified note, violating the scale of the original melody, or changing one interval or the melodic contour. Participants judge if the melodies are the same or different. Tests 4 and 5 target rhythm perception. In task 4, 30 pairs of melodies are presented, and half of the pairs contain a note with a different duration. As before, the participants judge if the melodies are same or different. In task 5, 30 short excerpts are presented (15 with a binary meter, and 15 with a ternary meter). The participants are asked to indicate if each excerpt is a march (in binary meter) or a waltz (in ternary meter). The stimuli were presented via Sennheiser EH2270 headphones. The responses were indicated by the experimenter on a response sheet. The administration of the MBEA lasted approximately 1 h.

3.2. Results and discussion

3.2.1. Tapping tasks

In the Synchronization tasks, 396 tapping time series overall (12 for each participant) were obtained. For each IOI/IBI and stimulus type the best performances were selected, based on the same criteria adopted in Exp. 1, and submitted to the following analyses. Synchronization accuracy and consistency were computed with circular statistics, as done in Exp. 1. Mean and variability of synchronization accuracy and consistency for the best performances with the three types of stimuli (isochronous sequence, music, amplitude-modulated noise) and at the different IOIs/IBIs are presented in Table 2.

Accuracy was analyzed as in Exp. 1 by using the Watson–Williams test to compare Poor synchronizers to Controls, and to test potential differences between pacing stimuli. All Poor synchronizers performed above chance when tapping with an isochronous sequence as assessed with the Rayleigh test. However, a few Poor synchronizers performed at chance when synchronizing with music (two participants at 450-ms and 600-ms IOIs and four at 750-ms IOI), and with amplitude-modulated noise (five participants at 450-ms IOI, one at 600-ms and two at 750-ms IOIs). Consequently, in these conditions a reduced number of trials could be analyzed for obtaining a measure of accuracy. Poor synchronizers did not significantly differ from Controls in terms of accuracy across pacing stimuli and IOIs, as attested by Watson–Williams tests. In addition, Controls' taps anticipated the pacing stimulus mostly when synchronizing with an isochronous sequence, but less with music and amplitude modulated noise (with 450-ms IOI, Watson–Williams $F(2,63)=15.65$, $p<.001$; 600-ms IOI, $F(2,63)=5.30$, $p<.01$; 750-ms IOI, $F(2,63)=3.31$, $p<.05$). Even though Poor synchronizers revealed a similar tendency, differences in accuracy between pacing stimuli did not reach significance.

Table 2
Exp. 2: Accuracy and consistency in the synchronization tasks obtained by Poor synchronizers ($n=10$) and Controls ($n=23$) at the different IOI/IBIs. Average accuracy was computed based only on the values of θ for participants synchronizing above chance.

	Poor synchronizers				**Controls**			
	Accuracy		Consistency		Accuracy		Consistency	
IOI/IBI (ms)	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
Isochronous sequence								
450	−28.6	8.8	.85	.04	−26.5	4.6	.95	.01
600	−35.4	12.4	.86	.07	−22.9	2.9	.95	.003
750	−22.1	3.7	.90	.02	−20.9	2.0	.95	.004
Music								
450	−1.9	19.0	.55	.11	4.1	4.1	.84	.05
600	−28.1	17.1	.48	.11	−5.2	5.6	.86	.05
750	−10.7	8.1	.43	.12	−8.9	5.2	.88	.04
Noise								
450	−4.9	23.2	.43	.12	8.5	5.3	.80	.05
600	11.0	19.8	.48	.10	4.2	5.3	.85	.05
750	11.1	14.9	.59	.11	−7.4	4.1	.86	.04

Values for consistency were submitted to an arcsine transformation, due to lack of normality in most conditions in the control group (with music and amplitude-modulated noise, Kolmogorov-Smirnov $ps<.05$). Transformed data were entered into a 2 (Group) × 3 (IOI/IBI) × 3 (Stimulus type) mixed-design ANOVA. Group (Poor synchronizers vs. Controls) was the between-subject factor, and IOI/IBI (450 vs. 600 vs. 750 ms) and Stimulus type (Isochronous sequence vs. Music vs. Amplitude-modulated noise) the within-subject factors. As can be seen in Table 2, Controls were typically more consistent than Poor synchronizers. However, this difference between the two groups varied with the stimulus type ($F(2, 62)=6.13$, $\varepsilon=.66$, $p<.05$).[6] The difference was more visible when participants tapped to isochronous sequences ($F(1,31)=15.34$, $p<.001$) and music ($F(1,31)=15.35$, $p<.001$), as compared to amplitude-modulated noise ($F(1,31)=12.41$, $p<.01$). Other interactions did not reach significance.

