The Musician Redefined: A Behavioral Assessment of Rhythm Perception in Professional Club DJs

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Abstract

Studies of musical training demonstrate functional advantages in rhythm tasks that result from enriched auditory experience. Anatomical correlates exist in brain areas involved in auditory perception, speech processing, motor control, attention, and emotion. However, these studies fail to include many classes of musicians that might undergo experience-related change. The current study examined rhythm processing in professional disc jockeys (DJs) who routinely engage in temporally-demanding tasks during practice and performance. In Experiment 1, DJs outperformed controls at detecting a deviation in a rhythmic pattern, and were no different than trained percussionists. In Experiment 2, participants receiving one week of DJ training trended toward outperforming untrained participants on this same measure. Across experiments, movement improved detection of rhythmic deviations, providing evidence of privileged auditory-motor connections, and underscoring the importance of motor areas to rhythm perception. It is clear that DJs show experience-dependent changes in perception that are comparable to more traditional musicians.

1. Introduction

The perception of time is critically important for perceiving music and much research focuses on sensorimotor synchronization, in which systems critical to the perception of time intervals are coupled with those responsible for executing

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actions. The ability of humans to synchronize action to an externally produced sound signal is an exquisite feat of millisecond-level timing (see Repp, 2005; Repp & Su, 2013, for reviews). Studies in this domain have often required listeners to tap along with an isochronous rhythm (such as a metronome). Untrained listeners are fairly good at such tasks, presenting with an onset asynchrony between stimulus and action on the order of tens of milliseconds, depending on tempo; however this asynchrony is often much smaller in musically trained listeners (Aschersleben, 2002; Krause et al., 2010; Repp, 2010; Repp & Doggett, 2007), and may be smaller still when musicians are asked to entrain using their own instrument (Stoklasa et al., 2012). An extension of this paradigm involves asking participants to continue tapping at the rate of the presented isochronous rhythm after that stimulus has been removed (referred to as *continuation tapping*; e.g., Chen et al., 2002; Snyder et al., 2006). Trained listeners also outperform untrained listeners on this task (Repp, 2010), which requires that information regarding the interstimulus interval be maintained in memory.

Information-processing approaches to sensorimotor synchronization posit that organizing movements into a series of discrete contacts requires a great deal of temporal control (Delignières et al., 2004) and appears to involve brain areas classically implicated in discrete time perception, such as the basal ganglia (see Coull et al., 2010, for a review) and the cerebellum (Spencer et al., 2003, 2005; Wiener et al., 2010). While there remains some debate on the issue, it appears that interval timing involves two neural systems: one which operates on a sub-second scale and which involves the cerebellum and motor cortices, and the other which functions over longer time intervals and which involves the basal ganglia, parietal cortex and prefrontal areas (Buhusi & Meck, 2005; Lewis & Miall, 2003). Recent studies suggest that the degree to which these systems contribute to the perception of rhythm depends on whether or not an underlying beat (which may span several seconds) is perceived (Grube et al., 2010; Teki et al., 2011). Cerebellar-cortical connections have been implicated not only in movement timing and temporal prediction, but also in feedback-based learning (Doya, 1999; Teki et al., 2012). Thus, it is not surprising that training in the rhythm domain leads to increased performance in the types of tasks described above.

Musical training provides a unique opportunity to examine the experience-dependent reorganization of the structure and function of neural systems related to music perception and production, as well as movement. Some of the changes occurring as a result of musical training are nonspecific across instrument played, such volumetric differences between musicians and non-musicians in primary auditory cortex (Gaser & Schlaug, 2003; Schneider et al., 2002), planum temporale (e.g., Meyer et al., 2012), Broca's area (e.g., Abdul-Kareem et al., 2011), and white matter tracts including the corpus callosum (e.g., Steele et al., 2013), and arcuate fasciculus (e.g., Halwani et al., 2011). Functionally, musicians show increased coupling between auditory and motor areas when perceptually

processing the beat of an auditory rhythmic sequence (Grahn & Rowe, 2009; James et al., 2012). In addition to such generalized effects, much of the reorganization associated with musical training is related to the demands of the instrument. For example, percussionists have been shown to outperform string musicians and control subjects on auditory duration judgment tasks, while string players show the best performance on tasks involving pitch judgments (Hinton & Rauscher, 2003). Percussionists have also been shown to display less variability than both pianists and controls when asked to tap along with isochronous (Krause et al., 2010), and nonisochronous (Repp et al., 2013) rhythms. In addition, Pantev and colleagues (2001) demonstrated that musicians show enhanced cortical representations for sounds of the same timbre as the instrument they are trained to play. Finally, instrument-specific anatomical plasticity has been observed. For example, Elbert and colleagues (1995) demonstrated that, relative to controls, string players have an over-representation of the fingers of the left hand in motor cortex.

An overwhelming majority of these studies examining differences between musicians and non-musicians have focused on classically trained players. However, there is reason to believe that large populations of performers, which have been overlooked in the literature, may also exhibit experience-dependent plasticity as a result of musical training. For example, like percussionists, professional disc jockeys (DJs) routinely perform complicated rhythm tasks including beat matching, whereby the tempo of one piece of music is altered in order to match the tempo of another piece being played simultaneously, using turntables. Additionally, they engage in beat sampling, whereby parts of a number of pieces (e.g., vocal lines, bass lines, hooks, etc.), that may differ significantly in their original tempi, are combined at a common tempo to create a novel piece of music. In each case, these practices place significant demands on a DJ's ability to perceive metrical levels within a musical piece. Moreover, they require impressive motor control to synchronize action to musical rhythm. These practices led Langois (1992) to conclude that DJs have "transformed the turntable from a record 'player' into a creative instrument, capable of combining different pieces of music in ways unimagined by the artists who originally recorded them." The experiments in the present study are the first to examine whether DJs benefit, in the same way as classically trained musicians, from a wealth of experience executing temporally demanding tasks.

