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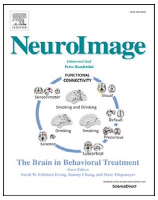

The cerebellum's contribution to beat interval discrimination

S. Paquette[a], S. Fujii[b], H.C. Li[a], G. Schlaug[a,*]

[a] *Music, Stroke Recovery, and Neuroimaging Laboratory, Neurology Department, Beth Israel Deaconess Medical Center, Harvard Medical School, Boston, MA, USA*
[b] *Faculty of Environment and Information Studies, Keio University, Fujisawa, Kanagawa, Japan*

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ABSTRACT

From expert percussionists to individuals who cannot dance, there are widespread differences in people's abilities to perceive and synchronize with a musical beat. The aim of our study was to identify candidate brain regions that might be associated with these abilities.

For this purpose, we used Voxel-Based-Morphometry to correlate inter-individual differences in performance on the Harvard Beat Assessment Tests (H-BAT) with local inter-individual variations in gray matter volumes across the entire brain space in 60 individuals.

Analysis revealed significant co-variations between performances on two perceptual tasks of the Harvard Beat Assessment Tests associated with beat interval change discrimination (faster, slower) and gray matter volume variations in the cerebellum. Participant discrimination thresholds for the Beat Finding Interval Test (quarter note beat) were positively associated with gray matter volume variation in cerebellum lobule IX in the left hemisphere and crus I bilaterally. Discrimination thresholds for the Beat Interval Test (simple series of tones) revealed the tendency for a positive association with gray matter volume variations in crus I/II of the left cerebellum.

Our results demonstrate the importance of the cerebellum in beat interval discrimination skills, as measured by two perceptual tasks of the Harvard Beat Assessment Tests. Current findings, in combination with evidence from patients with cerebellar degeneration and expert dancers, suggest that cerebellar gray matter and overall cerebellar integrity are important for temporal discrimination abilities.

1. Introduction

In recent years, many studies have focused on the ability to perceive or synchronize to a musical beat (e.g., Fujii and Schlaug, 2013; Tranchant et al., 2016). Studies have established the early onset of this skill in human development (Fujii et al., 2014; Hannon and Trehub, 2005; Kirschner and Tomasello, 2009; Phillips-Silver and Trainor, 2005; Winkler et al., 2009; Zentner and Eerola, 2010) while noting evolutionary advantages (e.g. human communication, group cohesion or sexual selection) and emphasizing its biological origins. While most infants can detect the beat in music (Winkler et al., 2009), there are widespread differences in people's abilities to perceive and synchronize with a musical beat, ranging from expert synchronizers (e.g., musicians: Chen et al., 2008; Kung et al., 2013) to individuals who cannot synchronize to music (i.e., beat deafness: Phillips-Silver et al., 2011). In this study, we aimed to utilize inter-individual differences in the normal population as a tool to identify the neural correlates associated with people's abilities to perceive and synchronize with a musical beat.

Generally speaking, while some progress has been made (for a review on the mechanisms enabling beat synchronization, see: Repp and Su, 2013), the manner in which the auditory system extracts the periodicity of a stimulus is to some extent unspecified. Several different mechanisms have been proposed, ranging from measurement of temporal intervals by a central timekeeper (Grube et al., 2010a; Ivry et al., 1988; Ivry and Keele, 1989; Molinari et al., 2007; Thaut et al., 2009) to the coupling of auditory stimuli with low-frequency neural oscillators found in the auditory cortex (Nozaradan et al., 2012). Some have focused on the cerebellum (e.g., Schwartze and Kotz, 2013) as an important brain area for temporal encoding reducing sensory input to a discrete, event-based representation of temporal structure that implicitly encodes the temporal relation between successive sensory events. However, it is clear that we are still lacking in our understanding of brain regions that could be involved in the ability to perceive/extract a musical beat.

The neuroimaging technique of voxel-based-morphometry (VBM) can be used to relate variations in a behavioral variable with variations in gray matter signal across the entire brain space (Ashburner and Friston, 2000). VBM studies are typically used to examine co-variations or changes in gray matter volume with a specific ability within a group

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* Corresponding author. Neurology Department, Beth Israel Deaconess Medical Center, Boston, MA 02215, United States.
E-mail address: gschlaug@bidmc.harvard.edu (G. Schlaug).

