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Synchronisation rythmique déficiente chez l'humain: Bases comportementales

par Pauline Tranchant

Département de Psychologie, Faculté des Arts et des Sciences

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Résumé

Les humains ont naturellement tendance à bouger sur le *beat* de la musique. Bien que spontané, ce comportement nécessite d'extraire une régularité d'un signal acoustique complexe, ainsi que d'aligner le mouvement à cette périodicité. Il n'est donc pas surprenant que certains individus éprouvent de la difficulté à se synchroniser au beat. Quelques cas ont été décrits ces dernières années. Des causes telles qu'une déficience intellectuelle, de l'ouïe, motrice, ou encore du traitement de la hauteur des notes musicales ont été écartées; leur difficulté semble donc spécifique au traitement du beat.

Le but de la thèse est de clarifier la nature d'un tel trouble comme moyen d'éclairer les théories du traitement du beat chez l'humain. Dans un premier temps, nous avons utilisé des mouvements naturels et de la musique populaire originale pour détecter, au sein d'un grand échantillon de jeunes adultes, des individus présentant une faible capacité de synchronisation au beat. Une gradation est apparue: certains cas ont échoué dans toutes les conditions tandis que d'autres ont échoué à plier les genoux mais pas à frapper des mains, sur certaines musiques.

Nous avons ensuite étudié un groupe de neuf jeunes adultes présentant une synchronisation déficiente à travers deux formes de mouvement (taper du doigt, rebondir en pliant les genoux). Nous avons évalué la capacité du groupe à juger si un métronome superposé à un extrait musical est ou non aligné sur le beat de celui-ci, et observé un moins bon résultat lorsque comparé à un groupe typique. Cette observation est compatible avec une théorie motrice du beat, où la perception dépend de l'oscillation de populations de neurones dans les régions motrices du cerveau. Néanmoins, six cas de synchronisation déficiente ont obtenu un résultat faible mais dans la norme au test de perception. A l'inverse, un résultat indiquant une perception déficiente malgré une synchronisation faible mais dans la norme a été observé chez deux participants faisant initialement partie du groupe typique. Ces dissociations remettent en question la théorie motrice du beat, pas fermement toutefois puisque les huit cas cités ont obtenu des scores généralement faibles. Nos résultats sont plutôt compatibles avec une origine centrale et commune du trouble de traitement du beat, affectant à la fois perception et synchronisation.

Nous avons finalement montré que le trouble est associé à une déficience du traitement temporel à un niveau fondamental, au moyen de deux conditions: taper du doigt de façon régulière sans stimulation et se synchroniser au métronome et maintenir les tapes après que les sons aient cessé, pour des intervalles couvrant le spectre des tempi accessibles (225-1709 millisecondes). Nous avons testé huit des neuf cas de synchronisation déficiente (étude précédente) et observé une moins bonne régularité ainsi qu'une moins bonne flexibilité au changement de tempo que chez des participants contrôles appariés.

Dans l’ensemble, nos résultats indiquent qu’une synchronisation et une perception déficientes du beat sont associées, et que le trouble pourrait provenir d'une altération de mécanismes fondamentaux du traitement temporel.

Mots-clés: musique, beat, synchronisation, mouvement, temporel, troubles sensori-moteurs

Abstract

Humans across cultures show the propensity to move in time with the beat of music. Despite the spontaneous nature of this behavior, it is one that requires the abstraction of periodicities from acoustically complex signals and the temporally precise coupling between auditory perception and motor action. It is therefore not surprising that some individuals exhibit difficulties to synchronize movements with the beat of music; a few such cases have been reported in recent years. Importantly, their lack of synchronization seems to be attributable to a disorder specific to beat processing, as these individuals did not present deficient intelligence, motor or hearing disabilities, or deficient pitch-related musical processing in previous studies.

The aim of this thesis was to clarify the nature of this beat synchronization impairment, as a way to shed light on theories of beat processing in humans. As a first step, we used ecological conditions - natural movements and commercially available music - to screen for synchronization deficits in a large pool of young adults. This approach revealed a gradient of synchronization difficulties across movement types and stimulus complexity. While some individuals displayed an inability to bounce their body and clap their hands with all stimuli, others failed to bounce to a few songs only.

Next, we studied a group of nine individuals ("beat-impaired") with deficient synchronization across tapping and bouncing movement forms. We tested their capacity to detect a misalignment of a superimposed metronome soundtrack to the beat of music. We found lower performance for this detection task in the beat-impaired group as compared to typical adults. This association of perception and production deficits is in line with a motor theory of beat finding, according to which beat perception depends on neural oscillations in motor regions of the brain. Nevertheless, we observed deficient synchronization in six beat-impaired cases who were able to perceive the beat normally, albeit in the low range. The opposite pattern, i.e. low but normal synchronization performance in spite of deficient detection, was observed in two other participants initially from the typical group. These dissociations question the motor theory of beat finding, albeit not strongly so, because the eight cases performed poorly in general. Our results thus point towards a central origin of beat impairments, which affects both perception and synchronization.

In line with this view, we also showed that deficient synchronization to a musical beat is linked to faulty timekeeping core mechanisms. In this last study, we used two tapping conditions: spontaneous production of a regular sequence and synchronization-continuation with metronome stimuli covering the range of predictive timing in humans (225-1709 milliseconds). By testing eight of the nine beat-impaired cases from the previous study, we found higher temporal variability across conditions and poorer rate flexibility in paced tapping, as compared to a group of closely matched control participants.

Altogether, our findings highlight an association between beat perception and synchronization impairments, which may emerge from disrupted timekeeping functions.

Keywords: music, beat, synchronization, movement, timekeeping, sensorimotor impairments

Table des matières

Liste des tableaux

Article 1:

Article 2:

Article 3:

Liste des figures

Chapitre 1:

Article 1:

Article 2:

Article 3:

Liste des abréviations

supp.: supplémentaire

ms: millisecondes

EEG: électroencéphalographie/elecroencephalography

MEG: magnétoencéphalographie

IRMf: imagerie par résonance magnétique fonctionnelle

ASAP: Action Simulation for Auditory Prediction

MBEA: Montreal Battery of Evaluation of Amusia

BAT: Beat Alignment Test

MMN: mismatch negativity

BRAMS: International Laboratory for Brain, Music, and Sound Research

SMS: sensorimotor synchronization

M: mean

BPM: beats per minute/beats par minute

IBI: inter-beat-interval

MIR: music information retrieval

W: watt

mm: millimeter

ANOVA: analysis of variance

Mdn: median

IIRI: inter-response-interval

SR: synchronization regularity

CV: coefficient of variation

SD: standard deviation

NSERC: Natural Sciences and Engineering Research Council of Canada

CRBLM: Center for Research on Brain, Language, and Music

n.s.: not significant

SMA: supplementary motor area

PMC: premotor cortex

FSR: force-sensing resistor

USB: universal serial bus

WAIS-III: Wechsler Adult Intelligence Scale - III

IOI: inter-onset-interval

ITI: inter-tap-interval

P0: spontaneous rate

S.T. spontaneous tapping

BI: beat-impaired

RPD: rhythm processing deficits

ADT: anisochrony detection task

BAASTA: Battery for the Assessment of Auditory Sensorimotor and Timing Abilities

H-BAT: Harvard-Beat Alignment Test

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Chapitre 1: Contexte théorique

1.1 Positionnement de la thèse

À travers les cultures, les humains ont naturellement tendance à bouger sur le rythme de la musique (Nettl, 2000). Taper des mains à un concert, se déhancher sur le *dancefloor,* ou encore marcher au pas d'une musique militaire sont autant d'exemples. Dans la plupart des situations, le mouvement est synchronisé à une forme de périodicité; le *beat* de la musique.

Malgré son apparente simplicité, la synchronisation au beat musical est un comportement qui repose sur des mécanismes cognitifs sophistiqués. Pour la plupart des styles musicaux il n'existe en effet pas de correspondance systématique entre le beat et les évènements (sons) formant le signal acoustique. C'est particulièrement le cas pour des rythmes dits syncopés, où la plupart des temps du beat coïncident avec des silences (Snyder & Krumhansl, 2001; Velasco & Large, 2011). Le beat musical est un construit perceptif exigeant de l'auditeur qu'il induise une périodicité à partir d'un signal complexe. Se synchroniser au beat n'est donc pas simplement réagir à des sons, mais bien un comportement nécessitant des capacités de prédiction dans le domaine temporel (van der Steen & Keller, 2013).

Il n'est dès lors pas étonnant que quelques individus puissent éprouver de la difficulté à bouger de façon synchronisée sur le beat de la musique. Bien des gens vous diront qu'ils connaissent au moins une personne "qui a deux pieds gauche en danse", ou encore "qui n'a vraiment pas le rythme dans la peau". Le premier cas d'un individu présentant une difficulté marquée à danser sur le beat a été décrit par une équipe de notre laboratoire il y a quelques années (Phillips-Silver, Toiviainen, Gosselin, Piché, Nozaradan, Palmer et al., 2011). Le mouvement testé consistait à se balancer verticalement en pliant les genoux ("*bouncing*"). L'individu en question, Mathieu, ne présentant aucun autre trouble diagnostiqué, que ce soit cognitif, neurologique ou moteur. En outre, il n'avait pas de difficulté à traiter la hauteur des notes musicales; sa condition était donc spécifique à la dimension temporelle du traitement musical. Quelques cas comparables à Mathieu ont été décrits depuis 2011 (Bégel, Benoit, Correa, Cutanda, Kotz & Dalla Bella, 2017a; Palmer, Lidji, & Peretz, 2014; Sowiński & Dalla Bella, 2013; Tranchant, Vuvan, & Peretz, 2016).

L'étude de tels cas constitue une opportunité de mieux comprendre les processus de la perception et de la synchronisation au beat de la musique, selon l'approche neuropsychologique consistant à fractionner les éléments formant un système cognitif normal par l'investigation de ses déficiences. Par exemple, l'étude de l'amusie congénitale, ou *pitch-deafness*, a permis de révéler l'importance d'une boucle récurrente entre cortex fronto-pariétal et auditif pour le traitement conscient de la structure mélodique (pour une revue récente voir Peretz, 2016).

L'objectif général de cette thèse est de documenter et clarifier la nature du trouble de synchronisation au beat de la musique. Pour cela, au Chapitre 2 sont présentés trois articles scientifiques constituant le corps de la thèse. Le présent chapitre est consacré aux connaissances actuelles sur les mécanismes de la perception et synchronisation au beat (Section 1.2), aux origines évolutive (Section 1.3) et développementale (Section 1.4) de ces capacités, à la revue des études, mentionnées plus haut, portant sur les troubles de la synchronisation au beat musical (Section 1.5), et enfin à l'exposé plus détaillé des objectifs de la thèse. Nous terminons au Chapitre 3 par une discussion générale des résultats, et par la présentation de perspectives pour de futures recherches.

1.2 Mécanismes et modèles de la synchronisation au beat

Le rythme en musique réfère aux motifs temporels des évènements qui constituent le signal acoustique. La perception du beat réfère quant à elle à la superposition d'une grille isochrone à une séquence rythmique qui la plupart du temps n'est pas isochrone (voir Figure 1 plus bas). La synchronisation au beat musical est un processus prédictif (Rankin, Large, & Fink, 2009; van der Steen & Keller, 2013; van der Steen, Jacoby, Fairhurst, & Keller, 2015), où le mouvement est aligné de façon précise avec les temps du beat (Snyder & Krumhansl, 2001), voire légèrement en avance sur ceux-ci (Patel, Iversen, Chen, & Repp, 2005). Le beat musical offre dès lors un référent temporel permettant la production d'actions motrices qui soient coordonnées entre individus (p. ex. orchestre, danse de couple, etc.).

Du point de vue cognitif, il est plus facile de mémoriser et reproduire des séquences complexes si elles permettent l'induction d'un beat, en comparaison à des séquences dont la structure rythmique ne favorise pas l'induction d'un beat (Chen, Penhune, & Zatorre, 2008b; Grahn & Brett, 2007; Grahn, & Brett, 2009). Du point de vue de la théorie de l'information, l'isochronie est en effet la forme la plus déterministe et prévisible de séquence rythmique (p. ex. Ravignani & Madison, 2017). Ceci explique peut-être le biais en faveur de l'isochronie qui est observé chez l'humain: des séquences composées d'intervalles irréguliers entre les sons subissent une distorsion vers un certain degré de régularité (Drake & Gérard, 1989; Drake & Bertrand, 2001; voir également Madison & Merker, 2002).

Au cours des années, les mécanismes qui sous-tendent le traitement du beat ont majoritairement été étudiés via un paradigme consistant à taper du doigt (*tapping*) sur le métronome (pour des revues, voir Repp, 2005; Repp & Su, 2013). De nombreuses études ont montré que les tapes sont produites en avance de quelques dizaines de millisecondes sur les sons, confirmant le caractère prédictif de la synchronisation audio-motrice. Ce phénomène a été qualifié d'asynchronie moyenne négative (Repp, 2005). L'asynchronie réfère à la différence temporelle entre le son et la tape; au plus elle est grande au plus la tape est distante du son. La taille de l'asynchronie est sujette à de larges différences entre individus et peut même être nulle chez certains musiciens (Repp, 2004). Elle dépend également du *feedback* sensoriel dont dispose celui qui se synchronise. Par exemple, l'asynchronie augmente considérablement lorsqu'une anesthésie supprimant la sensation tactile est administrée au doigt (Aschersleben, Gehrke, & Prinz, 2001). À l'inverse, la présence de feedback auditif (un son est généré à chaque tape) permet de réduire l'asynchronie (Aschersleben & Prinz, 1995; 1997; Mates, 1994). Ces observations suggèrent que l'asynchronie moyenne négative reflète une différence dans vitesse de traitement de l'information sensorielle entre modalités sensorielles (Aschersleben, 2002); auditive et tactile dans le cas du tapping sur métronome.

Une autre caractéristique du beat est qu'il peut être perçu à travers une assez large fourchette de tempi. Le tempo réfère à l'intervalle entre deux beats (la période): au plus l'intervalle est petit au plus le tempo est rapide. L'analyse d'une compilation de 12 148 morceaux de musique spécialement créés pour invoquer une forte sensation de beat (*dance music*) a révélé que pratiquement tous les morceaux ont une période se situant entre 320 et 760 ms, avec médiane à 451 ms (van Noorden & Moelants, 1999). La fourchette des tempi donnant lieu à la perception d'un rythme est cependant bien plus large, allant de 100 ms à environ 2500 ms (London, 2002; McAuley, 2010). En dessous de 100 ms, les évènements sonores sont difficiles à distinguer les uns des autres, tandis qu'au-dessus de 2500 ms ils apparaissent trop isolés.

Quant à la synchronisation, la limite inférieure (tempo rapide) se situe autour d'une période de 150-200 ms (McAuley, Jones, Holub, Johnston, & Miller, 2006; Repp, 2003) et serait en partie fixée par la vitesse maximale à laquelle le doigt peut effectuer les tapes (Cousins, Corrow, Finn, & Salamone, 1998). La limite supérieure (tempo lent) se situe autour d'une période de 1800-2000 ms. Au-delà, il devient difficile d'anticiper les sons du métronome si bien que la synchronisation devient réactive plutôt que prédictive; les tapes sont en retard sur les sons (Mates, Müller, Radil, & Pöppel, 1994). Il s'agirait donc de la limite supérieure d'un mécanisme cognitif capable de prédire l'intervalle entre deux beats.

Entre ces tempi extrêmes, il existe une zone pour laquelle la perception de séquences isochrones est optimale. Drake et Botte (1993) ont mesuré les seuils différentiels de tempo, c'est-à-dire la plus petite différence entre deux séquences de sons qu'un auditeur puisse détecter, pour des intervalles allant de 100 à 1500 ms. Ces chercheuses ont observé une zone de détection optimale se situant entre 300 et 800 ms (voir également Drake & Baruch, 1995 1997), ce qui correspond pratiquement à la fourchette de tempi décrite par Van Noorden et Moelants (1999) pour la musique de danse. Comme on peut s'y attendre, la zone de synchronisation optimale correspondrait à la zone de perception optimale (400-800ms; Fraisse, 1982).

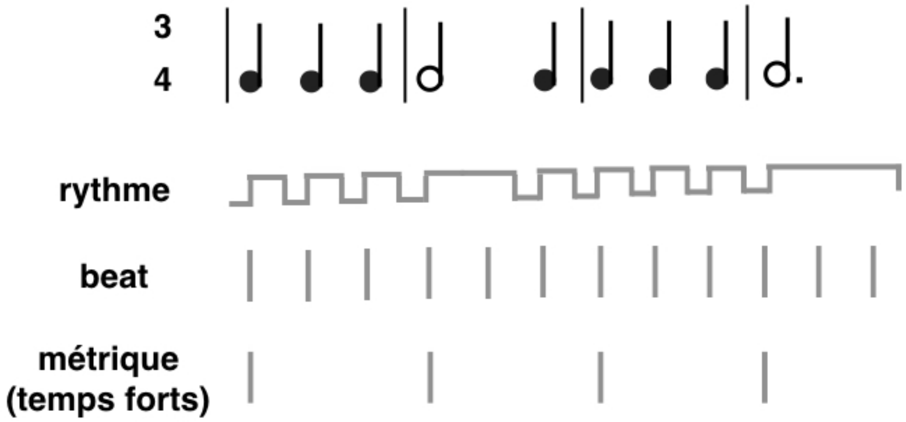
Enfin, il existe au sein de cette zone optimale une préférence encore plus serrée: le tempo préférentiel (perception) ou spontané (production). La valeur la plus communément rapportée dans la littérature se situe autour de 500-600 ms (Moelants, 2002). Le tempo préférentiel correspond à celui d'un métronome dont la vitesse semble la plus appropriée du point de vue perceptif, ni trop rapide, ni trop lent. Le tempo spontané est observé lorsqu'on fait produire une séquence régulière d'intervalles à la vitesse qui semble la plus naturelle. Bien qu'il s'agisse de mesures assez subjectives, elles sont relativement stables à travers le temps (Harrell, 1937; Smoll, 1975). Une étude a de plus montré que tempo préférentiel et spontané sont corrélés, suggérant une base commune à ces deux phénomènes (McAuley et al., 2006). Les auteurs de cette étude ont également montré que le tempo spontané ralentit avec l'âge: il se situe autour de 300ms chez les enfants de moins de huit ans pour ensuite rejoindre ce qui est observé chez les adultes, soit entre 500 et 600 ms (voir également Drake, Jones, & Baruch, 2000).

La zone optimale de perception et synchronisation ainsi que la préférence de tempo sont des phénomènes qui ont été interprétés suivant l'approche des oscillateurs pour l'étude de la coordination temporelle (p. ex. McAuley, 2010). Selon cette approche, le tempo préférentiel/spontané reflète la période naturelle d'un oscillateur interne et la synchronisation est le résultat du couplage unidirectionnel entre oscillateur interne et stimulation externe (p. ex. Large & Kolen, 1994; Drake et al., 2000; McAuley et al., 2006). Cette oscillation correspondrait à une modulation périodique de l'attention (Large & Jones, 1999), dont les pics de sensibilité (c. à d. les points dans le temps où l'attention est maximale) s'aligneraient sur les beats du stimulus. Ce couplage entre oscillation interne et stimulation externe s'effectue par un processus d'adaptation de la phase et de la période de l'oscillateur interne vers celles du stimulus.

Les mécanismes par lesquels s'opèrent ces adaptations ont typiquement été étudiés par l'introduction de perturbations temporelles dans des séquences de métronome. Ces perturbations prennent la forme d'un décalage local de la phase ou d'un changement de période (tempo). Un décalage de phase signifie qu'un des sons apparaît en retard ou en avance sur le moment attendu, avec conservation de la période initiale pour les intervalles suivant la perturbation. Un changement de période signifie qu'un intervalle et les suivants sont plus longs ou plus courts que ceux de la période initiale. Le processus de réalignement des tapes sur les sons après une perturbation de phase est rapide, automatique, et repose sur des mécanismes de relativement bas niveaux (Repp, 2002; 2005). Adapter la période de l'oscillateur après une perturbation de période est un processus plus lent (Large, Fink, & Kelso, 2002), requérant un contrôle actif et probablement des mécanismes cognitifs de plus haut niveau (Repp, 2005).

L'approche des oscillateurs n'est pas seulement utile pour décrire la synchronisation au métronome; elle l'est également pour décrire la perception et la synchronisation au beat musical. Le passage n'est cependant pas direct. Le rythme musical présente en effet une caractéristique importante qu'un simple oscillateur ne peut modéliser: l'organisation du beat en niveaux hiérarchiques, appelée métrique (Lerdahl & Jackendoff, 1983). Certains temps du beat sont perçus comme plus accentués que d'autres et constituent des temps forts (Figure 1). Une marche par exemple est caractérisée par l'alternance d'un temps fort et d'un temps faible; il s'agit d'une métrique binaire. Une valse est quant à elle caractérisée par l'alternance d'un temps fort et de deux temps faibles; il s'agit d'une métrique ternaire. Ces niveaux hiérarchiques peuvent être observés dans le mouvement produit en réponse à la musique. Pour un même morceau de musique, différentes personnes se synchroniseront spontanément sur différents niveaux du beat. Drake, Baruch et Jones (2000) ont par exemple montré que des enfants ayant une formation musicale synchronisent leurs tapes à un niveau plus lent que les enfants n'ayant pas reçu de telle formation. Des variations s'observent également en fonction de la partie du corps qui effectue le mouvement: typiquement les membres distaux bougent à un niveau correspondant à un tempo plus rapide que le tronc (Toiviainen, Luck & Thompson, 2010; Burger, Thompson, Luck, Saarikallio & Toiviainen, 2014). Pour rendre compte de l'existence de cette organisation hiérarchique du beat, un système cette fois non pas constitué d'un mais de plusieurs oscillateurs couplés les uns aux autres a été proposé (Large & Kolen, 1994; Large, 2000).

Figure 1: Séquence musicale: rythme, beat et métrique (exemple d'une valse).



L'approche des oscillateurs est également utilisée pour rendre compte des corrélats neuraux du beat musical. Selon la théorie de la "résonance neurale" (Large & Snyder, 2009; Large, 2010), la perception du beat résulterait du couplage temporel (communément appelé *entrainment* dans la littérature) entre l'activité oscillatoire de réseaux de neurones et la stimulation rythmique. Les pics d'amplitude correspondraient à de l'activité dans les basses fréquences (bande delta; < 4 Hz), et qui s'aligneraient sur les beats. La synchronisation d'une telle activité neurale à des stimulations rythmiques complexes a été observée dans plusieurs études d'électro-encéphalographie (EEG; Nozaradan, Peretz, & Mouraux, 2012; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Zerouali, Peretz, & Mouraux, 2013). Une étude en magnéto-encéphalographie (MEG) a également montré que des bouffées ("*bursts*") d'oscillation dans les bandes de fréquence beta (15-30 Hz) et gamma (> 30 Hz) sont couplées dans le temps avec les sons du métronome (Fujioka, Trainor, Large, & Ross, 2009). Les auteurs de cette étude ont proposé que la modulation d'activité dans la bande beta - traditionnellement associée à des tâches motrices - joue un rôle dans la communication entre zones auditives et motrices du cerveau lors de la perception du beat.

Il existe en effet un lien spécial entre aspects perceptifs et moteurs du beat. Lorsque nous entendons de la musique entraînante, nous éprouvons bien souvent l'envie spontanée de bouger sur son beat (Janata, Tomic, & Haberman, 2012). Plus qu'une simple réaction, le mouvement produit jouerait un rôle actif dans la prédiction des temps du beat (Manning & Schutz, 2013; Su & Pöppel, 2012), voire influencerait la représentation que l'on se fait de son organisation métrique (Chemin, Mouraux, & Nozaradan, 2014; Naveda & Leman, 2009; Phillips-Silver & Trainor, 2007). Par exemple, lorsqu'on présente à des participants un rythme ambigu, c'est-à-dire qui puisse être interprété selon une métrique binaire ou ternaire, leur perception sera biaisée en faveur de la métrique sur laquelle ils ont préalablement synchronisé leur mouvement (voir également Phillips-Silver & Trainor, 2005; 2007). Des études en imagerie fonctionnelle par résonance magnétique ont de plus démontré que, même en l'absence de mouvement, certaines aires motrices corticales (cortex prémoteur, aire motrice supplémentaire) et sous-corticales (cervelet, ganglions de la base) sont activées lors de la perception du beat même en l'absence de mouvement (Bengtsson, Ullén, Ehrsson, Hashimoto, Kito, Naito et al., 2009; Chen et al., 2008a; Grahn & Rowe, 2009; Kung, Chen, Zatorre, &

Penhune, 2013).

Se basant sur ces résultats d'imagerie, Patel et Iversen (2014) ont émis l'hypothèse selon laquelle l'activation des aires motrices jouerait un rôle causal dans la perception du beat ("Action Simulation for Auditory Prediction"; ASAP). Plus précisément, la prédiction du beat serait facilitée par la *simulation* de mouvement périodique, même lorsque qu'aucune action motrice n'est produite de façon manifeste. Cette facilitation aurait lieu grâce à une communication temporelle précise entre régions motrices et auditives dans les deux directions, possiblement via l'activité oscillatoire dans la bande beta (Fujioka, Trainor, Large, & Ross, 2012). Ce serait grâce à un réseau particulièrement développé de neurones reliant les régions auditives aux régions de planification motrice via le cortex pariétal (*auditory dorsal pathway*) que prendrait place cette communication.

En particulier, Patel & Iversen (2014) insistent sur le fait que certaines parties de ce réseau seraient moins développées chez les singes que chez les humains, ce qui constituerait une explication potentielle des capacités inférieures de prédiction du beat chez les premiers comparés aux seconds (voir également Merchant & Honing, 2014). Plus généralement, l'étude comparative des capacités rythmiques à travers les espèces permet de mieux comprendre la spécificité des mécanismes sous-tendant le traitement du beat musical, et d'aborder la question de leur origine évolutive. Nous présentons dans la prochaine section un aperçu des connaissances actuelles dans ce domaine.

1.3 Origine évolutive de la synchronisation au beat

Si elle a longtemps été considérée spécifique à l'espèce humaine (p.ex. Fitch, 2012), nous savons aujourd'hui que la capacité de synchronisation du mouvement à la musique est présente au sein du règne animal.

Patel, Iversen, Bregman & Schulz (2009) ont les premiers décrit le cas d'un cacatoès (une sorte de perroquet), Snowball, devenu star internationale de Youtube pour son petit balancement de tête sur le tube "Everybody" des Backstreet Boys. Dans les conditions du laboratoire, ces auteurs ont montré que le mouvement de Snowball est aligné de façon prédictive sur le beat, mais par intermittence seulement. En effet, des épisodes pour lequel le mouvement était synchronisé au beat n'ont été observés que pour un peu plus de la moitié (58%) des séquences musicales sur lesquelles du mouvement a été observé, et lorsque présents ces épisodes ne couvraient qu'une partie de la séquence. Ceci contraste avec ce qui est observé chez les humains adultes, chez qui la synchronisation tend à être stable à travers les séquences musicales (Burger et al., 2014; Snyder & Krumhansl, 2001). Les auteurs de l'étude ont appelé les épisodes transitoires de synchronisation "bouts", un terme que nous adopterons dans la suite du texte. De plus, un certain degré de flexibilité de tempo a été démontré chez Snowball, néanmoins moins grand que ce qui est typiquement observé chez les humains (voir section 1.2). En effet, alors que quelques bouts ont été observés sur des stimuli vingt pour cent plus rapides (462 ms soit 130 beats par minute; BPM) que le tempo original de la chanson (552 ms; 108.7 BPM), aucun bout n'a été observé pour des tempi dix pour cent (ou au-delà) plus lents (613 ms; 97.8 BPM). Notons que ce niveau de flexibilité, même si restreint, distingue la synchronisation chez Snowball du phénomène de *synchronous chorusing* observé chez certaines espèces d'insectes (pour plus de détails voir Ravignani, Bowling, & Fitch, 2014). Par exemple, les lucioles mâles tentant d'attirer les femelles émettent des flashs lumineux synchronisés au niveau du groupe, mais avec pratiquement aucune flexibilité de tempo. Enfin, notons qu'un comportement de synchronisation comparable à celui de Snowball a été montré chez un autre perroquet, Alex (Schachner, Brady, Pepperberg, & Hauser, 2009).

