Published in final edited form as:

Exp Brain Res. 2014 April ; 232(4): 1207–1218. doi:10.1007/s00221-014-3837-9.

Auditory-motor integration of subliminal phase shifts in tapping: Better than auditory discrimination would predict

Florian A. Kagerer*,

Department of Kinesiology / Neuroscience Program Michigan State University, East Lansing, MI 48824

Priya Viswanathan,

Department of Physical Therapy and Rehabilitation Science University of Maryland School of Medicine, Baltimore, MD 21201

Jose L. Contreras-Vidal, and

Laboratory for Noninvasive Brain-Machine Interface Systems Department of Electrical & Computer Engineering University of Houston, Houston, TX 77204-4005

Jill Whittall

Department of Physical Therapy and Rehabilitation Science University of Maryland School of Medicine, Baltimore, MD 21201

Abstract

Unilateral tapping studies have shown that adults adjust to both perceptible and subliminal changes in phase or frequency. This study focuses on the phase responses to abrupt/perceptible and gradual/subliminal changes in auditory-motor relations during alternating bilateral tapping. We investigated these responses in participants with and without good perceptual acuity as determined by an auditory threshold test. Non-musician adults (9 per group) alternately tapped their index fingers in synchrony with auditory cues set at a frequency of 1.4 Hz. Both groups modulated their responses (with no after-effects) to perceptible and to subliminal changes as low as a 5° change in phase. The high threshold participants were more variable than the adults with low threshold in their responses in the gradual condition set ($p=0.05$). Both groups demonstrated a synchronization asymmetry between dominant and non-dominant hands associated with the abrupt condition and the later blocks of the gradual condition. Our findings extend previous work in unilateral tapping and suggest (1) no relationship between a discrimination threshold and perceptible auditory-motor integration and (2) a noisier subcortical circuitry in those with higher thresholds.

Keywords

sensory-motor synchronization; modulation; bilateral finger tapping; auditory perceptual thresholds; subliminal change

Bimanual finger tapping to an external cue is a highly specialized motor skill where only minimal inertial properties need to be managed and where spatial accuracy requirements are low. This allows the experimenter to study the relationship between sensory information and motor response without the constraints of large inertial forces and visuo-motor targeting being imposed.

*Correspondence: F. A. Kagerer, Department of Kinesiology, Michigan State University, East Lansing, MI 48824, fkagerer@msu.edu.

An intriguing finding in unilateral tapping studies is that participants adjust their motor response even if the changes in an auditory stimulus sequence are subliminal, i.e. not consciously perceived by an individual. For example, randomized phase changes of different magnitudes (unknown to the subject) were introduced in a finger tapping task and participants were found to apply different strategies with small (10–20 ms or 2–4% respectively) and large phase changes (50 ms or 10%) in inter-stimulus intervals of 500ms (Thaut et al. 1998). Interestingly, Thaut and colleagues observed immediate response corrections to the small phase changes that should be difficult or impossible to detect by participants. A follow-up study using magnetoencephalography indicated a discriminatory capacity of the auditory cortex for interstimulus interval changes as small as 10 ms, despite participants not having conscious access to these small changes. (Tecchio et al., 2000). Work by Repp investigated whether these small, subliminal changes are made use of in controlling the timing of motor behavior. He demonstrated that, in an isochronous auditory sequence, subliminal changes in interval duration were rapidly compensated for when the changes were between 0.8–2% of a 500ms inter-stimulus interval (corresponding to a change of 4–10ms) (Repp 2000). A subsequent series of experiments (Repp 2001a; Repp 2001b; Repp 2002a; Repp 2002b; Thaut and Kenyon 2003) have confirmed the earlier basic finding that auditory timing information is accessible to the auditory/motor system at levels below conscious perception. We expand this line of research in two main aspects.