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(jugglers: Draganski et al., 2004; taxi drivers: Maguire et al., 2000). In the musical domain, previous studies have observed gray matter volume differences between expert, amateur, and non-expert musicians; and expert or non-expert dancers (Gaser and Schlaug, 2003; Nigmatullina et al., 2015; Sluming et al., 2002). Furthermore, VBM studies (Hyde et al., 2006; Mandell et al., 2007) have examined co-variation of gray matter volume with participant performance on a musical assessment test (Peretz et al., 2003) to identify candidate brain regions that are related to the phenotypic expression of congenital amusia or tone-deafness (a pitch perception deficit, Vuvan et al., 2017).

In order to determine the neural correlates associated with people's abilities to perceive and synchronize with a musical beat, we used VBM in combination with our recently developed beat assessment test. The Harvard Beat Assessment Test (H-BAT: Fujii and Schlaug, 2013) was developed to investigate the individual differences in people's abilities to perceive and synchronize with a musical beat. The H-BAT assesses beat perception and production abilities in tests that are matched with regard to material and assessing thresholds via psychophysical adaptive staircase methods. H-BAT consists of four sub-tests: 1 - music tapping test, 2 - beat saliency test, 3 - beat interval test, and 4 - beat finding and interval test (sub-tests are further described in the method section).

Our subjects consisted of a large number of young individuals with varying levels of performance on the H-BAT. We examined co-variations between performance on the (H-BAT) and inter-individual variations in gray matter volume on a voxel-by-voxel basis across the entire brain space using VBM, to identify candidate brain regions that are related to people's abilities to perceive and/or synchronize with a musical beat. These brain regions and the networks they are involved in could then become the basis of further exploration to examine their precise role in the expression of this ability.

2. Method

2.1. Participants

The study group consisted of 62 healthy individuals who responded to newspaper advertisements for a variety of studies on music processing. Two participants were excluded because they did not complete the full protocol of tests. A data set derived from 60 subjects (29 females, 58 right handed) with a mean age of 27.3 (range: 21–58), with on average of 9.4 years of musical training (range: 0–53) was available for final data analysis. All volunteers gave signed, informed consent and the Institutional Review Board of Beth Israel Deaconess Medical Center, Boston, MA, approved this study.

2.2. Behavioral evaluation

All subjects were screened for neurological, psychiatric, and hearing disorders before being enrolled, and subsequently underwent the Shipley/Hartford vocabulary and abstraction tests (Shipley, 1940) which correlate highly with the Wechsler Adult Intelligence Scale full-scale IQ (Paulson and Lin, 1970); all had an IQ of 99 or above. Each subject completed all subtests of the H-BAT using the same H-BAT apparatus described by Fujii and Schlaug (2013).

The H-BAT consists of four sub-tests: (1) a music tapping test (MTT) where the participant has to tap the quarter-note beat underlying musical excerpts, (2) a beat saliency test (BST) where the participant has to first discriminate a duple/triple meter, then produce that meter by changing tap amplitudes, (3) a beat interval test (BIT) where the participant has to first perceptually discriminate a temporal change (within a series of tones that consists of only quarter notes), then tap in synchrony with the tones and adapt to the temporal change (slower/faster), and (4) a beat finding and interval test (BFIT) where the participant has to first discriminate a temporal change pattern (within a series of tones that consists of one quarter note, two eighth notes, one dotted-quarter note, and one eighth note) and then find and produce the quarter note and adapt to the temporal change (slower/faster). Note that BFIT is more complex than BIT because the former includes a beat-finding ("the F") component. MTT measures the degree of tapping synchronization with the musical beat; whereas BST, BIT, and BFIT measure perception and production thresholds via psychophysical adaptive staircase methods. For a more detailed description of the different tests see Fujii and Schlaug (2013).

Since raw score distributions were significantly different from normal (Shapiro-Wilk, $p < .001$), scores were normalized by log-transformation, as presented in the H-BAT introduction paper (Fujii and Schlaug, 2013). Because BIT production and MTT scores were still not normally distributed after log 10 normalization, log 2 normalization was used. For all reported scores, a smaller value indicates a better synchronization (MTT), discrimination (perceptual tasks), or adaptation (production tasks) ability (see Table 1 for group averages).

Table 1
Group average score at the different H-BAT sub-tests presented with the group lowest and highest score and standard deviation.

	MTT (SI*)	BST (log2db)		BIT (log2ms)		BFIT (log2ms)	
	MTT	Perception	Production	Perception	Production	Perception	Production
Mean	−1.5	1.2	1.6	−1.6	−3.0	−2.0	−2.5
Min	−2.6	−0.9	−1.9	−5.0	−6.3	−5.4	−5.7
Max	−1.0	3.3	3.9	1.3	0.3	0.6	1.3
Stdev	0.4	1.0	1.3	1.4	1.2	1.3	1.6

SI* Synchronization Index (entropy of relative phase distribution) in degrees (log2 transformed).