To examine further potential differences between Poor synchronizers and Controls regarding short-term correction processes during synchronization, lag-1 autocorrelation of the ITIs was computed for the three pacing stimuli. Poor synchronizers and Controls alike exhibited negative lag-1 autocorrelation when synchronizing with the isochronous sequences ($rs=-.19$, $SE=.0,4$, and $-.24$, $SE=.02$, respectively), which is indicative of functional short-term correction mechanisms (e.g., Vorberg & Wing, 1996). However, Poor synchronizers did not exhibit negative lag-1 autocorrelation when they tapped along with music or noise (average $r=.05$, $SE=.09$), thus significantly departing from the performance of Controls (average $r=-.18$, $SE=.04$; $t(12.9)=2.41$, $p<.05$). Notably, Poor synchronizers who tapped most consistently with music or noise were also those who showed greater correction, as attested by a significant correlation between vector length and lag-1 autocorrelation (with music, $r=-.83$, $p<.01$; with noise, $r=-.76$, $p=.01$).

In the Spontaneous tapping task, 66 tapping time series were obtained (two per participant). The best of the two performances for each participant (i.e., the one showing the lowest CV of the ITIs) was considered. The mean ITI was 622 ms (CV=.046) for Poor synchronizers, and 627 ms for Controls (CV=.041). No significant

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[6] The Greenhouse–Geisser correction for inhomogeneity of variance was applied whenever appropriate. Uncorrected degrees of freedom, epsilon value, and probability level following correction are reported.

differences between the groups were observed. In addition, Poor synchronizers and Controls did not differ in terms of lag-1 autocorrelation ($rs=.07$ and.06, respectively).

In summary, the results of the synchronization tasks confirmed that, at a group level, Poor synchronizers identified in Exp. 1 had major difficulties in synchronizing with a variety of rhythmical auditory stimuli (more and less complex), and across different tempos, relative to Controls. Poor synchronizers exhibited very low accuracy (i.e., only three out the 10 Poor synchronizers tapped above the chance level with all the pacing stimuli). In addition, they tapped in an inconsistent fashion along with various stimuli and reduced correction of the ITI with complex stimuli (i.e., music and noise). The observed difference between Poor synchronizers and Controls cannot be ascribed merely to general motor abilities. Both groups were similarly accurate and consistent in tapping at a spontaneous pace.

3.2.2. *Rhythm perception task*

Data from the anisochrony detection task were analyzed by calculating the discriminability index (d') at each level of change (i.e., 8, 12, 16% of the IOI/IBI) and for each IOI. Values of d', computed separately for isochronous sequences and for music, are reported in Fig. 4. These data were entered into two 2(Group) × 3(Change) × 3 (IOI) mixed-design ANOVAs, one for each stimulus type. Group (Poor synchronizers vs. Controls) was the between-subject factor; Change (8% vs. 12% vs. 16%) and IOI/IBI (450 vs. 600 vs. 750 ms) were the within-subject factors. With the isochronous sequence, both groups were less accurate when the change to detect was smaller (main effect of Change, $F(2,62)=90.31$, $\varepsilon=.65$, $p<.001$), and the performance was slightly but significantly higher at the fastest tempos as compared to the slower ones (main effect of IOI; $F(2,62)=4.01$, $\varepsilon=.96$, $p<.05$). Poor synchronizers tended to perform slightly worse than Controls. However, this difference did not reach significance ($F(1,31)=3.16$, $p=.09$). None of the interactions reached significance. With music, for both Poor synchronizers and Controls, the sensitivity to the amount of the change was dependent on tempo, as indicated by a Change × IBI interaction ($F(4,124)=11.30$, $\varepsilon=.57$, $p<.001$). The effect of Change was observed at 450-ms and 600-ms IBIs ($F(2,64)=37.90$, $\varepsilon=.75$ $p<.001$, and $F(2,64)=3.83$, $p<.05$, respectively), but not at 750-ms IBI, thus indicating higher sensitivity to anisochronies at the fastest tempos. Neither the effect of Group nor other interactions were significant.