The accurate perception of musical rhythm appears to involve not only brain areas involved in timing, but privileged connections between auditory and motor cortices; this may explain why listening to auditory rhythms makes people want to entrain their motor movements to the beat. Functional imaging studies have revealed that simply listening to a rhythmic stimulus activates areas in the motor cortex (e.g., Bengtsson et al., 2009; Chapin et al., 2010; Chen et al., 2008, 2009; Fujioka et al., 2012; Grahn & Brett, 2007). Furthermore, MEG studies indicate that

increases and decreases in induced oscillatory activity in the beta band (around 20 Hz) predict the onset timing of the next beat (Fujioka et al., 2012; Iversen et al., 2009). Interestingly, this activity spans auditory and motor regions, providing additional evidence for the critical role of the motor system in rhythm processing.

The interaction between auditory and motor cortices appears to be bidirectional; in both infants and adults, the timing of movements to an otherwise ambiguous rhythmic pattern influences the perception of an underlying beat (Phillips-Silver & Trainor, 2005, 2007). In addition, MEG responses from auditory cortex show that adults learn to perceive auditory melodies and rhythmic patterns better if learned in a sensorimotor context (i.e., when producing them) than if learned in a perceptual context alone (i.e., when asked to make discriminative judgments about them; Lappe et al., 2008, 2011). The current study examines the contribution of auditory-motor interactions to rhythm perception in DJs who may not produce music directly, but who have experience manipulating and matching previously recorded tracks. Moreover, it compares DJs to non-musicians and to percussionists who produce rhythmic sounds directly, through action.

Finally, the origins of the differences between musicians and non-musicians discussed above, and the extent to which they are the result of experience-based plasticity or genetic predisposition, remains an open question. However, music training typically involves a large amount of experience across a number of modalities (e.g., auditory, motor, visual, haptic), and the specialized processing in both auditory and motor regions of the brain is often presumed to be in large part the result of this specialized training (e.g., Herholz & Zatorre, 2012). The vast majority of studies on the effects of musical training compare adult musicians and non-musicians but, for the most part, the training took place long before the experimental testing and, therefore, the researchers could not control who engaged in musical training and who did not through random assignment. However, studies indicating instrument-specific effects (e.g., Elbert et al., 1995; Hinton & Rauscher, 2003; Pantev et al., 2001) are highly suggestive that the differences between musicians and non-musicians are due in large part to musical training. As well, studies of musical training in children using random assignment and/or longitudinal designs (e.g., Fujioka et al., 2006; Gerry et al., 2012; Schellenberg, 2004; Trainor et al., 2012) also suggest a significant role of experience in musician/non-musician differences.

If the turntable is the DJ's instrument, then the auditory-motor experience DJs accumulate while practicing their craft would be expected to lead to particularly good rhythm processing. In Experiment 1, we compare rhythm processing in DJs, percussionists, and non-musicians. In Experiment 2, we use a training paradigm to begin to address more directly the causal link between DJ experience and rhythm processing.

2. Experiment 1

Experiment 1 examined the abilities of professional DJs to behaviorally detect deviations from a repeating rhythmic pattern. Figure 1 shows the experimental paradigm. On each trial, participants were entrained to an auditory rhythm, asked to maintain a mental representation of that rhythm through a silent period, and to judge whether a final, target stimulus occurred on-time (as the first downbeat in the third measure in Fig. 1) or whether it occurred too early. Additionally, the role of movement in the maintenance of the mental representation of rhythm was examined.

2.1. Materials and Methods

2.1.1. Participants

Ten professional club DJs (all male; aged 31.0 +/− 2.9 years; 12.0 +/− 3.5 years of experience) were recruited from across North America to participate in this experiment with the help of documentary filmmaker Courtney James. Only three of these participants had any musical training on an instrument other than turntables (these three having received between 3 and 12 years of piano lessons during adolescence). DJs reported practicing an average of 10.8 hours per week, and while half of participants noted that they composed by ear, none reported having perfect pitch. In addition, ten percussionists matched for musical experience on their primary instrument (all male; aged 24.0 +/− 3.9 years; 12.7 +/− 4.3 years of experience) and ten age-matched controls (all male; aged 28.2 +/− 1.9 years) were recruited to participate. Best efforts were made to match the amount of non-percussion musical training in the percussionist group to the amount of training on instruments other than turntables in the DJ group; a *t*-test confirmed that no significant difference existed [$t(18) = 0.24$, $p = 0.8$]. No control subject reported any history of musical training. All experimental procedures were approved by the McMaster Research Ethics Board.

2.1.2. Stimuli and Design

The stimulus was a sequence of alternating downbeats and upbeats, with onset-to-onset of each beat being 200 ms (Fig. 1). The downbeat consisted of a 100 ms synthesized bass drum sound produced by GarageBand (Apple Inc., USA), presented at 70 dB(A). The upbeat was created by shifting the pitch of the downbeat upwards by four semitones, and was presented at 67 dB(A) at the position
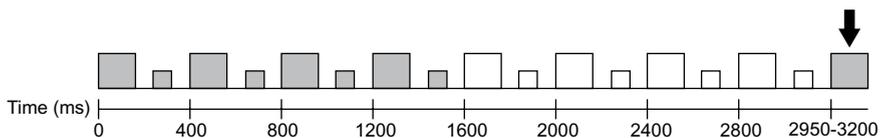
Figure 1. A representation of the stimulus sequence presented in Experiments 1 and 2. Large and small squares represent downbeats and upbeats, respectively. The target stimulus at the end of the sequence is denoted with an arrow. Participants entrained to the acoustic stimuli (grey boxes) and were asked to judge whether the target stimulus presented following a period of silence (white boxes) occurred on-time, or too early.

of the participant's head. The sequence consisted of four downbeat/upbeat pairs presented every 400 ms, followed by a silent period that lasted between 1350 and 1600 ms, followed by a single downbeat. This final, target stimulus occurred either on-time, as the first beat of the third measure after a 1600 ms silent period (3200 ms from sequence onset), or was temporally offset to occur 12.5% (3150 ms), 25% (3100 ms), 37.5% (3050 ms), 50% (3000 ms) or 62.5% (2950 ms) early, relative to the inter-downbeat interval.