Que ce soit chez Snowball ou Alex, la synchronisation à la musique s'est manifestée de façon spontanée, comme c'est le cas chez l'humain. Chez le singe, mesurer la synchronisation à une séquence rythmique auditive requiert en revanche un effort considérable d'entraînement. Il a fallu de onze à 25 mois d'entraînement avant que (Zarco, Merchant, Prado, & Carlos Mendez, 2009) puissent observer une synchronisation au métronome (cinq tapes en tout) chez trois singes rhésus. Ceux-ci ont démontré une bonne flexibilité de tempo (de 450 à 1000 ms), cependant, leurs tapes étaient systématiquement en retard d'environ 250 ms sur les sons. Le délai entre sons et tapes restait cependant inférieur aux temps de réaction observés avec des séquences au décours temporel imprévisible. Donc, la synchronisation chez ces singes n'était pas entièrement réactive, mais pas ne présentait pas non plus le niveau de prédiction qui caractérise la synchronisation chez l'humain et les perroquets.

La capacité restreinte pour la synchronisation chez les singes va dans le sens du lien entre apprentissage vocal et synchronisation proposé par Aniruddh Patel (2006; 2014). L'apprentissage vocal désigne la production par la voix de sons nouveaux, guidée par l'expérience auditive et la rétroaction sensorielle (p. ex. Janik & Slater, 1997; Merker, 2005). Selon A. Patel, seules les espèces animales ayant la capacité d'apprentissage vocal, incluant les perroquets mais pas les singes, seraient capables de synchronisation prédictive à un beat musical. Le circuit cérébral sous-tendant la perception du beat et connectant les régions auditives aux régions motrices (auditory dorsal pathway; voir section 1.2), se serait initialement développé au cours de l'évolution aux fins de l'apprentissage vocal (Patel, 2006; Patel & Iversen, 2014).

Cette vision va dans le sens d'une fonction évolutive non-adaptative du beat musical. Non-adaptative signifie que le traitement du beat ne serait pas apparu parce qu'il favorise la survie de l'espèce mais parce qu'il recrute des circuits qui se sont développés pour sous-tendre des fonctions, elles, utiles à la survie. L'apprentissage vocal n'est cependant pas la seule fonction candidate à ce titre. David Huron (2001) mentionne par exemple la "théorie non-adaptative de recherche du plaisir" pour expliquer l'origine de la musique. Bouger sur le beat de la musique est source de plaisir intense (Janata et al., 2012), peut-être parce que l'alignement du mouvement avec le beat informe le cerveau que la prédiction qu'il a formée est correcte (Salimpoor, Zald, Zatorre, Dagher, & McIntosh, 2015). Le beat musical pourrait donc être apparu parce qu'il active les circuits cérébraux de la récompense (Salimpoor, van den Bosch, Kovacevic, McIntosh, Dagher & Zatorre, 2013) qui se seraient développés pour des fonctions servant directement à la survie, comme le sexe ou l'ingestion de nourriture, par exemple.

Notons finalement que le lien entre apprentissage vocal et synchronisation rythmique est remis en question par des études menées auprès d'espèces animales ne présentant pas la capacité d'apprentissage vocal. Large et Gray (2015) ont mesuré le tempo spontané ainsi que la synchronisation visuelle avec un expérimentateur chez un bonobo (espèce n'ayant pas démontré la capacité d'apprentissage vocal), Kuni. Bien que Kuni ait produit des bouts synchronisés pour l'ensemble des tempi testés, la grande majorité des bouts a été observée pour les tempi proches de son tempo spontané (222 ms). Malgré des différences importantes dans les méthodologies employées, les résultats de Kuni présentent des similarités importantes avec ceux obtenus chez les perroquets: synchronisation intermittente, proportion et longueur des bouts comparables, et flexibilité à travers les tempi présente mais restreinte.

Enfin, Cook, Rouse, Wilson & Reichmuth (Cook, Rouse, & Wilson, 2013) ont entraîné par conditionnement opérant l'otarie Ronan (à nouveau, pas d'apprentissage vocal démontré chez cette espèce) à synchroniser le mouvement de tête avec des séquences auditives (métronome et musique). Les auteurs de l'étude ont montré que Ronan est capable de se synchroniser à l'entièreté des stimuli présentés (420 à 833 ms). Donc, la synchronisation a eu lieu pour une fourchette de tempi au moins aussi large que chez les perroquets, et de façon stable plutôt que par bouts. Néanmoins, pour les tempi plus rapides (< 462 ms) le mouvement était légèrement en retard par rapport aux temps du beat, contrairement à ce qui a été observé pour les tempi plus lents. Ces résultats montrent donc un bon degré de flexibilité, mais avec une dépendance au tempo pour le caractère prédictif de la synchronisation, contrairement à ce qui est observé chez les humains où la synchronisation reste prédictive pour les tempi rapides.

Les deux études présentées ci-dessus (Large & Gray, 2015; Cook et al., 2013) montrent donc que les capacités de synchronisation rythmique pourraient être plus répandues que précédemment conjecturé (p. ex. Fitch, 2012, Patel 2006). Patel (2014) mentionne toutefois que l'otarie est une espèce apparentée à la baleine et au morse, qui ont la capacité d'apprentissage vocal, et qu'il se pourrait donc que des circuits cérébraux sous-tendant l'apprentissage vocal soient présents chez elle. Pour ce qui est des singes, il reste à vérifier si la synchronisation à un beat *musical* est possible pour que l'hypothèse du lien entre apprentissage vocal et synchronisation motrice proposée par Patel (2006) puisse être définitivement remise en question.

On voit donc que l'origine évolutive de la synchronisation au beat musical n'est pas encore bien comprise et que la recherche comparative auprès des animaux génère des débats au sein de la communauté scientifique. Il s'agit d'un domaine de recherche en pleine expansion qu'il sera intéressant de suivre au cours des prochaines années.

1.4 Origine développementale de la synchronisation au beat

Nous avons exposé jusqu'ici les principales caractéristiques de la synchronisation au beat chez l'humain adulte et vu en quoi elles sont ou non présentes chez les animaux. Nous allons à présent décrire la trajectoire développementale des capacités de synchronisation chez l'humain.

Deux études ont étudié le mouvement spontané précoce en réponse à la musique: chez les bébés (3-4 mois; Fujii, Watanabe, Oohashi, Hirashima, Nozaki & Taga, 2014) et chez les tout jeunes enfants (5-24 mois; Zentner & Eerola, 2010). Seuls deux des 30 bébés inclus dans l'étude de Fujii et al. (2014) semblaient produire une réponse motrice à la musique par des mouvements rythmiques des jambes et des bras (les bébés étaient allongés sur le dos). La réponse n'a cependant été observée que par bouts, qui étaient systématiquement synchronisés au beat chez un des deux bébés seulement. Les enfants dans l'étude de Zentner & Eerola (2010) étaient assis sur les genoux de leurs parents et bougeaient le torse, les bras et les jambes, à nouveau par bouts non-synchronisés au beat des stimuli musicaux. Ces deux études montrent donc qu'avant l'âge de deux ans, la synchronisation spontanée du mouvement à la musique est un phénomène probablement assez rare.

Kirshner et Tomasello (2009) ont étudié des enfants un peu plus âgés (deux ans et demi à quatre ans et demi), et montré qu'un incitatif social permet d'améliorer la synchronisation. La tâche consistait à taper des mains sur un tambour avec soit un partenaire adulte, soit une machine imitant un bras tapant sur le tambour, soit un stimulus auditif dispensé par un haut-parleur. Les auteurs de l'étude ont montré que, bien que l'alignement entre tapes et sons était en général inférieur à ce qui est typiquement observé chez l'adulte, la synchronisation était possible quel que soit l'âge. Surtout, ils ont observé une synchronisation de meilleure qualité dans la condition avec partenaire humain.

Enfin, McAuley et collaborateurs (2006) ont montré qu'entre les âges de quatre et huit ans, la synchronisation (tapping) est restreinte à une fourchette de tempi plus étroite que pour des âges un peu plus avancés (neuf à 12 ans et âge adulte). Chez les plus jeunes enfants testés dans l'étude (quatre à cinq ans) la synchronisation n'apparaissait possible que pour des séquences dont le tempo était le plus proche du spontané, soit une période de 337 ms. Chez les enfants un peu plus âgés (six à sept ans) la synchronisation, bien que relativement peu précise, semblait possible pour une fourchette un peu plus large (225-1139 ms).

Chez les enfants de huit à douze ans la synchronisation semblait possible pour l'ensemble des tempi testés (150-1709ms), même si à nouveau un peu moins précise que ce qui a été observé chez les adultes[1]. Ces résultats confirment donc que les capacités de synchronisation motrice se développent relativement lentement dans l'enfance. Notons qu'un tel étirement de la trajectoire développementale pourrait être dû à une acquisition tardive des capacités de coordination motrice nécessaires à la synchronisation, sans que cela ait nécessairement un rapport avec le traitement du beat musical. Les approches permettant de tester la perception sans recours à la synchronisation sont éclairantes sur ce point, et indiquent que la perception du beat serait très précoce.

Par exemple, Hannon & Johnson (2005) ont montré que des bébés de sept mois préfèrent les séquences rythmiques ayant une métrique (binaire ou ternaire) identique à celle de séquences auxquelles ils ont précédemment exposés. Phillips-Silver & Trainor (2005) ont de plus montré qu'une même séquence rythmique sera interprétée comme binaire ou ternaire par des bébés de sept mois selon qu'ils aient préalablement été bercés en deux ou en trois temps sur cette séquence. Cirelli, Spinelli, Trainor et Nozaradan (2016) ont étudié la réponse cérébrale au beat chez des bébés du même âge (sept mois). Ces chercheuses ont observé des pics dans le domaine fréquentiel sélectivement plus élevés aux fréquences correspondant au beat et à la métrique, comme chez les adultes (Nozaradan et al., 2013). De plus, Cirelli et collaborateurs (2016) ont observé que l'amplitude du pic à la fréquence de la métrique était plus importante chez 14 bébés ayant participé à un entraînement musical (adapté à leur très jeune âge) qu'au sein du reste du groupe (total de 60 bébés). Des bébés de 15 mois ont également été testés, ce qui a permis de montrer que l'expérience musicale des parents

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[1] Notons que dans l'étude de McAuley et collaborateurs (2006) les asynchronies n'ont pas été rapportées et que la majorité des résultats était basée sur les tapes de continuation, pas de synchronisation. Les résultats résumés ici sont une interprétation des graphiques présentés dans le matériel supplémentaire en ligne de l'étude.

influence l'amplitude de la réponse cérébrale aux fréquences d'intérêt chez les bébés de cet âge. Cette étude indique donc que les circuits cérébraux impliqués dans la perception du beat semblent déjà présents à sept mois, et que leur développement subséquent dépend, sans surprise, de l'expérience musicale et de l'environnement (voir également Hannon & Trehub, 2005a,b).

Enfin, Winkler, Háden, Ladinig, Sziller & Honing (2009) ont mesuré la réponse électrique du cerveau (EEG) à l'écoute de séquences isochrones où différents sons percussifs marquent les beats, chez des nouveaux-nés. Ces séquences étaient répétées en boucle et, de façon occasionnelle, un son était omis (paradigme de type *oddball*). Les auteurs de l'étude ont montré que le cerveau des nouveaux-nés répondait spécifiquement à des omissions se produisant sur les temps forts (début du motif), similairement à ce qui est observé chez les adultes (Ladinig, Honing, Háden, & Winkler, 2009). Ces résultats suggèrent un pré-câblage des circuits nécessaires à la perception du beat chez l'humain - en d'autres termes - qu'il s'agirait d'une capacité innée plutôt qu'acquise. Il faut cependant noter que dans cette étude l'omission du beat sur les temps forts correspondait également au retrait de plusieurs instruments, contrairement aux omissions sur les temps faibles. Ce qui a été interprété par les auteurs comme la réponse cérébrale à une violation de métrique pourrait donc être la réponse à une anomalie purement acoustique. Aucune étude à ce jour n'a permis d'éclaircir ce point (à notre connaissance).

En conclusion, la question du caractère inné ou acquis de la perception du beat est à l'heure actuelle source de débat (pour une discussion, voir Hannon, Nave-Blodgett et Nave, 2018), la seule étude ayant suggéré l'inné (Winkler et al., 2009) comportant des faiblesses méthodologiques qui n'ont pas été dépassées (peut-être parce que l'étude du cerveau du nouveau né n'est pas évidente à réaliser en pratique).

1.5 Troubles de la synchronisation au beat

Plusieurs études portant sur la synchronisation déficitaire au beat de la musique sont parues dans la dernière décennie. Notons qu'ici l'intérêt est porté aux troubles dits congénitaux, c'est-à-dire dont l'origine ne peut être attribuée à un diagnostic de dégénérescence neuronale ou de traumatisme crânien.

La première étude (Phillips-Silver et al., 2011) a décrit le cas d'un étudiant universitaire, Mathieu, présentant une incapacité à se synchroniser au beat de plusieurs extraits musicaux malgré une audition, une intelligence et des fonctions motrices et sociales normales. Le mouvement testé consistait à déplacer le tronc de bas en haut en pliant les genoux (*bouncing*). La séquence motrice était considérée comme synchronisée au beat si les variations de l'amplitude d'accélération verticale étaient conformes au tempo de la chanson. La synchronisation chez Mathieu était intermittente: le mouvement n'était consistant avec le tempo que pour trois des dix chansons testées, contrairement à un groupe de dix participants contrôles chez qui les mouvements étaient synchronisés à toutes les chansons.

Le bouncing spontané (pas de stimulus) et la synchronisation au métronome ont quant à eux été décrits comme normaux chez Mathieu, même si une comparaison directe au groupe contrôle n'a pas été effectuée pour ces conditions. Les auteurs de l'étude ont donc conclu que le trouble ne pouvait être attribué à une difficulté à produire une régularité, ou à un trouble plus général d'intégration sensori-motrice. Mathieu présentait également des scores dans la norme aux trois premiers tests de la *Montreal Battery of Evaluation of Amusia* (MBEA; Peretz, Champod, & Hyde, 2003) évaluant le traitement de la hauteur des notes en musique. Donc, contrairement à ce qui a été observé auprès de certains cas d'amusie congénitale (Dalla Bella & Peretz, 2003), l'incapacité à se synchroniser à la musique telle qu'observée chez Mathieu n'est pas due à un défaut de perception du *pitch*. Il ira de même pour les différents cas présentés dans la présente section.

La perception rythmique dans l'étude de Phillips-Silver et collaborateurs (2011) a été évaluée par les tests rythmique et métrique de la MBEA. Dans le test rythmique, le participant doit décider si deux courtes mélodies présentées l'une après l'autre sont identiques ou non, la différence étant créée dans la longueur de deux intervalles entre les notes consécutifs. Le nombre de notes, leur hauteur, et surtout l'organisation métrique sont eux maintenus identiques. Dans le test métrique le participant doit déterminer pour chaque mélodie présentée s'il s'agit d'une marche (métrique binaire) ou d'une valse (métrique ternaire).

Mathieu a obtenu un résultat normal pour le test rythmique, mais a échoué au test métrique, selon les normes établies par Peretz et collaborateurs (2003). Mathieu a également obtenu un résultat inférieur au groupe contrôle à une tâche consistant à déterminer si le mouvement de l'expérimentateur, enregistré sur vidéo, était synchronisé à la musique de la bande sonore. L'échec de Mathieu au test métrique, qui d'après les auteurs de l'étude nécessite d'extraire le beat sous-jacent à la mélodie, ainsi que sa difficulté au test de détection visuelle ont été interprétés comme l'indication d'un trouble perceptif ("*beat-deafness*").

Mathieu a fait l'objet d'une deuxième étude, plus récente. Palmer, Lidji & Peretz (2014) ont cette fois évalué le tapping dans quatre conditions: spontané, métronome, métronome avec perturbation de phase, et métronome avec perturbation de tempo. Les perturbations de tempo consistaient à augmenter ou diminuer l'intervalle entre deux sons par rapport à celui de base pour six intervalles consécutifs, avec retour à l'intervalle de base par la suite.

Les tapes de Mathieu étaient alignées de façon prédictive avec les sons du métronome (asynchronie négative) en l'absence de perturbations, bien qu'avec une variabilité des intervalles entre les tapes légèrement plus élevée que chez les contrôles. Surtout, Palmer et collaborateurs (2014) ont observé que revenir à l'alignement entre tapes et sons après les perturbations prenait plus de tapes chez Mathieu que chez les contrôles. Ce résultat était attendu pour les perturbations de tempo, il l'était moins pour les perturbations de phase étant donné le caractère automatique du processus de réalignement de phase.

Les auteurs de cette étude ont conclu à un défaut de couplage entre l'oscillateur interne et la stimulation externe durant le processus de synchronisation. La modélisation du décours temporel des tapes par un oscillateur harmonique amorti (Large et al., 2002) a en effet permis de caractériser le défaut de couplage (rétablissement anormalement lent après perturbation). Étant donné le niveau minimum de complexité rythmique dans un métronome, de tels résultats suggèrent un problème de coordination temporelle assez basique, une possibilité qui sera explorée plus en détail dans l'Article 3 de la présente thèse.

Sowiński & Dalla Bella (2013) ont décrit quatre cas présentant un profil comparable à celui de Mathieu. La tâche de synchronisation consistait à taper sur un extrait de musique classique, un extrait de bruit blanc modulé en amplitude (même enveloppe acoustique que le stimulus musical), et un métronome. L'alignement des tapes avec le beat de la musique et du bruit modulé était significativement plus variable chez ces quatre cas comparés à un groupe de participants contrôles.

La perception dans cette étude a été évaluée par le test rythmique de la MBEA ainsi qu'une tâche de détection de perturbation d'isochronie (musique et métronome). Deux des cas (S2 et S9) ont obtenu un score inférieur au *cut-off* (deux déviations standard sous la moyenne du groupe contrôle) pour la tâche de perturbation d'isochronie. Les auteurs de l'étude ont conclu à des capacités de perception du beat dégradées. Les deux autres cas (S1 et S5) ont par contre obtenu des scores dans la norme, au test rythmique de la MBEA et au test de perturbation de l'isochronie. Les auteurs ont conclu à des capacités de perception du beat préservées chez ces deux cas, et à un défaut d'intégration audio-motrice pour expliquer la synchronisation dégradée. Si cette conclusion semble tout à fait plausible, il faut toutefois souligner que les deux tests de perception utilisés dans l'étude ne sont pas les plus appropriés pour déterminer que la perception du beat est préservée (voir Annexe 1)[2]. Il reste donc à confirmer l'existence d'une dissociation entre capacités de synchronisation (déficiente) et perception (préservée).

La dissociation inverse a été décrite dans une étude très récente. Bégel et collaborateurs (2017a) ont décrit trois individus présentant de faibles scores à la tâche de perturbation d'isochronie ainsi qu'à une version adaptée du *Beat Alignment Test* (BAT; Iversen & Patel, 2008) comportant deux extraits de musique classique à trois tempi différents. La tâche dans le

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[2] Notons que le test métrique de la MBEA comporte également des défauts, soient des éléments permettant de détecter la structure métrique sans que la perception du beat ne soit nécessaire. Notamment, une accentuation acoustique des temps forts et l'utilisation du mode majeur pour la plupart des marches et du mode mineur pour la plupart des valses.

BAT consiste à déterminer si un métronome superposé à l'extrait musical est ou non aligné sur le beat de cet extrait. Le non-alignement est créé de deux façons: soit le tempo du métronome ne correspond pas à celui du beat (décalage de période), soit les deux tempi sont identiques, mais les sons du métronome sont systématiquement en retard ou en avance par rapport aux temps du beat (décalage de phase). Des versions adaptées du BAT ont été utilisées dans plusieurs études visant à mesurer les capacités de perception du beat (Grahn & Schuit, 2012). Dans les études où la synchronisation a également été mesurée, une corrélation entre scores de perception et synchronisation a été montrée (Leow, Parrot, & Grahn, 2014). Une telle observation va dans le sens de l'hypothèse ASAP, proposée par Patel et Iversen (2014; voir section 1.2). Pourtant, chez deux des trois cas (L.A. et L.C.) rapportés par Bégel et collaborateurs (2017a), la perception du beat déficiente n'était pas accompagnée d'une synchronisation déficiente (score supérieur au cut-off établi auprès de sept participants contrôles). Ces deux cas indiquent qu'un défaut de perception n'est pas nécessairement accompagné par un défaut de synchronisation.

Une forme de "traitement implicite" de l'isochronie a été testée dans l'étude de Bégel et collaborateurs (2017a). La tâche consistait à réagir le plus rapidement possible à un son-cible à la suite d'une séquence soit isochrone soit irrégulière de sept sons. Les temps de réaction chez les trois cas testés n'étaient pas différents de ceux de trois participants contrôles, avec dans les deux groupes un avantage des séquences isochrones sur les séquences irrégulières, tel qu'attendu. Bégel et collaborateurs (2017a) en ont conclu à forme implicite de traitement de l'isochronie préservée qui aurait donc pu guider la synchronisation chez L.A. et L.C. Les auteurs ont également suggéré que les basses performances de perception du beat chez ces deux cas pourraient résulter d'un défaut d'accès conscient à une représentation implicite qui, elle, serait intacte. Il s'agit d'une interprétation déjà avancée pour le traitement déficient du pitch chez des cas d'amusie congénitale (Omigie, Pearce, & Stewart, 2012; Tillmann, Gosselin, Bigand, & Peretz, 2012).

Enfin, il n'existe à ce jour qu'une seule étude portant sur les corrélats neuraux du trouble de la synchronisation au beat musical. Mathias, Lidji, Palmer & Peretz (2016) ont mesuré la réponse EEG à des omissions de beats (paradigme oddball) dans des séquences rythmiques, chez Mathieu ainsi que dix participants contrôles. Deux conditions ont été utilisées: pré-attentive durant laquelle les participants visionnaient un film, et attentive durant laquelle les participants devaient rapporter les omissions du beat. Au niveau comportemental, une détection moins bonne des omissions a été observée chez Mathieu en comparaison au groupe contrôle (condition attentive). Cette différence était accompagnée d'une composante P3b anormale. La P3b est connue pour apparaître lorsqu'un évènement auditif inattendu est détecté de façon consciente (Polich, 2007; Pritchard, 1981; E. Snyder & Hillyard, 1976) et reflèterait la mise à jour de la représentation du stimulus en mémoire de travail (context updating theory; Donchin & Coles, 1988). La composante *Mismatch Negativity* (MMN), reflétant la détection pré-attentive (non consciente) d'irrégularités telles que l'omission d'un beat, a en revanche été décrite comme normale chez Mathieu. Les auteurs de l'étude en ont conclu que certains mécanismes faisant appel à l'accès à la conscience (reflétés par la P3b) pourraient être altérés chez les personnes présentant un trouble du traitement du beat. Cette conclusion rappelle des résultats obtenus auprès de personnes présentant une amusie congénitale (pitch-deafness), et dont le cerveau semble normalement équipé pour détecter des petites déviations de pitch sans perception consciente (Moreau, Jolicoeur, & Peretz, 2013; Peretz, Brattico, Jarvenpaa, & Tervaniemi, 2009).

En résumé, plusieurs études de cas ont confirmé l'existence d'individus avec difficulté marquée à se synchroniser au beat musical. Cette difficulté semble émerger d'un défaut de perception du beat dans certains cas mais pas d'autres (dissociation). À l'inverse, il existerait des individus présentant une difficulté à percevoir le beat sans que la synchronisation s'en trouve affectée. Il reste cependant à confirmer l'existence de telles dissociations, et notamment à montrer qu'elles ne se limitent pas à la musique classique et au tapping, qui sont des conditions assez éloignées de la danse. Enfin, une des études (Palmer et al., 2014) suggère que des mécanismes plus basiques de coordination temporelle pourraient être altérés.

1.6 Objectifs et présentation des articles

L'objectif général de cette thèse est de mieux comprendre les mécanismes cognitifs qui sous-tendent le processus de synchronisation à la musique. Pour cela nous étudions les personnes présentant une difficulté marquée et spécifique à se synchroniser, selon l'approche neuropsychologique consistant à étudier un système déficient pour en révéler l'organisation fonctionnelle normale par fractionnement des éléments qui constituent le système. Ce travail est présenté à travers trois articles scientifiques.

Le premier article, publié dans la revue *PloS One*, avait pour objectif principal de diagnostiquer de nouveaux cas. Pour la robustesse et la généralisation des résultats, l'étude de groupes est en effet préférable à celle de cas. De plus, l'objectif poursuivi à plus long terme par notre laboratoire est d'étudier le cerveau des personnes présentant un trouble de la synchronisation par des techniques d'imagerie, pour lesquelles un nombre minimal de participants est requis. Un second objectif était de comparer deux gestes naturels, taper des mains (*clapping*) et plier les genoux (bouncing). Pour cela nous avons testé la synchronisation à des musiques de genres différents ainsi qu'au métronome chez 100 jeunes adultes ne présentant pas de trouble de la perception du pitch.

L'objectif du deuxième article était de confirmer l'existence de dissociations entre capacités de perception et de synchronisation au beat, ou à l'inverse de montrer que ces deux composantes sont intimement liées. Pour cela nous avons utilisé une version adaptée du Beat Alignment Test (Iversen & Patel, 2008) pour mesurer la perception. Notons que pour mesurer la synchronisation, le tapping a été choisi à des fins de comparaison avec la littérature existante dans le domaine de la coordination temporelle. Huit cas préalablement diagnostiqués ou déclarant avoir un trouble de la synchronisation à la musique ont été comparés à un large groupe de participants contrôles.

Enfin, la troisième étude visait à tester la flexibilité de tempo chez les personnes présentant un trouble de synchronisation à la musique. La fenêtre maximale de tempi testée jusque-là était de 450-750 ms (chez Sowiński & Dalla Bella, 2013), donc bien en deçà des tempi pour lesquels la synchronisation est possible (200-1800ms pour le tapping). Les études montrant une flexibilité réduite chez les animaux (Section 1.3) et chez l'enfant (Section 1.4) suggèrent que la capacité à coordonner le mouvement à des tempi en dehors d'une zone optimale pourrait reposer sur un processus sophistiqué d'adaptation de la période de l'oscillateur. Notre hypothèse était donc celle d'une flexibilité réduite chez les personnes avec trouble de synchronisation à la musique.