In order to test whether the detection of anisochronies varied as a function of the direction of the change (i.e., when the penultimate sound/musical beat occurred earlier or later than expected), d' data across different IOIs were entered in two 2(Group) × 3(Change) × 2 (Direction) ANOVA, one for each stimulus type. Group (Poor synchronizers vs. Controls) was the between-subject factor; Change (8% vs. 12% vs. 16%) and Direction (anticipation vs. delay) the within-subject factors. With the isochronous sequence, both Poor synchronizers and Controls were more sensitive to anisochronies when the penultimate sound/beat was anticipated (mean $d'=.76$, $SE=.06$) than when delayed (mean $d'=.62$, $SE=.06$), as attested by a main effect of Direction ($F(1,31)=8.32$, $p<.01$). With music, both groups were affected by the direction of the change. This effect depended on the amount of change ($F(2,62)=4.23$, $\varepsilon=.98$, $p<.05$). Unlike what was observed with the isochronous sequence, anisochronies were detected less easily when the change was an anticipation (mean $d'=.93$, $SE=.04$) than a delay (mean $d'=1.06$, $SE=.03$) when the change was 12% of the IOI/IBI ($t(32)=2.7$, Bonferroni-corrected $p<.05$). For other changes, no significant differences were observed. In summary, Poor synchronizers did not significantly differ from

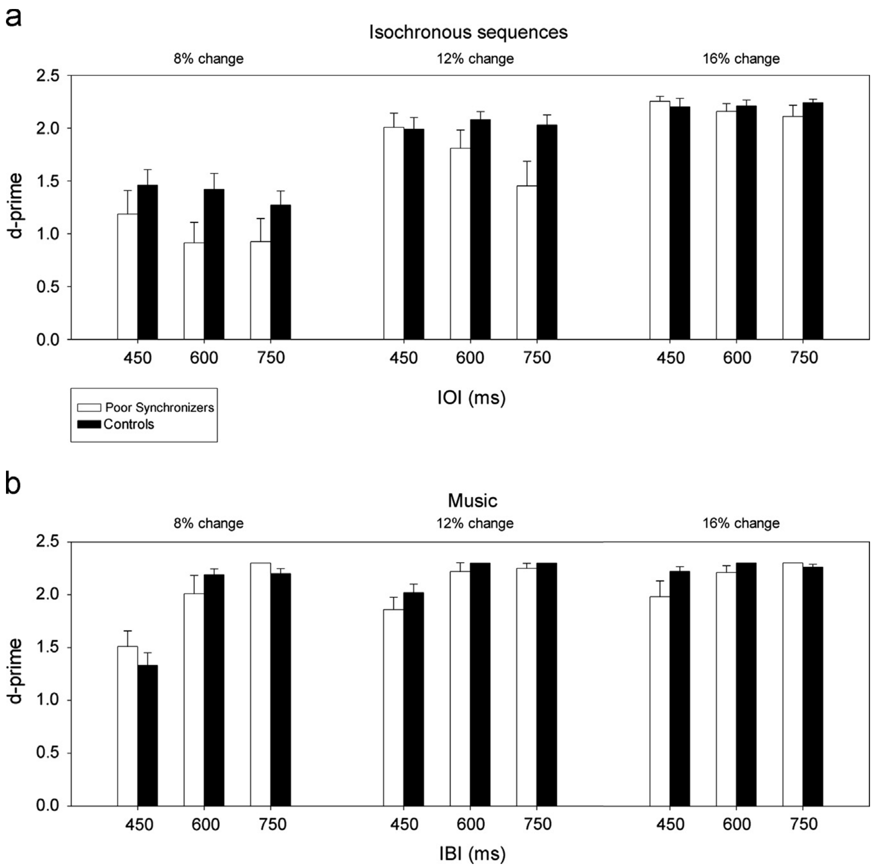

Fig. 4. Exp. 2: Values of d' obtained by Poor synchronizers and Controls in the Rhythm perception task at different IOIs/IBIs, (a) with the isochronous sequence, and (b) with music. Error bars indicate S.E.M.