First, we determine whether adjustments will also occur in bilateral tapping where the task complexity of two-finger tapping may influence the results. In the context of previous findings that auditory information can guide unilateral finger tapping without being consciously perceived (Repp 2000; 2001a; 2001b; 2002a; 2002b), our primary aim was to examine the response modulation to auditory beats that changed their phase relationship between hands in an alternating tapping task, either in an abrupt or gradual way, the former of which was consciously perceived, the latter not. The goal was to examine auditory-motor coupling by assessing concomitant changes in motor responses when synchronizing bilateral finger taps to auditory cues that were either perceptibly or subliminally changed in their phase relationship on a trial-to-trial basis. That is, the phase of the auditory cues was changed at the beginning of each trial. We also expanded the subliminal paradigm by examining the influence of incremental changes in auditory phase providing a gradual/subliminal condition in contrast to one that was readily, and hence abruptly perceived. In this way, we could examine whether the accumulation of a phase difference was needed for a motor response to occur.

Variables of interest included the modulation and the speed of modulation defined by the between-finger phase relationship and trial/block number respectively and the stability of the modulation defined by the variability of the phase per trial. We predicted that the abrupt condition would result in an immediate phase change while the gradual condition would result in a phase change at some subliminal level. Based on the finding of decreased stability at intermediate phase relationships (Yamanishi et al. 1980), we predicted increased variability in the abrupt condition compared to baseline, which was the stable antiphase condition (Whitall et al. 1999; Forrester and Whitall 2000). As the gradual condition consisted of subliminal changes, we hypothesized that an increase in trial variability would not occur until the incremental change became perceptible even though a motor response would occur before then. We also assessed the synchrony (accuracy) of the bilateral finger modulation with respect to the signal and the individual synchrony between signal and finger to further characterize the nature of the modulation in these two conditions.

The second major extension of the previous work in unilateral tapping is related to the idea that one's ability to perceive a particular phase change is related to the ability to adjust to the perceptible/abrupt condition since the phase change needs to be perceptible in the first place.

We hypothesized that those with a lower threshold (detecting a smaller change of rhythm) might adjust more quickly and more accurately to a perceptible change. Whether individuals with a low threshold would also adjust more quickly to subliminal/gradual phase changes was an open question. In most of the previously referenced studies, participants have been musicians who are known to have very sharp perceptual acuity. In several of these studies, either no assessment of acuity was taken (Thaut et al. 1998; Repp 2000; 2001a; Thaut and Kenyon 2003) or participants were known to have an acuity of 20ms (Repp 2002a; Repp 2002b). In the present study, we attempted to relate perceptual acuity to motor response, and therefore measured the auditory discrimination of phase change in our participants prior to the experiment and recruited only adults without extensive musical training. This population, we reasoned, would have a larger range of auditory phase discrimination ability that would allow grouping of high and low thresholds as well as provide a more appropriate comparison control for future studies addressing the development of auditory-motor coupling.

MATERIALS AND METHODS

Participants

Eighteen healthy adults, (nine males, nine females, mean age 24.46 ± 2.75 years) participated in the study; all were non-musicians with less than six months of instrumental training. An additional six participants tested had to be excluded due to problems with corrupted data. The experiments were approved by the University of Maryland Institutional Review Board, and all participants provided informed consent. Hand preferences was established by a modified Edinburgh Inventory (Oldfield 1971), consisting of six questions designed to test for hand preference in activities of daily living. Sixteen participants were right-handed, one male and one female were left-handed.

Procedure

Participants were seated comfortably at a table, facing a custom-designed plexiglas tapping board with arm extensions to support both forearms and hands. The arms were strapped at the forearm and the distal portion of the metacarpals to restrict motion in the metacarpophalangeal joints. Both index fingers were splinted by attaching Q-tips to the lateral border of fingers to ensure extension at the interphalangeal joints of fingers. Finger tapping was measured with an electromagnetic tracking system (FOB, Burlington VA), which provided 3D position data of the tapping fingers via small sensors attached to the tapping fingers, at a sampling rate of 100 Hz per hand. The data were collected and stored through the Motion Monitor™ system; subsequent off-line analysis was done using custom-built software.

Stimuli

A custom-made stimulus generator provided auditory signals at a frequency of 1.4Hz (based on previous studies), which were fed to headphones at a comfortable loudness that all participants stated they could hear clearly. While the timing of the beats to one headphone speaker was always kept unchanged (static), the timing could be changed in the other speaker (dynamic). The headphone speaker providing the dynamic stimuli was always placed on the ear ipsilateral to the dominant hand. The timing of the beats in the dynamic headphone could be manipulated in order to produce different phase relationships between the beats from the two speakers. An 180° phase relationship thus resulted in a stimulus pattern where the beats alternated regularly between the two speakers ('antiphase pattern'). A 0° or a 360° relationship would result in an inphase pattern of beats, i.e. the beats would occur simultaneously in both headphone speakers.