Chapitre 2: Méthodologie et résultats

Article 1: Keeping the beat: A large sample study of bouncing and clapping to music

Pauline Tranchant, Dominique T. Vuvan et Isabelle Peretz

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Keeping the beat: A large sample study of bouncing and clapping to music

Pauline Tranchant[1,2], Dominique T. Vuvan[1,2], Isabelle Peretz[1,2]

1 Département de psychologie, Université de Montréal, Montréal, Québec, Canada

2 International Laboratory for Brain, Music and Sound Research (BRAMS), Université de Montréal, Montréal, Québec, Canada

Running Title: Bouncing and clapping to music

Corresponding author: Isabelle Peretz, isabelle.peretz@umontreal.ca

Abstract

The vast majority of humans move in time with a musical beat. This behaviour has been mostly studied through finger-tapping synchronization. Here, we evaluate naturalistic syn- chronization responses to music–bouncing and clapping–in 100 university students. Their ability to match the period of their bounces and claps to those of a metronome and musical clips varying in beat saliency was assessed. In general, clapping was better synchronized with the beat than bouncing, suggesting that the choice of a specific movement type is an important factor to consider in the study of sensorimotor synchronization processes. Performance improved as a function of beat saliency, indicating that beat abstraction plays a significant role in synchronization. Fourteen percent of the population exhibited marked difficulties with matching the beat. Yet, at a group level, poor synchronizers showed similar sensitivity to movement type and beat saliency as normal synchronizers. These results sug- gest the presence of quantitative rather than qualitative variations when losing the beat.

Introduction

Humans move to musical rhythms by nodding the head, clapping the hands or dancing in time with perceived periodicities in musical stimuli–that is, with the musical beat. Such movements are spontaneous and observed across cultures [1]. Infants show a rhythmic motor response to music before the age of two [2] but it is only between the ages of 2.5 and 4.5 that the flexibility required to match their movement tempo to those of the stimuli starts to develop [3].The behavioural and neural mechanisms required by the capacity for rhythmic sensorimotor synchronization (SMS) are presently the topic of intense research (see [4, 5] for reviews).

The vast majority of the studies conducted in this area have investigated finger tapping. Yet, finger tapping leaves out important aspects of the processes involved in SMS to music, such as the diversity of natural movements and the feedback they provide, as well as the pleasurable aspect of moving to music.

Different movements may recruit different mechanisms. For example, different timing and motor control mechanisms may underlie the production of continuous versus discrete periodic movements (such as tapping). Emergent properties of the movement dynamics and the representation of event-based timing seem to differentiate continuous from discrete movements [6–9]. This distinction is supported by several findings. Temporal precision in finger tapping and continuous drawing is not related within individuals [10, 11], and different auto-correlation patterns characterize the period and asynchronies for discrete versus continuous synchronization [12, 13]. Furthermore, patients with cerebellar damage show preserved circle drawing (continuous) but impaired finger tapping (discrete) when asked to time their movement to isochronous tones [14].

Second, vestibular stimulation, which varies when bending the knees to move the trunk up and down in bouncing, is constant in finger tapping and clapping. Yet vestibular stimulation appears to drive beat finding in music. Indeed, bouncing to a specific meter while listening to a rhythmic pattern can affect perceptual meter judgments [15, 16]. This is also found for motion of the head only (as opposed to the legs) and whole-body passive motion [17], suggesting that it is the manipulation of vestibular information that is playing a crucial role.

Last but not least, the desire to move to certain types of music, a phenomenon referred to as groove [18], is a highly pleasurable experience [19]. When exposed to music, people spontane- ously start to move their foot, head and/or trunk [20]. Preventing listeners from moving their body actually reduces their ability to find the beat [21]. Moreover, participants prefer to move freely with music rather than to be directed to make hand-tapping movements only [20]. Restricting a participant’s movements such that they may only move their finger, as is the case in tapping studies, is likely to restrain this participant’s feeling of 'being in the groove'. This is not only because participants are required by the experiment to perform a specific gesture, but also because that gesture may not be one that arises spontaneously in non-experimental contexts. As groove is an important aspect of motor engagement during music listening [22] and of the quality of sensorimotor coupling [20], the experimental study of movements that occur spontaneously outside of the lab may help improve the understanding of some important aspects of SMS to music in humans.

In sum, the way we move has an influence on how we interpret, enjoy and synchronize to musical rhythms. A few studies have explored the effects of using different effectors, such as finger versus foot [23] or finger versus drumstick [24] on the quality of isochronous synchroni- zation, and there is a growing literature on the synchronization of gait (e.g. [25, 26]) and dance-like movements (e.g. [16, 27, 28]) to music. However, no studies so far have compared different forms of naturalistic but qualitatively distinct movement, such as bouncing and clapping during synchronization to music. This comparison was the primary goal of the current study.

A second goal of the current study was to explore the effect of beat saliency on clapping and bouncing. Synchronization to music requires the perceptual encoding of a periodic beat struc- ture from the musical stimulus. This beat structure is neither consistently periodic in reality [29] nor does it systematically contain acoustic energy at beat locations, such as in syncopated rhythms [30,31]. Since there is no one-to-one relationship between beats and sounded events in music, an important task for the perceptual system is to track the beat in music in order to synchronize to it. Moreover, there are considerable variations in beat saliency (i.e., the percep- tual clarity of the beat) across musical genres. Compare, for example, techno dance in which there is generally a strong bass kick marking each beat, to jazz, in which the beat is much more subtle.

Previous studies have assessed the effect of rhythmic complexity, which is conceptually related to beat saliency, on synchronization by comparing metrical to non-metrical rhythmic sequences [32,33] and by comparing metronome to musical sequences [34,35]. These studies generally show better synchronization for lower rhythmic complexity. In a similar vein, Fitch and Rosenfeld [30] studied how syncopation in single-tone rhythms, i.e., “rhythmic events that violate one’s metrical expectations” [19] affected synchronization, and showed that higher tapping accuracy was associated with lower degrees of syncopation. Specifically, increasing the number of un-syncopated isochronous “streams” in computer-generated rhythms tends to improve tapping accuracy [36].

Less is known about the role of beat saliency on synchronization. Chen et al. [32] and more recently Fujii and Schlaug [37] assessed the effect of beat saliency on tapping behaviour by periodically increasing the intensity of isochronous tones to create accent patterns. In both studies, the louder (more salient) accents led participants to increase the duration [32] and pressure [37] of their taps. In the same vein, Burger et al. [38] found that beat saliency ("pulse clarity" in their paper) positively correlates with the amount and speed of movement. However, in these three studies the accuracy of synchronization was not assessed. Van Dyck et al [28] showed that better tempo entrainment of the head is found when increasing the sound level of the bass drum in a club-like dance context. Finally, better period-matching with a beat is found for high- compared to low-groove music [20, 25]. Although beat saliency has been associated with groove in music [20, 39], these two concepts may recruit beat finding mechanisms differently. Indeed, syncopated rhythms have been shown to elicit a higher perception of groove than rhythms with a straight-ahead beat [19]. For example, a metronome has the most salient beat but is not groovy. Moreover, groove is bound to movement whereas beat saliency relates to perception. Therefore, in the current study we used stimuli that varied in beat saliency in order to gain insights into the perceptual component of SMS. Keeping in line with our attempt to study SMS in a naturalistic context, our goal was to evaluate synchronization to naturalistic musical stimuli (i.e., commercially available music) that were distributed along a spectrum of beat saliency.

To these aims, we tested 100 healthy young adults on their ability to match the tempo of musical pieces when asked to bounce or clap the hands in time with the beat of the stimuli. We predicted the occurrence of synchronization difficulties in a minority of individuals, as previ- ously found with finger-tapping [35] and bouncing [34]. Rather than excluding the data of such individuals, as is usually the case in SMS studies, we applied a neuropsychological approach to study these impaired cases as a way of gaining insight into the mechanisms of normal synchronization.

Materials and Methods

Experiment

A large group of young unselected university students were invited to bounce and clap to a set of music excerpts varying in beat saliency. We also measured their ability to (a) maintain a regular movement without music and (b) to perceptually infer the meter from short musical excerpts taken from the Montreal Battery of Evaluation of Amusia (the metric test; [40]).

Participants

We tested 101 healthy university students (Aged 18–34, M = 23.4; 56 female) who provided written informed consent and received financial compensation for their participation. None of them reported any neurological problems or motor deficits. They all self-reported having nor- mal hearing. A description of their musical and dance background is presented in Table 1.

All participants completed the on-line test of amusia [41] to screen for music perceptual dif- ficulties, and completed the MBEA metric test in the lab [40]. The on-line test assesses out-of- key tone discrimination and off-beat detection, both in a melodic context. In the MBEA metric test, participants are asked to find the underlying pattern of strong and weak beats in 32 piano sequences, in order to judge them as being marches (strong beat on every other beat) or waltzes (strong beat on every third beat). Nine individuals obtained poor scores on the on-line pitch tests and were further tested with the entire MBEA. One participant obtained a melodic com- posite score (i.e. mean of the scale, contour, and interval tests, each comprising 30 trials) of less than 22 (out of 30). This participant was hence diagnosed with “pitch-deafness” and was therefore excluded from the study. Thus, the final sample included 100 individuals with no perceptual pitch impairment. The research protocol was approved by the Comité d’éthique de la recherche de la Faculté des arts et des sciences (CÉRFAS) at Université de Montréal.

[Insert Table 1 here]

Stimuli

There were six musical stimuli varying in musical style and tempo and two metronomes. Detailed descriptions of the stimuli are presented in Table 2. We selected four stimuli previously used to measure bouncing synchronization in 33 good and one poor synchronizers [34]. These were Metronome (116 and 125 BPM), Suavemente (Merengue, 116 and 124 BPM), What a Feeling (Pop dance) and The Flow (Dance lounge). Merengue and Metronome stimuli were presented at two different tempi in order to assess the effect of tempo on synchronization. Stimuli were constructed by looping initial selections at a stable tempo, so that the period between the last beat of any one excerpt and the first beat of the next excerpt in the loop was equal to the inter-beat period, maintaining the beat across excerpts for 115 seconds. In order to vary musical genres as well as beat saliency, we added two stimuli that also had previously been used in our lab (unpublished data): Since You've Been Gone (Soul) and Brand New Carpet (Pop rock). All stimuli were chosen in a relatively narrow tempo range, typical of dance music [42] and around people's perceptual preferred tempo (120 BPM, see [43]). The inter-beat intervals (IBIs) varied from 455 to 517 milliseconds, corresponding to tempi between 116 and 132 BPM. The tempi were determined using the mirtempo function from the MIR toolbox [44] in Matlab (MathWorks).

[Insert Table 2 here]

In order to best map the relation between beat saliency and synchronization performance, we decided to derive an empirical measure of beat saliency from participants with similar levels of musical training as those in the synchronization experiment. This method was favoured over acoustical analysis methods that have been developed and validated using trained musicians' ratings (for example the mirpulseclarity function in the MIR toolbox). To do so, 14 university students (Aged 20–26, M = 22.3, 7 female) who did not take part in the bouncing and clapping synchronization experiment but were screened according to the same criteria, participated in an additional pilot study. They were asked to indicate ‘how clear and salient’ the beat of each stimulus was by moving a slider potentiometer (10 K Ohm, 0.5W, 10 mm) controlled by customized Python scripts from left to right while listening to the stimulus. The slider value ranged from zero (least salient beat) to 1023 (most salient beat). Z-scores for each stimulus are provided in Table 2. Paired-sample t-tests revealed no difference between the two Merengue stimuli (t(13) = -0.4, p = 0.66) or between the two Metronome stimuli (t(13) = 0.6, p = 0.58), indicating that the tempo difference did not affect the saliency of the perceived beat. Therefore, the values were collapsed over the two tempi, producing a single value for the Merengue and Metronome (Table 2). A one-way repeated-measures ANOVA with 6 levels (Merengue, Metronome, Dance lounge, Pop Dance, Soul and Pop Rock) for the Stimulus factor revealed a significant effect of Stimulus, F(5,65) = 28.2, p < 0.001. There was a significant linear trend in the Stimulus factor, t(78) = 10.1, p < 0.0001.

Finally, familiarity with the musical stimuli was assessed in a separate pilot study including 27 participants (aged 20–38, M = 25.6, 18 female) who did not take part in the synchronization experiment or the beat saliency experiment but were screened according to the same criteria. They rated how familiar they were with the stimuli on a 1 to 100 scale (1 = not familiar at all, 100 = very familiar). Responses were made on the keyboard. Results revealed that two of the stimuli, Suavemente (Merengue) and Since You've Been Gone (Soul), were more familiar than the others (Table 2).

Bouncing and clapping synchronization

Movement condition presentation order was counter-balanced between participants, with half of the participants starting with the bouncing and the other half starting with the clapping. Each participant received the same set of stimuli. We kept the order of stimulus presentation constant across tasks and participants (except for the two Merengue and Metronome that were counter-balanced for tempo). The stimuli presentation order was as follows: Merengue (two tempi), Metronome (two tempi), Pop Dance, Dance Lounge, Soul, Pop Rock. The main reason for this design was that the musical selections vary in beat saliency, and this variation may have unpredictable carry-over effects. For example, a musical stimulus with an easy beat to track may prime beat finding in the next excerpt; conversely, a difficult beat to track in one musical stimulus may impair beat tracking in the next excerpt. Since our main goal was to compare bouncing and clapping, we used the same order of presentation for the stimuli in both tasks. This procedure insured that any carry-over effects that existed between stimuli would be stable across the tasks, and any carry-over effects that existed between tasks would cancel out across participants. Participants were instructed to move in time with the ‘strong and regular beat’ of the stimulus and to continue the same movement throughout the stimulus. Before starting each synchronization condition they were asked to bounce or clap “regularly at their own preferred rate”, for two minutes. The testing session lasted approximately one hour.

Equipment

The experiment took place in a large sound-attenuated studio, with the experimenter present but facing away from the subject to avoid distraction. Stimuli were presented in free field from Genelec speakers at a comfortable volume level. An accelerometer was used to capture move- ment. This accelerometer was contained in the remote of a Nintendo Wii and was strapped to the trunk of the subject’s body in the bouncing condition, and to the forearm of the dominant hand in the clapping condition (see S1 Fig). This device continuously measured the acceleration produced by participants’ movements in the three spatial dimensions, at 100 frames per second. Acceleration data were transmitted to an Apple computer via Bluetooth and recorded by a customized program written in MAX (Cycling ‘74). Because of a technical error with the triggering between stimuli and movement capture, phase values provided by our system were not accurate enough for analysis. Nevertheless, we collected data in 1600 files (8 stimuli x 2 movement types x 100 participants). Of these, 7 files were corrupted and were not considered in the analyses.

Data Analyses and Results

The current section is divided into four parts. In the first part, we report the metrical levels observed in produced movement. In the second part, we describe the procedure we applied to each trial (i.e., a participant’s synchronization response to each stimulus) to determine whether participants successfully matched their movements to the tempo (‘Normal Synchronization’) or not (‘Poor Synchronization’). Next, we describe the procedure we applied to each participant to determine whether they were a Normal Synchronizer or a Poor Synchronizer. Finally, we analyze synchronization performance separately in normal and poor synchronizers.

Metrical levels observed in produced movement

Participants produced movement either at the beat level or at the two-beat level. Bounces or claps that occurred at a rate corresponding to the beat frequency were considered to occur at the beat level, whereas bounces or claps that occurred at half the beat frequency (i.e., every second beat) were considered to occur at the two-beat level. For each participant and each stimulus, the level at which the participant moved was determined by calculating the Fourier transform of the acceleration data. Fourier analysis was performed with Matlab. This procedure produced a power spectrum with the maximal peak appearing at the frequency of the participant’s movement.

Two participants produced movement at a very slow rate, close to the four-beat level (beat frequency/4). Further analysis revealed that one of these participants (participant 21) was accu- rately matching the tempo of all stimuli at the four-beat level: we decided to exclude her in sub- sequent analyses because her behaviour was not comparable to the rest of the group. In contrast, Participant 18’s responses were not tempo-matched to any of the stimuli. This participant was identified as a ‘Poor Synchronizer’ and excluded from the current analysis. One additional participant produced movement at tempi that did not match the stimulus tempi but from the experimenter's report this was due to an obvious lack of motivation in performing the tasks rather than a synchronization difficulty, and he was excluded from subsequent analysis.

For the remaining 97 participants, the chosen metrical level was not always the same across stimuli. Furthermore, for some trials, it was impossible to determine which level was produced by the participant, because the chosen level was not constant throughout the trial (3 cases) or was produced at a tempo that was not constant or that did not correspond to the beat or two- beat level (48 cases). These trials were excluded. Note that more trials had to be excluded in the bouncing (total of 37 over 20 participants, out of 97*8 = 776 trials) as compared to the clapping condition (total of 14 over 12 participants, out of 776 trials).

The distribution of metrical level (beat-level, two-beat level) displayed in participants' movements are presented in Table 3. There was a higher proportion of movement at the beat-level (versus two-beat level) in all conditions, and particularly so in the clapping condition (*Mdn* = 82) as compared to the bouncing condition (*Mdn* = 54), $U = 62.50$, $p < .001$. The number of trials on which participants synchronized at the beat versus two-beat level was not affected by the differential effects of the two movement types over the course of the stimulus presentation order, $\chi 2(7) = 2.59$, $p = 0.92$. Thus, having moved for some time did not impact participants' chosen synchronization level in a different way for the bouncing compared to the clapping movement.

[Insert Table 3 here]

Normal versus poor synchronization

Synchronization performance was quantified by analyzing the acceleration data to determine the degree to which the tempo of the produced movement matched the stimulus tempo. For each stimulus, the first 10 seconds were discarded from the analysis, leaving 105 seconds of data for analysis. First, the timing of maximal flexion of the knee (bouncing) or hand impact (clapping) were extracted from the acceleration data. These time points were called responses and the interval between two responses was called the inter-response interval (IRI).

The response series was analyzed using circular statistics [45, 46] and the CircStat Toolbox [47] for Matlab. The timing of the responses was converted to vectors on the unit circle. For beat level synchronization trials, one stimulus inter-beat-interval (IBI) corresponded to one circle length (i.e., 2*pi radians). For two-beat level synchronization trials, two IBIs corresponded to one circle length. For beat level synchronization we segmented each trial into four consecutive segments, while two-beat level synchronization were segmented into two consecutive segments, so that each segment had the same number of responses within a trial. The assessment of synchronization across segments allowed us to catch trials in which the beat was lost after a certain duration, or in which participants required a very long duration to achieve synchronization.

When IRIs are close to the stimulus IBI (or 2*IBI in two-beat synchronization), corresponding vectors are clustered around a preferred direction (Fig 1C). Conversely, if IRIs are consistently different from the stimulus IBI, corresponding vectors are increasingly distributed around the circle (Fig 1A). A Rayleigh test (null hypothesis = random distribution of vectors around the circle) is used to assess whether performance on a particular segment is period-matched to the stimulus. When performance is period-matched (i.e., vectors clustered around a preferred direction, Fig 1C), the Rayleigh test yields a significant result. When performance is not period-matched (i.e., vectors randomly distributed around the circle, Fig 1A), the Rayleigh test yields a non-significant result. Note that the time between responses and beat locations (i.e., phase) was not taken into account here. This means that the preferred direction of the vector series can be located anywhere on the circle. However, in a few trials (20 bouncing and 15 clapping trials) two preferred directions (bimodal distribution) were observed within the trial (Fig 1B). Bi-modal trials were excluded from further analysis. Two more participants were excluded because at least 3 of the 8 clapping or bouncing trials were bimodal, resulting in too much missing data. Finally, each trial for a given participant was categorized as ‘poor synchronization’ if the Rayleigh test was not significant for any one of the segments, and ‘normal synchronization’ if the Rayleigh test was significant for all segments. This procedure detected 53 poor synchronization trials in the bouncing condition (7.4% of trials), and 23 in the clapping condition (3.1% of trials).

[Insert Figure 1 here]

A participant was categorized as a ‘Poor Synchronizer’ if s/he had at least 3 poor synchronization trials out of the 6 music trials for at least one movement type (bouncing or clapping). Following this procedure, 13 participants were identified as Poor Synchronizers, in addition to participant 18 (see previous section), yielding 14 Poor Synchronizers. The remaining 82 participants made up the Normal Synchronizers group.

Normal synchronizers

We analyzed the synchronization data of the 82 normal synchronizers in order to establish a normal profile of performance to which we could compare the performance of poor synchro- nizers. As in the previous analysis, synchronization failure trials were excluded (18 bouncing and 6 clapping trials). The circular variance, a measure of angular dispersion (see [46] for a description) was calculated for the responses of the entire un-segmented trial, and was used as our index of movement regularity. The distribution of the circular variance, for all stimuli and both movement types, corresponded to a lognormal function. To normalize the distributions, the inverse logarithm of the circular variance was taken as a measure of regularity, with a higher value representing more regularity. This variable will henceforth be referred to as 'synchronization regularity' (SR). A description of log-transformed SR scores are provided in S1 Table. There was no correlation between SR (all stimuli averaged) and musical training or dance training, and as those factors were not of primary interest in the present study they were not included in our statistical model.

Scores for the two Merengue and the two Metronome stimuli were averaged across tempi (no significant difference between tempi). We assessed the impact of movement type (bouncing vs. clapping) and beat saliency (Table 2) on SR by conducting a two-level hierarchical linear regression with Movement Type and Beat Saliency as predictors, and with all data nested within participant. We performed this statistical analysis with the lme4 package [48] in R (http://cran.r-project.org/). A trial synchronized at the beat level contains twice as many responses as a trial synchronized at the two-beat level; this was taken into account by weighting the variance based on the number of responses in each trial, using the weights parameter of the lmer function. We tested a series of increasingly elaborated models (as recommended by [49]), in which a random intercept was modeled for each participant, and both fixed and random slopes were tested for the main effects of Movement Type and

Stimulus Type, as well as their interaction. The final, best-fitting model included a random intercept for participants, fixed effects of both Movement Type and Beat Saliency, and a random slope for Movement Type. All analysis steps leading to the final model and its specifications are provided in S2 Table. According to the fixed effects, SR was predicted significantly by the main effect of Movement Type (b = 0.44, SE = 0.06, p < .001), with clapping being more regular than bouncing, and by the main positive effect of Beat Saliency (b = 0.23, SE = 0.08, p = 0.0087). There was no significant interaction between these two factors (b = 0.02, SE = 0.05, p = 0.68). The significant random slope for Movement Type indicated that the relation between bouncing and clapping scores is different from person to person. When collapsing bouncing and clapping SR, post-hoc comparisons (Bonferroni adjusted, p = .05) indicated that all stimuli differed from one another, except for the Metronome, Dance Lounge and Pop Rock. SR to these three stimuli were statistically equivalent, and furthermore were better than for the other musical stimuli. Thus, though beat saliency was a significant positive predictor of SR, some stimuli elicited higher SR than others with relatively higher beat saliency (Fig 2). Interestingly, the two most familiar stimuli (Merengue and Soul) elicited the worse synchronization scores. Note that because stimulus presentation order was kept constant between participants and conditions, there is a possibility that uncontrolled parameters played a role in these findings. Finally, there was a correlation between bouncing and clapping synchronization for music (using the averaged score for the 6 musical stimuli), $r(82) = 0.39$, $p < 0.001$, but not for the metronome (averaged score for the 2 metronome stimuli), $r(82) = -0.078$, $p = 0.48$.

[Insert Figure 2 here]

Poor Synchronizers

The goal of this section is to assess whether the 14 Poor Synchronizers' profile paralleled the Normal Synchronizers' profile in terms of the effects for Movement Type and Beat Saliency. Whereas normal synchronization performance could be assessed with synchronization regu- larity scores, this could not be done in Poor Synchronizers because they had many trial seg- ments with failed synchronization trials (i.e., non-significant Rayleigh tests), and to compare SRs that have been calculated from failed synchronization segments is meaningless because it involves comparing the degree to which performance was random. Therefore, we used propor- tion of synchronization successes (i.e., trials for which every segment had a significant Ray- leigh's test) as a measure of performance in each movement type and beat saliency condition. This analysis revealed that clapping (*Mdn* = 8.5) was less impaired than bouncing (*Mdn* = 3), *U* = 154.50, *p* = 0.0073. In particular, four Poor Synchronizers (25, 38, 46 and 62) had normal synchronization (i.e., no synchronization failures) when clapping. Like for the Normal Synchronizers' group, beat saliency seemed to play a role: we found a higher proportion of normal performance trials on Metronome and Pop Dance stimuli (i.e., the stimulus with the highest level of beat saliency; Fig 3). At the group level, the Poor Synchronizers' profile thus seems to parallel that of Normal Synchronizers'. Note that because stimulus presentation order was kept constant between participants and conditions, there is a possibility that uncontrolled parameters played a role in these findings.

[Insert Figure 3 here]

At the individual level, Poor Synchronizers presented a variety of behavioural profiles, ranging from synchronization failures on all trials to synchronization failures when bouncing to music only. In order to classify poor synchronizers into subgroups of converging profiles, a cluster analysis was conducted on the proportion of failed synchronization trials for each participant when bouncing to music, bouncing to metronome, clapping to music and clapping to metronome. An agglomerative hierarchical cluster analysis determined that a 4-cluster solution was ideal and cluster centroids were estimated with a k-means cluster analysis (MacQueen algorithm). The final centroids for each cluster and Poor Synchronizers' classification into clusters are presented in Table 4. The first cluster included two Poor Synchronizers, who exhibited poor tempo matching in all of the conditions. The second cluster included four Poor Synchronizers, who presented poor tempo matching when bouncing and clapping to music, but normal performances with the metronome. The impairment thus seemed to emerge for music only. The third cluster included four Poor Synchronizers who were less impaired on clapping as compared to bouncing and less impaired on metronome as compared to music. The fourth and last cluster included four Poor Synchronizers who showed normal clapping performance across all stimuli but impaired performance in bouncing (to both music and metronome). Thus, the impairment in these cases seems to be specific to bouncing.

[Insert Table 4 here]

In summary, scrutiny of Poor Synchronizer's data reveals different individual profiles, sug- gesting that poor synchronization is not a uniform impairment. However, at the group level bouncing is more difficult than clapping and music is more difficult than metronome, suggest- ing a parallel with the Normal Synchronizer's group profile. A summary of each Poor Synchro- nizer's performance on the Synchronization tasks, the Metric perception test (see results below) and self-paced motor production (see results below) tasks is provided in

Supporting Information (S3 Table).

Self-paced motor production

In order to assess whether Poor Synchronizers were able to maintain regularity in the absence of an external pacing stimulus, we measured their regularity when asked to regularly bounce and clap in silence. The produced rate can be considered to reflect participant's subjective tempo, called the referent period [50]. We compared Poor Synchronizers' produced period and regularity to those of Normal Synchronizers to detect potential anomalies of their referent period, such as an extremely slow or an extremely fast tempo, or irregular IRIs. There was one missing file in each of the bouncing and clapping conditions due to equipment error, both for Normal Synchronizers. The mean IRI of the first 30 events was calculated to determine the produced tempo while the coefficient of variation (CV), i.e. standard deviation (SD) of the IRIs divided by the mean IRI, of the first 30 events was used to assess regularity. Normal and Poor Synchronizer group IRIs and CVs are summarized in Fig 4.

Normal synchronizers. A paired-sample t-test revealed that the mean IRI was shorter in the clapping condition ($M = 681$, $SD = 243$) compared to the bouncing condition ($M = 758$, $SD = 237$), $t(79) = 2.6$, $p = 0.011$, paralleling the tendency of all participants to bounce at the two-beat level and to clap at the beat-level in the synchronization tasks. Two Normal Synchronizers bounced at a tempo slower than 2 SD from the mean, and four Normal Synchronizers clapped at a tempo slower than 2 SD from the mean.

The distributions of the CV for the bouncing and clapping conditions were consistent with a lognormal function. This was expected because the CV was bounded by zero. To normalize the distribution, we calculated CV's inverse logarithm. This normalized CV was used as the index of regularity (higher values represent lower variability).