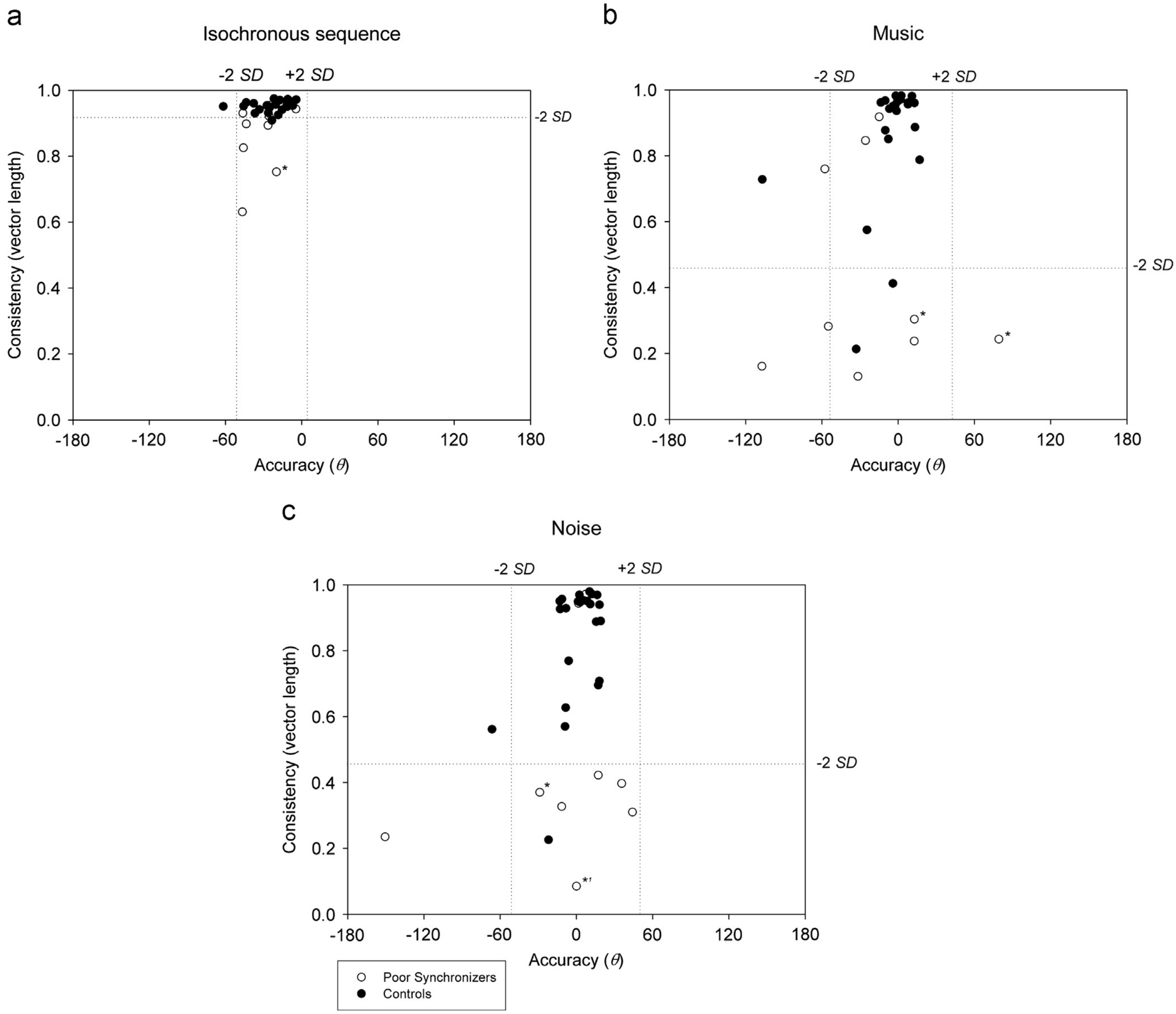

Fig. 5. Exp. 2: Individual data for synchronization accuracy and consistency with (a) the isochronous sequence, (b) music, and (c) amplitude-modulated noise. Stars indicate beat-deaf participants with unimpaired perception.[1]The performance of this beat-deaf individual was at chance. Thus, accuracy (θ) cannot be interpreted. By default, here θ was set to 0.

Controls in detecting an anisochrony embedded in an isochronous sequence or in a musical context.

3.2.3. MBEA

Two measures of pitch and rhythm perception were obtained from the MBEA. To compare our results with the performance of Mathieu from a previous study (Phillips-Silver et al., 2011), who did not show impaired pitch processing, correct responses in Tasks 1, 2, and 3 (contour, interval, and scale) were averaged to obtain the Pitch-composite score. On average, Poor synchronizers revealed poorer pitch perception (Pitch-composite score=21.4, SD=2.0) as compared to Controls (25.0, SD=2.3) (U=193.50, $p<.001$). Rhythm perception was tested by considering the number of correct responses in Task 4 (rhythm), a measure of duration discrimination abilities in a musical context. Poor synchronizers (with 25.4/30 correct responses, on average) did not differ from Controls (26.3) in that task. The average Pitch-composite score and the performance in Task 4 for Poor synchronizers are still above the cut-off threshold for impairment (20.1 and 19.9, respectively) as indicated in a previous study where the MBEA was administered to a comparable group of 100 university students who reported that they are non-tone-deaf (Cuddy, Balkwill, Peretz, & Holden, 2005).[7]

3.2.4. Individual differences