2.1.3. *Experimental Procedure*

All participants were asked to fill out a survey outlining their history of musical training, language experience, relevant medical history, and general demographic information. Following this, participants were seated comfortably in the centre of a sound-attenuating room. Stimuli were presented by a program written in E-Prime (Psychology Software Tools, USA), running on a Dell computer (Audigy 2 Platinum sound card, Creative Labs, Singapore) through a loudspeaker (WestSun Jason Sound, JSIP63, Canada) located 1 m in front of them. Responses were recorded on a keypad with buttons labelled 'on-time' and 'early'.

There were two blocks of trials, the order of which was counterbalanced within each group of participants. In one block, participants were asked to sit still and move only to make their on-time/early discrimination. In the other block, participants were instructed that they were free to move as they normally would to help keep time, provided that movement did not produce an audible noise. Within each block, the order of trial-type was randomized with each of the five temporal offsets being presented 20 times, and the on-time condition being presented 100 times, for a total of 200 trials per block. At the end of each trial the program paused and waited for the participant to respond; a new trial was not initiated until a response to the previous trial was made. While this experiment was to some degree self-paced, the experiment typically lasted between 25 and 30 minutes.

2.2. *Results*

Table 1 shows the raw hit rates and false alarm rates at each temporal offset for all three groups, and across both movement conditions. Figure 2 shows the sensitivity of each of the three groups across each temporal offset for both the movement and no-movement conditions. In each case, the sensitivity (d') to each temporal offset was calculated to provide an unbiased estimate of performance. The metric d' is calculated as the difference between the z-transforms of the hit and false alarm rates [$d'=z(H)-z(F)$]. In some cases, participants correctly identified all of the early stimuli for a particular temporal offset. Because a hit rate of 100% results in an infinite value of d', these values were replaced with a value of $(1-0.5/n)$, where n is the number of signal trials (Macmillan & Kaplan, 1985). The temporal offset of 62.5% appeared to represent ceiling-level performance for some groups in some conditions. Consequently, these offsets were eliminated from statistical analysis. A repeated-measures analysis of variance (ANOVA) was conducted with the remaining temporal offsets (12.5, 25, 37.5, and 50%) and movement condition (movement, no movement) as within-subject factors, and group (DJs, percussionists, controls) as a between-subjects factor. This analysis revealed significant interactions between movement condition and temporal offset [$F(2.14, 57.90) = 6.14$, $p = 0.003$, $\eta_p^2 = 0.185$] and between temporal offset and group [$F(4.29, 57.90) = 2.80$, $p = 0.031$, $\eta_p^2 = 0.172$]. To explore

Table 1.

Percent correct performance and false alarm rates (FA) with standard errors by group for each temporal offset

		Temporal Offset					
		12.5 %	25%	37.5%	50%	62.5%	FA
DJ	move	38 ± 7.7	59 ± 8.2	82 ± 4.6	93 ± 1.5	88 ± 3.4	14 ± 3.1
	no move	39 ± 5.6	50 ± 5.8	70 ± 3.1	82 ± 4.8	91 ± 3.1	23 ± 5.6
Perc	move	48 ± 10.2	70 ± 7.9	90 ± 4.6	92 ± 2.6	98 ± 1.7	19 ± 6.8
	no move	56 ± 7.2	67 ± 7.6	80 ± 7.8	87 ± 7.5	88 ± 6.7	35 ± 7.1
Control	move	34 ± 5.1	53 ± 7.1	67 ± 7.4	72 ± 7.2	84 ± 6.3	21 ± 3.6
	no move	36 ± 6.7	45 ± 6.0	52 ± 7.5	64 ± 7.7	85 ± 3.3	22 ± 2.9
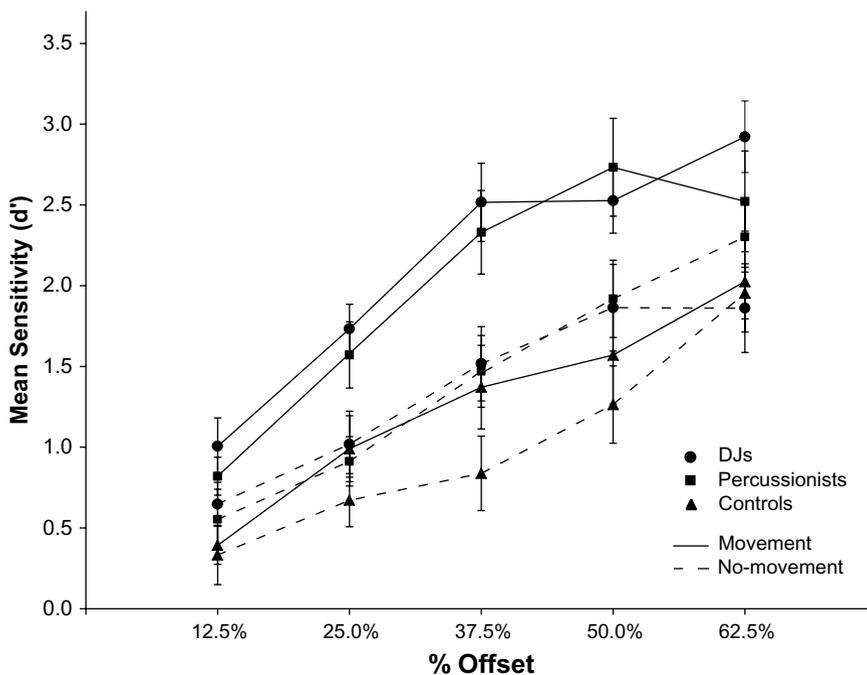
Figure 2. Mean sensitivity (d') of participants in Experiment 1 to different temporal offsets in a rhythmic sequence. Sensitivity measures are presented for DJs (circles), percussionists (squares), and control subjects (triangles), in the movement (solid) and no-movement (dashed) conditions.