Clapping was marginally more regular than bouncing, $t(79) = 1.96$, $p = 0.054$. However, three Normal Synchronizers produced regularity scores more than two SD below the mean in the clapping condition and four Normal Synchronizers did so in the bouncing condition. Self-paced regularity did not predict synchronization regularity, justifying its non-inclusion in the multilevel modeling of the normal synchronization data presented previously. There was no significant correlation between self-paced regularity and synchronization to a metronome (scores averaged across the two tempi), and no significant correlation between self-paced regularity and regularity in synchronization to music (scores averaged across all musical stimuli), all $p > 0.34$. Moderate correlations were obtained when standard deviations of the IRIs rather than CV were considered, but here we report CV because it is the standard measure used in this field (e.g. [51]). No correlations were found between regularity and musical or dance training, all $p > 0.28$.

[Insert Figure 4 here]

Poor synchronizers. We compared Poor Synchronizers' self-paced performance to cut-off scores established by the performance of the Normal Synchronizers (mean minus 2 SD).

In the bouncing condition, self-paced tempo did not differ between Poor Synchronizers and Normal Synchronizers, $t(92) = 0.65$, $p = 0.51$. Two Poor Synchronizers (18 and 53) were slower than the cut-off. In the clapping condition, self-paced tempo did not differ between Poor Synchronizers and Normal Synchronizers, $t(92) = 0.4$, $p = 0.69$. One Poor Synchronizer

(80) was slower than the cut-off.

In the bouncing condition, regularity was significantly worse in Poor Synchronizers than in Normal Synchronizers, *t*(92) = 2.6, *p* = 0.011. One Poor Synchronizer (80) had regularity below the cut-off for bouncing. However, in the clapping condition, this participant's score was above the mean of the normal synchronization group, indicating that participant 80's poor reg- ularity was limited to bouncing. In the clapping condition, regularity was not significantly dif- ferent between Poor Synchronizers and Normals, *t*(92) = 0.86 *p* = 0.39. One Poor Synchronizer (31) presented regularity below the cut-off.

Metric perception

The Normal Synchronizers' mean score was 27.4 out of 30 (*SD* = 3.65). This distribution is highly asymmetric with negative skewness and a mode of 30. Therefore, as a group, Normal Synchronizers performed well on this task. However, six normal synchronizers performed poorly with a score inferior to two standard deviations below the mean (cut-off: 20). Note that there is not enough variability in the normal group to perform a correlation with synchronization scores. Moreover, no correlation was found between synchronization and the off-beat detection test of the on-line test of amusia.

The mean score of the 14 poor synchronizers was 24.07 (*SD* = 5.41) and was significantly worse than normal performance, *t*(94) = 2.91, *p* = 0.0045. Two Poor Synchronizers, 6 and 46, obtained a score inferior to the cut-off of 20, with scores of 13 and 12, respectively. The other Poor Synchronizers obtained a score superior to the cut-off, and in particular participants 25, 62 and 93 scored above the Normal Synchronizers' mean.

Discussion

In the present study, we examined the role of movements and beat saliency in synchronization to music using naturalistic stimuli and movements. We found that the vast majority of young adults are able to match their bounces and claps to the tempo of musical and metronome stimuli, in line with a previous study from our lab [34]. Here, we further show that the matching was less accurate in bouncing than in clapping. Several factors may account for this finding. Bouncing requires more force or physical endurance because each bounce requires the individual to work against gravity to propel the trunk upwards. Indeed, previous work has demonstrated that forearm movement synchronization is less stable when performed against gravitational forces, regardless of the movement's direction (up or down) [52]. Another possible factor is the absence of auditory and tactile feedback in bouncing compared to clapping, whereby the physical impact between the hands produces a sound for each clap. Sensory feedback plays an important role in the anticipatory timing of synchronized movements [53, 54]. During bouncing, both gravity and the absence of sensory feedback may have counteracted the contribution of vestibular stimulation, which is known to play a role in meter perception [17]. Synchronization may be better facilitated by sensory feedback, as is present in clapping, than it is by vestibular stimulation, as is present in bouncing. Clapping, however, does not only benefit from sensory feedback; it is also a discrete movement. Previous research has shown that motor control develops earlier for discrete than continuous forms of movement during childhood [55] and that the variability of movement timing during synchronization is lower for discrete than continuous forms of movement [56, 57]. Therefore, the fact that clapping is a more discrete movement than bouncing may explain why synchronization was more accurate in clapping. Further research is required to disentangle the respective role of discreteness and feedback in synchronization.

In addition to the difference in the accuracy of tempo matching between bouncing and clapping, the two forms of movements often occurred at different levels. Specifically, there was a tendency to clap to every beat but to bounce to every other beat. The latter result is consistent with the observation that the torso moves at higher metrical level (slower tempo) than the arms in dancing [58]. The authors of the study interpreted this in terms of the body's inertial and biomechanical properties, with the torso having a higher period of oscillation than the extremities. In our case, one alternative and novel explanation may be that bouncing to every other beat is a way to "discretize" the time course of the bouncing motion. Whereas bouncing on every beat requires continuous movement, bouncing half as fast allows for discrete movement by introducing a short break between each bounce. Since separate mechanisms seem to drive discrete and continuous forms of SMS, and better synchronization accuracy is associated with the former, the discretization observed with bouncing may reflect a natural tendency to use discrete movements as a strategy for optimal synchronization.

Bouncing and clapping were found to be similarly affected by the musical beat saliency. This result suggests that higher beat saliency facilitates perceptual beat extraction, thereby removing one source of cognitive load on the SMS process. However, synchronization perfor- mance did not strictly follow the beat saliency gradient. For instance, tempo-matching was more accurate to the Dance Lounge and Pop Rock stimuli than to the metronome, which has the most salient beat. Other factors such as groove may play a role. As mentioned in the introduction, high-groove music elicits better SMS coupling than low-groove music [20, 25] and groove is associated with pleasure, which is an important component of musical engagement [59, 60]. It is thus possible that higher beat saliency was associated with better performances not only because beat extraction was easier but also because it was much more enjoyable. Groove might in particular explain why the metronome, which was given the highest ratings of beat saliency, did not lead to the highest synchronization scores. Not only a metronome is unlikely to elicit much pleasure, but previous work indicates that inter-beat event density (of which the metronome has none) is highly correlated with groove [39].

In sum, optimizing the way researchers measure SMS in participants depends on the specific research question under study. Clapping seems optimal for the characterization of the fine-tuning of SMS. In contrast, bouncing constitutes a more challenging task and may therefore be more sensitive to individual differences. Indeed, all 14 individuals (out of 100) who exhibited poor synchronization performance did so in bouncing, but not necessarily in clapping. Qualita- tively, poor synchronization paralleled normal performance, with clapping being better than bouncing and better for music with high beat saliency. These results support the earlier sugges- tion [61] that poor synchronization may correspond to the low tail of a normal distribution of beat perception abilities. It is also consistent with Poor Synchronizers' lower performance, as compared to Normal Synchronisers, on the MBEA metric test, and the recent observation that poor beat perceivers have weak period-matching abilities compared to good beat perceivers [25].

The present findings question the methods currently used to identify individuals with syn- chronization difficulties. So far the existing test batteries assess synchronization abilities through finger tapping (e.g., [37, 62, 63]). Our findings suggest that researchers may be missing whole categories of individuals showing synchronization difficulties, as would have been the case in the present study if we had used clapping only. Therefore, the development and validation of test batteries assessing synchronization via multiple movement forms should be an important goal for researchers in this field. In particular, the recent spread of portable devices containing accelerometers (e.g. smartphones) in the general population may constitute an avenue for the study of synchronization impairments through multiple types of movements on a very large scale.

To conclude, our results show that not all movement types and musical stimuli are equiva- lent when it comes to synchronizing body motion to external rhythms. A goal for future studies will be to understand why synchronization is more accurate via certain movement types over others, and whether these effects reflect distinct underlying mechanisms or rather a continuum of difficulty along a single mechanism. Indeed, the heterogeneity observed in our poor syn- chronizers' sample calls for clarification of the origin of these difficulties, as well as their speci- ficity to music (as compared to speech and other non-auditory modalities).

Supporting Information

S1 Fig. Wii set-up. Clapping (left) and bouncing (right) (PDF)

S1 Table. Description of Normal synchronizers' performances. Log-transformed circular variance mean score (standard deviation) for all conditions (Metronome and Merengue averaged). The higher the score the better the performance. The log-transformed coefficient of variation mean score is also provided.

S2 Table. Model specifications for bouncing and clapping synchronization. Prediction of SR by Movement Type and Beat Saliency factors in Normal Synchronizers.

S3 Table. Description of Poor Synchronizers' performances. A '-' indicates a failure to match the tempo of at least three (out of six) of the musical trials, or a failure to match the tempo of both metronome trials. A '+ /-' indicates a failure to match the tempo of one or two of the musical trials or one of the metronome trials. For Spontaneous motor production, only singu- lar performances are described. For the Metric Perception task, scores below the cut-off are in bold.

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Author Contributions

Conceptualization: PT IP. Data curation: PT. Formal analysis: PT DV. Funding acquisition: IP. Investigation: PT. Methodology: PT IP. Project administration: IP. Resources: IP. Software: PT DV. Supervision: DV IP. Validation: PT DV IP. Visualization: PT. Writing - original draft: PT DV IP. Writing - review & editing: PT DV IP.

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Article 1: Tableaux et Figures

Tableau I. A1: Description de l'expérience musicale et de danse des participants

Table 1. Musical and dance experience of participants

Musical training	**Number of participants**
No training	29
Self-learned (more than 7 years of practice)	7
0.5 to 5 years of formal music classes	39
More than 5 years of formal music classes	20
Professional musicians and graduate music students	6
Dance training	
No training	62
0.5 to 5 years of formal dance classes	25
More than 5 years of formal dance classes	13

Tableau II. A1: Caractéristiques des stimuli

Table 2. Characteristics of stimuli

Table 2. Characteristics of stimuli

Stimulus name	**Genre**	**Tempo (BPM)**	**Familiarity (Z-score)**	**Beat Saliency (Z-score)**
Metronome	-	125/116		1.14
What a feeling[1]	Pop dance	132	-0.50	0.49
The flow[1]	Dance lounge	120	-0.40	0.41
Suavamente[1]	Merengue	124/116	1.16	-0.13
Brand new carpet	Pop rock	126	-0.68	-0.76
Since you've been gone	Soul	117	0.42	-1.15

[1] musical excerpts derived from [34].

Tableau III. A1: Niveaux de métrique produits

Table 3. Produced metrical levels

Stimulus, tempo (BPM)	**Bouncing**		**Clapping**	
	Beat level[1]	**Two-beat level**[1]	**Beat level**[1]	**Two-beat level**[1]
Metronome, 125	55	39	95	2
Metronome, 116	57	38	89	7
Pop Dance, 132	68	25	85	11
Dance lounge, 120	61	27	90	4
Merengue, 125	52	38	78	16
Merengue, 116	52	38	75	19
Pop, 125	49	44	65	28
Soul, 117	44	47	56	38
Median	**54**	**38**	**82**	**14**

[1] Number of participants

Tableau IV. A1: Profils des participants du groupe synchronisation faible

Table. 4. Poor Synchronizers' profiles.

Cluster	**Participants**	**Bouncing to Music**[1]	**Clapping to Music**[1]	**Bouncing to Metronome**[1]	**Clapping to Metronome**[1]
1	18, 93	0	0	0	0
2	31, 37, 80, 92	16.7	37.7	100	100
3	5, 25, 62, 97	33.5	87.5	100	100
4	6, 38, 46, 53	12.5	83.3	33.5	100

[1] Centroïds calculated on the proportion of success trials

Figure I. A1: Exemples de distribution des vecteurs sur le cercle

Fig 1. Example distributions of response vectors. A: random distribution, B: bimodal distribution, C: unimodal distribution.

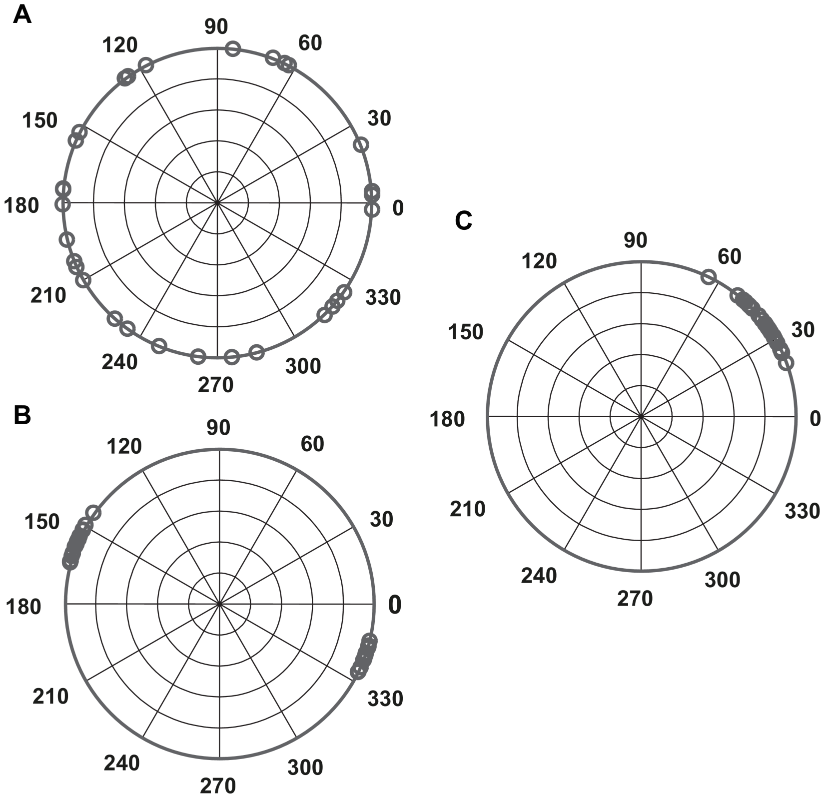


Figure II. A1: Groupe contrôle: alignement de la période

Fig. 2. Period matching in Normal Synchronizers' group. Bouncing and clapping scores were averaged for each stimulus and each participant (no interaction between Movement Type and Beat Saliency factors). Error bars represent standard deviations corrected for repeated measures.

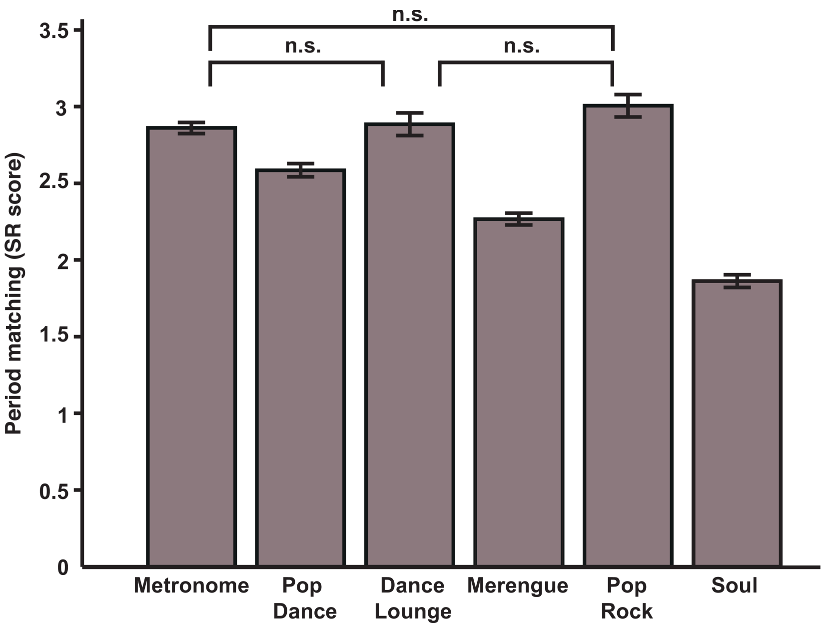
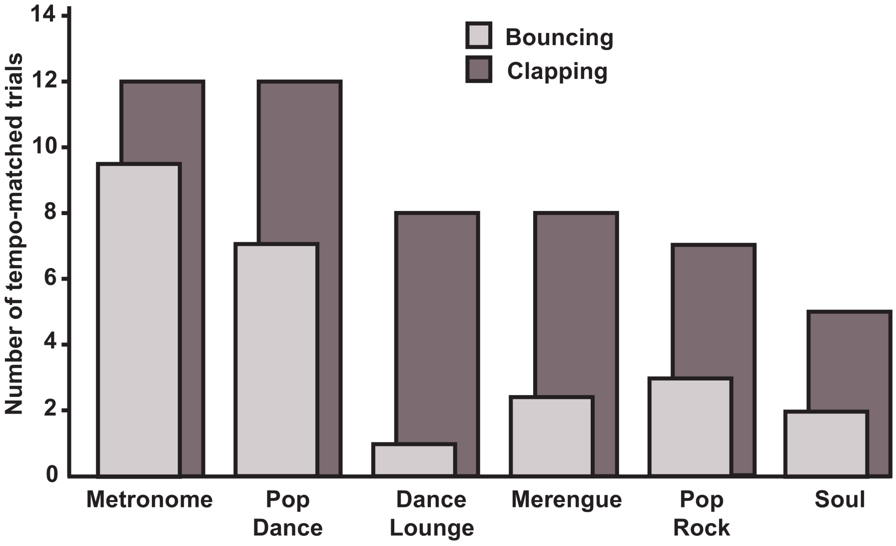


Figure III. A1: Groupe synchronisation faible: alignement de la période

Fig. 3. Period matching in Poor Synchronizers' group. We presented the number of success trials (i.e. period-matched), for each movement type and for all stimuli (maximum is 14, i.e. the number of poor synchronizers). The two Merengue and two Metronome were averaged.



Matériel supplémentaire (Article 1)

Tableau V. A1: Matériel supp. 1: Performance de synchronization du groupe contrôle.

S1 Table. Description of Normal synchronizers' performances. Log-transformed circular variance mean score (standard deviation) for all conditions (Metronome and Merengue averaged). The higher the score the better the performance. The log-transformed coefficient of variation mean score is also provided.

		Metronome	**Pop Dance**	**Dance Lounge**	**Merengue**	**Pop Rock**	**Soul**
Bouncing	Coefficient of Variation	2.93 (0.40)	3.00 (0.40)	2.97 (0.43)	2.99 (0.35)	2.88 (0.48)	2.90 (0.50)
	Circular Variance	2.54 (0.60)	2.44 (0.63)	2.56 (0.77)	2.12 (0.63)	2.59 (0.91)	1.80 (0.65)
Clapping	Coefficient of Variation	3.16 (0.39)	3.17 (0.38)	2.99 (0.54)	3.12 (0.43)	3.08 (0.56)	3.22 (0.49)
	Circular Variance	3.07 (0.44)	2.73 (0.47)	3.21 (0.63)	2.28 (0.50)	3.42 (0.89)	1.93 (0.66)

Tableau VI. A1: Matériel supp. 2: Spécification du modèle statistique

S2 Table. Model specifications for bouncing and clapping synchronization. Prediction of SR by Movement Type and Beat Saliency factors in Normal Synchronizers.

Model	***b* (*SE*)** **(fixed effects)**				Model Statistics **χ^2(*df* = 1)**
Step 0 :	2.61(0.04)***				
Data ~ (1| participant)					
Step 1 :	Intercept		Beat Saliency		65.48***
Data ~ Beat Saliency + (1| participant)	2.62(0.04)***		0.25(0.03)***		
Step 2 :	Intercept	Beat Saliency	Mov. Type		84.98***
Data ~ Beat Saliency + Mov. Type + (1| participant)	1.99(0.08)***	0.26(0.03)***	0.43(0.03)***		
Step 3 :	Intercept	Beat Saliency	Mov. Type	Beat Saliency*Mov. Type	0.09
Data ~ Beat Saliency * Mov. Type + (1| participant)	1.99(0.08)***	0.23(0.09)**	0.43(0.05)***	0.02(0.06)	
Step 4 :	Intercept	Beat Saliency	Mov. Type	Beat Saliency*Mov. Type	29.83***
Data ~ Beat Saliency * Mov. Type + (1+ Mov. Type | participant)	1.97(0.11)***	0.23(0.08)**	0.44(0.06)***	0.02(0.05)	

Note: ****p* < .001, ***p* < .01, **p* < .05, †*p* < .10;

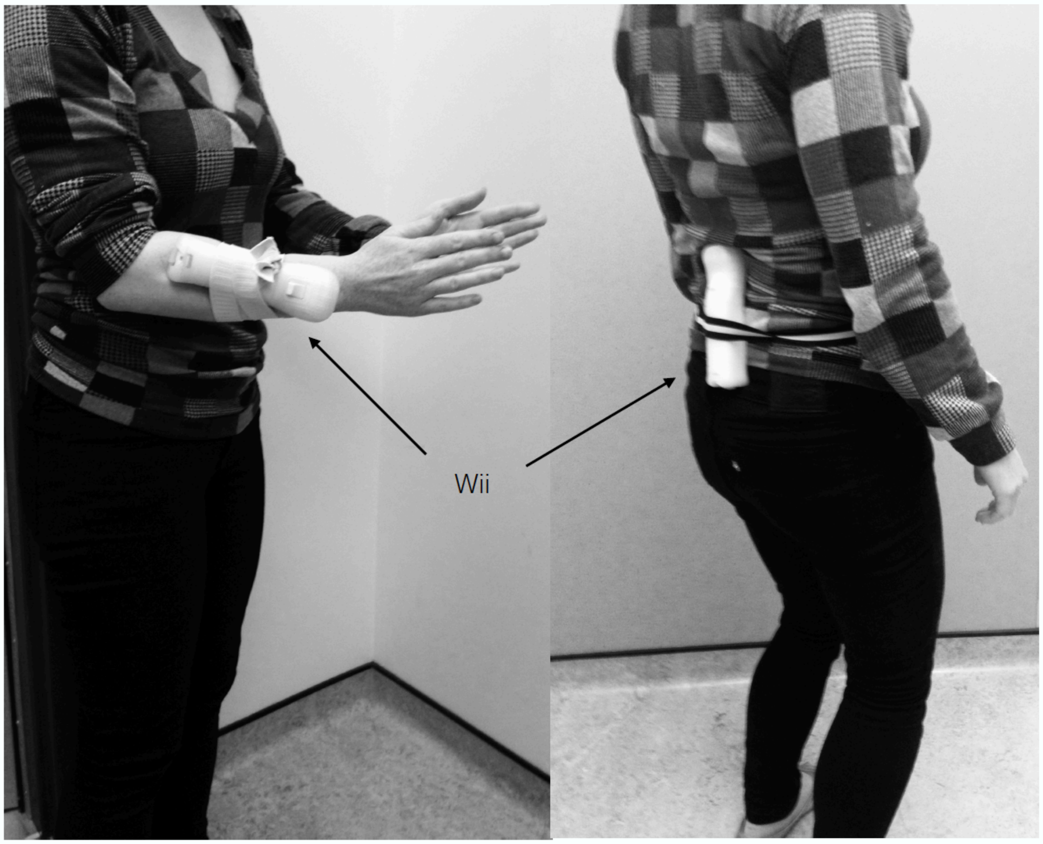
Tableau VII. A1: Matériel supp. 3: Description de la performance du groupe synchronisation faible

S3 Table. Description of Poor Synchronizers' performances. A '-' indicates a failure to match the tempo of at least three (out of six) of the musical trials, or a failure to match the tempo of both metronome trials. A '+ /-' indicates a failure to match the tempo of one or two of the musical trials or one of the metronome trials. For Spontaneous motor production, only singular performances are described. For the Metric Perception task, scores below the cut-off are in bold.

Participant	Synchronization				Spontaneous Motor Production	MBEA Meter Test (cut-off=22)
	Bouncing		Clapping			
	Musique	Metronome	Musique	Metronome		
P18	-	-	-	-	Slow (bouncing)	24
P93	-	-	-	-		**20**
P31	-	+	-	+	Regularity - (clapping)	27
P37	-	+	-	+		26
P80	-	+	-	+	Regularity – (bouncing) & slow (clapping)	25
P92	-	+	-	+		30
P05	-	+	+ /-	+		26
P25	-	+	+ /-	+		30
P62	-	+	+	+		28
P97	-	+	+ /-	+		26
P06	-	+ /-	+ /-	+		**13**
P38	-			+		27
P46	-	+ /-	+	+		**12**
P53	-	-	+/-	+	Slow	22

Figure IV PA1: Matériel supp. 4: Placement de la Wii.

S1 Fig. Wii set-up. Clapping (left) and bouncing (right).



Article 2: Beat alignment test of the motor origin of musical entrainment deficits

Pauline Tranchant, Marie-Élaine Lagrois, Antoine Bellemare, Isabelle Peretz

Beat alignment test of the motor origin of musical entrainment deficits

Pauline Tranchant[1,2], Marie-Élaine Lagrois[1,2], Antoine Bellemare[1,2], & Isabelle Peretz[1,2]

1 Département de psychologie, Université de Montréal, Montréal, Québec, Canada

2 International Laboratory for Brain, Music and Sound Research (BRAMS), Université de Montréal, Montréal, Québec, Canada

Keywords: music, beat, synchronization, perception, sensorimotor deficits

Abstract

The main goal of this study was to assess the motor origin of disorders in music entrainment. To this aim, we adapted the Beat Alignment Test (BAT; Iversen & Patel, 2008) and tested a large pool of typical adults as well as nine individuals with evidence of a deficit in synchronization to music. The tasks consisted of tapping (Experiment 1) and bouncing (Experiment 2) in synchrony with the beat of non-classical music that varied in genre, tempo and groove, and of judging whether a superimposed metronome sounded on or off the beat of the same selection of music. The results point to deficits in both beat synchronization and detection of a misaligned metronome, in line with the idea that the motor system plays a *causal* role in beat perception (Patel & Iversen, 2014). However, support for this theory is weakened by the co-occurrence of deficient synchronization despite normal perception and, conversely, of deficient perception with normal synchronization.

Introduction

Humans across cultures spontaneously move to music. The movement is coordinated with perceived musical regularities that correspond to the beat. Despite the apparent simplicity of this behavior, synchronizing movements to a musical beat is complex and may be unique to humans and a few animal species (Patel, 2014) . Indeed, in many musical contexts one needs to *find* the beat in the auditory signal, as there is no one-to-one correspondence between beats and sounded events. This is particularly the case for syncopated rhythms, in which accents occur at non-beat locations. Furthermore, beats are anticipated during synchronization, relying on predictive timing mechanisms (van der Steen & Keller, 2013). Thus, beat finding is likely to recruit sophisticated cognitive and neural mechanisms, and its study can advance our understanding of predictive timing, which is crucial for numerous human behaviors including communication and sports.

Accumulating evidence suggests that beat perception cannot be understood in isolation from movements. The motion, more than being a mere reaction, may play an active role for predicting the beat (Su & Pöppel, 2012; Patel & Iversen, 2014). Indeed, the way we move the whole body to a rhythm can shape the internal representation of its beat structure (Chemin, Mouraux, & Nozaradan, 2014; Phillips-Silver & Trainor, 2005; 2007). In these prior studies, the same rhythmical sequence was internally represented as a march (One-two-One-two) or a waltz (One-two-three-One-two-three), depending on whether one bent their knees every two (march) or three (waltz) beats. Conversely, occupying the motor system by a pursuit task can disrupt beat perception (Walker, Stillerman, Patel, & Iversen, 2014). Altogether these behavioral results indicate an active role of the motor system in beat perception.