Tasks and Procedure

Auditory Perception Threshold paradigm—Prior to the tapping task, participants were tested for their ability to discern the change in phase relationship between two auditory trials. Participants listened to two 10sec-long trials, the first always consisting of a regular antiphase pattern (reference trial), while the second trial exhibited a phase change (test trial). The experiment was run as a forced choice staircase method (Treutwein 1995), with participants always listening to a set of two trials and deciding whether the second trial with the phase change was the same as the reference trial, or not. The thresholding procedure always started with a clearly perceptible phase change (around 270), and, upon correct identification ('unequal'), the phase in the set presented next decreased or increased in steps of 5° with each repetition. Each time the subject answered incorrectly ('same'), the phase difference was increased again, and was decreased only when the subject answered correctly for 2 consecutive trials. The threshold procedure was stopped when the subject identified a test trial incorrectly three times in a row. For example, if the individual answered "same" three times when actually presented with a phase of 185 ($185 - 180^\circ = 5^\circ$), but had identified the previous higher intervals correctly as 'different', then the phase change of 10, was defined as the first detectable signal, was considered to be the auditory perception threshold for that individual. The distribution of auditory discrimination thresholds in our participant pool allowed for dividing it into two groups: those who could detect a phase change ≤ 20 (< 80 ms, low threshold group), and those who could detect a phase change only ≥ 20 (> 80 ms, high threshold group). Previous studies suggest that musically experienced adults can detect a temporal discrepancy of at least 20 ms for successful temporal order judgment (Drake and Botte 1993; Repp 1999). The 20 cut-off was chosen a priori firstly, because it was above the threshold previously reported in the literature representing a change corresponding to a 5.6% (about 40ms) phase change; secondly, in the gradual condition it allowed for the increments to reach the same threshold without having too many steps so that fatigue or inattention would be an issue.

Tapping paradigm—At the beginning of the tapping experiment, participants were instructed to synchronize their taps with the auditory stimuli by alternately tapping each index finger – left finger with a stimulus in the left headphone speaker, and right finger with a stimulus in the right speaker. The participants were not informed that there would be a change in the phase relationship between the beats in some trials. After two baseline trials of 180° phase difference, the phase relationship was changed either abruptly or gradually for the next eight trials (modulation phase); each experimental condition ended with another presentation of two baseline trials.

In the abrupt condition, each of the eight modulation phase trials presented either 20 (≈ 80 ms)- or 45 (≈ 178 ms)-shifted stimuli, depending on the individual's auditory threshold. In the gradual condition, the modulation phase began with a 5 (≈ 20 ms) phase shift, increasing by 5 in each subsequent trial. Consequently, in the fourth set of trials (i.e. in trials nine and ten) the phase of the auditory stimuli was shifted to 200. Each trial lasted 30 seconds. The order in which the two conditions were presented was counterbalanced across participants; there was a short rest break between the two conditions.

Data processing and reduction

The first five seconds of each trial were excluded from analysis to account for initial adjustment effects, and only the last 25 seconds were analyzed. The time series obtained were dual-pass filtered with a low-pass filter (4th order Butterworth $f_{3db} = 10$ Hz) through customized Matlab scripts used for analyses. A digital video camera recorded the tapping activity and was used later for verification purposes. The dependent variables for each trial were: mean relative phase (MRP), a measure of the phase relationship between the index

fingers of the right and left hand; the variability of this between-finger phase (MRPV), given by the standard deviation of the between-finger phase within a trial, serving as a measure of the consistency of performance across the trials; accuracy of between-finger phase relative to the acoustic stimuli, measured in percent absolute error (AE) to determine how synchronous the finger-coupling was compared to the beat, and mean relative synchrony (MRS) for each side/finger, expressed as the constant phase relationship between the acoustic stimulus and the 'associated' finger. For relative synchrony, a phase relationship of 100% would indicate that the finger taps were perfectly synchronized with the acoustic stimuli; a relationship <100% or >100% would indicate that the finger taps were either leading the stimuli, or lagging behind them, respectively.