these interactions, separate repeated-measures ANOVAs were carried out at each temporal offset with movement condition (movement, no movement) as a within-subjects factor, and group (DJs, percussionists, controls) as a between-subjects factor. These analyses revealed that across all three groups, participants performed significantly better when allowed to move than when asked to remain still for the 25% [$F(1, 27) = 25.13$, $p < 0.001$, $\eta_p^2 = 0.482$], 37.5% [$F(1, 27) = 60.49$, $p < 0.001$, $\eta_p^2 = 0.69$], and 50% offsets [$F(1, 27) = 17.39$, $p < 0.001$, $\eta_p^2 = 0.392$]. While movement characteristics were not directly recorded in the current experiment, we can report anecdotally that movement across all groups typically consisted of head bobbing and/or silent foot tapping, with no noticeable differences between groups. Although there was a trend, performance at the 12.5% offset did not differ significantly between movement conditions [$F(1, 27) = 3.90$, $p = 0.059$, $\eta_p^2 = 0.126$], which probably reflects the near floor performance level at this offset. In addition, significant group differences were observed at all temporal offsets. These effects were examined further using Fisher's LSD tests. Percussionists were found to outperform control subjects across all temporal offsets (all ps < 0.05), while DJs outperformed controls at both the 37.5% [$t(27) = 2.47$, $p = 0.02$] and 50% [$t(27) = 2.98$, $p = 0.006$] temporal offsets. Percussionists and DJs were not significantly different at any temporal offset tested.

3. Experiment 2

Experiment 1 demonstrated that DJs perform similarly to percussionists, and that both groups outperform controls on a rhythm perception task at multiple temporal offsets. While the maximum and minimum offsets employed in Experiment 1 proved to result in ceiling- and floor-level performance, respectively, both the DJs and percussionists outperformed controls at intermediary offsets. However, the question remained whether this advantage was, in fact, due to their experience or to pre-existing enhanced rhythmic ability. Experiment 2 sought to answer this question by determining whether short-term training on rhythmic tasks similar to those employed by professional DJs would improve the performance of naïve participants.

3.1. Materials and Methods

3.1.1. Participants
A total of 28 participants with no prior DJ experience were split into two groups. One group ($N = 14$) received training in the rhythmic skills employed by DJs, while the remaining participants ($N = 14$) served as a control group. All experimental procedures were approved by the McMaster Research Ethics Board.

3.1.2. Stimuli and Design
The stimuli and testing procedure were identical to those of Experiment 1 (see Section 2.1.2.).

3.1.3. Experimental Procedure

Each of the participants in the training group completed the behavioral task exactly as described in Experiment 1 to provide a baseline measure of rhythm perception. This group then received 20 hours of hands-on, group instruction in the rhythmic skills employed by professional DJs over five consecutive days. The training program began with lessons in beat finding and coordinating movement to auditory rhythms, followed by practice in beat matching and blending. Thus, the training was multimodal, combining focused listening with motor activities executed on turntables. By the end of the training period, participants were able to create continuous musical 'sets' by manually equating the tempi of five different musical pieces and coordinating the onset of tracks to maintain a continuous beat. While participants varied somewhat on their proficiency at this exercise, this variability was not quantified during training. All training was provided by an instructor from the Scratch Lab DJ Institute (Toronto, Ontario). A soon as possible following this training period, the participants completed a follow-up behavioral task identical to the baseline task (mean time between measures was 10.40 ± 1.69 days, as in some cases baseline measures were taken several days before the onset of training). The control group also completed the baseline and follow-up behavioral tasks, but did not receive any training in between (mean time between measures = 10.00 ± 1.51 days).

3.2. Results

Figure 3 shows the mean accuracy at baseline and follow-up for both the training (panel A) and control (panel B) groups. In order to provide an unbiased estimate of performance, the sensitivity (d′) to each temporal offset was determined for each participant. As in Experiment 1, performance approached ceiling-level when the target stimulus was temporally offset by 62.5%. Consequently, this offset was eliminated from statistical analysis. In order to address potential outliers, the most and least sensitive participant in each group across the remaining temporal offsets was removed from statistical analysis (Brown & Forsythe, 1974; Field, 2013), leaving a total of 12 participants in each group. Shapiro–Wilk tests confirmed that the resulting trimmed data sets were normally distributed (all ps > 0.05). A repeated-measures ANOVA was conducted with temporal offset (12.5, 25, 37.5, and 50%), movement condition (movement, no movement), and time of measure (baseline, follow-up) as within-subject factors, and group (training, control) as a between-subjects factor.