The motor system also shows activity during beat *perception*, even when no overt movement is produced (Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009). For instance, the perception and production of a regular rhythm both activate brain areas implicated in motor processing, including the supplementary motor area (SMA), premotor cortex (PMC), the cerebellum, and the basal ganglia (Grahn & Brett, 2007; Grahn & Rowe, 2009). According to Patel and Iversen (2014), the recruitment of the motor system, rather than being the result of co-activation with auditory regions, sharpens the perception of a beat. These authors propose the "Action Simulation for Auditory Prediction" (ASAP) model according to which prediction of upcoming beats is facilitated by the simulation of periodic movement, in the form of neural oscillations in motor planning regions of the brain. Specifically, neuronal activity in the motor system entrains to the frequency of the beat, which is communicated to the auditory region in a temporally precise way via the auditory dorsal pathway.

The ASAP model is an attractive framework because it can explain why people often experience a compelling drive to move along to the beat when listening to music (Janata et al., 2012). Moving along with music is a human universal, appearing in very young children (Drake, Penel, & Bigand, 2000; Kirschner & Tomasello, 2009) and across the world cultures (Nettl, 2000). Here, we test one straightforward prediction of the ASAP model: if motor oscillations to the beat are altered, its perception should equally suffer. Yet, in recent years, individuals showing poor beat synchronization abilities with preserved perception have been reported (Sowinski & Dalla-Bella, 2013; (Tranchant, Vuvan, & Peretz, 2016). However, the tasks used in these prior studies were not optimal for distinguishing perceptual from motor entrainment to music (Tranchant & Vuvan, 2015). Thus, the observation of intact beat perception in case of anomalous synchronization remains to be confirmed. This was the goal of the present study.

To this aim, we developed a customized version of the Beat Alignment Test (BAT; Iversen & Patel, 2008). The BAT assesses beat alignment in perception and production. It requires participants to align their taps to preselected music (production task) or to detect a misalignment of a superimposed metronome soundtrack to the beat of the same music. The musical selections varied in genre, groove and tempo. Indeed, classical music, as used in some prior tests of beat perception (Bégel, Benoit, Correa, Cutanda, Kotz & Dalla Bella, 2017; Sowiński & Dalla Bella, 2013; Tranchant et al., 2016) may not be optimal for studying motor entrainment. Other musical styles, like R&B or Jazz for example, have high groove and induce a pleasant sense of wanting to move along with the music (Janata et al., 2012). Furthermore, in high-groove contexts (e.g., dance club, music festivals), motion is rarely limited to finger tapping but typically involves whole-body motion (e.g., Butler, 2006; Van Dyck et al., 2013). Thus, here, we investigated beat alignment through both tapping (Experiment 1) and bouncing (Experiment 2). We tested eight "beat-impaired" young adults and a large group of controls. Based on previous studies (Sowiński & Dalla Bella, 2013; Tranchant et al., 2016), we expected to find a few beat-impaired cases with normal beat misalignment detection. In addition, we expected to find a few beat-impaired cases among so-called typical participants because beat finding deficiencies can occur in individuals who are not aware of their condition (Bégel et al., 2017).

Experiment 1: Beat synchronization and perception

Methods

Participants

We tested 42 young adults without suspected beat finding difficulties (typical beat finders group, 23 females, mean age: 26.6 years, range 20-39 years, *SD* = 4.4) and 9 beat-impaired cases of synchronization (7 females, mean age: 26.4 years, range 22-30 years, *SD* = 2.6). All participants were non-musicians and had no history of neurological, cognitive, hearing or motor disorders. Four beat-impaired cases (case 1, 2, 3 and 5 in Table 1) were identified on the basis of poor bouncing and clapping synchronization to music, according to the criterion described in Tranchant, Vuvan & Peretz (2016). Two cases (4 and 6) were identified in a pilot experiment investigating tapping synchronization, using the musical stimuli presented in the present study. Two cases (7, 8) were recruited on their self-declared inability to follow the beat in music. The last beat-impaired case (T.B.) was initially recruited to be part of the typical group but was shifted to the beat-impaired group because her score was two standard deviations below the mean of the typical group (see Results section) in tapping.

All participants were assessed for the presence of musical deficits with standard tools. Typical participants were tested with the On-line Test of Amusia (Peretz & Vuvan, 2017). Scores were within normal variations (Table 1), except for two participants who were subsequently tested with the Montreal Battery of Evaluation of Amusia (MBEA; Peretz, Champod, & Hyde, 2003) in the laboratory and obtained normal scores on the latter battery. Beat-impaired cases were assessed with the MBEA (Table 1). They obtained a normal melodic composite score, which is an averaged score for three tests (scale, contour and interval) assessing pitch processing in a melodic context (Vuvan et al., 2017). All beat-impaired cases obtained a normal score in the discrimination of melodies by their rhythm whereas two of them (case 6 and 7) scored two *SD* below the population mean on the Metric test (below cut-off according to Vuvan et al., 2017).

[Insert Table 1 here]

All beat-impaired individuals were tested for their ability to synchronize finger taps with a metronome. Stimulus consisted in sequences of 31 isochronous tones, with two inter-tone-intervals (476 and 506 ms, corresponding to 126 and 119 BPM respectively). Since successful period matching was observed with both metronome sequences, the presence of a basic sensorimotor deficit can be excluded in the beat-impaired group.

Stimuli

Ten songs that varied in genre (see Table 2) were selected from previous research (Janata et al., 2012; Phillips-Silver et al., 2011; Tranchant et al., 2016; Einarson & Trainor, 2016). Beats were identified by a beat tracking algorithm (Ellis, 2007) implemented in Matlab (MathWorks). Eight songs had a simple meter in 4/4 while two had a more complex one: "Sollsbury Hill" in 5/4 and "Take Five" in 7/4. In order to obtain groove information, an independent sample of 64 adults unselected for their musical experience (35 females, mean age: 24.2 years, *SD* = 5.3) had to move a slider potentiometer (10 K Ohm, 0.5W, 10 mm) controlled by customized Python scripts while the participant listened to each stimulus twice in separate blocks, in a randomized order. Slider values ranged from zero (least groovy) to 1023 (most groovy). Groove was defined as "that aspect of the music that induces a pleasant sense of wanting to move along with the music" (Janata et al., 2012). Ratings were averaged across the two presentations then transformed into z-scores within participant. These values were then averaged across participants in order to obtain a groove score for each song (Table 2).

[Insert Table 2 here]

For the perception test, the 10 songs were presented with a metronome track constituted of pure tones (100ms, 1000Hz) that was superimposed on the last 24 beats of each stimulus, except for "Take Five" where 36 beats were considered because it had a faster tempo. In order to give participants some time to build their internal representation of the beat, the metronome track started five seconds after the beginning of each stimulus. Each song was presented eight times, four times with misaligned metronome tones (off-beat conditions) with ±15% phase shift or ± 5% period shift, and four times with aligned metronome tones (on-beat conditions), twice on each beat and once for each of two alternating beat arrangements, for a total of 80 trials. The two alternating arrangements (on-beat conditions) consisted of metronome tones occurring every two beats, either starting on the first or the second beat of the song. Creating more than one on-beat condition was done to equate the ratio of on-beat and off-beat conditions without presenting the same condition more than twice. A schematic description of on-beat and off-beat conditions is provided in Figure 1.

[Insert Figure 1 here]

For the tapping test, the songs did not have a superimposed metronome and were 10s longer: five seconds were added at the beginning (to give participants enough time to find the beat) and at the end of the excerpt. Note that these extra seconds were not included in the analyses.

Tasks and Procedure

Participants completed the tapping test before the perception test on the same day. Tapping was always administered first in order to avoid biases or clues provided by the metronome in the perception test. Participants were instructed to tap in time with the beat of the music. There were four familiarization trials on different songs than the experiment stimuli. After each of these four trials, the participant listened to a metronome superimposed on the beat of the same song, to ensure that she/he understood the concept of beat. The actual test started right after the practice session. Each stimulus was played twice in two distinct blocks, for a total of 20 trials. Order of stimuli was randomized within each block. Participants were invited to take a short break between the two blocks.

In the perception test, participants judged whether the superimposed metronome was aligned with the beat of the music or not. The task consisted in choosing one of four choices: *always on the beat (1), mostly on the beat (2), sometimes on the beat (3)* and *rarely or never on the beat (4)*. For the analysis, the first two choices were considered as "on-beat" responses and the last two choices were considered as " off-beat" responses. We provided four choices rather than just on- or off-beat options because for off-period trials some metronome tones could happen to be on a beat (Figure 1). Participants received two on-beat trials, two off-phase trials, and two off-period trials for familiarization before the experimental trials. The songs used in the familiarization session were different from the experimental stimuli, and were identical to the tapping familiarization songs. Feedback was given after each familiarization trial to ensure that the participant understood the task. The actual test started right after, with no feedback. The test was divided in four blocks, with 20 trials in each block. The order of presentation of the stimuli was pseudo-random so that no song was presented twice consecutively. Participants were instructed not to move to the music in order to reduce the contribution of body movements to the perception task. There were three breaks of at least five seconds between blocks and participants were given the opportunity to take longer breaks if needed.

The tapping test lasted for approximately 20 minutes, and the perception test lasted for approximately 40 minutes. The tapping test was programmed with MAX/MSP (Cycling' 74) and the perception test was programmed with Matlab. Taps were made on a square force sensitive resistor (3.81 cm, Interlink FSR 406) connected to an Arduino Duemilanove (arduino.cc) transmitting timing information to the computer via the serial USB port. This system had a 1-ms temporal resolution. The square resistor was placed on a table in front of the participant. Stimuli were delivered through headphones (DT 770 PRO, Beyerdynamics).

Participants provided written informed consent and received financial compensation for their participation. The research was approved by the local ethics committee at Université de Montréal.

Data analyses

We used Matlab for data processing and R for statistical analyses. There was no missing data in the perception test, with 80 responses (10 per stimulus) recorded per participant. For the tapping test, six trials (0.5% of the total) from three typical participants were missing due to a technical error. Trials for which less than eight taps were recorded (0.8% of the total) were also excluded from the analyses. This happened in one trial of a beat-impaired case and in eight trials from five typical participants. Tapping data were analyzed with circular statistics, using the Circular statistics Toolbox for Matlab (Berens, 2009). Mixed effects models were computed using the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R. Degrees of freedom were calculated with the Satterthwaite approximation using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017).

Results

Synchronization

We used the Rayleigh test to assess whether taps were period-matched with the beat period of each musical stimulus, after transforming taps into vectors on the circle. A significant Rayleigh test ($p < .05$) indicates success in matching the inter-tap intervals with the stimulus inter-beat-interval (i.e., the period). Less than three out of 20 trials per participant failed to be period-matched in the typical group to one notable exception (Figure 2). One participant initially from the typical group (T.B.) failed to period-match her taps in seven trials. As it turned out that the synchronization performance of this participant was characteristic of the beat-impaired group (Figure 2), we shifted her in this latter category, as mentioned previously.

[Insert Figure 2 here]

Synchronization of the taps to the song beat was calculated with circular statistics. Individual taps were expressed as angles on a polar scale from 0 to 360 deg., considering that the full circle corresponds to the inter-beat interval. Angles were treated as unit vectors and used to calculate the mean resultant vector *R*. The length of vector *R*, ranging from 0 to 1, indicates *synchronization consistency* (i.e., the reciprocal of variability). A value of 1 means that all the taps occurred exactly at the same time interval before or after the pacing stimulus (maximum consistency); 0 means absence of synchronization (the taps are randomly distributed between the beats). Before statistical analyses, synchronization consistency was submitted to a log transformation, as circular variance was positively skewed, it was transformed using a log function (log score = -1*log circular variance). A higher score now indicates higher consistency. For each participant, the log-transformed score was averaged across the 20 trials. The scores are summarized in Figure 3. The beat-impaired group performed largely below the typical group. All participants from the beat-impaired group (including T.B.) obtained a score of two *SD* below the mean of the typical group.

[Insert Figure 3 here]

Synchronization varied across songs. In order to better understand which aspects of the stimuli contributed to this variability, we performed a mixed-effects regression on the transformed circular variance in the typical group, with Groove and Tempo as predictors and Participants as random factor. Block (first versus second block of tapping) was also entered in the model to assess the potential effect of practice. Note that the song "Solsbury Hill" and "Take Five" were not considered in this analysis because of their complex metrical structure. We observed a positive effect of Repetition, $\beta = .15$, $SE = .058$, $t(601) = 2.52$, $p = .012$, indicating superior performance in the second block, a negative effect of Tempo, $\beta = -.23$, *SE*

= .030, *t*(601) = -8.21, *p* < .0001, indicating higher performance for slower stimuli, a negative effect of Groove, *β* = -.12, *SE* = .056, *t*(601) = -2.17, *p* =.031, indicating an unexpected higher performance for lower groove music, and an interaction between Tempo and Groove, *β* = -.13, *SE* = .039, *t*(601) = -3.47, *p* < .001. Unfortunately, the observed interaction between Tempo and Groove could not be broken down, as these factors were not manipulated independently from each other. At any rate, tempo seems to have a more linear effect than groove on synchronization (Figure 4). Similar statistical modeling for the effects could not be performed in the beat-impaired group because there were too few period-matched trials to be considered.

[Insert Figure 4 here]

Perception

The sensitivity index (*d'*) was calculated, as an unbiased measure of detection performance, based on the number of Hits (when unaligned tones were correctly detected) and False alarms (when lack of alignement was incorrectly reported). The scores are presented in Figure 5. As can be seen, the *d'* was highly variable in the typical group. Two participants obtained a near perfect score with only one or two incorrect responses out of 80 trials, while five participants from the typical group performed at chance (being 48/80, by binomial test).

[Insert Figure 5 here]

In the beat-impaired group, two participants (cases 6 and 7) performed at chance, with accuracy scores of 40 and 43/80, respectively. Interestingly, these two participants were also the ones showing a deficit on the Meter Test of the MBEA (Table 1). As can be seen in Figure 5, two additional participants (cases 1 and 5) performed above chance but with a *d'* score that was below the cut-off computed from typical scores. The other five beat-impaired cases performed above the cut-off albeit with low scores, which suggests normal but low beat perception abilities. A Welch's two-sample t-test confirmed that the d' score was lower in the beat-impaired group (M = 1.22) compared to the typical group (M = 2.40), $t(15.25) = 4.17$, $p < .001$. Altogether these results indicate low perception abilities in the beat-impaired group.

Because chance performance may reflect poor understanding of task demands, the five typical individuals and the two beat-impaired ones were invited to take the test a second time, on a different day; we made sure that the instructions were clear to them. One beat-impaired participant still performed at chance (case 6, with 46/80 correct response) while the other one performed slightly above chance (case 7, with 50 correct responses). Nevertheless, the *d'* score remained below the cut-off for both of them (.41 and .78, respectively), confirming a perception deficit. Three participants from the typical group performed above chance, but only two of them (identified in Figure 6) obtained a score above the cut-off (d' = 2.1 and 1.88). Therefore, a perception deficit is confirmed in two participants from the typical group. The fifth participant from the typical group was unavailable for retest. Note that the two participants (cases T.N. and M.B.) from the typical group who failed the perception test twice were further tested with the MBEA; their scores were within the normal range.

A different measure of sensitivity than *d'* was used to assess the role of tempo and groove on beat perception, because there was only eight responses per stimulus and participant to consider. A correct response corresponded to "always/mostly on the beat" when metronome tones were on-beat and to "sometimes/rarely on the beat" when the metronome was off-beat. Participants who failed to perform above chance (five in the typical group and two in the beat-impaired group) were not considered in this analysis. In the typical group, we found an effect of Tempo, $\beta = -.15$, $SE = .050$, $t(249) = -3.04$, $p < .01$, indicating higher accuracy for slower tempi, no effect of Groove, $\beta = -.025$, $SE = .094$, $t(249) = -.27$, $p = .79$ and no interaction between the two factors, $\beta = .091$, $SE = .066$, $t(249) = 1.38$, $p = .17$. In the beat-impaired group, there were no effect of Tempo, $\beta = -.14$, $SE = .15$, $t(46) = -.97$, $p = .34$, no effect of Groove, $\beta = -.47$, $SE = .27$, $t(46) = -1.73$, $p = .091$, and no interaction between the two factors, $\beta = -.24$, $SE = .19$, $t(46) = -1.29$, $p = .20$.

[Insert Figure 6 here]

Despite the fact that performance in the two tasks appears related (Figure 6), the correlation obtained by the 36 typical participants performaning above chance did not reach significance, $r(34) = 0.26$, $p = 0.13$.

To summarize, we confirmed poor tapping performance in eight beat-impaired cases by objective testing and discovered a new case of deficient synchronization without awareness (T.B.). Four of them showed impaired beat perception and the other five obtained a low but normal perception score. The reverse pattern - impaired perception with a low but normal tapping score - was observed in two individuals initially recruited to be part of the typical group. Nevertheless, all these participants performed poorly in general. This raises the possibility that the disturbance is not confined to either auditory or motor beat finding mechanisms but rather arises from a more central timekeeping mechanism.

Experiment 2. Bouncing

Synchronization performance was assessed with bouncing movements to the same songs in order to ascertain the generality of the beat impairment found with tapping in Experiment 1. Synchronization performance may vary somewhat across movement types (Repp & Su, 2013; Tranchant et al., 2016) and may depend on how natural the movement feels to the participant. Thus, finding a deficit in both tapping and bouncing would provide convergent evidence for the presence of a disorder and for the abstract nature of the processes involved.

Methods

Participants

The nine beat-impaired cases from Experiment 1 and nine matched control participants (6 females, 3 males; mean age: 27 years, range: 22-32 years) participated to the bouncing task. This control group did not differ from the other typical participants tested in Experiment 1 on tapping performance, $t(19.73) = 1.67$, $p = .11$ (Welch's two-sample t-test).

Material and Procedure

Participants were standing in the middle of a large room, facing away from the experimenters. The room was equipped with an optical infrared motion capture system (Qualisys Oqus). The cameras detected three-dimensional positions of the markers, at a 200 Hz sampling rate. The 10 songs were delivered at a comfortable volume through two loudspeakers (Genelec 8040A) controlled by an audio interface (RME Fireface 800). Data from the markers was synchronized with the stimuli via a Qualisys Analog interface, and recorded by the Qualisys Track Manager software (http://www.qualisys.com).

Participants wore a reflective marker on the right knee, which served to measure bouncing. The bouncing consisted in a vertical full-body movement by bending the knees. Participants were instructed to bounce in time with the beat of the music, keeping the knees parallel and hips facing forward with the arms resting at their sides. Before starting with the music, participants were instructed to bounce in a regular fashion for 40 seconds in silence ("spontaneous"), to confirm that they could perform the movement. Then a procedure similar to the tapping test (Experiment 1) was followed, except that the stimuli were presented only once (10 trials in total). Stimulus order differed for each participant, and matched the order followed for Experiment 1 first tapping block. There were four practice trials. After each practice trial, the participant was presented with the same stimulus but this time with a metronome track aligned with the beat. The actual test without metronome started right after the practice. The session had a duration of approximately 40 minutes. The bouncing test was performed one to two weeks after Experiment 1.

Data Analyses

The Qualisys Track Manager software for markers identification and the Motion Capture (MoCap) Toolbox (Burger & Toiviainen, 2013) in Matlab, and Matlab and R were used for data processing and statistical analyses. For each trial, displacement data of the marker placed ont the right knee was extracted and linearly interpolated to 1000Hz in order to obtain the same resolution of 1ms as in tapping (Experiment 1). The component of maximal movement amplitude was selected, and corresponded to the horizontal direction perpendicular to the wall faced by the participant. For each trial, time points of maximal flexions of the knee were extracted (zero-crossings of the backward horizontal velocity), and were used to calculate vectors on the circle, as done for tapping.

Results

As in Experiment 1, the Rayleigh test was used to assess whether the bounces were period-matched with the stimulus beat for each song. We found a significant Rayleigh test ($p < .05$) for only 18% of the trials in the beat-impaired group and for 96% of the trials in the control group, with no overlap between the group's scores (Figure 8). Note that one case, T.B., failed to match the period of all ten songs, although she managed to synchronize with five out of ten songs in tapping in Experiment 1. This failure to bounce in-synch with the music could not be attributed to mechanical limitations. Her ability to produce a regular bouncing movement was normal in the spontaneous condition: she obtained a coefficient of variation (corresponding to the variance of the inter-bounce-intervals divided by the mean interval) of 0.034, which indicates a slightly higher regularity than the control group (*M* = 0.040). More generally, the coefficient of variation for spontaneous bouncing in the beat-impaired group (*M* = 0.053) did not differ from the control group, *t*(16) = 1.44, *p* = .17 (same result by non-parametric testing).

[Insert Figure 7 here]

In order to compare bouncing and tapping performance we used the log-transformed circular variance (log score = -1*log(circular variance)), averaged across the ten bouncing trials and across the first block of 10 tapping trials of Experiment 1. As expected, performance was lower in the beat-impaired compared to the typical controls in both experiments (Figure 9). Bouncing scores were generally lower than tapping scores in the beat-impaired group, whereas the reverse pattern was observed in the control group. This was confirmed by a mixed-design ANOVA (type III sum of squares), in which we found a main effect of Group, *F*(1,16) = 759.1, *p* < .0001, no effect of Condition, *F*(1,16) = 0.040, *p* = 0.32, and an interaction between the two factors, *F*(1,16) = 16.15, *p* < 0.001. The difference between tapping and bouncing scores within each group was confirmed by post-hoc comparisons (with bonferroni correction): *t*(8) = 2.80, *p* = 0.047 in the beat-impaired group and *t*(8) = -2.91, *p* = 0.039 in the control group.

Correlations between tapping and bouncing performances did not reach significance in the beat-impaired, $r(7) = -.38$, $p = .32$ nor in the control group, $r(7) = -.22$, $p = .58$ ($r = -.35$, $p = .36$ and $r = -.27$, $p = .49$ by non-parametric tests).

[Insert Figure 8 here]

In sum, the deficits in aligning taps to the musical beat generalize, and are even amplified, in aligning whole body movements. In contrast, typical synchronization was higher in bouncing than in tapping.

Discussion

The goal of this study was to test the reliance of perception on motor entrainment to a musical beat, as framed in the "Action Simulation for Auditory Prediction" (ASAP) model of Patel & Iversen (2014). To this aim, we used a classic neuropsychological procedure which consists in testing whether dissociations can be found between beat perception and production in nine individuals with clear evidence of a deficit in motor entrainment. According to the ASAP model, a deficit in motor entrainment should impair beat perception. This prediction was born out by the finding of a co-occurrence of deficit in judging beat alignment of metronome tones to the same songs on which the beat-impaired cases exhibited problems in tapping and bouncing to the beat. This poor performance in both production and perception suggests that poor motor entrainment might be at the root of the deficit.

However, typical performance in beat tracking production and perception did not correlate. Moreover, in some cases, perception did not appear as off-synch as movements were, which suggests a dissociation according to the usual criterion of a score below two standard deviations of the normal population's mean as indicative of a deficit. In particular, five individuals with severe motor entrainment deficits managed to perform in the normal range in the detection of an off-beat metronome tone. Conversely, we found two cases who were unable to detect the off-beat tones but tapped to the beat within normal variations. Note that the evidence is not strong because these seven cases performed poorly in general. Thus, these dissociation patterns may question the ASAP model, albeit not firmly so.

This raises the thorny question concerning the diagnostic test that should be used in the future to identify disorders in musical beat processing. In this respect, it is worth mentioning that the meter test of the MBEA, which is the current standard tools for the identification of musical disorders, is not sensitive enough to the presence of a deficit. Two of the four cases with a clear-cut deficit in beat perception on the Beat Alignment Test also failed the MBEA Meter test. The rhythm test of the MBEA had even less, if no, sensitivity to the presence of the beat processing impairment; all beat-impaired participants performed in the normal range, including those with deficient beat perception on the BAT test. This shows that the Rhythm test of the MBEA is not appropriate to prove normal beat perception abilities as done in prior research (Sowinski & Dalla Bella, 2013). The findings suggest that MBEA meter test might constitute a good complement but cannot replace the Beat Alignment Test for the diagnosis of beat perception deficits.

For synchronization, both tapping and bouncing to the music were diagnostic of a problem. The evidence is compatible with the idea that the difficulty is more cognitive than motoric, in accordance with the ASAP model and with previous research (Iversen & Patel, 2008; Fujii & Schlaug, 2013; Leow, Parrot, & Grahn, 2014). It is also consistent with the normal performance found in spontaneous tapping and bouncing without metronome or music. The movements were as regular in the individuals with a synchronization deficit as in the matched controls. Therefore, little support for a basic timing deficit was found in the present study. However, by collecting larger amounts of tapping sequences we observed a difficulty to maintain regularity and limited flexibility in tapping speeds among beat-impaired cases (Tranchant & Peretz, in preparation).

To conclude, our study confirms that beat perception and synchronization abilities are tightly coupled so that a congenital anomaly can hardly dissociate them. Now that we have a good description of the beat impairment at the behavioral level, future research should be brought to the next level by delineating its neural correlates and its training potential.

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Disclosure statement

The authors declare no competing interests

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Article 2: Tableaux et Figures

Tableau I. A2: Résultats à la MBEA et au Test en Ligne .

Table 1. Musical Processing. Beat-impaired participants' scores on the Montreal Battery of Evaluation of Amusia (MBEA) and scores of the typical group (N = 41) on the Online Test of Amusia. Scores below the cut-off are in bold.

Beat-Impaired Participants	**Melodic Composite Score (/30) cut-off : 21.4**	**Rhythm (/30) cut-off : 22**	**Meter (/30) cut-off : 17**
1	26	22	25
2	24.7	26	24
3	26.3	28	20
4	25	26	19
5	24.3	25	21
6	23. 7	27	**13**
7	23	26	**16**
8	25.3	25	23
9 (T.B.)	29	25	23
Typical Group (N = 40)	**Scale (%)**	**Off-beat (%)**	**Off-key (%)**
Mean	90.5	84.5	82.6
SD	7.2	6.5	11.5

Tableau II. A2: Description des stimuli.

Table 2. Description of stimuli.

Song Name	**Genre**	**Tempo (BPM)**	**Duration (in s)**	**Groove mean (*SD*)**
Party at your mama's house	Rock	82	22	-1.0 (.76)
Superstition	Pop	100	19	.86 (.62)
Solsbury hill	Rock	103	18	-.33 (.73)
Since you've been gone	Soul	117	17	.00 (.68)
The flow	Dance lounge	129	16	.02 (.70)
Suavemente	Merengue	124	16	.63 (.91)
Brand New Carpet	Pop rock	126	16	-.70 (.60)
What a feeling	Pop dance	132	15	-.01 (.91)
Don't stop me now	Rock	156	14	.63 (.80)
Take five	Jazz	170	17	-.02 (.94)

Figure I. A2: Représentation schématique de l'alignement du métronome sur le beat des stimuli.

Figure 1. Schematic representation of beat alignment of the metronome soundtrack (Experiment 1).