Despite the general differences reported above at group level, important discrepancies emerged among Poor synchronizers, which deserve particular attention. Individual synchronization accuracy and consistency with isochronous sequences, music, and noise, averaged across IOIs, for Poor synchronizers and

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[7] The results obtained in Task 5 (meter) of the MBEA, though potentially interesting, were not considered here. Indeed, Controls were variable on this task (SD=5.4), which is likely more difficult than the others (see also Cuddy et al., 2005, for comparable variability). The cut-off threshold for impairment in this task (i.e., 2 SD below the average of the control group) is at chance level. This paradoxically entails that a participant immediately above the cut-off score, but still performing around chance, would be considered as unimpaired. Thus, the results obtained with this task are difficult to interpret.

Table 3
Exp. 2: Summary of the individual results obtained by Poor synchronizers. The performance of participants with unimpaired perception are indicated in bold.

	Synchronization (*vector length*)			**RHYTHM PERCEPTION (d') (change %)**		**MBEA**	
Poor synchronizer	Isochr. sequence	Music	Noise	Isochr. sequence	Music	Pitch-Composite	Rhythm (Task 4)
S1	**.75**	**.30**	**.37**				
S2		.28	.40	.22 (8)	1.92 (16)		
S3	.63	.16	.33		1.71 (12) 1.98 (16)	20	21[a]
S4							
S5		**.24**	**.09**				
S6		.24	.31			20	
S7							
S8	.90		.42	.24 (8) 1.20 (12) 1.67 (16)		17	22[a]
S9	.89	.13	.24		1.38 (8) 1.92 (12) 1.92 (16)		
S10	.83						

[a] Below the cut-off score relative to Controls' performance, but not to 100 non-tone-deaf participants in Cuddy et al. (2005).