The improvement in performance between baseline and follow-up measures across experimental conditions was larger for participants who received training (an increase in d′ sensitivity of 0.35 across conditions) than for control subjects (an increase of 0.10). This difference approached conventional levels of statistical significance [$F(1, 22) = 3.361$, $p = 0.08$, $\eta_p^2 = 0.133$]. The failure to reach the 0.05 level was likely due to the relatively small sample size available for the current study, combined with variability across participants and a significant increase in performance across both groups between the baseline and follow-up measures [$F(1, 22) = 11.26$, $p = 0.003$, $\eta_p^2 = 0.338$]. It is important to note that, despite these challenges, a moderate effect size related to training was observed in the current experiment ($\eta_p^2 = 0.133$), and this effect approached the value considered by Cohen (1969) to reflect a large effect ($\eta_p^2 = 0.138$). The ANOVA also revealed a
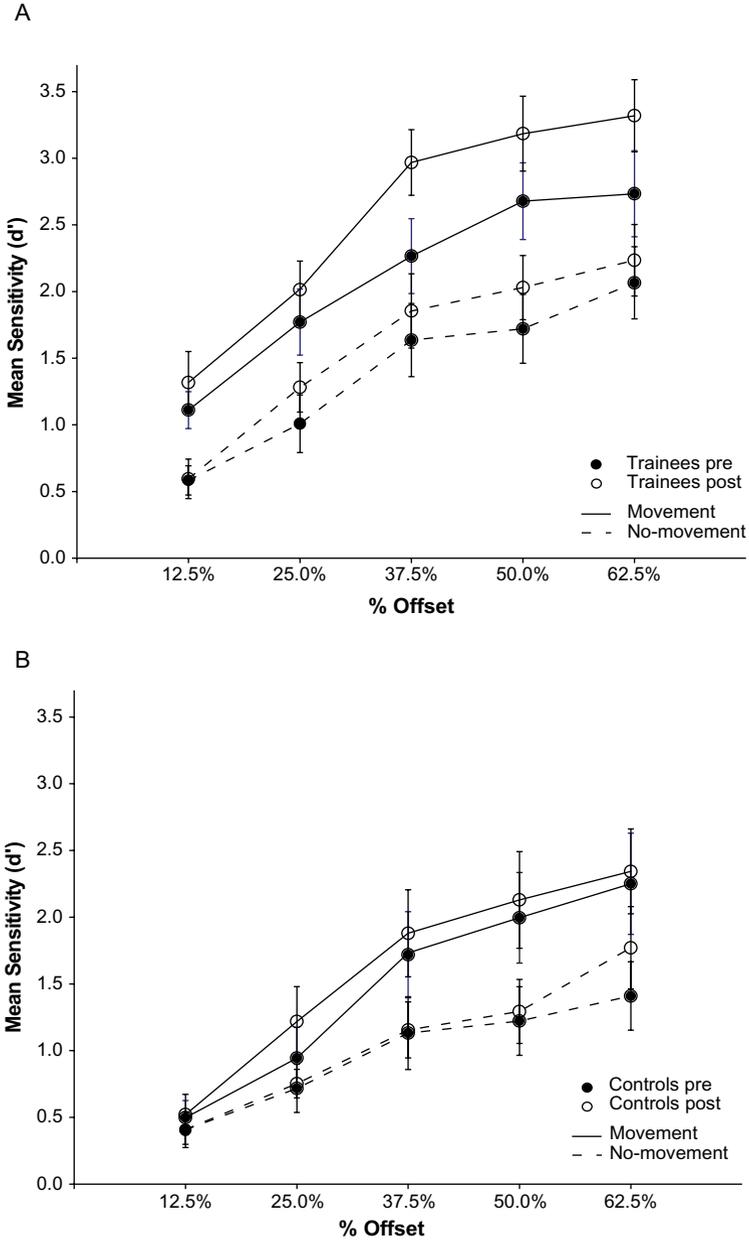
Figure 3. Mean sensitivity (d') of participants in Experiment 2 to different temporal offsets in a rhythmic sequence. Panel A shows the sensitivity of participants before (filled symbols) and after (open symbols) receiving DJ training. Panel B shows the sensitivity of control subjects at baseline (filled symbols) and follow-up (open symbols) measures. In both panels, data are presented from the movement (solid lines) and no-movement (dashed lines) conditions.

significant interaction between group and movement condition [$F(1, 22) = 5.16$, $p = 0.03$, $\eta_p^2 = 0.190$], with the group who received training outperforming the control group across experimental conditions only when they were allowed to move [$F(1, 22) = 6.47$, $p = 0.02$, $\eta_p^2 = 0.227$]. It is worth noting that although the ANOVA did not reveal a significant difference in baseline performance between groups, those participants who received training did show somewhat better baseline performance, at least at some temporal offsets (Figure 3).

4. Discussion

4.1. *Experience-Dependent Functional Advantages in DJs*

Experiment 1 demonstrated that professional DJs outperform age-matched control subjects when asked to detect deviations in a rhythmic pattern; in fact, no statistically significant difference was observed between the performance of DJs and percussionists matched for duration of experience. Participants in the present experiment were required to imagine the continuation of a beat pattern and determine whether a probe stimulus occurred on or off the beat. The demands of this task are similar to continuation tapping paradigms in which participants tap in synchrony with a metronome, and are then asked to continue tapping at that same rate in the absence of the external stimulus. In continuation tapping studies, when the cue from the metronome is removed, an accelerated rate of tapping is typically observed in non-musicians across a wide range of frequencies (e.g., Flach, 2005), while those with musical training are much less affected (Repp, 2010; Repp & Doggett, 2007). In each trial of the current paradigm, participants were presented with a sequence of four downbeats and four upbeats on which to base a mental representation of the rhythm they were asked to maintain through the period of silence. While this represents only a brief sequence upon which to form a mental representation of rhythm, previous work has demonstrated that rhythmic entrainment can occur to a train of as few as three stimuli (Fraisse, 1966).

   The musician advantage in continuation tapping paradigms, as well as that demonstrated by DJs and percussionists in Experiment 1 of the current study, likely reflects a combination of better thresholds for detecting small-scale differences in time intervals (e.g., Hinton & Rauscher, 2003), and a superior ability to maintain an accurate representation of rhythm through a period of silence (see Wing & Kristofferson, 1973, for a possible model). While experience-dependent plasticity can result from simple exposure (e.g., listening), functional changes of the type described herein appear to be greatly enhanced by sensorimotor-auditory experience such as those involved in musical performance (e.g., Lappe et al., 2008, 2011; Stoklasa et al., 2012). When examining the raw data from DJs and

percussionists (Table 1), it is evident that the freedom to move results in an increase in the identification of mistimed stimuli and concurrent decrease in false alarm rate. Interestingly, the effect of movement demonstrated in control subjects appears to be the result of an increased hit rate in the absence of any change in the rate of false alarms. The finding that DJs show similar advantages as percussionists suggests that the movements that they need to make in order to perform their art, such as beat matching between tracks, may be critical to their enhanced perceptual abilities as compared to controls.