Consistent with Fujii and Schlaug (2013), most perception-production scores from the H-BAT were significantly correlated with each other. For example, BFIT perception was correlated with BFIT production, $p < .05$). Exceptions were that BIT production was not significantly correlated with BIT and BFIT perception; and BIT perception was not significantly correlated with MTT. These exceptions may indicate, in part, a possible dissociation between beat perception and production as measured on the H-BAT (Fujii and Schlaug, under review).

2.3. MRI image acquisition and preprocessing

Imaging participants were scanned with a 3 T General Electric (Fairfield, CT) MRI scanner using a standard radio frequency head coil. Anatomical scans were acquired using a strongly T1-weighted magnetization prepared gradient-echo (MPRAGE) volume acquisition with a voxel resolution of 0.93 × 0.93 × 1.5 mm.

All preprocessing steps except for the smoothing step were computed using the CAT12 Toolbox. T1 images were first segmented. Then, gray and white matter tissue segments for all subjects were used to create a population template of gray matter from the entire image dataset using the DARTEL algorithm. All images were normalized into Montreal Neurological Institute (MNI) stereotactic space and modulated (non-linear only) by Jacobian determinants derived from the spatial normalization step. Modulated normalized images were then smoothed by convolution with an isotropic Gaussian kernel of 8-mm full-width at half maximum in SPM12 software. Only the smoothed gray matter images were used in the statistical analyses.

2.4. *MRI image analysis*

Seven simple regression analyses were performed across the entire gray matter space. The 60 preprocessed gray matter maps were regressed on their corresponding H-BAT scores, using each sub-test score on a voxel-by-voxel basis with an absolute masking threshold of 0.1 as suggested by the developers. Global effects were estimated with SPM mean voxel value.

3. Results

3.1. *Voxel-based-morphometry: regression results*

Whole-brain regression analysis of variations in gray matter volume with performance on the different H-BAT tests showed significant covariation in the cerebellum for one of the perceptual tests (Fig. 1). Discrimination thresholds on the perceptual portion of the BFIT were positively associated ($T_{58} = 4.93$, $p < 0.005$, FWE cluster level) with gray matter volume variations predominantly in the left cerebellum in lobule IX (peak: −6, −46, −52; Fig. 1C) and in crus I of the left (peak: 26, −56, −34) and right (peak: 45, −44, −36) cerebellum (Fig. 1A and B; left: $T_{58} = 4.60$, $p < 0.01$, FWE cluster level; right $T_{58} = 4.60$, $p < 0.01$, FWE cluster level). Discrimination thresholds for the BIT perception task showed a similar tendency in crus I/II of the left (peak: 28, −58, −39; Fig. 1A) cerebellum ($T_{58} = 4.50$, $p = 0.06$, FWE cluster level).

3.2. *Voxel-based-morphometry: group comparison*

Additionally, for both tests (BFIT perception, BIT perception) where co-variation between gray matter and performance was observed, planned gray matter comparisons were done between the 10 best (BFIT: m = −3.9 [range: −5.4 to −3.1]; BIT: mean score = −3.8 [range: −5.0 to −2.7]) and 10 worst (BFIT: m = −0.3 [range: −0.8 to 0.6]; BIT: m = 0.27 [range: −0.3 to 1.3]) performers of each test in the regions identified in the previous analysis (using volume correction to the cluster images).

Analysis for the BFIT task, using its associated regression clusters (Fig. 1-green; crus I [right, left]) as a mask, revealed that poor performers also had significantly more gray matter in the regions of interest (right: $T_{18} = 4.98$, $p < 0.01$; left: $T_{18} = 5.83$, $p < 0.005$, FWE peak level). The same was found for lobule IX (Fig. 1-green; $T_{18} = 4.07$, $p < 0.05$, FWE peak level). Similarly, for the BIT task, using its associated regression cluster (Fig. 1-blue; crus I/II as a mask, revealed that poor performers had significantly more gray matter in the region of interest ($T_{18} = 4.42$, $p < 0.01$, FWE peak level).