For each condition, the twelve trials were grouped into six trial blocks (the first trial block comprising of the first and second trials, and so on); the data of the two trials were averaged. We also checked for possible 'drift-like' gradual changes within trial blocks, but did not see this in any of the blocks, justifying our averaging approach. Consistent with previous experiments (Whitall et al. 1999), we converted the phase change to percent change in phase, and reported the absolute relative phase as a deviation from antiphase. Thus, a 180° phase relationship would correspond to a phase change of 0%, a 200° relationship to 5.6%, and 225° to a 6.9% phase change; expressed in a temporal dimension, 1.0% would be equivalent to 14.27ms phase difference (or 3.57°).

Statistical analysis

Both one-way and two-way repeated measures ANOVAs were used to compare the dependent variables. Separate one-way ANOVAs were used to examine block effects for all variables in the abrupt condition (as this condition was set differently for both groups), while two-way ANOVAs were used to test for main effects for group, block, and interactions in the gradual condition. Whenever statistically significant main effects or interactions were found, post-hoc pairwise comparisons were conducted using Tukey's test, together with Bonferroni adjustment for multiple comparisons.

RESULTS

Auditory Perception Threshold

The temporal threshold for detecting a phase change, defined as the phase shift that was the lowest detected, ranged from 10° to 45° deviation from antiphase (equating 2.8% to 12.5%), which translates to about a 40–178 ms time difference between the reference and the test beat that was necessary to detect the phase change (Figure 1). The mean temporal perception threshold in the low threshold group was 11.2° (3.1% ±0.9, which translates to 44.2ms) with 1 individual detecting 10°, five detecting 15° and 3 detecting 20°. For the high threshold group the mean was 26.3° (7.3% ±1.6, which translates to 104.2ms), with 2 detecting 25°, 5 detecting 30°, 1 detecting 35° and 1 detecting 45°. A ttest confirmed that the thresholds were significantly different between the two groups ($t=6.55$, $p<0001$).

Mean Relative phase (MRP)

As shown in Figures 3 and 4, the phase relationship (MRP) of the fingers changes with the phase shift in both the abrupt and the gradual condition; within the abrupt condition, both groups (low/high perception threshold) exhibit very similar MRP changes. In the gradual condition, both groups also adjusted very similarly to the gradually increasing phase change.

Abrupt Condition—For the low threshold group, a one-way repeated measures ANOVA showed a significant main effect for trial block [$F(5, 35) = 17.34$, $p<0.001$, partial $\eta^2=0.71$]. Post-hoc tests revealed that the group's MRP during trial blocks with phase shift was

significantly higher than during the baseline conditions (blocks 1 and 6, both $p < 0.001$), indicating that the participants adjusted their MRP values in response to the phase-shifted auditory signals for the middle four trial blocks.

Similarly, for the high threshold group, a one-way ANOVA showed a significant main effect for trial block as well [$F(5, 40) = 85.56$, $p < 0.001$, $\text{partial } \eta^2 = 0.91$], with all middle blocks being significantly different from blocks 1 and 6 (both $p < 0.001$), again reflecting that participants adjusted to the phase change.

Gradual Condition—A two-way ANOVA showed a significant main effect for trial block [$F(5, 75) = 18.11$, $p < 0.001$, $\text{partial } \eta^2 = 0.54$], but no group or interaction effects. Post-hoc tests revealed that MRP of blocks 2–5 was significantly higher than in blocks 1 and 6; within the middle blocks, trial blocks 2 and 3 were different from 4 and 5, with trial block 4 also being different from block 5 ($p = 0.04$). This indicates that participants both the low threshold and the high threshold group (for whom all stimuli were subliminal) adjusted to the increment in phase change between blocks 2 and 5. See Table 1 for descriptive statistics.

Variability of between-finger phase (MRPV)

The variability of between-finger phase within a trial block, averaged across all participants, for the abrupt and gradual conditions is shown in Figure 5, representing the performance of the two groups for the two tapping conditions.

Abrupt Condition—For the low-threshold group, one-way ANOVA showed a significant main effect for trial block [$F(5, 40) = 11.27$, $p < 0.001$, $\text{partial } \eta^2 = 0.62$], indicating that the participants became more variable during trials with phase change. Post-hoc tests revealed that participants' performance was significantly more variable during trial blocks 2, 3 and 4 than during baseline (all $p < 0.001$).