Controls are presented in Fig. 5. As can be seen, most Poor synchronizers departed by at least 2 *SD* from the performance of Controls, in particular when they synchronized with music and with amplitude-modulated noise. Here we examined on a subject-by-subject basis to what extent Poor synchronizers exhibited impaired synchronization and poor perception as compared to Controls. Therefore, we focused on synchronization consistency. This measure, reliable and available from all Poor synchronizers, has proven to be particularly sensitive to individual differences. Consistency was averaged across the different tempos, since the IOI/IBI did not significantly affect synchronization. The results obtained in the Rhythm perception task at each change level were similarly averaged across the different IOIs/IBIs. Finally, the Pitch-composite score, and the average number of correct responses in Task 4 were considered. To test whether each poor synchronizer was impaired in the Synchronization and in the Rhythm perception tasks, her/his performance was compared to that of Controls via corrected t-tests (Crawford & Garthwaite, 2002). In the Rhythm perception task the following criterion was adopted to determine if Poor synchronizers showed impairment: they had to show a deficiency as compared to Controls at one of the Change levels (i.e., 16%, 12%, or 8% of the IOIs). Finally, to determine if Poor synchronizers were impaired in pitch or rhythm perception as indicated by the MBEA (Pitch-composite score and Task 4), individual results were compared with the performance of Controls and with norms obtained with a comparable group of university students (Cuddy et al., 2005). A cut-off score for identifying impaired performance (i.e., below 2 *SD* relative to the average of the comparison group) was set, as done in previous studies on congenital amusia (e.g., Peretz et al., 2003).

A summary of the individual performance of the ten Poor synchronizers is presented in Table 3. For clarity, values on the different tests are reported only when Poor synchronizers performed significantly worse than Controls. This analysis reveals intriguing results, showing different profiles of impairment. Two individuals (S3 and S8) synchronized poorly with most of the pacing stimuli and overall revealed poor pitch and rhythm perception. This profile matches well to the pattern previously observed in congenital amusia (Ayotte et al., 2002; Dalla Bella & Peretz, 2003). In this case, poor synchronization may stem from general difficulties in pitch and rhythm perception. A different pattern was shown by S2 and S9. They also had major difficulties with synchronization and with perceiving deviations from isochrony. Yet they could normally process pitch information (i.e., with average Pitch-composite score = 21.7). This profile is reminiscent of the performance showed by Mathieu (Phillips-Silver et al., 2011), who was similarly more impaired when synchronizing to a complex stimulus, such as music, than to a metronome. However, a more intriguing profile, never described before, also emerged. S1 and S5 performed like Controls when asked to detect anisochronies (on average, showing d' values of 2.2, 2.0, and 1.5 for 8, 12, and 16% changes, respectively); their performance was also normal in the MBEA (with average Pitch-composite Score = 22.0; Task 4 = 25.5). Nevertheless, they showed very poor synchronization, particularly when tapping to music and to amplitude-modulated noise. In particular, S5′s performance was at chance (significance threshold = .19 vector length) when synchronizing with noise (at all IOIs), and just above chance with music (at chance with 750-ms IBI). It is noteworthy that S1 and S5, despite their poor synchronization, could tap at a spontaneous tempo as the Controls did, hence revealing unimpaired motor control. Notably, because poor synchronization can occur without degraded perceptual functions, the term ‘beat deafness’ is no longer appropriate for characterizing the performance of individuals like S1 and S5. As a more adequate alternative, we propose here ‘pure sensorimotor coupling disorder’; this term will be used below to refer to this condition. S6 and S10 performed similarly to S1 and S5. However, S6, albeit showing poor synchronization with spared beat perception, also exhibited poor pitch perception. S10 manifested poor synchronization limited to isochronous sequences. Yet there are reasons to doubt that S10 is a genuine case of poor synchronization with spared perception. Her poorer performance when synchronizing with a metronome relative to Controls may result from low variability in this task for Controls, most of which performed at ceiling (with vector length around .95 – 1). By any means, S10 synchronized quite consistently (vector length = .83 as compared to.95 for Controls). Finally, two participants (S4 and S7) did not reveal any synchronization or perceptual deficits. The discrepancy of the results obtained with these two participants in Exp. 2 and Exp. 1 is likely to result from the fact that Poor synchronizers were preliminarily identified in Exp. 1 based on accuracy and/or consistency. In particular, S4 and S7, though revealing low accuracy, still exhibited high consistency in Exp. 1. However, in Exp. 2, only consistency was sensitive to synchronization disorders and eventually used to identify Poor synchronizers. Thus, it is not surprising that based on this criterion, S4 and S7 showed unimpaired performance.