The ability to maintain an accurate auditory memory of a previously established rhythm through a silent period places demands on processes associated with executive function. Musical training that involves periods of focused instruction followed by considerable practice engages these same processes, as a great deal of attention and control needs be directed toward the task (see Corrigall et al., 2013; Schellenberg & Weiss, 2013; Trainor & Corrigall, 2010; Trainor & Hannon, 2013, for discussions). This explicit training leads to enhanced acoustic encoding across a number of auditory music and language tasks (e.g., Kraus & Chandrasekaran, 2010; Parberry-Clark et al., 2011; Patel, 2011). However, these gains are not limited to the auditory domain; functional changes in related modalities occur as a result of musical training, such as improvements in verbal and tonal working memory (Schulze et al., 2010), and are often explained using near transfer mechanisms between associated skills (e.g., Schellenberg, 2004). Thus, systems subserving executive functions are engaged through musical training, and may lead directly to benefits in auditory processing, as well as indirectly to enhanced memory for rhythmic sequences and time intervals such as those demonstrated by DJs and percussionists in the present study.

Studies comparing musician and non-musician adults are typically unable to address the question of whether musical experience caused any differences measured, or whether these differences were preexisting and contributed to the musicians' decision to train musically. In Experiment 2, we sought to determine whether the advantages demonstrated by DJs could indeed arise from experience. After one week of DJ training, participants' accuracy on a behavioral rhythm task increased, with the greater pre-post difference in DJs compared to controls approaching conventional levels of significance ($p = 0.08$) and a moderate effect size. It is likely that a longer training period would have led to a more robust effect. For example, evidence of cortical plasticity has been demonstrated following two weeks of sensorimotor training for both tonal (Lappe et al., 2008) and rhythmic (Lappe et al., 2011) stimuli. We expect that extending the period of training in Experiment 2 would have resulted in a larger group difference, as trainees gained further experience and consolidated expertise with complex rhythmic tasks, while any test/retest gains experienced by those participants receiving no training would be further attenuated by an increased time between baseline and follow-up testing. Unfortunately, circumstances dictated that the training period in the

current study be limited to five days, and thus the impact of an extended training period remain speculative at this point. In any case, the results reported here are suggestive of a causal link between DJ training and the ability to accurately maintain an auditory beat in memory.

4.2. *The Role of Movement*

For all groups of participants in Experiment 1 and Experiment 2, allowing movement during the behavioral task improved performance in comparison to when movement was not permitted. This is not surprising, as a number of neuroimaging studies have demonstrated that the perception of a musical rhythm results in neural activity in areas typically associated with the motor system, including premotor cortex, supplementary motor areas, cerebellum, and basal ganglia (e.g., Chen et al., 2008; Fujioka et al., 2012; Grahn & Brett, 2007; Schubotz & von Cramon, 2001). Moreover, the maintenance of an internal representation of rhythm may involve a widely distributed network comprised of sensory, motor, and higher-level cognitive areas of the brain (see Grahn, 2012, for a review). Thus, it is probable that motor activity associated with moving to a beat combines with auditory activity related to the perception of the auditory stimuli to create a stronger mental representation of the rhythm, which in turn leads to increased performance in the movement condition. This combined effect likely underlies the fact that movement can influence the way in which otherwise ambiguous rhythms are perceived (Phillips-Silver & Trainor, 2005, 2007) and that participants can more easily identify deviations from an isochronous rhythm when allowed to tap along with that rhythm (Manning & Schutz, 2013). Thus, engaging the motor system to entrain to an external acoustic stimulus serves to reinforce auditory perception and improve performance in this task.

Interestingly, although performance in Experiment 1 was overall superior for DJs and percussionists compared to control participants, all three groups benefited to a similar degree when allowed to move. There are several possible explanations for this finding. Perhaps the benefit derived from engaging the motor system during a rhythm perception task, at least for simple rhythms as in the present study, is universal to both trained and untrained listeners, and not dependant on experience. This idea is supported by studies demonstrating the effects of engaging the motor system on rhythm perception in infancy (Phillips-Silver & Trainor, 2005). Still, other studies have demonstrated that the coupling between auditory and motor cortices is strengthened following musical training (Grahn & Rowe, 2009; James et al., 2012). An alternative explanation is that the type of movement allowed during behavioural testing in the current experiments was not sufficient, or was too dissimilar to performance-related movements to be of benefit (participants were told they could move any way they chose, but were required to remain seated and to avoid making any noise). In any case, the important finding is that movement helped all participants to maintain an auditory beat in memory.

5. Conclusions

Collectively, the results presented here demonstrate that DJs are superior to non-musician controls and, indeed, as good as trained percussionists at accurately maintaining a rhythm in working memory as measured by their detection of whether a probe tone is on or off the beat. Moreover, the results of the training study presented in Experiment 2 suggest that this advantage is at least in part the result of dedicated training on complex rhythmic tasks practiced by DJs. Across trained and untrained groups, performance was significantly better when participants were allowed to move, highlighting the importance of the strong coupling between the auditory and motor systems for rhythm perception. To date, traditionally defined musicians have provided a useful model of structural and functional neural plasticity across a number of domains. The current study adds to this literature, and suggests that the field would benefit from expanding beyond traditional, orchestral instrumentalists to include nontraditional musicians, such as DJs, who demonstrate similar experience-dependent enhancements.