4. Discussion

Our results showed positive correlations between gray matter volume variations in sub-regions of the cerebellum (crus I, lobule IX) mostly on the left, and H-BAT beat interval change discrimination tasks (BFIT, BIT) scores. VBM studies associating variations in gray matter with performance in cross-sectional analyses have varied with regard to whether or not poor performance on a test was associated with either higher or lower regional gray matter volume. For example, higher gray matter volume in the left inferior temporal gyrus has been found to be associated with poor performance on a reading task (Silani et al., 2005). In another study (Hyde et al., 2006), congenital amusics were found to have more gray matter relative to controls in the inferior frontal gyrus and this was interpreted as a possible consequence of a microscopic malformation or dysgenesis in cortical development (Hyde et al., 2007, 2006). However, there are also studies that have found lower gray matter volume to be associated with poor performance on a musical discrimination task (e.g., Mandell et al., 2007). Overall, whether or not higher or lower gray matter volume is associated with the variation in performance might depend on the region of the brain that is most affected and on the presumed underlying pathology (e.g., migration disorder, abnormalities of specific

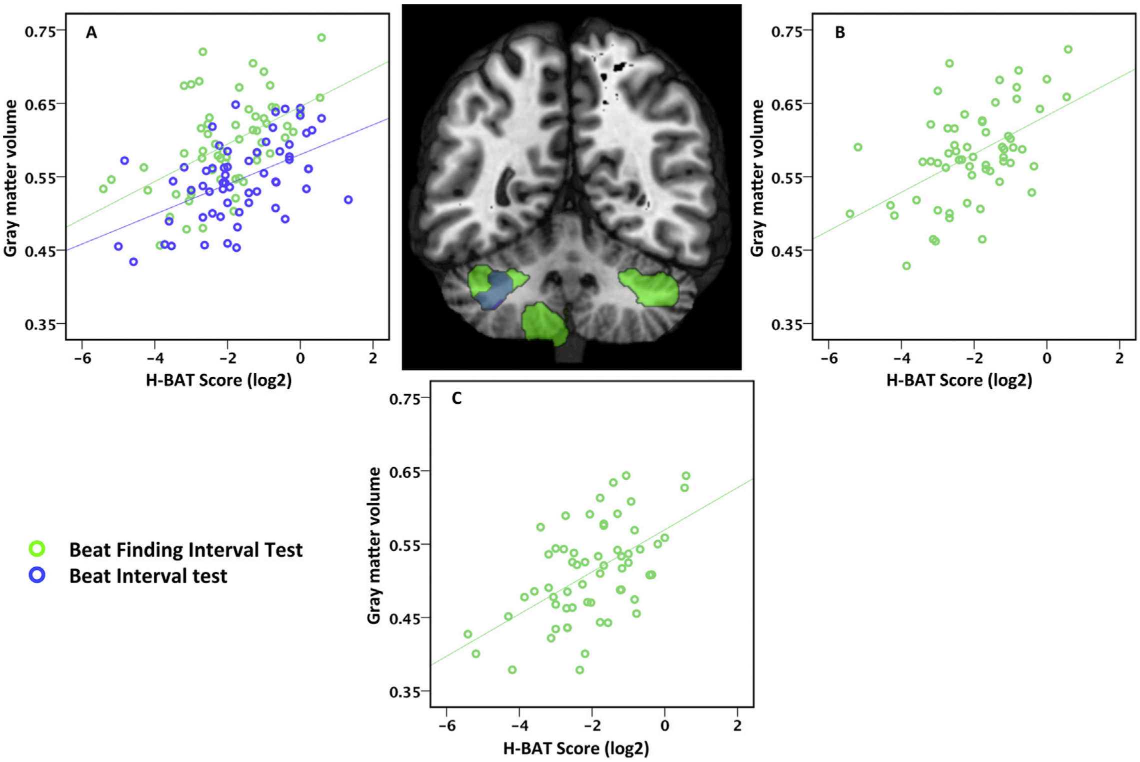

Fig. 1. Representation of the clusters associated with the regression analysis, presented alongside a graphical representation of the positive association with the corresponding H-BAT test (y = Gray matter volume; x = Log2-transformed scores). BFIT test scores are presented in green in figures A, B, C; and BIT scores in blue in figure A.

neuron populations, connectivity or connection abnormalities). All of these processes could potentially have an effect on the gray matter signal, but they might affect the gray matter signal in different directions.