To sum up, the analysis of individuals differences revealed that seven out of the 10 Poor synchronizers selected in Exp. 1 had indeed difficulties in synchronizing to the beat of auditory sequences. Poor synchronization was more visible with complex auditory stimuli, like music or amplitude-modulated noise, than with a simple metronome. Different patterns of impairment were found. In some of them, perception and action were disrupted. However, for at least two individuals, poor synchronization was clearly not accompanied by poor perception. This dissociation is in favour of the hypothesis that in some cases poor synchronization may result from inaccurate auditory-motor mapping.

3.3. General discussion

In the present study, we sought to test the hypothesis that poor coupling of movement to the beat of auditory stimuli may result from impaired mapping of perception to action timing. The majority of participants could move synchronously to the beat of auditory stimuli. Yet among approximately 100 participants, seven displayed major difficulties in tapping to the beat of a variety of auditory stimuli, in particular with music and with a rhythmical complex non-musical stimulus (i.e., amplitude-modulated noise), as revealed by the analysis of individual performances (see Table 2). Notably, poor synchronization was associated with reduced error correction, as indicated by a lack of negative lag-1 autocorrelation when participants tapped along with music or noise. These findings indicate that tapping along with complex auditory stimuli, as compared to an isochronous sequence, is more sensitive to timing disorders. However, whether this dissociation is the result of a genuine malfunctioning of specific mechanisms underlying synchronization with complex rhythmical stimuli (e.g., involving several periodicities at different embedded time scales), or merely result of differences in task difficulty, is unknown.

Three Poor synchronizers showed concurrent signs of impoverished pitch perception (as in Dalla Bella & Peretz, 2003). Their difficulty in processing rhythm may stem from inaccurate perception of pitch-variation in music (see Foxton et al., 2006). However, the remaining Poor synchronizers showed normal pitch processing. This finding extends the observation of the single-case reported by Phillips-Silver et al. (2011), thus providing compelling evidence that some individuals in the general population have difficulties in synchronizing the movement to the beat, a phenomenon observed in 4% of the tested sample.

We documented that beat deafness is not a monolithic phenomenon. Among the four Poor synchronizers, two showed the same profile observed in Mathieu (Phillips-Silver et al., 2011), and thus can be qualified as beat deaf. However, the other two, though they could hardly couple their movement to the beat, performed within the normal range in tasks involving perceiving small temporal anisochronies and rhythm discrimination. This condition, reported here for the first time in otherwise unimpaired individuals, has been referred to as 'pure sensorimotor coupling disorder'. The only indication of a similar dissociation comes from a short single-case report of a patient, an amateur musician, with right temporal brain damage extending to the basal ganglia (Fries & Swihart, 1990). The patient, despite unimpaired rhythm recognition, imitation, and discrimination, could not tap along with a metronome and with the beat of a musical excerpt.

These findings show that inaccurate beat perception is not a mandatory condition for showing poor synchronization. Difficulties in coupling movement to the beat cannot exclusively be the result of a faulty beat perception system (as also suggested by Phillips-Silver et al., 2011). A mere disturbance in motor planning or implementation is also unlikely to be the cause of poor synchronization. Indeed, participants with a pure sensorimotor coupling disorder could tap at a very regular spontaneous tempo in absence of a pacing stimulus. A sensorimotor account for explaining this condition seems more likely, whereby an accurate perceptual representation of the beat would be erroneously matched to a motor movement. Note that the possibility of malfunctioning sensorimotor integration/matching mechanisms has been advocated as an important cause of other forms of congenital music disorders in the general population, namely to account for the dissociation between pitch perception and production (i.e., singing) in congenital amusia (e.g., Pfordresher & Brown, 2007; for reviews, see Dalla Bella et al., 2011; Hutchins & Peretz, 2011). Inaccurate singers typically display poor-pitch singing accompanied by poor pitch discrimination (Ayotte et al., 2002; Dalla Bella et al., 2009). This finding led initially to the hypothesis that inaccurate singing may result from the inability to perceive pitch relationships. However, a few cases have been described of highly inaccurate singing coexisting with normal perception (Bradshaw & McHenry, 2005; Dalla Bella et al., 2007; Pfordresher & Brown, 2007). Hence, poor-pitch singing in tone deafness cannot result from a deficit of perception per se. Rather, the mistranslation of auditory pitch information into motor gestures would be responsible for inaccurate singing. A similar explanation is likely to extend to the domain of rhythm perception and production. We suggest here that a mismapping of the extracted beat information from a rhythmical auditory stimulus on to movement timing may lead to poor synchronization to the beat, in absence of degraded perception.