References

Abdul-Kareem, I. A., Stancak, A., Parkes, L. M., & Sluming, V. (2011). Increased gray matter volume of left pars opercularis in male orchestral musicians correlate positively with years of musical performance. *J. Magn. Reson. Imaging*, *33*, 24–32.

Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. *Brain Cogn.*, *48*, 66–79.

Bengtsson, S. L., Ullén, F., Ehrsson, H. H., Hashimoto, T., Kito, T., Naito, E., Forssberg, H., & Sadato, N. (2009). Listening to rhythms activates motor and premotor cortices. *Cortex*, *45*, 62–71.

Brown, M. B., & Forsythe, A. B. (1974). Robust tests for the equality of variances. J. *Am. Stat. Assoc.*, *69*, 364–367.

Buhusi, C., & Meck, W. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nat. Rev. Neurol.*, *6*, 755–765.

Chapin, H. L., Zanto, T., Jantzen, K. J., Kelso, S. J. A., Steinberg, F., & Large, E. W. (2010). Neural responses to complex auditory rhythms: The role of attending. *Front. Psychol.*, *1*, 224.

Chen, Y., Repp, B. H., & Patel, A. D. (2002). Spectral decomposition of variability in synchronization and continuation tapping: Comparisons between auditory and visual pacing and feedback conditions. *Hum. Mov. Sci.*, *21*, 515–532.

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Listening to musical rhythms recruits motor regions of the brain. *Cereb. Cortex*, *18*, 2844–2854.

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2009). The role of auditory and premotor cortex in sensorimotor transformations. *Ann. N. Y. Acad. Sci.*, *1169*, 15–34.

Cohen, J. (1969). *Statistical power analysis for the behavioural sciences*. New York, NY, USA: Academic Press.

Corrigall, K. A., Schellenberg, E. G., & Misura, N. M. (2013). Music training, cognition, and personality. *Front. Psychol.*, *4*, 222.

Coull, J. T., Cheng, R.-K., & Meck, W. H. (2010). Neuroanatomical and neurochemical substrates of timing. *Neuropsychopharmacology*, *36*, 3–25.

Delignières, D., Lemoine, L., & Torre, K. (2004). Time intervals production in tapping and oscillatory motion. *Hum. Mov. Sci.*, *23*, 87–103.

Doya, K. (1999). What are the computations of the cerebellum, the basal ganglia, and the cerebral cortex? *Neural Netw.*, *12*, 961–974.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307.

Field, A. (2013). *Discovering statistics using IBM SPSS statistics*, 4th ed. Sussex, UK: SAGE Publications Ltd.

Flach, R. (2005). The transition from synchronization to continuation. *Hum. Mov. Sci.*, *24*, 465–483.

Fraisse, P. (1966). L'anticipation de stimulus rhythmiques: Vitesse d'établissement et précision de la synchronization [Anticipation of rhythmic stimuli: Rate of establishment and precision of synchronization]. *Annee Psychol.*, *66*, 15–36.

Fujioka, T., Ross, B., Kakigi, R., Pantev, C., & Trainor, L. J. (2006). One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain*, *129*, 2593–2608.

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *J. Neurosci.*, *32*, 1791–1802.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *J. Neurosci.*, *23*, 9240–9245.

Gerry, D., Unrau, A., & Trainor, L. J. (2012). Active music classes in infancy enhance musical, communicative and social development. *Dev. Sci.*, *15*, 398–407.

Grahn, J. A. (2012). Neural mechanisms of rhythm perception: Current findings and future perspectives. *Top. Cogn. Sci.*, *4*, 585–606.

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *J. Cogn. Neurosci.*, *19*, 893–906.

Grahn, J. A., & Rowe, J. B. (2009). Feeling the beat: Premotor and striatal interactions in musicians and nonmusicians during beat perception. *J. Neurosci.*, *29*, 7540–7548.

Grube, M., Cooper, F. E., Chinnery, P. F., & Griffiths, T. D. (2010). Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration. *Proc. Natl Acad. Sci.*, *107*, 11597–11601.

Halwani, G. F., Loui, P., Ruber, T., & Schlaug, G. (2011). Effects of practice and experience on the arcuate fasciculus: Comparing singers, instrumentalists, and non-musicians. *Front. Psych.*, *2*, 39–47.

Herholz, S. C., & Zatorre, R. J. (2012). Musical training as a framework for brain plasticity: Behavior, function, and structure. *Neuron*, *76*, 486–502.

Hinton, S. C., & Rauscher, F. H. (2003). Type of music training selectively influences perceptual processing. In R. Kopiez, A. C. Lehmann, I. Wolther & C. Wolf (Eds), *Proceedings of the 5th Triennial ESCOM conference* (pp. 89–92). Hanover, Germany.

Iversen, J. R., Repp, B. H., & Patel, A. D. (2009). Top-down control of rhythm perception modulates early auditory responses. *Ann. N. Y. Acad. Sci.*, *1169*, 58–73.

James, C. E., Michel, C. M., Britz, J., Vuilleumier, P., & Hauert, C.-A. (2012). Rhythm evokes action: Early processing of metric deviances in expressive music by experts and laymen revealed by ERP source imaging. *Hum. Brain. Map.*, *33*, 2751–2767.

Kraus, N., & Chandrasekaran, B. (2010). Music training for the development of auditory skills. *Nat. Rev. Neurosci.*, *11*, 599–605.

Krause, V., Pollok, B., & Schnitzler, A. (2010). Perception in action: The impact of sensory information on sensorimotor synchronization in musicians and non-musicians. *Acta Psychol.*, *133*, 28–37.

Langois, T. (1992). Can you feel it? DJs and house music culture in the UK. *Pop Music*, *11*, 229–238.

Lappe, C., Herholz, S. C., Trainor, N. J., & Pantev, C. (2008). Cortical plasticity induced by short-term unimodal and multimodal musical training. *J. Neurosci.*, *28*, 9632–9639.