For example, neuronal migration disorders are the result of misplacement and faulty differentiation of neurons affecting the cortical gray matter during development (Copp and Harding, 1999). Neuronal migration can be affected at its beginning, while the migration process is ongoing, and in multiple steps near completion of the migration. This includes the stage at which neurons penetrate through the subplate and the cortical plate (Gleeson and Walsh, 2000); where and when this penetration happens can affect the gray matter signal in different directions. For example, clumping of cells in cortical layers without a clear neuropil having formed around them, as well as processes that interfere with the natural pruning of neural cells during development, can lead to a higher gray matter signal. Furthermore, disturbance of local connections in GABAergic circuits (mediating the activity-dependent maturation of cortical circuits; Hensch and Stryker, 2004) or long-range connections (modifying the expression of axon guidance molecules; Hensch, 2005) might have similar consequences and might lead to less separation of neurons from each other or less neuropil around the neurons, again potentially increasing the gray matter signal. Specific systems' vulnerability might be linked to the timing of circuit assembly in particular cortical regions (Rakic, 2002) and also to the underlying etiology (e.g., genetic defects, differential expression of genes, or other structural injuries that could interfere with neuronal migration and synapse formation.

Our findings support the idea that the cerebellum is involved in optimizing sensory input from the auditory system and perhaps other modalities (Bower, 1997; Gao et al., 1996; Penhune et al., 1998) to facilitate comparison of time intervals in working memory (Rao et al., 2001) and perhaps help coordinate sensory and motor areas. All cerebellum subregions identified in this study are associated with regions of the cerebellum that are functionally connected (Buckner et al., 2011) to cerebral association networks (e.g. lateral temporal cortex, the inferior parietal lobule, and an extended region along medial prefrontal cortex) - networks that integrate auditory, visual, and somatic sensory information into complex perceptions (Kandel et al., 2000).

4.1. The role of the cerebellum

While the role of the brain's internal “pacemaker'' is usually attributed to the basal ganglia, Kotz et al. (2009) brought forward the idea that this “pacemaker'' can be influenced by the cerebellum when predictable sensory cues (e.g. a metronome beat) are present. The cerebellum would be responsible for the precise encoding of a perceived temporal structure that is required for efficient predictive adaptation of a behavior (Schwartze and Kotz, 2013).

Further support for a role of the cerebellum in the precise encoding of temporal structure that allows time interval discrimination comes from patient studies. Patients with neurological disorders that lead to cerebellar atrophy show impairments in conscious perception of tempo changes, despite preserved tapping performances (Molinari et al., 2005). Although, as in our study, Molinari and colleagues did not aim to analyze the ability to consciously perceive temporal changes, their data indicate, as ours do, that the ability to detect/discriminate tempo or beat changes might be linked to variations in cerebellar volume. The role of the cerebellum in timing tasks has also been demonstrated experimentally. Disrupting the cerebellar vermis using transcranial magnetic stimulation or continuous transcranial magnetic theta-burst stimulation has been reported to have an impact on performance on timing tasks by affecting participants' ability to estimate/reproduce time intervals (Grube et al., 2010b; Koch et al., 2007; Lee et al., 2007; Théoret et al., 2001).

4.2. The cerebellum and task complexity

Although both BIT and BFIT scores were positively associated with the gray matter volume variation in the cerebellum; results were slightly different between the two tests. While BFIT scores correlated with various clusters in lobule IX and crus I, correlation results for BIT were only marginally significant. To interpret this, it is important to discuss the task difference between the BIT and BFIT.

For example, in case of the BIT, if the inter-beat interval (IBI) of the stimulus was 500 msec and the tempo was slowing down by 10 msec per beat, the first four inter-stimulus intervals (ISIs) would be 500, 510, 520, and 530 msec c (all quarter notes). In case of the BFIT in the same setting, the first five ISIs would be 500 ms (quarter note), $510/2 = 255$ ms (eighth note), $510/2 = 255$ ms (eighth note), $520 + 530/2 = 785$ ms (dotted-quarter note), and $530/2 = 265$ ms (eighth note). Thus, the BFIT is more complex than the BIT in terms of the pattern of change in the stimulus intervals; the participant had to listen to ISIs that varied more than those in the BIT to discriminate the temporal changes. In other words, the BFIT requires brain networks to encode more variable time intervals in the BFIT than in the BIT.