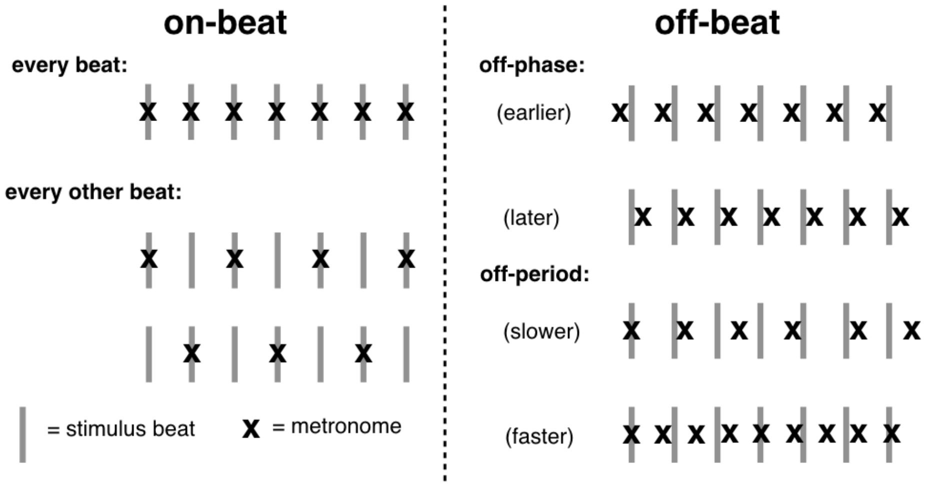


Figure II. A2: Nombre d'essais alignés à la période par participant (tapping).

Figure 2. Number of period-matched trials (out of 20) in the tapping test. Each dot corresponds to a participant.

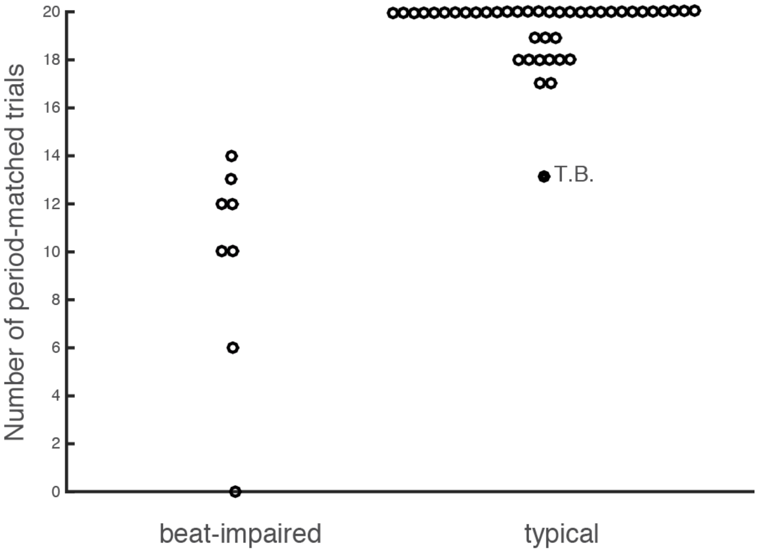


Figure III. A2: Performance en tapping dans les deux groupes.

Figure 3. Tapping performance. Scores in beat-impaired cases (N = 9) and in the typical group (N = 41). The vertical grey line indicates cut-off scores (i.e. two *SD* below the mean, as computed from the typical group).

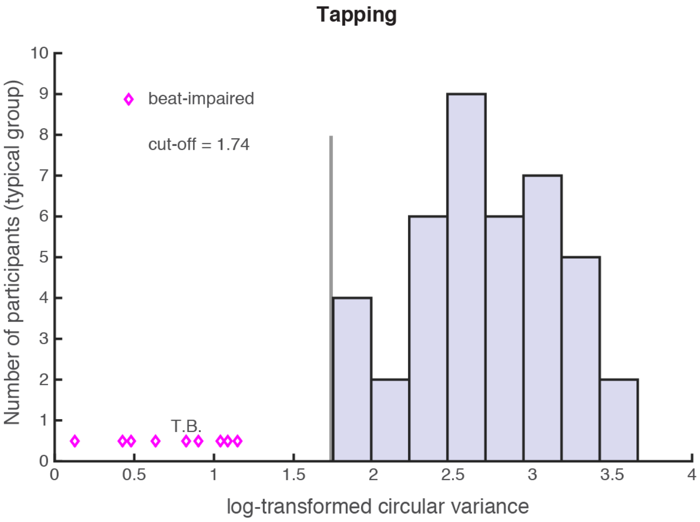


Figure IV. A2: Performance en tapping, en fonction du tempo et du groove.

Figure 4. Tapping synchronization as a function of the stimulus tempo and groove. Standard errors are represented by bars (typical group only, $N = 41$).

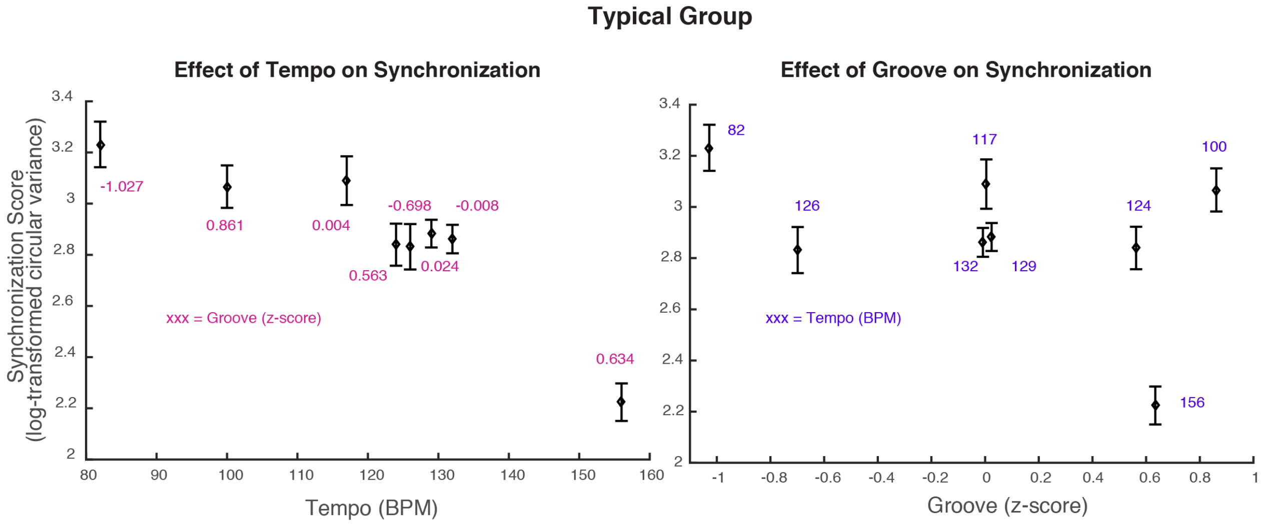


Figure V. A2: Performance au test de perception.

Figure 5. Distribution of Perception scores. The vertical grey line indicates cut-off score of 1.29 corresponding to two SD below the typical mean. Participants from the typical group who performed at chance are identified by black stars.

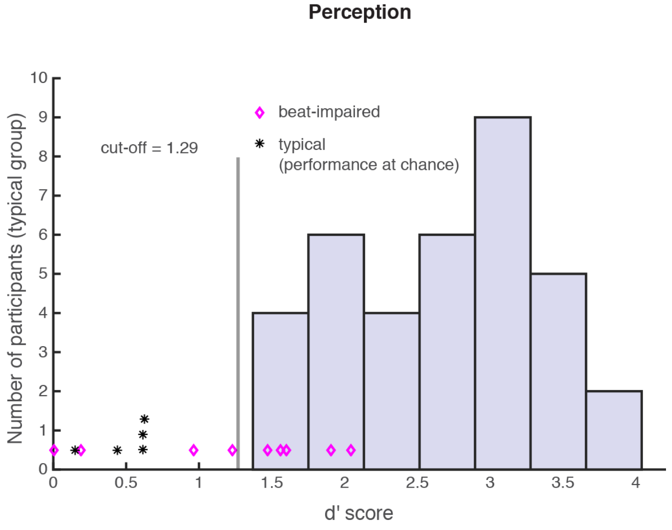


Figure VI. A2: Performance en perception, en fonction du tapping.

Figure 6. Individual scores in perception as a function of tapping. Grey lines indicate cut-off scores. Perception: participants who performed above the cut-off on re-test are identified by grey vertical arrows and the participant who has not been re-tested is identified by the grey star.

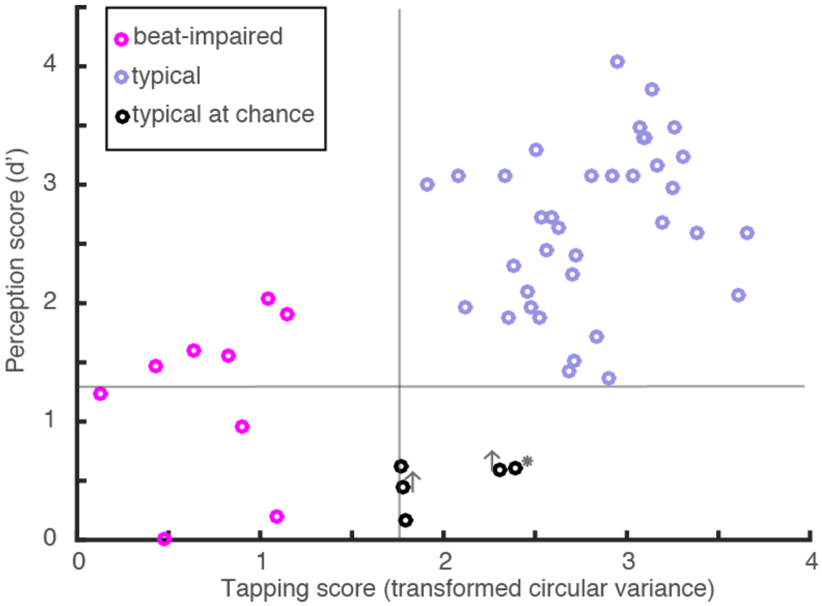


Figure VII. A2: Nombre d'essais alignés à la période par participant (bouncing).

Figure 7. Number of period-matched trials (out of 10) in bouncing. Each dot corresponds to a participant.

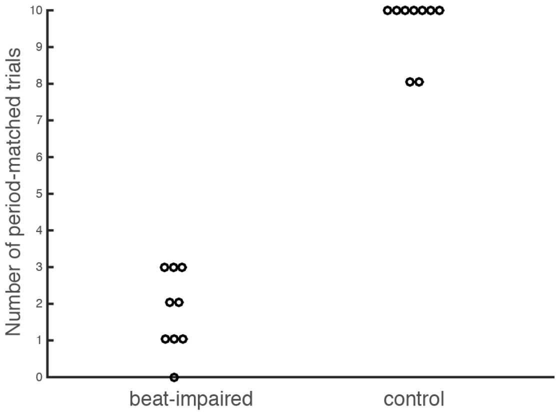
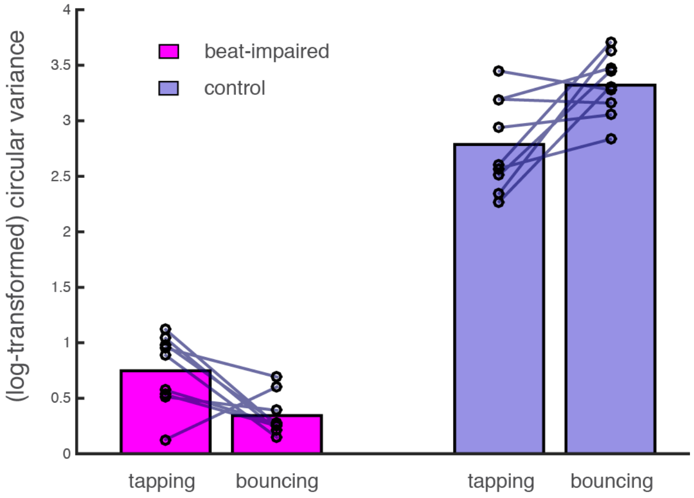


Figure VIII. A2: Performance de synchronisation: bouncing et tapping.

Figure 8. Tapping and bouncing alignment to the musical beat as a function of group. Dots indicate individual scores (averaged across stimuli).



Article 3: Faulty mechanisms of timekeeping in the beat-based form of congenital amusia

Pauline Tranchant, Isabelle Peretz

Faulty mechanisms of timekeeping in the beat-based form of congenital amusia

Pauline Tranchant[a,b] **& Isabelle Peretz**[a,b]

1 Département de psychologie, Université de Montréal, Montréal, Québec, Canada

2 International Laboratory for Brain, Music and Sound Research (BRAMS), Université de Montréal, Montréal, Québec, Canada

Keywords: beat, music, isochrony, timekeeping, movement, sensorimotor deficits

Abstract

Humans master the capacity to move in time with the beat of music. Yet some individuals show marked difficulties to synchronize simple body movements with musical beats. The causes of this phenomenon are still largely unexplained. Here we investigated internal timekeeping capacities, which are driving all rhythmic motor behaviors, in a group of eight beat-impaired and a group of 14 matched control participants. Beat-impaired cases were recruited for their poor ability to tap with the beat of music, and did not present any neurological, auditory or musical pitch-related deficits. Groups were compared for two finger tapping tasks: spontaneous production of regular sequences (no stimulus) and synchronization-continuation to a metronome spanning a large range of interval periods (225-1709 ms). Higher inter-tap variability was observed across tasks in the beat-impaired group. Synchronization was in addition characterized by unsuccessful matching of the fastest metronome's period and larger asynchronies between taps and tones of slow metronomes. A lower capacity to maintain the period of slow metronomes was as well observed during the continuation (i.e. after tones had stopped). Altogether these results indicate a low capacity for isochrony and limited rate flexibility in the beat-impaired group, and suggest a disruption of basic timekeeping mechanisms.

Introduction

Humans are particularly good at producing stable periodicities in synchrony with others (Kirschner & Tomasello, 2009; Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007; Su, 2014). This skill is biologically useful for cooperation (Cirelli, Einarson, & Trainor, 2014) and events prediction (Konvalinka, Vuust, Roepstorff, & Frith, 2010; van der Steen & Keller, 2013). It appears universally mastered to the exception of a few deviant individuals (Phillips-Silver et al., 2011). In the advent of a neurodevelopmental anomaly, synchronization skills can be disrupted. The disorder typically affect beat finding in music (Phillips-Silver et al., 2011; Sowiński & Dalla Bella, 2013) but it may also occur in synchronization to a metronome in which timing is strictly isochronous (Palmer, Lidji, & Peretz, 2014; Tranchant, Vuvan, & Peretz, 2016). Here we tested the basic mechanisms underlying the aptitude for isochrony in eight individuals who have been diagnosed with deficient musical beat finding, which is a form of congenital amusia.

The most common form of congenital amusia concerns the processing of the pitch structure of music, not isochrony (Hyde & Peretz, 2004; Phillips-Silver, Toiviainen, Gosselin, & Peretz, 2013). It is a neurodevelopmental disorder that affects the processing of musical pitch in both perception and production. It is associated to abnormal connectivity between the auditory cortex and inferior frontal cortex mostly in the right cerebral hemisphere (for a review see Peretz, 2016). The pitch disorder is hereditary (Peretz, Cummings, & Dubé, 2007) and molecular analyses are in progress in order to identify the responsible genes. Thus, pitch deafness is instructive regarding causal links between musical pitch, brain networks and genes. Likewise, impairments in isochrony represent a complementary and distinct chance to study the neurobiological foundations of musical rhythm.

The core mechanisms underlying musical beat arises from the aptitude to impose an isochronous grid to a rhythmic sequence. The aptitude for isochrony, where all intervals between events are equal like those of a steady metronome, rests on the interaction between acoustical cues and higher-level cognitive organization. One key feature of this high-level organization is anticipation. Humans tap in advance of metronome clicks by a few tens of milliseconds (Repp, 2005). This typical behavior is thought to compensate for the time lag introduced by sensory processes (Aschersleben, 2002; Aschersleben & Prinz, 1995; Aschersleben, Gehrke, & Prinz, 2001). Such anticipatory tendency is considered to be unique to humans and a few animal species, specifically those with the capacity for vocal learning (Patel, 2014; Patel, Iversen, Bregman, & Schulz, 2009), although recent findings with a sea lion (Cook, Rouse, & Wilson, 2013), a chimpanze (Hattori, Tomonaga, & Matsuzawa, 2013), and a bonobo (Large & Gray, 2015), who are not vocal learners, are challenging this view (Rouse, Cook, Large, & Reichmuth, 2016). In the two beat-impaired cases we have tested so far, normal anticipation of steady metronome's clicks was observed (Palmer et al., 2014).

Another key feature of the aptitude for isochrony is rate flexibility (McAuley, Jones, Holub, Johnston, & Miller, 2006). It is still unknown whether beat-impaired individuals lack flexibility, since they_were tested with a narrow range of isochronous rates, which lie around the optimal tempo of 500-600 ms between events (Baruch, Panissal-Vieu, & Drake, 2004; Moelants, 2002). The largest range tested with beat-impaired cases is 450-750 ms for which large individual differences are obtained (Sowiński & Dalla Bella, 2013). This range is still limited in regard to what adults can typically achieve when synchronizing taps with a metronome (Repp, 2005).

Here, we compare the performance of eight new beat-impaired cases with those of a control group in terms of anticipatory tapping (synchronization) and continuation to metronome-like stimuli in reference to their spontaneous tapping rate. First, based on previous studies (Palmer et al., 2014; Phillips-Silver et al., 2011; Sowiński & Dalla Bella, 2013; Tranchant et al., 2016) we predict that no difference will be observed for spontaneous tapping between the beat-impaired group and a group of matched control participants. This is assessed in Study 1. Second, we predict that synchronization and continuation performance may be normal initially around beat-impaired participants' spontaneous (comfortable) tapping rate but should deteriorate for stimulus rates rolling away from it. In study 2, we test to what extend synchronization-continuation degrades for rates that are distant from the individually defined spontaneous rate.

Methods

Participants

Eight beat-impaired cases (6 females, 2 males; mean age: 27.1 years, *SD* = 2.2) were matched for years of education and years of musical and dance training to 14 control participants (9 females, 5 males; mean age: 26.6 years, range 23-33 years, *SD* = 2.3). All participants were university students or recent graduates, and none had history of neurological or motor disorders. Six beat-impaired cases were selected on the basis of poor synchronization to music in our laboratory, two cases self-declared their inability to follow the beat in music. In order to confirm the presence or absence of a beat finding disorder, all participants' synchronization abilities were assessed with 20 songs, with the instruction to tap to the beat. Ten musical stimuli, which varied in genre and tempo, were presented twice over two blocks. Their duration was between 24 and 32 seconds, and the first and last five seconds of tapping were removed from the analyses. A detailed description of musical stimuli is provided in Table 1. We used circular statistics (Batschelet, 1981) to assess tapping synchronization to the beat.

We used the Rayleigh test to assess whether taps were period-matched with the beat period of each musical stimulus, after transforming taps into vectors on the circle. A significant Rayleigh test ($p < .05$) indicates success in period matching (i.e. inter-tap intervals are consistent with the stimulus inter-beat-interval). As can be seen in Figure 1, there was not overlap between the number of trials that were period-matched with the beat of the musical excerpts by beat-impaired cases and controls. To confirm the synchronization deficit, the circular variance was used to compare the performance of beat-impaired cases to normative scores obtained in our laboratory from 41 typical synchronizers (23 females, mean age: 26.6 years, *SD* = 4.4). The circular variance is a measure of consistency between inter-tap and inter-beat intervals, and is bounded by zero and one. A value close to zero indicates high consistency while a score close to one usually corresponds to a non-significant Rayleigh test and indicates a random distribution of vectors (one vector = one tap) around the circle. The circular variance score was positively skewed and therefore transformed using a log function (log score = -1*log circular variance), a higher score now indicates higher consistency. For each participant, the log-transformed values were averaged across the 20 trials, providing an index score of individual performance. All of our eight beat-impaired cases were below *SD* under the mean of the typical group (cut-off = 1.54), which confirms their poor beat-finding abilities.

[Insert Figure 1 here]

All participants were screened for the presence of other musical deficits than synchronization to music. Beat-impaired cases were evaluated with the Montreal Battery of Evaluation of Amusia (MBEA; Peretz, Champod, & Hyde, 2003). They obtained a normal melodic composite and rhythm score (Table 1; Vuvan et al., 2017). The melodic composite score is an averaged score for three tests (scale, contour and interval) assessing pitch processing in a melodic context. The rhythm test evaluates a participant's ability to judge whether two short melodies are similar or not, differences being created by manipulating the duration of two adjacent intervals while maintaining the beat structure. Contrary to what has been found in a previous study (Phillips-Silver et al., 2011), only two out of the eight cases scored two standard deviations below the mean on the Meter test, which assesses a participant's ability to judge whether short melodies have an underlying pattern of strong and weak beats that corresponds to either a march (One two One two) or a waltz (One two three One two three). Controls' musical abilities were tested with the Online Test of Amusia for which they all obtained normal scores (Peretz & Vuvan, 2017). Finally, all participants performed in the normal range for verbal working memory and non-verbal reasoning (Progressive Matrix and Digit Span tests from the WAIS-III Wechsler adult intelligence scale; Wechsler, Coalson & Raiford, 1997).

[Insert Table 1 here]

The research was approved by the local ethics committee at Université de Montréal and participants provided written informed consent. They received financial compensation for their participation.

Material and procedure

The design of the study is schematized in Figure 2. First, each participant was instructed to tap in silence (no stimulus) at her most comfortable rate, in a constant and regular fashion "as if she were a metronome". A sounded beep indicated when to start and when to stop, that is after 31 taps were made. Twenty such spontaneous tapping sequences were recorded over two sessions, with three in a row at the beginning of each session to measure the spontaneous period (P0).

[Insert Figure 2 here]

Next, each participant was invited to tap with a metronome (synchronization) and to continue thereafter (continuation). Before each trial, she was primed with a short version of the stimulus (10 tones) and instructed to listen without moving. Then, she was invited to tap in synchrony with 31 isochronous tones (440 Hz, 200 ms duration) with an inter-onset-interval (IOI) corresponding to her spontaneous tempo (P0) as computed from her own pace just before. She also tapped to tones series corresponding to P0 plus 50 ms (P0+50) and P0 minus 50 ms (P0-50). The order of P0+50 and P0-50 was counter-balanced between participants and inverted in the second testing session. After the tones had stopped, participants continued tapping at the same rate. A beep indicated to stop tapping after 31 continuation taps. Participants were instructed to maintain the tempo and regularity during the continuation.

The session ended by six synchronization-continuation trials of varying IOI and by seven spontaneous tapping sequences. Stimulus IOIs were fixed here and consisted of 225, 337, 506, 759, 1139, and 1709 ms as in (McAuley et al., 2006). A short version (10 tones) of the stimulus was presented before each synchronization-continuation trial for preparation. The stimuli were presented in a descending (fast to slow) or ascending (slow to fast) order, which was counter-balanced between participants and inverted in the second session. The spontaneous sequences were performed before, between and after synchronization-continuation sequences (see Figure 2).

Each participant was tested in all conditions twice over two separate sessions, with a minimum of six days between sessions. Each session lasted about 30 minutes. Taps were made on a square force sensitive resistor (3.81 cm, Interlink FSR 406) placed on a table in front of the participant. The resistor was connected to an Arduino Duemilanove transmitting timing information to a PC (HP ProDesk 600 G1, Windows 7) via the serial USB port. Tap times were recorded and stimuli were generated with a customized program in MAX/MSP (Cycling' 74) at a sound level of 88 dB SPL through headphones (DT 770 PRO, Beyerdynamics).

Data Analysis

For each participant, there were 20 spontaneous tapping sequences, 18 synchronization-continuation sequences, and four (two slow, two fast) accessible tapping rates. The data were analyzed in Matlab (R2014b, Mathworks) with linear and circular methods, using the CircStat Toolbox (Berens, 2009). Statistical analyses were performed with linear mixed-effects models, using the "lme4" package (Bates, Maechler, Bolker, & Walker, 2015) in R (R Core Team, 2015). Plotted residuals indicate unequal variance across the range of predicted values for the circular variance. Therefore, circular variance scores were transformed using the reverse log function (new score = -1*log(old score), the higher the score the better the consistency). The models include a random term for Participant to account for repeated measures. Factor IOI (Study 2) was centered and scaled using the *scale* function in R before running mixed-effects statistical models, so that factors Group and IOI were on comparable scales. We used mixed-effects models rather than ANOVA because they do not require prior averaging of the data and have more statistical power in case of unbalanced designs such as different group sizes. Corresponding p-values and degrees of freedom are computed from the Satterthwaite approximations, using the "lmerTest" package (Kuznetsova, Brockhoff, & Christensen, 2017) in R. For post-hoc analyses, pairwise comparisons were performed with the "lsmeans" package (Lenth, 2016) in R, which computes least-square rather than arithmetic means to account for unbalanced designs.

Study 1: Internal timekeeping

The goal of Study 1 was to test participants' regularity in their spontaneous rate of tapping. To this aim, the first three tapping sequences collected at the beginning of each session were analyzed in order to avoid potential carry-over effects of synchronization-continuation rates on spontaneous rate.

Results

There were large variations in mean spontaneous inter-tap-interval (ITI), ranging from 471ms to 996ms in the beat-impaired group (M = 754ms) and from 391 ms to 1214 ms in the control group (M = 670ms; Figure 3A); the group difference was not significant, $\beta = -84.15$, $SE = 66.23$, $t(20) = -1.42$, $p = .22$. In contrast, the two groups differed in regularity (Figure 3B). The coefficient of variation (CV), which corresponds to the standard deviation of the ITIs divided by the mean ITI of a sequence, indicated higher variability, hence poorer regularity in the beat-impaired (M = 0.074) as compared to the control group (M = 0.052). The difference in CV between the two groups reached significance, $\beta = -.022$, $SE = .0046$, $t(20) = -4.63$, $p < .001$.

This difference between groups contrasts with previous studies. For example, in Sowiński & Dalla Bella (2013) the variability of spontaneous tapping in four beat-impaired participants (synchronization profile comparable to our beat-impaired group) was described as normal. This discrepancy may be due to the larger amount of data considered in the present study. To check for that, we compared our groups on the spontaneous sequence showing the lowest CV from the two first produced sequences (instead of six sequences), following the procedure of Sowiński & Dalla Bella. This analysis revealed no statistical difference between groups, $t(14) = -1.75$, $p = 0.10$ (Welch's two-sample t-test). Thus, higher statistical power (the six sequences were individually considered in the statistical model above) likely contributed to the finding of larger inter-tap variability in our beat-impaired group.

Regularity was unrelated to the individual spontaneous rate. There was no significant correlation between CV and spontaneous rate; $r(20) = .26$, $p = .23$ across all participants and $r(6) = .28$, $p = .50$ for the beat-impaired group only. The CV remained higher in the beat-impaired group ($M = 0.088$) as compared to the control group ($M = 0.057$) throughout the sessions, considering the averaged CV over the other 14 sequences performed in silence, $\beta = -.030$, $SE = .006$, $t(20) = -5.03$, $p < .0001$.

[Insert Figure 3 here]

Note that in both groups, the average spontaneous rate (745 and 670ms) was slower than the standard 500-600 ms mentioned in the introduction (e.g. Moelants, 2002). Thus, individually produced spontaneous rate (P0) needs to be taken into consideration when evaluating synchronization abilities, which was the goal of Study 2.

Study 2: Flexibility

The higher variability in spontaneous tapping observed in beat-impaired individuals as compared to controls suggests that basic timekeeping mechanisms are impaired in the beat-related form of congenital amusia. Providing an external aid from metronome sounds may assist timekeeping and hence decrease variability in tapping. To be effective as an aid, it is likely that the metronome rate should be proximal to the spontaneous rate (P0). Furthermore, continuation (i.e. without the external aid) is expected to be disrupted, especially for stimulus rates distant from P0._The goal of Study 2 was to examine these predictions.