A sensorimotor account of poor synchronization is compatible with the existing cognitive models of synchronization based on synchronized tapping (e.g., Jacoby & Repp, 2012; Repp, 2005, 2006; Vorberg & Wing, 1996; Vorberg & Schulze, 2002). According to these models, coupling movement to a regular auditory stimulus involves general-purpose perceptual and motor implementation processes, an internal timekeeper, and correction mechanisms (i.e., phase and period correction). The internal timekeeper generates periodic pulses, which adjust to the temporal properties of the pacing stimulus (e.g., an isochronous sequence). Correction mechanisms allow maintaining synchronization via the adjustment of the phase or of the period of the internal timekeeper, for example when confronted with a perturbation of the pacing stimulus. These mechanisms are underpinned by both subcortical brain networks (e.g., the basal ganglia and the cerebellum) and by cortical regions (e.g., the supplementary motor area, the superior temporal gyrus, and dorsal premotor cortex) (see Chen, Zatorre, & Penhune, 2006; Chen, Penhune, & Zatorre, 2008; Wing, 2002; Zatorre, Chen, & Penhune, 2007).

Our findings indicate that poor synchronization dissociates from both poor beat perception and impaired rhythm production (e.g., in spontaneous tapping). Thus, poor synchronization, at least in some cases, cannot be the outcome of poor perception or impaired motor implementation. Deficient synchronization in this condition may rather result from increased timekeeper variability or from a malfunctioning of automatic phase correction mechanisms or period correction processes more relying on attention and awareness (Repp & Keller, 2004). The finding that Poor synchronizers showed positive lag-1 autocorrelation when synchronizing with complex stimuli in indicative of malfunctioning correction mechanisms, a possibility that should be examined in further studies. These processes are likely under the control of subcortical regions such as the basal ganglia and the cerebellum in connection with premotor cortical regions (Middletone & Strick, 2000; Zatorre et al., 2007). For example, there is evidence of increased variability in synchronization tasks linked to disrupted phase correction or period correction in patients with Parkinson's disease or with focal lesions of the basal ganglia (e.g., Diedrichsen, Ivry, & Pressing, 2003; Schwartze, Keller, Patel, & Kotz, 2011). The basal ganglia may also play a relevant role in the understanding of poor synchronization, given their role in beat-based timing as indicated in a growing number of neuroimaging studies (e.g., Grahn & McAuley, 2009; Grahn & Rowe, 2009). So far, little is known about the neuronal substrates of synchronization disorders. However, that cases of poor synchronization can be identified easily with a sensitive set of synchronized tapping tasks, as demonstrated in our study, should stimulate further research on the neuronal underpinning of this condition in the coming years.

To conclude, the results of the present study show that a small number of individuals in the general population have major difficulties in moving to the beat of music (or of a comparable complex auditory stimulus), without impaired pitch processing. Poor sensorimotor coupling has been found, particularly with complex auditory stimuli. An open question to be investigated in future studies is whether this deficit extends to other domains (e.g., to linguistic stimuli) or modalities (i.e., visual and tactile). Moreover, poor synchronization to the beat may have different causes, such as perceptual disorders (i.e., beat deafness), or faulty auditory-motor mapping (i.e., pure sensorimotor coupling disorder). These findings stimulate further research to uncover whether perception and action in timing are subserved by separate neuronal pathways, as has been suggested for pitch processing (Griffiths, 2008; Loui et al., 2008).

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