Lappe, C., Trainor, N. J., Herholz, S. C., & Pantev, C. (2011). Cortical plasticity induced by short-term multimodal musical rhythm training. *PLoS ONE*, *6*, e21493. doi:10.1371/journal.pone.0021493.

Lewis, P., & Miall, R. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Curr. Opin. Neurobiol.*, *13*, 250–255.

Macmillan, N. A., & Kaplan, H. L. (1985). Detection theory analysis of group data: Estimating sensitivity from average hit and false-alarm rates. *Psychol. Bull.*, *98*, 185–199.

Manning, F., & Schutz, M. (2013). "Moving to the beat" improves timing perception. *Psychon. Bull. Rev.*, *20*, 1133–1139.

Meyer, M., Elmer, S., & Jäncke, L. (2012). Musical expertise induces neuroplasticity of the planum temporale. *Ann. N. Y. Acad. Sci.*, *1252*, 116–123.

Pantev, C., Roberts, L. E., Schulz, M., Engelien, A., & Ross, B. (2001). Timbre-specific enhancement of auditory cortical representations in musicians. *Neuroreport*, *12*, 169–174.

Parberry-Clark, A., Strait, D. L., & Kraus, N. (2011). Context-dependent encoding in the auditory brainstem subserves enhanced speech-in-noise perception in humans. *Neuropsychologia*, *49*, 3338–3345.

Patel, A. D. (2011). Why would musical training benefit the neural encoding of speech? The OPERA hypothesis. *Front. Psychol.*, *2*, 142.

Phillips-Silver, J., & Trainor, L. J. (2005). Feeling the beat in music: Movement influences rhythm perception in infants. *Science*, *308*, 1430.

Phillips-Silver, J., & Trainor, L. J. (2007). Hearing what the body feels: Auditory encoding of rhythmic movement. *Cognition*, *105*, 533–546.

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychon. Bull. Rev.*, *12*, 969–992.

Repp, B. H., (2010). Sensorimotor synchronization and perception of timing: Effects of music training and task experience. *Hum. Mov. Sci.*, *29*, 200–213.

Repp, B. H., & Doggett, R. (2007). Tapping to a very slow beat: A comparison of musicians and non-musicians. *Music Percept.*, *24*, 367–376.

Repp, B. H., & Su, Y.-H. (2013). Sensorimotor synchronization: A review of recent research (2006–2012). *Psychon. Bull. Rev.*, *20*, 403–452.

Repp, B. H., London, J., & Keller, P. E. (2013). Systematic distortions in musicians' reproduction of cyclic three-interval rhythms. *Music Percept.*, *30*, 291–305.

Schellenberg, E. G. (2004). Music lessons enhance IQ. *Psych. Sci.*, *15*, 511–514.

Schellenberg, E. G., & Weiss, M. W. (2013). Music and cognitive abilities. In D. Deutsch (Ed.), *The psychology of music*, 3rd ed. (pp. 499–550). Amsterdam, Netherlands: Elsevier.

Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat. Neurosci.*, *5*, 688–694.

Schubotz, R. I., & von Cramon, D. Y. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cereb. Cortex*, *11*, 210–222.

Schulze, K., Zysset, S., Mueller, K., Friederici, A. D., & Koelsch, S. (2010). Neuroarchitecture of verbal and tonal working memory in nonmusicians and musicians. *Hum. Brain Map.*, *32*, 771–783.

Snyder, J. S., Hannon, E. E., Large, E. W., & Christiansen, M. H. (2006). Continuation tapping to complex meters. *Music Percept.*, *24*, 135–146.

Spencer, R. M. C., Zelaznik, H. N., Diedrichsen, J., & Ivry, R. B. (2003). Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. *Science*, *300*, 1437–1439.

Spencer, R. M. C., Ivry, R. B., & Zelaznik, H. N. (2005). Role of the cerebellum in movements: Control of timing or movement transitions? *Exp. Brain Res.*, *161*, 383–396.

Steele, C., Bailey, J. A., Zatorre, R. J., & Penhune, V. B. (2013). Early musical training and white-matter plasticity in the corpus callosum: Evidence for a sensitive period. *J. Neurosci.*, *33*, 1282–1290.

Stoklasa, J., Liebermann, C., & Fischinger, T. (2012). Timing and synchronization of professional musicians: A comparison between orchestral brass and string players. Paper presented at the 12th International Conference on Music Perception and Cognition. Thessaloniki, Greece.

Teki, S., Grube, M., Kumar, S., & Griffiths, T. D. (2011). Distinct neural substrates of duration-based and beat-based auditory timing. *J. Neurosci.*, *31*, 3805–3812.

Teki, S., Grube, M., & Griffiths, T. D. (2012). A unified model of time perception accounts for duration-based and beat-based timing mechanisms. *Front. Int. Neurosci.*, *5*, 90.

Trainor, L. J., & Corrigall, K. A. (2010). Music acquisition and effects of musical experience. In M. Riess-Jones & R. R. Fay (Eds), *Springer handbook of auditory research: Music perception* (pp. 89–128). Heidelberg, Germany: Springer.

Trainor, L. J., & Hannon, E. E. (2013). Musical development. In D. Deutsch (Ed.), *The psychology of music*, 3rd ed. (pp. 423–498). Amderdam, Netherlands: Elsevier.

Trainor, L. J., Marie, C., Gerry, D., Whiskin, E., & Unrau, A. (2012). Becoming musically encultured: Effects of music classes for infants on brain and behaviour. *Ann. N. Y. Acad. Sci.*, *1252*, 129–138.

Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010). The image of time: A voxel-wise meta-analysis. *Neuroimage*, *49*, 1728–1740.

Wing, A. M., & Kristofferson, A. B. (1973). Response delays in the timing of discrete motor responses. *Percept. Psychophys.*, *14*, 5–12.