Beat finding is another component which makes the BFIT more complex than the BIT. During the BIT, the beat timing corresponds to the tone (all quarter notes) timing. But, during the BFIT, the participants had to infer the beat timing based on the perceived pattern of tone intervals (not all tones were quarter notes). In the H-BAT introduction paper, Fujii and Schlaug (2013) added this beat-finding component to investigate the individual differences of beat processing. This idea was based on previous functional MRI studies showing that musicians were better at finding the beat in a pattern of time intervals compared to non-musicians (Chen et al., 2008; Grahn and Rowe, 2009), and that the superior beat-finding ability was associated with greater involvement of the prefrontal activity (Chen et al., 2008) and increased connectivity between the auditory and premotor areas (Grahn and Rowe, 2009). These functional MRI studies led us to expect that the BFIT score might be associated with a more complex network of cortical region regions for which the cerebellum might be the hub and the center of the time duration task.

It is important to remember that both the BIT and BFIT in the H-BAT battery require the processing of absolute time of tone intervals rather than relative time. Previous studies suggest that the cerebellum is particularly critical to perception of absolute duration of time intervals, whereas the basal ganglia-thalamo-cortical network may be more critical for perception of time intervals relative to a regular, constant beat (Grube et al., 2010a, 2010b; Teki et al., 2011). The perception of absolute timing is a fundamental process in BIT and BFIT because the tempo is not constant but changes gradually and therefore there is no identical time interval in the series of tones. Perception of absolute timing may be what differentiates BIT and BFIT most from other tests and batteries.

The observed selective gray matter variation in crus I for the BFIT beat discrimination tests may be linked to higher processing demands for variable time intervals. Crus I has been described as central to auditory processing by Petacchi et al. (2005). The results of their meta-analysis suggest that activation patterns in crus I should scale with the demand for high-quality sensory data (related to the degree of complexity of the auditory task). Hence, it is not surprising that its size (gray matter volume) is likely to affect fundamental aspects of auditory processing, such as time interval discrimination.

Additional support comes from a study (Parsons, 2001) involving musicians and non-musicians that investigated the functional neuroanatomy associated with the perception of different rhythmic components (meter, pattern, duration, tempo). Although cerebellar activation was seen for all participants in the conditions testing for meter, tempo, and pattern discrimination, this activation was stronger in non-musicians than in musicians (even though task difficulty was controlled across groups). Even more revealing, the opposite was found for the duration discrimination task (perceived as more complex/novel by musicians) where musicians showed stronger activation than non-musicians. Hence, task novelty/complexity seems to have an effect on how the cerebellum processes information, which would explain the significant clusters of gray matter variation-associated with participant performance on the

BFIT. The need to find the underlying quarter-note beat and discriminate its temporal change patterns in a series of various notes of different time intervals in the BFIT makes it more complex, potentially requiring more resources and more connections with both sides of the dentato-thalamic-cortical axes. Of note, this ability to find a musical beat is particularly relevant to dancers and it has been observed that expert dancers were found to have reduced gray matter density in these regions of the cerebellum (lobules IX; Nigmatullina et al., 2015).

4.3. Conclusion

In conclusion, the cerebellum, or more precisely the gray matter volume in Crus I and lobule IX, might become the basis of further exploration in studies examining fine timing discrimination abilities. Perceiving differences in time duration (tempo/beat detection) might be linked to variations in gray matter volume in the cerebellum, while the ability to detect asynchrony– a task that was not included in the H-BAT - may either be linked with the same regions or could be associated with other brain structures that yet have to be determined (Lerens et al., 2014; Patel et al., 2005; Phillips-Silver et al., 2011; Tierney and Kraus, 2013). For example, it has been observed in blind individuals (Lerens et al., 2014) that early visual deprivation was associated with improved beat asynchrony detection but not with auditory duration discrimination. This might perhaps indicate that beat asynchrony detection may involve higher-level processes that may be separate from duration discrimination tasks.

The same is true for perception and production: the ability to anticipate and accurately reproduce or synchronize with intervals might be due to a more distributed system that involves implicit motor responses for explicit tempo detection/comparison and constant error correction (Repp, 2005). Hence, the wide-ranging abilities associated with beat production/synchronization cannot be directly associated with variation in gray matter in a specific area. Support for this hypothesis also comes from the current study, where participant perception and production scores at the H-BAT did not always correlate. BIT perception and production only shared 4.8% of variance ($r = 0.22$, $p = 0.9$) and BFIT perception and production only shared 10.7% of variance ($r = 0.33$, $p = 0.01$); these would qualify as weak correlations according to Evans (1996). This might suggest that these two processes, perception and production of a beat, may not draw on exactly the same neural structures.

The specific role of the cerebellum in timing discrimination supports theories that consider it as an optimization and coordination system with regard to the fine-tuning and integration of sensory information, particularly when it involves the time domain (Bower, 1997).

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