For the high-threshold group, one-way ANOVA showed a significant main effect for trial block [$F(5, 40) = 12.00$, $p < 0.001$, $\text{partial } \eta^2 = 0.60$], indicating that the higher phase change (as compared to baseline) was associated with increased variability. Post-hoc tests revealed that all middle blocks were more variable than block 1, and blocks 2, 3, and 4 were more variable than block 6 (all $p < 0.05$).

Gradual Condition—Two-way ANOVA showed a significant main effect for trial block [$F(5, 75) = 8.39$, $p < 0.001$, $\text{partial } \eta^2 = 0.36$] and a marginally significant main effect for group, [$F(1, 15) = 5.16$, $p = 0.04$, $\text{partial } \eta^2 = 0.26$]. Post-hoc tests revealed that the blocks 3 and 4 were more variable than the baseline blocks 1 and 6. Block 5 was significantly more variable than block 1 (but not different from block 6). Trial block 4 was also more variable than blocks 2 and 5 ($p = 0.03$). Overall, the high threshold group was found to perform more variable than low threshold group, indicating that this group appeared to be more challenged by the low-threshold phase shift employed during the gradual condition than the low-threshold group. See Table 1 for descriptive statistics.

Absolute error (AE)

AE represents the accuracy (or synchronicity) of the phase change relative to the auditory cues. Generally, AE increased during the phase shift away from 180° for both groups in similar ways during both abrupt and gradual condition, as can be seen in Fig. 6.

Abrupt Condition—For the low-threshold group, a one-way ANOVA showed a significant main effect for trial block [$F(5, 35) = 5.68$, $p < 0.001$, $\text{partial } \eta^2 = 0.45$]. Post-hoc tests revealed that blocks 2, 3, 4 & 5 were significantly different from blocks 1 and 6

($p=0.03$), indicating that participants' accuracy decreased substantially during the trials with the phase shift, compared to the baseline condition.

A one-way ANOVA for the high-threshold group also showed a significant main effect for trial block [$F(5, 40) = 4.23$, $p<0.001$, $\text{partial } \eta^2=0.37$], with post-hoc tests revealing that absolute error was significantly higher (i.e., accuracy decreased) in blocks 2, 3 and 4, compared to the baseline blocks; AE values in block 5 were higher as well, albeit not statistically significant. AE during block 2 was higher than during blocks 5 and 6, and higher during block 4 compared to block 6 (all $p<0.05$).

Gradual Condition—A two-way ANOVA showed a significant main effect for trial block [$F(5, 75) = 10.82$, $p<0.001$, $\text{partial } \eta^2=0.42$], without any group or interaction effects. Post-hoc tests revealed that only trial blocks 4 and 5 were performed with significantly higher AE compared to the baseline blocks, and blocks 2 and 3. Participants performed with higher errors during block 5 than block 4 ($p=0.01$). See Table 1 for descriptive statistics.

Mean Relative Synchrony (MRS)

The main results for MRS of each finger with its respective signal, for each condition, are summarized in Table 2.

Abrupt Condition—For the low-threshold group, a repeated measures ANOVA with finger (non-dominant, dominant) and block (1–6) as within subjects factor showed a marginally significant main effect for finger [$F(1, 7) = 5.25$, $p=0.05$, $\text{partial } \eta^2=0.43$] only, indicating that the non-dominant finger, across all six blocks, tended to anticipate the stimuli less than the dominant one.

For the high-threshold group, this analysis showed a significant main effect for finger [$F(1, 8) = 12.29$, $p=0.01$, $\text{partial } \eta^2=0.60$], indicating more anticipation in the dominant compared to the non-dominant finger, and a significant Finger x Block interaction [$F(5, 40) = 11.72$, $p<0.001$, $\text{partial } \eta^2=0.59$]; post-hoc tests indicated that there was significantly more anticipation for blocks 3 and 5 of the dominant finger (all $p<0.05$, Bonferroni-adjusted), compared to the baseline trial blocks. No block effects were found for the non-dominant finger. The means and standard deviations for each finger, and each group are shown in Table 2.