Results

The individual P0 was computed from the sequence with highest regularity (lowest CV) over the three first spontaneous sequences of each session. P0 ranged from 553 to 882 ms in the beat-impaired group and from 426 to 983 ms in the control group, with no difference between groups, $\beta = -84$, $SE = 66$, $t(20) = -1.27$, $p = .22$.

The CV (synchronization) of Inter-Tap-Intervals (ITI) for the Inter-Onset-Intervals (IOI) set to individual P0 and P0±50ms was again higher in the beat-impaired ($M = .068$) than in the control group ($M = .052$), $\beta = -.016$, $SE = .0031$, $t(20) = -5.15$, $p < .0001$. However, the CV does not capture anticipation and accuracy of synchronization because it does not take the stimulus into account. For example, a sequence of taps could be highly regular (low CV) but not synchronized with the tones. Thus, the log transformed circular variance (see Data Analysis) was considered here as the main variable. These scores indicate lower consistency in the beat-impaired compared to the control group, $\beta = 0.70$, $SE = .19$, $t(20) = 3.77$, $p = .0012$

(Figure 4). Furthermore, the beat-impaired group anticipated the tones in an anomalously large degree of magnitude. The asynchronies between taps and tones, computed by subtracting the closest tone onset time from the tap time, indicated a negative trend with a tap occurring before the tone onset, which was much larger in the beat-impaired compared to the control group, $\beta = -48$, $SE = 11$, $t(20) = -4.15$, $p < .001$ (Figure 4). Thus, taps tended to be further away from the tones in the beat-impaired compared to the control group when tapping to tones at the individual spontaneous tempo.

[Insert Figure 4 here]

Continuation performance was similar to synchronization, with higher CV (lower regularity) in the beat-impaired ($M = .069$) compared to the control group ($M = .056$), $\beta = -.013$, $SE = .0045$, $t(20) = -3.01$, $p < .01$. Yet, the ability to maintain the stimulus rate, as measured by the distance between the mean ITI and the stimulus IOI (i.e. continuation error), did not differ between groups, $\beta = -12$, $SE = 9$, $t(20) = -1.39$, $p = .18$. Thus, higher CV in the beat-impaired group was due to poor regularity rather than a constant drift towards a faster or slower tempo than the stimulus.

To summarize, the results show that even at a participant's most comfortable rate and with the external aid of isochronous tones, tapping performance remains poorer in the beat-impaired group as compared to controls. In what follows, we assessed to what extent less comfortable stimulus rates disrupted performance.

The synchronization-continuation performance for the six pacing rates in the range of 225-1709 ms is presented in Figure 5. The results indicate limited flexibility in the beat-impaired group, particularly at fast paces. Actually, for the fastest pace (IOI = 225 ms), the Rayleigh test revealed a failure to period-match ($p > .05$) in six of the eight beat-impaired cases whereas none of the participants in the control group failed the Rayleigh test at that rate. Note that the failure to tap regularly does not seem to arise from biomechanical or motor limitations because beat-impaired participants were producing fast rates when tapping to fast stimuli (see Table 2).

[Insert Figure 5 here]

[Insert Table 2 here]

Because sequences were unsuccessfully period-matched with the fastest stimulus rate (IOI = 225 ms) in most beat-impaired individuals, this rate was not included in subsequent analyses of synchronization consistency and accuracy. Synchronization difficulties were also observed for the second fastest rate (337 ms; Figure 5); a failure to period-match with that stimulus rate was observed in three beat-impaired cases. These failed sequences were not included in the following analysis of synchronization consistency and accuracy.

As can be seen in Figure 5, synchronization consistency, measured by log-transformed circular variance, was generally lower in the beat-impaired group as compared to the control group, $\beta = .90$, $SE = .14$, $t(20) = 6.52$, $p = <.0001$, with an effect of Stimulus Rate, $\beta = .19$, $SE = .040$, $t(192) = 4.67$, $p = <.0001$, and no interaction between Group and Stimulus Rate factors, $\beta = -.089$, $SE = .080$, $t(192) = -1.11$, $p = .27$. Post-hoc comparisons for the effect of Stimulus Rate (with Bonferroni-holm p-value adjustment) showed lower consistency in both groups for 337ms compared to 759, 1139 and 1709 ms (all $p < .05$) and for 506 ms compared to 1139ms ($p < .01$) across groups.

Anticipation of tone onsets was observed in both groups: mean asynchronies were negative for 84% and 85% of the sequences in the beat-impaired and control groups, respectively. Thus, taps again tended to precede tones onsets in both groups, but again to an anomalously larger degree in the beat-impaired group for slow metronome rates. A summary of mean asynchronies by rate for each group is provided in Table 3. There was an effect of Group on asynchronies (synchronization accuracy), β = -40, *SE* = 14, $t(20) = -2.89$, p = .00091, an effect of Stimulus Rate, β = 27, *SE* = 2.66, $t(192) = 10.13$, $p < .0001$, and an interaction between Group and Stimulus Rate factors, β = -29, *SE* = 5.31, $t(192) = -5.54$, $p <$ .0001. The distance between taps and tones increased with the IOI in the beat-impaired group but not in the control group (Figure 5). There was no group difference for 337 and 506 ms (both $p > .05$ by post-hoc comparisons with Bonferroni-holm p-value adjustment), but significantly larger asynchronies in the beat-impaired group for 759 ($p = .028$), 1039 (p = .0038), and 1709 ms ($p < .0001$). Because the mean asynchrony was negative (see Table 3), larger asynchronies for slow rates in the beat-impaired group indicate a tendency to underestimate the stimulus IOI.

[Insert Table 3 here]

The CV of ITIs during continuation was higher in the beat-impaired compared to the control group, β = -.021, *SE* = .0031, $t(20) = -6.58$, $p = <.0001$, with no effect of Stimulus Rate or of Tempo (both $p > .22$). Thus, continuation was generally less regular in the beat-impaired than in the control group, like observed in spontaneous and synchronization tapping. Continuation error was computed by subtracting the mean ITI from the stimulus IOI (in magnitude). While the error tended to increase with larger IOIs (slower rates) in both groups, the effect was generally larger in the beat-impaired group (Figure 5), as supported by an interaction between Group and Stimulus Rate factores, β = -42, *SE* = 10, $t(216) = -4.36$, $p <$ 0.0001. The two groups did not differ for the fast rates (225, 337, 506 and 759ms rates; all $p >$ .05) but did so for the slow rates (1139 ms; $p = .0028$ and 1709 ms; $p < .0001$). Thus, contrary to predictions, beat-impaired participants were as capable as controls to maintain fast and moderate rates after the stimulus had stopped. Of note is that, because the number of taps is fixed, the length of continuation sequences increases with slower rates. We checked whether keeping only the first half of continuation taps for the 1139 and 1709 ms stimuli suppressed the difference between groups, and it did not.

Note that all the analyses presented above were performed with groups of similar sizes, by considering eight control participants instead of 14. All results are maintained except for the larger asynchronies during synchronization at 759 ms IOI in the beat-impaired group.

Discussion

The main finding of the present study is that individuals with anomalous difficulties to tap to the beat of music have more basic problems with timekeeping mechanisms. We found a lower capacity for isochrony (higher inter-tap variability) in the beat-impaired group across conditions. We also found evidence that rate flexibility is limited in the beat-impaired group: larger negative asynchronies as well as poor tempo retention were observed for slower metronome rates, and a striking limitation was observed for synchronization to fast rates.

Our results can be interpreted within a nonlinear dynamical approach to beat-based coordination of motor actions (Drake, Jones, & Baruch, 2000; Large & Jones, 1999; Loehr, Large, & Palmer, 2011; McAuley, 2010; McAuley et al., 2006). In this approach, synchronization to a regular beat is considered to rely on an internal oscillator, which is capable to generate an intrinsic beat and to adapt the period of this beat to match that of the stimulus. The intrinsic period of the oscillator is captured by spontaneous tapping, while period adaptation is measured by synchronization-continuation, with higher adaptation demands for extreme fast and slow rates. The operation of this internal oscillator may be the faulty mechanism in the beat-impaired cases.

First, higher inter-tap variability (CV) across conditions reveals a disrupted capacity of the oscillator for isochrony. In particular, high variability during spontaneous tapping indicates that the impairment goes beyond poor sensorimotor coupling with external signals. This finding contrasts with prior reports of beat impairments (Phillips-Silver et al., 2011; Sowiński & Dalla Bella, 2013; Tranchant et al., 2016). In Phillips-Silver et al. (2011), the variability of spontaneous whole-body bouncing movement in one beat-impaired case (Mathieu) was described as normal, although comparison to the control group was not considered. In Tranchant et al. (2016), the variability of spontaneous bouncing as well as hands clapping did not differ between beat-impaired and control groups. It is possible that differences between movement forms contributed to the discrepancy between prior and present studies. The beat-impaired case (Mathieu) from Phillips-Silver et al. (2011) was later tested by Palmer et al. (2014) with finger tapping. His inter-tap variability (CV) in spontaneous production was then above one standard deviation from the mean of the control group, and very close to findings in our beat-impaired group (0.072 in Mathieu compared to a mean of 0.074 in our beat-impaired group). Finally, higher statistical power in the present study, as for example compared to Sowiński & Dalla Bella (2013), may have contributed to highlight the difference between groups in spontaneous tapping.

Second, limited rate flexibility in the beat-impaired group reflects poor period adaptation of the oscillator, for rates that are beyond the optimal range. In other terms, the range for which period adaptation is optimal is narrower in beat-impaired cases. We indeed observed poor synchronization and/or continuation performances at extreme slow and fast rates. A severe difficulty to synchronize with the fastest stimulus rate (225 ms) could not be attributed to pure motor or biomechanical limitations, because produced periods were close or sometimes even shorter than the target. The limitation thus likely emerges from faulty period adjustment mechanisms. For slow rates, beat-impaired cases showed a lower capacity to use error signals for synchronization, as indicated by larger asynchronies, and showed low period stability in the absence of the external aid, as indicated by large deviations from the target period in continuation. Altogether, these findings point toward faulty period adaptation mechanisms at extreme slow and fast rates.

The absence of such a difference between groups for fast rates, as found here, may seem against this conclusion. For example, McAuley et al. (2006) observed larger continuation errors with extreme slow *and* fast rates, as compared to older children and to adults. These authors concluded of a narrower range of optimal adaptation in young children. Yet continuation errors in children below eight were much larger for slow as compared to fast rates in that study (see Figure 7) and were very similar to findings in our beat-impaired group. It is thus possible that the limited size of our groups was responsible for the difference between groups not being significant for the fastest rates.

Additional support for the faulty period adaptation hypothesis also comes from previous studies of beat impairments. For example, Mathieu (Phillips-Silver et al., 2011) showed poor adjustment of bouncing movements for a gradual 10% tempo change applied to a musical excerpt, but not for a 20% tempo change. However, in that study period matching was not precisely assessed (only the direction of speed change) and comparison to a control group was not considered. Thus, it is possible that adaptation to gradual tempo changes was even more severe than the findings suggest. Palmer et al. (2014) further assessed Mathieu's tapping to sudden (unpredictable) perturbations in otherwise isochronous sequences of tones. Perturbations consisted in small increases or decreases (3%, 8% or 15%) from the baseline of 500 ms IOI (i,e. by 15, 40 or 75ms). The number of taps required to return, after the perturbation, to baseline alignment with tones was longer in Mathieu than in controls. In addition, this difference between Mathieu and the control group was successfully captured by a damped harmonic oscillator model. The findings of Palmer et al. (2014) thus fit the hypothesis of poor period adaptation of an internal oscillator in the beat-impaired condition.

A challenge for future research will be to identify the neural bases underlying beat impairments. In the nonlinear dynamical approach, temporal coordination is supported by self-sustained ongoing neural oscillations which entrain to the pulse of an external rhythmic signal (for a recent review see Haegens & Zion Golumbic, 2018). Which of the brain areas are generating and/or supporting this mechanism is not fully understood yet. In a meta-analysis of 43 functional neuroimaging studies, Chauvigné, Gitau & Brown (2014) contrasted regions showing activations during spontaneous versus synchronization tapping. They found a dissociation between two subcortical structures frequently associated to motor timing: the cerebellum (e.g. Buonomano & Mauk, 1994; Paquette, Fujii, Li, & Schlaug, 2017; Penhune, Zatorre, & Evans, 1998) and basal ganglia (e.g. Hausdorff, Cudkowicz, Firtion, Wei, & Goldberger, 1998; Schwartze, Keller, Patel, & Kotz, 2011). This analysis revealed that while basal ganglia seem to be important for the two types of motor tasks, the cerebellum seems involved in synchronization tapping only. Functional imaging studies of beat impairments are a rare chance to provide causal links between brain regions and behavior. In particular, because a poor capacity for isochrony was found for both spontaneous and synchronization tapping, we predict that anomalies related to the basal ganglia will be detected in a beat-impaired group.

To conclude, we showed that deficient synchronization to music can be traced back to human's core timekeeping mechanisms. The hypothesis of a faulty internal oscillator provides a useful model to interpret the findings. Deficiencies in timekeeping and temporal coordination are a rare chance to better understand human timing, which is essential for numerous human activities, including dancing, music making or even speech. For example, smooth turn-taking in conversations requires a form of temporal coordination thought to rely on synchronization between oscillators in the brains of people taking part in the conversation (Wilson & Wilson, 2005). Future studies of the beat-impaired brain should advance our understanding of the neural circuits that are essential for beat finding and timekeeping in general.

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The authors declare no competing interests

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Article 3: Tableaux et Figures

Tableau I. A3: Résultats à la MBEA des participants avec trouble de la synchronisation.

Table 1. MBEA scores. Individual scores of the 8 beat-impaired cases for the melodic (scale, contour, interval) tests, the rhythm and meter test of the Montreal Battery of Evaluation of Amusia. Scores below cut-off (2 *SD* below the mean; Vuvan et al., 2017) are in bold.

Participant	Melodic Composite Score	Rhythm	Meter
1	26.0	22	25
2	24.7	26	24
3	26.3	28	20
4	25.0	26	19
5	24.3	25	21
6	23.7	27	13
7	23.0	26	16
8	25.3	25	23

Tableau II. A3: Intervalle entre les tapes - tempo rapide.

Table 2. ITIs when tapping to the fastest stimulus IOI.

	ITI (ms)
Beat-impaired cases:	
1	206
2	233
3	254
4	301
5	199
6	233
7	231
8	210
Controls:	
M (range)	225 (223-227)

Tableau III. A3: Asynchronie moyenne

Table 3. Mean asynchrony between taps and tone onsets. A negative value indicates that taps precede tone onsets.

Group:	IOI:	337 ms	506 ms	759 ms	1139 ms	1709 ms
Beat-impaired	***M (SD)***	-16 (32)	-49 (39)	-78 (67)	-101 (67)	-136 (129)
Control	***M (SD)***	-19 (21)	-39 (30)	-33 (30)	-46 (31)	-43 (61)

Figure I. A3: Nombre d'essais avec alignement de période.

Figure 1. Number of period-matched trials (out of 20) per participant. Each participant is indicatd by a dot.

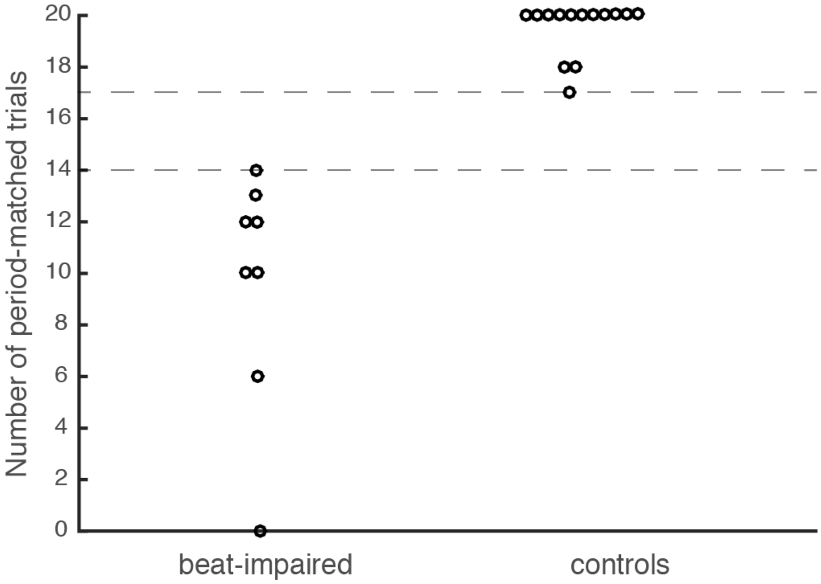


Figure II. A3: Description de la procédure

Figure 2. Procedure. S.T. = Spontaneous Tapping

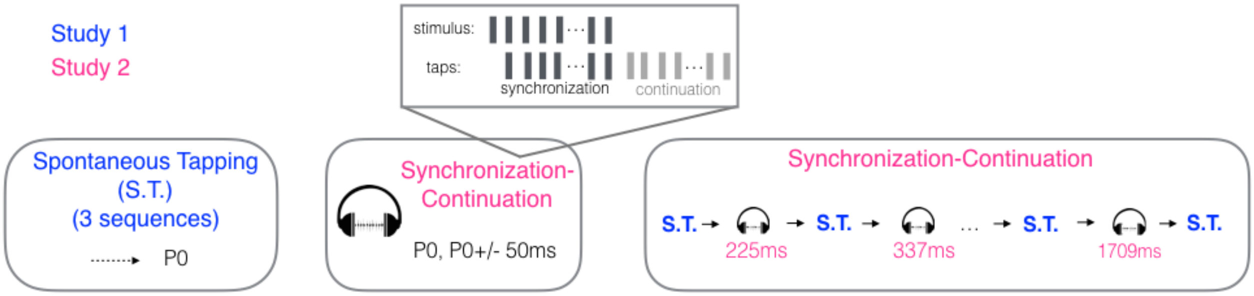


Figure III. A3: Tapping spontané

Figure 3. Spontaneous tapping. Each cross represents the mean score of one individual.

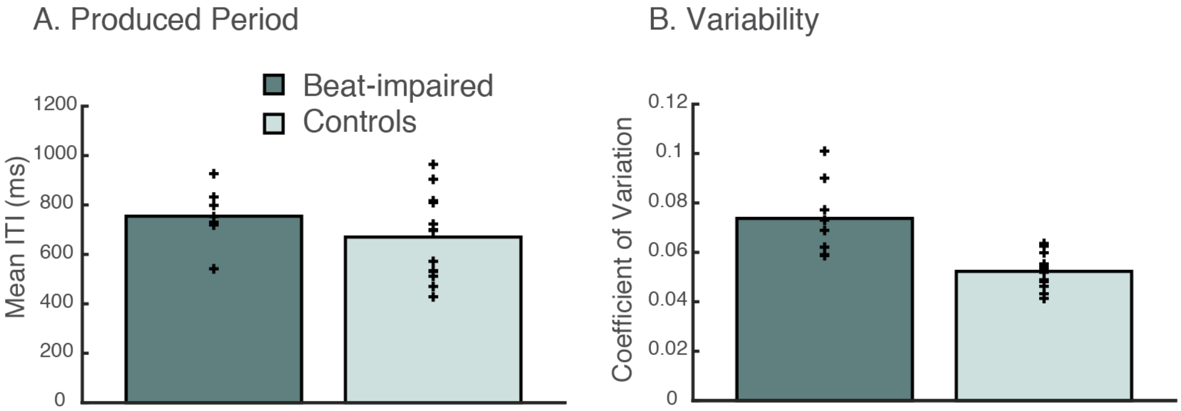


Figure IV. A3: Synchronisation-continuation au tempo spontané

Figure 4. Synchronization-continuation at participant's spontaneous tempo (P0). The average score obtained for six sequences (three per session) for each participant is represented by a dot. Bar graphs represent arithmetic means. For synchronization consistency, the higher the score the better the performance. For synchronization accuracy and continuation error, the lower the score the better the performance.

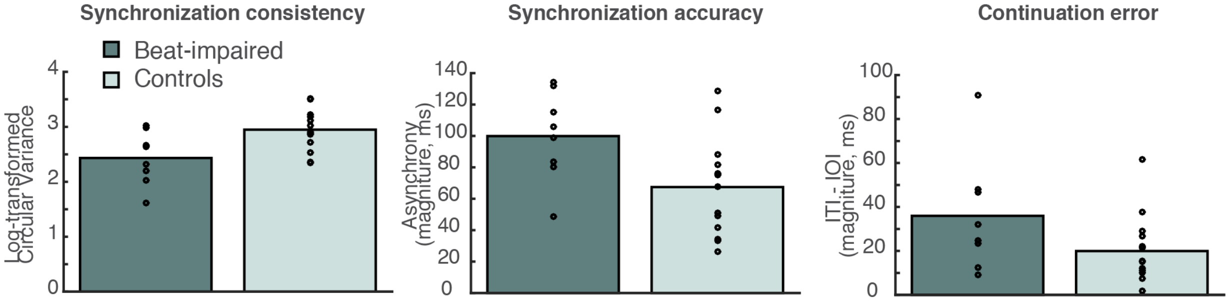
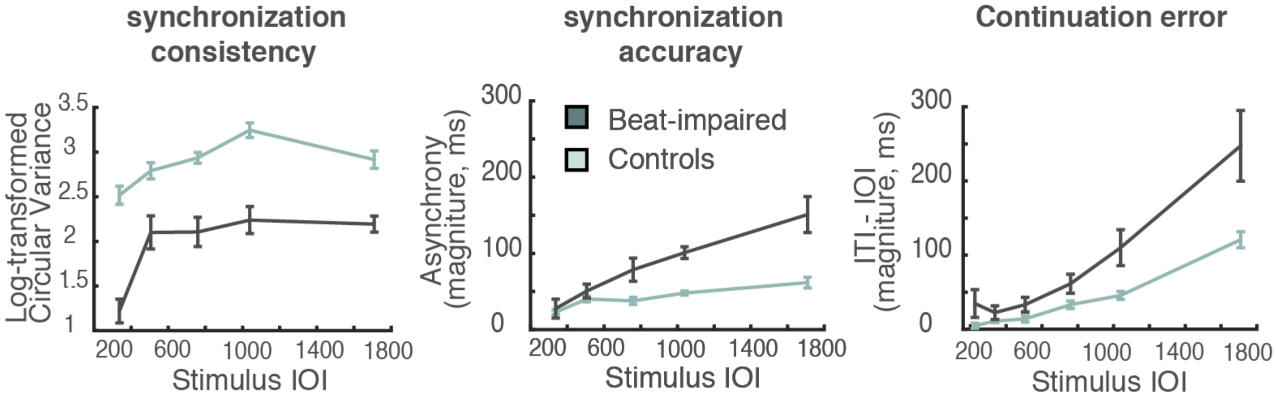


Figure V. A3: Synchronisation-continuation aux tempi fixes.

Figure 5. Synchronization-continuation. IOIs of 225 (continuation only), 337, 506, 759, 1139, and 1709 ms. The graphs show arithmetic means and standard error bars (corrected for repeated measures).



Chapitre 3: Discussion générale

3.1 Rappel des objectifs et intégration des résultats

L'objectif général de la thèse était de clarifier la nature du trouble de synchronisation au beat de la musique, comme moyen de mieux comprendre les mécanismes cognitifs sous-tendant le traitement du beat chez l'humain. Pour cela, trois études ont été présentées.

La première étude (Article 1) avait pour objectifs principaux d'identifier un groupe de personnes présentant une synchronisation déficiente à la musique, ainsi que de comparer la performance de synchronisation à travers deux formes de mouvement naturel (clapping et bouncing). Nous avons testé 100 jeunes adultes et identifié 14 cas présentant une synchronisation dégradée au beat de la musique. Nous avons observé une meilleure qualité de synchronisation (alignement au tempo) en clapping qu'en bouncing, au sein du groupe avec synchronisation dégradée ainsi qu'au sein du reste des participants de l'étude (*N* = 82; groupe contrôle). Ainsi, alors qu'une difficulté en bouncing a été observée chez les 14 cas le clapping n'était affecté que pour six d'entre eux.

Nous avons de plus observé un effet des stimuli musicaux beat sur la synchronisation, au sein des deux groupes. La performance de synchronisation était en général supérieure pour des stimuli musicaux avec un beat davantage marqué. Certains styles musicaux sont en effet caractérisés par un beat très clair (p. ex. techno, dance) alors que d'autres beaucoup moins (p. ex. jazz). Enfin, nous avons observé une déficience très marquée de la coordination temporelle à un beat parmi deux des 14 cas identifiés: en plus d'une incapacité à se synchroniser au beat des stimuli musicaux, la synchronisation au métronome (bouncing et clapping) s'est avérée déficiente également. Nos résultats suggèrent donc qu'il existe un gradient dans la sévérité du trouble de la synchronisation au beat, qui s'observe à travers les formes de mouvement et la complexité rythmique des stimuli utilisés pour l'examiner. Cette étude a donc permis de mettre en évidence l'importance de ne pas restreindre la diversité des conditions expérimentales (formes de mouvement, stimuli) utilisées pour caractériser le trouble de la synchronisation à la musique.

La seconde étude (Article 2) avait pour but principal d'évaluer la perception du beat chez les personnes présentant une synchronisation à la musique déficiente (qualifiées dans l'Article 2 de "*beat-impaired*"; BI dans la suite du texte). Nous souhaitions en cela confirmer l'existence d'une dissociation entre capacités de perception et de synchronisation au beat de la musique. Notons ici que seulement deux des 14 cas identifiés dans l'étude 1 ont répondu présent pour l'étude 2, car au moment où nous avons entamé la seconde vague de cueillette des données bon nombre d'entre eux n'étaient plus disponibles (étudiants provenant de l'extérieur de Montréal et rentrés dans leur région, désormais jeunes travailleurs manquant de temps, etc.). Des deux personnes ayant manifesté leur disponibilité, une seule a été recrutée pour l'étude 2; l'autre ne répondant plus à nos critères de sélection[3]. Sept nouveaux cas BI ont néanmoins pu être identifiés grâce à un effort de recrutement continu au cours des trois premières années de la thèse (petites annonces, bouche-à-oreille, etc.). Un neuvième cas a été détecté parmi les participants formant le groupe contrôle initial ("groupe typique", $N = 42$) de l'étude.

La synchronisation à la musique a été testée au moyen du tapping car il s'agit de la forme de mouvement la plus communément utilisée dans la recherche sur la synchronisation

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[3] Cette personne nous a informés avoir entammé la prise d'un traitement médicamenteux psychoactif à la suite d'un trouble psychiatrique.

sensori-motrice (Repp, 2005; Repp & Su, 2013). Nous souhaitions effet pouvoir mettre nos résultats en perspective de la littérature existante, d'une part, et que les normes obtenues avec notre groupe contrôle puissent servir de repère aux chercheurs dans d'autres laboratoires, d'autre part (nous comptons rendre disponibles sur Internet les tests et normes associées de l'Article 2). Nous avons toutefois confirmé au moyen du bouncing, largement affecté chez tous les cas BI testés dans cette étude, que le trouble de synchronisation n'est pas spécifique à une forme de mouvement. La perception du beat a quant à elle été évaluée au moyen d'une version adaptée du Beat Alignment Test (BAT; Iversen et Patel, 2008), qui évalue la capacité à juger si un métronome superposé à la musique est aligné ou pas sur le beat.