Gradual Condition—A repeated measures ANOVA with finger (non-dominant, dominant) and block (1–6) as within subjects factor, and group (low threshold, high threshold) as between subjects factor showed a significant main effect for finger [$F(1, 15) = 10.21$, $p=0.01$, $\text{partial } \eta^2=0.40$], and a significant Finger x Block interaction [$F(5, 75) = 7.36$, $p<0.001$, $\text{partial } \eta^2=0.33$]. The finger effect indicated that, across all trial blocks, the non-dominant finger overall anticipated less than the dominant finger. Post-hoc tests comparing the baseline trial blocks (1&6) with the middle blocks in the dominant finger showed significantly greater beat anticipation in trial block 4 ($p<0.01$, Bonferroni-adjusted); no statistically significant differences were found for the non-dominant finger. See Table 2 for descriptive statistics.

DISCUSSION

In this study, we examined the ability of adults to modulate their motor response to an abrupt (perceptible), or to a gradual (subliminal) change in auditory phase cues in a bilateral tapping task. Additionally, we investigated whether these responses were influenced by differences in auditory discrimination thresholds of the phase change. The results show that when the phase change was introduced abruptly, participants with both low and high

auditory phase detection thresholds adjusted their bilateral tapping to the changes; these adjustments were accompanied by increased variability and increased absolute errors. In the gradual condition, both groups showed a change in bilateral finger response to the subliminal temporal shifts in the auditory stimuli that began as early as 10°, or 40ms (reflecting a 2.8% phase change). Participants' accuracy and variability did not change substantially until the phase change had reached 15°, or 60ms (i.e. a 4.2% phase change). Regarding synchronization of the finger taps with the respective stimulus, a phase change revealed a synchronization asymmetry between dominant and non-dominant hands: During the later trials in the abrupt condition, the dominant hand in the high-threshold group showed anticipation, compared to baseline. This was also the case (for both groups) during the later trials in the gradual condition.

Non-musically trained adults demonstrate a wide range of auditory phase perception thresholds

Participants could perceive the change in phase between the two sets of auditory cues within a rather broad range of 20–160ms (equivalent to 5° – 40° phase change). This average perceptual threshold is much higher than the 10–20 ms range reported by authors of unilateral tapping studies (e.g., Thaut et al. 1998). One reason for the wide range of perception thresholds may be the non-musician background of our participants, unlike the participants in the previously reported unilateral studies (Repp 2000; Repp 2001b; Repp 2002a; Thaut and Kenyon 2003). The perception threshold paradigm in our study was also different in the sense that the participants were not required to detect the difference in the onset of two sounds but the difference between two sets of beats, which in effect constituted a subtle change of rhythm. At the same time, our estimates may be slightly skewed since we only used a descending protocol and did not follow with an ascending protocol. We think it is plausible that the wide range of thresholds is at least partly reflective of the different experiences with rhythm that existed within our sample that was controlled for by an absence of intense musical training.

Participants respond similarly to a perceptible phase change regardless of their perceptual auditory threshold

Contrary to our expectations there was no obvious difference between the high and low threshold participants in their ability to adjust in the first trial during the abrupt, perceptible change. Inspection of individual trials showed no tendency for the taps early in the sequence to be less accurate than those at the end. Rather, the participants from both groups were able to detect the change from antiphase cues and adjusted their movements within the initial five seconds of the first trial. It is plausible, however, that there could be differences in the response time if we changed the phase relationship in the middle of a trial or if we did not allow a 5 second start-up time. Nevertheless, visual observation suggested an immediate response.

Neither group showed any carry-over effects when they returned to baseline, indicating that the auditory-motor network did not learn the new phase relationship to the extent that a new “temporally stable” phase relationship was induced. This may be due to the relatively low number of repetitions for each finger (8 trials x 21 taps). Studies inducing changes in sensorimotor coupling, as indicated by the presence of after-effects, involve many more repetitions for rhythmic finger movements (e.g., Zanone and Kelso 1997). In this study, the authors found that at least 200 practice trials over a 2-day-period were needed to learn a new sensory-motor map in a bilateral ‘finger wagging’ paradigm, that is, a 90° out-of-phase change in a sensory-motor map that was temporally more attractive than the 0 or 180 phase. However, it is also known that learning a 90° change is easier than a 20° or 45° change,

presumably because it is exactly half of the stable 180° phase. Our results on variability of phase around the different phase relationships support this fact.