Comme pour la première étude, des extraits de chansons provenant de genre musicaux variés ont été utilisés pour tester synchronisation et perception. Une telle diversité au sein des stimuli nous a permis d'observer des variations de performance liées aux stimuli au sein du groupe contrôle: une qualité de synchronisation supérieure a été observée pour les chansons avec tempo plus lent. À notre connaissance un tel effet n'avait pas encore été rapporté dans la littérature et peut sembler surprenant, car la fourchette de tempi testés est largement dans les limites d'une synchronisation optimale. Il faut néanmoins noter que le tempo n'a pas été manipulé de façon contrôlée dans l'étude, puisqu'il variait en même temps que d'autres attributs des stimuli comme le groove (Janata et al., 2012; Madison, 2006; Madison, Gouyon, Ullén, & Hörnström, 2011) ou la familiarité, par exemple. Il resterait donc à vérifier si un tel effet du tempo continue à se manifester lorsque tous les autres facteurs dont maintenus constants.

Cette étude a de plus permis la mise en évidence d'une association des troubles de la synchronisation et perception du beat. Au niveau des groupes la performance de perception était moins bonne chez les participants BI que chez les participants typiques. Ce résultat est en accord avec le modèle ASAP (Patel & Iversen, 2014) qui prédit qu'une perturbation des oscillations motrices engendrées par un beat aurait des répercussions sur la perception de ce beat. Néanmoins, chez six des participants BI le score de perception était faible mais supérieur au cut-off établi sur la base des scores du groupe typique. Le profil de ces participants rappelle celui des cas S1 et S5 décrits par Sowiński & Dalla Bella (2013). Ces auteurs ont proposé que la synchronisation déficiente soit le résultat d'un couplage sensori-moteur altéré chez les individus présentant un tel profil de dissociation. Le profil inverse, soit un score de perception déficient malgré un score de synchronisation bas mais supérieur au cut-off, a été montré chez deux participants initialement recrutés pour faire partie du groupe contrôle. Ce profil ressemble à celui des cas L.A. et L.C. décrits par Bégel et collaborateurs (2017a), et rappelle celui de personnes amusiques capables de chanter juste malgré une perception déficiente du pitch dans un contexte mélodique (Ayotte, Peretz, & Hyde, 2002; Dalla Bella, Giguère, & Peretz, 2009). Cette dernière observation suggère que, dans le cerveau, la voie auditive nécessaire à la production vocale serait au moins en partie distincte de celle responsable de la perception consciente du pitch (Griffiths, 2008; Loui, Guenther, Mathys, & Schlaug, 2008), similairement à la distinction proposée entre les voies de la perception consciente et de l'action au niveau du système visuel (Goodale & Milner, 1992). La distinction entre perception consciente et action (synchronisation) pourrait également s'appliquer à la dimension du beat musical, en plus de s'appliquer à celle du pitch.

Ces cas de dissociation semblent aller à l'encontre de l'hypothèse d'une communication de type causale et bi-directionnelle entre régions auditives et motrices du cerveau, tel que proposé par le modèle ASAP. Toutefois, les cas de dissociation observés dans l'Article 2 ne remettent que faiblement en question le modèle ASAP, car les performances des participants concernés étaient généralement faibles, en synchronisation aussi bien qu'en perception.

Pour finir, la troisième étude (Article 3) visait à tester la flexibilité de tempo chez les personnes BI. Huit des neuf cas avec synchronisation déficiente présentés dans l'Article 2 ont pris part à cette étude, et ont été comparés à un groupe de 14 participants contrôles. Nous avons utilisé le métronome pour sa simplicité rythmique, afin que les potentiels effets observés ne puissent être attribués qu'au facteur d'intérêt (le tempo), et le tapping afin de pouvoir comparer nos résultats à la littérature existante (p. ex. Repp, 2005; McAuley et al., 2006).

Avant de tester la synchronisation et la continuation, nous avons mesuré le tempo spontané des participants en leur demandant de produire des séquences les plus régulières possibles au tempo qui leur est naturel, confortable. Nous avons mesuré une plus grande variabilité au niveau de l'intervalle entre les tapes (coefficient de variation) dans le groupe BI que dans le groupe contrôle. Ce résultat a été interprété comme un manque de régularité de l'oscillateur interne. Il est en accord avec ce qu'ont obtenu Palmer et collaborateurs (2014) avec Mathieu. En effet, le coefficient de variation correspondant à son tapping spontané était plus d'une déviation standard au-dessus de la moyenne du groupe contrôle, et du même ordre que ce qui a été décrit dans notre groupe BI. Ce manque de régularité en tapping spontané contraste néanmoins avec ce qui a été observé par Sowiński & Dalla Bella (2013) chez quatre cas présentant une synchronisation déficient, et par Bégel et collaborateurs (2017) chez un cas additionnel. Cette inconsistance dans les résultats pourrait être dû à la quantité de données collectées - un nombre plus important d'essais spontanés ont été utilisés dans notre étude - ou à l'existence de plusieurs profils parmi les personnes présentant un trouble de synchronisation à la musique, certaines présentant un manque général de régularité motrice mais pas d'autres.

La variabilité accrue de l'intervalle entre les tapes s'est également manifestée, dans notre étude, lors de la tâche de synchronisation-continuation et cela aussi bien au tempo spontané propre à chaque participant qu'à travers les tempi fixes couvrant les limites de la synchronisation chez l'humain (225-1800 ms)[4]. En plus de la variabilité accrue, des performances de synchronisation dégradées aux tempi très lents et très rapides ont également qualifié le groupe BI. Au tempo le plus rapide, une incapacité à faire correspondre l'intervalle entre les tapes à l'intervalle entre les sons (225 ms) a été observée. Ceci n'était pas dû à une limitation motrice car les intervalles produits par les participants BI correspondaient à un tempo très rapide (mais pas celui de la séquence). Aux tempi lents (>1139 ms) nous avons trouvé des asynchronies (négatives) anormalement larges ainsi qu'une difficulté à maintenir le tempo durant la continuation. Nous avons interprété de tels résultats comme un défaut de l'oscillateur interne à adapter sa période pour atteindre des intervalles très petits ou très grands. En d'autres termes, nous avons montré que la zone d'adaptation optimale de la période est plus étroite chez les participants avec synchronisation à la musique déficiente.

Les résultats présentés dans l'Article 3 pointent donc vers un trouble lié à des mécanismes centraux du traitement et de la production d'intervalles temporels (*timekeeping*), qui affecterait à la fois la production et la perception du beat musical (Article 2).

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4 Nous avons testé la synchronisation à un intervalle plus petit, 150ms, lors d'une étude pilote. Nous avons observé une difficulté à se synchroniser à ce tempo extrêmement rapide chez des participants contrôles et avons décidé sur cette base de ne pas inclure d'intervalle inférieur à 225ms dans notre étude.

3.2 Contributions originales, limites, et directions futures

Cette thèse se distingue par la nature écologique des tâches utilisées pour mesurer le traitement du beat musical, ce qui augmente le caractère généralisable des résultats obtenus. À l'exception de Phillips-Silver et collaborateurs (2011) toutes les études portant sur les troubles liés au beat ont eu recours au tapping et/ou à la musique classique uniquement. Si le tapping est pratique à enregistrer (nécessite peu d'équipement) et à analyser (points dans le temps), c'est un mouvement assez peu naturel contrairement au bouncing, qui se rapproche de la danse, et au clapping, fréquemment observé dans des concerts de musique, par exemple. L'utilisation exclusive de musique classique aurait été un autre facteur limitant, puisque ce sont d'autres genres musicaux (p ex. pop, rock) que l'on retrouve dans les contextes où une réponse motrice de la part de l'audience est attendue (concerts, clubs de danse, etc.).

Il est par contre une caractéristique écologique dont nous n'avons pas tenu compte dans la thèse: le caractère social de la danse (Leman, 2007). La synchronisation entre individus permet d'augmenter les sentiments d'appartenance au groupe (Hove & Risen, 2009), de compassion envers autrui (Valdesolo & Desteno, 2011), et de développer les comportements de collaboration entre humains (Cirelli, Wan, & Trainor, 2014b; Kirschner & Tomasello, 2010; Wiltermuth & Heath, 2009). Cirelli, Einarson & Trainor (2014) ont par exemple démontré que bercer des jeunes enfants sur de la musique et en synchronie avec un adulte favorise l'entraide de l'enfant envers cet adulte par la suite. La danse pourrait donc avoir joué un rôle adaptatif au cours de l'évolution (Honing, Cate, Peretz, & Trehub, 2015), cohésion de groupe et entraide constituant des facteurs cruciaux à la survie de l'espèce dans les temps ancestraux (notons néanmoins que le moment où la danse est apparue dans l'histoire n'est pas connue, puisque danser ne laisse pas de traces fossiles).

Si la synchronisation entre individus favorise l'interaction sociale, l'inverse est vrai aussi. Un contexte qui est social encourage les individus à bouger sur la musique et favorise, voire facilite, la synchronisation au beat (De Bruyn, Leman, Moelants et Demey, 2009; Kirschner & Tomasello, 2009). Selon Kirschner et Tomasello (2010), bouger sur le beat de la musique permet aux individus la communication par voie audio-visuelle des intentions de chacun, satisfaisant par la même occasion le désir profondément humain de partager des expériences, des activités, et surtout des émotions avec autrui. Il serait donc intéressant d'évaluer si le trouble de la synchronisation au beat avoir des répercussions sur la vie sociale des personnes présentant cette condition.

Il serait également intéressant d'évaluer si, d'autre part, le fait d'effectuer la synchronisation avec d'autres individus permet d'améliorer la qualité de celle-ci chez les personnes BI. Un facteur propre aux contextes sociaux est l'accès visuel au mouvement effectué par les gens qui nous entourent. Il pourrait s'agir d'un facteur facilitant pour les personnes BI si l'on suppose que la synchronisation en modalité visuelle est préservée chez elles. Il s'agit d'un autre un aspect que nous n'avons pas évalué dans la thèse. Phillips-Silver et collaborateurs (2011) ont mesuré la synchronisation à un expérimentateur chez Mathieu. Les résultats sont apparus normaux, ce qui suggère que la synchronisation en modalité visuelle pourrait être préservée chez les personnes présentant une difficulté à trouver le beat. Notons néanmoins qu'une comparaison au groupe contrôle n'ait pas été effectuée pour cette condition, et que la synchronisation visuelle n'a pas été évaluée indépendamment de la modalité auditive ni de l'aspect social de la condition dans laquelle elle a été testée.

Préciser la spécificité du trouble de synchronisation à la modalité auditive, ou au contraire montrer qu'il se généralise à d'autres modalités perceptives (Iversen, Patel, Nicodemus, & Emmorey, 2015; Tranchant, Shiell, Giordano, Nadeau, Peretz & Zatorre, 2017) est une piste de recherche intéressante pour la compréhension des mécanismes de traitement des intervalles temporels chez l'humain (pour une revue voir par exemple Grondin, 2010). La performance de Mathieu (Phillips-Silver et al., 2011) lorsqu'il s'agit de suivre l'expérimentateur visuellement suggère qu'il pourrait y avoir dissociation entre modalités auditive et visuelle. Nos résultats suggèrent plutôt un dysfonctionnement du mécanisme en charge de produire une régularité motrice, et qui donc devrait altérer la synchronisation quelle que soit la modalité perceptuelle.

Une autre question intéressante touchant à la spécificité du trouble de synchronisation est s'il s'applique ou non à la régularité dans le langage parlé. Bien que la parole soit beaucoup moins régulière que le langage, certains auteurs ont proposé que les mécanismes sous-tendant le traitement du beat musical sont les mêmes que ceux permettant l'encodage efficace des signaux acoustiques dans la parole (p. ex. Wilson & Wilson, 2005; Goswami, 2012). L'évaluation du traitement de la régularité rythmique dans le langage parlé et chanté chez les personnes BI est un travail en cours dans notre laboratoire (thèse de doctorat de Marie-Élaine Lagrois). Des résultats préliminaires indiquent que le tapping sur la parole serait moins bon chez ces personnes que chez des participants contrôles, et vont donc dans le sens d'une généralité à travers les domaines du trouble de la synchronisation au beat.

Un autre point qui sera à clarifier dans le futur concerne un potentiel lien de causalité, et surtout le sens de ce lien, entre le trouble de synchronisation au beat musical et le manque de flexibilité de tempo, démontré ici pour la première fois. En d'autres termes: est-ce le manque de flexibilité qui cause le trouble de synchronisation à la musique, ou l'inverse? Répondre à cette question nécessiterait de connaitre la trajectoire développementale des capacités rythmiques chez les personnes BI. Drake et collaborateurs (2000) ont montré que la pratique musicale favorise la flexibilité de tempo chez les enfants, et en particulier l'accès aux niveaux de métrique supérieurs correspondant à des intervalles plus longs entre les beats. Il semble donc que l'expérience musicale interagisse avec la trajectoire développementale de l'adaptation de période à un stimulus externe. Dans ce contexte, il se pourrait qu'une incapacité trouver le beat de la musique limite les occasions de développer la flexibilité de tempo. À l'inverse, il est possible que ce soit le manque de flexibilité de tempo, reflétant un défaut d'adaptation de l'oscillateur interne, qui soit à l'origine du trouble de la synchronisation au beat. Des études longitudinales seront nécessaires pour préciser la direction d'un très probable lien de causalité entre flexibilité de tempo limitée et défaut de synchronisation au beat.

De façon plus générale, il n'existe pas à notre connaissance d'étude longitudinale s'étant intéressée au développement des capacités de perception et de synchronisation au beat. L'apparition de technologies comme les tablettes ou les téléphones intelligents comportant accéléromètre et écran sensible au toucher (Bégel, Di Loreto, Seilles & Dalla Bella, 2017b) pourrait bien faciliter la mise place de telles études. Ces outils technologiques, permettant de tester à distance, seraient de plus un atout pour le recrutement à large échelle de nouveaux cas présentant une synchronisation et/ou perception déficiente au beat musical. Une telle entreprise permettrait de dresser un portait plus global des troubles liés au traitement du beat.

Un groupe plus conséquent d'individus BI constituera en outre une opportunité d'étudier les corrélats neuraux associés à ces conditions, et éventuellement de mettre en évidence les structures cérébrales nécessaires au traitement du beat. Il existerait deux mécanismes distincts pour le traitement des intervalles temporels, associés à des circuits cérébraux différents (Teki, Grube, & Griffiths, 2011a; Teki, Grube, Kumar, & Griffiths, 2011b). Il s'agit, pour le premier, d'un mécanisme de perception dit absolu des durées ("duration-based") par lequel les intervalles sont traités sans référence à un beat, pour le second, d'un mécanisme dit relatif par lequel les intervalles sont traités par rapport à un beat. Le premier mécanisme serait supporté par un réseau sous-cortical comprenant olive inférieure, vermis et noyaux profonds du cervelet. Le second serait quant à lui supporté par un réseau cortical et sous-cortical comprenant putamen et noyau caudé (ganglions de la base), thalamus, aire motrice supplémentaire, cortex prémoteur et cortex préfrontal dorso-latéral (Teki et al., 2011b).

Cette distinction en deux mécanismes émane notamment d'observations neuropsychologiques. Les patients avec atteinte du cervelet présentent une déficience spécifique au traitement absolu des intervalles (duration-based) spécifiquement (Grube, Cooper, Chinnery, & Griffiths, 2010a; Grube, Lee, Griffiths, Barker, & Woodruff, 2010b), tandis que les patients avec maladie de Parkinson (atteinte des ganglions de la base) semblent ne pas être sensibles au beat (Grahn & Brett, 2009).

L'étude des personnes BI permettrait de tester ce modèle à deux mécanismes ainsi que de préciser les corrélats neuronaux associés à chacun d'eux. En effet, nous prédisons qu'une difficulté de synchronisation à la musique est associée à une altération du mécanisme relatif au beat (beat-based) mais pas du mécanisme de perception absolue des durées (duration-based).

Nous basons cette prédiction sur l'observation que toutes les personnes BI testées dans la thèse ont obtenu des scores dans la norme au test rythmique de la MBEA (Peretz et al., 2003). Ce test évalue la capacité à déterminer si deux mélodies sont pareilles ou différentes, les différences étant créées en manipulant la durée de deux intervalles adjacents. Si la perception d'un beat constitue certainement un facteur facilitant pour cette tâche (p. ex. Grahn & Brett, 2009), celle-ci peut être réussie par comparaison des durées absolues des intervalles. Nous pensons donc qu'un mécanisme intact de perception absolue des durées est responsable des résultats normaux au test rythmique de la MBEA, tel qu'observé chez les cas BI.

Le paradigme mis au point par Teki et collaborateurs (2011b) permettrait de vérifier cette prédiction de façon solide. Il consiste en une tâche de comparaison de durées. Le participant doit juger si le dernier intervalle d'une séquence de quelques sons est plus court ou plus long que l'avant-dernier intervalle. Dans la moitié des séquences, les intervalles précédant la cible sont isochrones et donnent lieu à la perception d'un beat. Dans l'autre moitié, ces intervalles sont irréguliers et ne donnent pas lieu à la perception d'un beat. Dans une étude pilote, Teki et collaborateurs (2011b) ont observé une meilleure discrimination de la durée pour les séquences isochrones comparées aux séquences irrégulières, lorsque la différence entre les intervalles à comparer est constante à travers les deux conditions. Chez les personnes BI nous prédisons un avantage moins important des séquences régulières sur les séquences irrégulières, en comparaison à un groupe contrôle. Cette différence comportementale devrait être accompagnée d'anomalie(s) au sein du réseau cérébral sous-tendant le mécanismes beat-based (ganglions de la base, thalamus, aire motrice supplémentaire, cortex pré-moteur et cortex pré-frontal dorso-latéral).

Une attention particulière devrait être portée aux ganglions de la base. Après avoir effectué une méta-analyse de 43 études de neuro-imagerie, Chauvigné, Gitau & Brown (2014) ont suggéré que cette structure jouerait un rôle important dans la production motrice (tapping) de séquences isochrones, que ce soit en synchronisation ou en tapping spontané. Le cervelet en revanche ne semble être actif qu'en synchronisation. Or, nos résultats (Article 3) ont montré que synchronisation *et* tapping spontané sont deux conditions dans lesquelles la variabilité motrice (intervalle entre les tapes) est anormalement élevée chez les personnes BI. Nous prédisons donc des anomalies au niveau des ganglions de la base auprès de cette population. Enfin, une attention devrait également être portée aux régions jouant un rôle dans l'intégration audio-motrice (auditory motor pathway, voir par exemple Zatorre, Chen, & Penhune, 2007), et en particulier à la connectivité entre régions auditives et de planification motrice (modèle ASAP; Patel & Iversen, 2014).

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Annexes

Annexe 1: Current conceptual challenges in the study of rhythm processing deficits

Pauline Tranchant et Dominique T. Vuvan

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Current conceptual challenges in the study of rhythm processing deficits

Pauline Tranchant[1,2] **& Dominique T. Vuvan**[1,2]

1 Département de psychologie, Université de Montréal, Montréal, Québec, Canada

2 International Laboratory for Brain, Music and Sound Research (BRAMS), Université de
Montréal, Montréal, Québec, Canada

Running Title: Conceptual challenges in rhythm deficit research

Abstract

Interest in the study of rhythm processing deficits (RPD) is currently growing in the cognitive neuroscience community, as this type of investigation constitutes a powerful tool for the understanding of normal rhythm processing. Because this field is in its infancy, it still lacks a common conceptual vocabulary to facilitate effective communication between different researchers and research groups. In this commentary, we provide a brief review of recent reports of RPD through the lens of one important empirical issue: the method by which beat perception is measured, and the consequences of method selection for the researcher's ability to specify which mechanisms are impaired in RPD. This critical reading advocates for the importance of matching measurement tools to the putative neurocognitive mechanisms under study, and reveals the need for effective and specific assessments of the different aspects of rhythm perception and synchronization.

Keywords: rhythm, rhythmic grouping, beat, meter, beat deafness, auditory-motor mapping, dysrhythmia, sensorimotor synchronization, poor synchronization

Introduction

Scientific interest in rhythm processing in music has exploded in the last decade. This has been accompanied by growing interest in rhythm processing deficits (RPD), which may serve as a powerful tool for the investigation of the normal processing of rhythm. Because the study of RPD is in its infancy, the empirical approach to its study has been inconsistent, particularly with respect to the methods used to measure beat perception. These inconsistencies invoke challenges for RPD researchers, particularly concerning the identification of which rhythm-related mechanisms (beat perception or synchronization, for instance) are impaired, and how the different mechanisms might interact. In this commentary, we discuss how these tensions are exemplified in three recently published reports (Phillips-Silver et al., 2011; Sowiński and Dalla Bella, 2013; Launay et al., 2014).

One constant across these studies is their use of the Montreal Battery of Evaluation of Amusia (MBEA; Peretz et al., 2003) to assess rhythm perception. The MBEA has been designed to diagnose music processing disorders along two distinct processing pathways; one related to melodic organization and the other related to temporal organization (the rhythm). This separation was motivated by neuropsychological dissociations (see Peretz, 2013 for a recent review; see Phillips-Silver et al., 2013 for a recent empirical report). Within the temporal dimension the assessment of rhythm perception is divided into two subtests: the rhythm test and the metric test. Like the MBEA's division of pitch and temporal processing, this division was motivated by previous neuropsychological dissociations (Fries and Swihart, 1990; Peretz, 1990; Liégeois-Chauvel et al., 1998) suggesting two separable mechanisms for the processing of musical rhythm: the tendency to cluster the sounded events that constitute a rhythm into figural patterns according to temporal proximity (grouping) and the emergence of regularly recurring psychological events in response to a rhythm.

In the rhythm test, participants have to judge whether two short piano excerpts are the same or different, with different trials containing alterations produced by manipulating the durations of two adjacent tones, so that the rhythm is changed but the total number of sounds and the meter are preserved. Importantly, although beat perception may be helpful to perform this task in normal participants, it is not necessary. Specifically, the comparison of the pattern of durations in each sequence to be judged is sufficient for task success. In contrast, the metric test targets beat perception by asking participants to judge whether short piano excerpts are marches (binary metrical organization: alternation of a strong beat and a weak beat) or waltzes (ternary metrical organization: one strong beat followed by two weak beats). Interestingly, like for the rhythm test, an alternative strategy that does not tap beat perception is possible. Specifically, the perception of the acoustic accents used to mark strong beats and the counting of the intervening events would be sufficient for task success.

The first study of congenital RPD (Phillips-Silver et al., 2011) reported the case of a university student, Mathieu, unable to synchronize simple whole-body movement (bouncing) with a musical beat despite preserved cognitive, motor, and pitch-related musical abilities. Mathieu performed comparably to controls on the MBEA rhythm test, but performed poorly on the metric test. The authors thus proposed that “an inability to detect an underlying beat” may be responsible for his disorder, which they labeled “beat deafness.”

In the second paper, Sowiński and Dalla Bella (2013) reported four participants who exhibit poor synchronization to a beat. Rhythmic perception was assessed with both the rhythm test of the MBEA and with an “anisochrony detection task.” Two cases (S2 and S9) performed poorly at an anisochrony detection task (henceforth ADT) and the authors concluded that they were thus comparable to Mathieu (i.e., synchronization deficit due to perception deficit). We argue that this conclusion may not be valid for two reasons. First, although Phillips-Silver et al. (2011) proposed the perceptual origin of Mathieu's disorder on the basis of his poor performance on the metric test of the MBEA, Sowiński and Dalla Bella (2013) did not report S2 and S9's performance on this test. The reason for this is that these authors' sample performed with high variability on the metric test, which might compromise the use of 2 SD below the mean as the impairment threshold. However, this does not invalidate the use of the MBEA metric test as a measure of beat perception. Rather, this indicates that a different threshold that takes this high variability into account should be sought, particularly because the distribution of performance on this task is non-normal (skewed to the left, as indicated by unpublished norms from our group with n = 432). Second, like the MBEA rhythm and meter tests, beat perception may facilitate performance but it is not necessary to succeed at the ADT. Indeed, it can be performed by comparing the durational values of adjacent inter- tone-intervals, and for the musical sequences, by noting the acoustic cue produced by the jittered onsets of the high and low voices on anisochronic trials (these stimuli were acquired through personal correspondence with Sowiński and Dalla Bella, 2013). This proposition is consistent with work by Grahn and McAuley (2009) showing that strong and weak beat perceivers do not differ in their ability to judge whether the final interval in a metronome sequence is different from the intervals preceding it.

Sowiński and Dalla Bella further concluded that the synchronization deficits observed in two additional cases (S1 and S5) might be due to a disorder of auditory-motor mapping rather than a beat perception disorder. We argue that caution should be exercised before making this claim. This conclusion can only be reached if an impairment of beat perception has been excluded, which is not the case because, as noted above, both the MBEA rhythm test and anisochrony detection tasks can be performed without beat perception.

Finally, Launay et al. (2014) screened participants for rhythm perception impairments using the MBEA rhythm test and showed that three individuals identified through this procedure exhibited impaired synchronization when tapping to a beat. The authors named this condition "dysrhythmia." These authors inferred that the deficit observed in their three impaired participants "seems to lie specifically in extracting the correct (intended) meter from non-isochronous metrical rhythms," despite the fact that, as discussed above, the capacity to perceive a beat is not necessary to perform the MBEA rhythm test. Therefore, the locus of the dysrhythmic deficit thus remains unclear. In particular, a clear model for how poor beat perception and consequently poor synchronization might result from poor temporal duration perception abilities is lacking. For instance, the perception of temporal duration may be necessary for beat extraction and hence for synchronization to the beat. Alternatively, if duration perception is dissociable from beat perception, or if perception is dissociable from synchronization, then the perception of interval duration perception may be unrelated to a beat synchronization deficit. Regardless, without the adequate measurement of beat perception, a strong conclusion cannot be reached about the source of the observed synchronization deficit.

Conclusions

We anticipate an explosion of studies on rhythm deficits in the coming years, as was the case for pitch-related deficits after the original introduction of the MBEA (Peretz et al., 2003). A primary goal for researchers in the years to come will be to find ways to clarify the origin of such deficits, driving the development of myriad research questions. For example, which temporal mechanisms are specifically impaired? Is the deficit purely perceptual or does it involve impaired sensorimotor coupling? Is the disorder music-specific or domain- general? The ability of such research to illuminate important research questions regarding timing behavior depends critically on the careful use of measurement tools to assess the specific mechanisms hypothesized to underlie various components of this behavior. One tool that has much potential for the measurement of beat perception in RPD is the Beat Alignment Test (BAT; Iversen and Patel, 2008), which tests beat perception through the judgment of whether or not an isochronous train of beeps superimposed upon a musical extract sounds "on the beat" or not. The BAT is particularly promising because of the lack of obvious strategies, other than beat perception, that can be deployed to perform this task. Two further potentially interesting tools are the Battery for the Assessment of Auditory Sensorimotor and Timing Abilities (BAASTA; Benoit et al., 2014) and the Harvard Beat Assessment Test (H-BAT; Fujii and Schlaug, 2013). The BAASTA provides a package of tests including the BAT, anisochrony detection, and a task that explicitly assesses duration discrimination in the absence of a beat. The H-BAT assesses beat perception and production using both musical excerpts and psychophysically-controlled woodblock stimuli. In sum, the use of untapped tools, such as the BAT, the BAASTA, and the H-BAT, as well as the development of novel tools for the measurement of beat perception must be a central aim of RPD research for the near future.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Annexe 2: Autres projets réalisés durant le parcours doctoral

Tranchant, P., Shiell, M. M., Giordano, M., Nadeau, A., Peretz, I., & Zatorre, R. J. (2017). Feeling the beat: bouncing synchronization to vibrotactile music in hearing and early deaf people. *Frontiers in neuroscience*, *11*, 507.

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