Based on the Haken-Kelso-Bunz (HKB) model (Haken et al. 1985; Schoner et al. 1986), we expected and found that in the abrupt condition both low and high threshold groups were more variable at a non-attractor phase. Participants clearly became less well-tuned when they had to modulate their responses to a perceived non-attractor phase change.

Absolute error increased for both groups in the abrupt condition, and with ongoing trials, they tended to become a little more accurate. This tendency was a little more pronounced in the group with a low threshold. These results suggest that the ability to detect and respond to the auditory phase change facilitates the ability to maintain synchrony with the cue. This is inconsistent with the finding in unilateral tapping that the period rather than the phase relationship with the cue is the dominant parameter. In our study, the participant had to make two adjustments, one is in relation to the cue and the other is in relation to the finger of the other hand. It appears that the finger-relationship is slightly stronger than the cue phase relationship for both groups.

Finally, both groups responded similarly in how each finger synchronized to the beat during baseline and the trials with the phase change. The baseline responses suggest that participants usually anticipated the stimulus with their dominant fingers as reported in previous studies on unilateral tapping (Fraisse 1966; Fraisse 1980; Hary and Moore 1985; Peters 1989; Kagerer et al. 1990; Mates et al. 1992; Aschersleben 2002), and also with their non-dominant fingers. During the trial blocks with the phase change, the responses of the dominant finger anticipated the stimulus more than the non-dominant finger during the abrupt condition in the high threshold group, and across both groups during the gradual condition. The fact that the dominant finger anticipated the beat more in these trials does not necessarily imply that its modulation is less skilled, but rather that it is the key finger for making the initial adjustment in an anticipatory manner because the change in phase occurred in the ear on the dominant side. Thus, from a spatial compatibility viewpoint this would argue for adjustment of the dominant finger.

Participants respond quickly to subliminal phase changes with some differences according to their perceptual auditory threshold

In the gradual change condition, both low and high threshold groups modulated their tapping to the a change of 10° (40ms, trial block 3), indicating that most participants responded to temporal changes that were smaller than their auditory thresholds. This replicates findings of unilateral tapping studies that demonstrated that the auditory phase change need not be consciously registered in order to produce corrective motor responses, and is also consistent with visuomotor adaptation studies using discrete movements, and a gradual adaptation paradigm (Kagerer et al. 1997). Our finding that the high threshold group could respond to as low a subliminal threshold as quickly as the low threshold group suggests that there is a response mechanism to auditory cues in place that is independent of the, presumably learned, ability to perceive a change of phase difference between auditory cues.

Although the overall tendency to respond with a relative phase change was present in the gradual condition by trial block two, neither group showed reduced accuracy, increased variability, or change in finger synchronization until trial block 4 (i.e., 15°, representing a change of 60ms). In other words, the subliminal phase changes away from true antiphase were, up to block 4, as accurate, stable and synchronized as well as the antiphase baseline. It is probable that most if not all of the participants in the low threshold group could likely detect the change by block 4, and certainly by block 5, resulting in a conscious modulation that had some errors. However, this explanation would not account for the high threshold

group where most should not have detected consciously the phase change even at block 5 according to the initial perceptual threshold paradigm. Thus, it seems that the receiving-operating characteristics (ROC) for detection of phase changes would be the same for both low and high-threshold groups, albeit, shifted by the threshold detection difference.

The increased amount of variability as one moves away from antiphase is certainly predicted by the HKB model of tapping (Haken et al. 1985; Schoner et al. 1986), although this has previously only been demonstrated in perceptible phase changes. As predicted, the high threshold group is more variable than the low threshold group across all the trials. Finally, one noteworthy difference in the subliminal/gradual trials versus the perceptible/abrupt trials was the fact that only the dominant finger seemed to make adjustments in synchronization, rather than both fingers. This suggests that the cortical circuitry responsible for this change operates in a lateralized way, consistent with the spatial source of the unperceived error.

Taken together, there are several novel findings from our study. First, our psychophysical determination of perceptual threshold suggests the presence of a large range of auditory phase perception thresholds in adults without extensive musical training. Second, regardless of detection abilities, adults are able to modulate their responses to both consciously perceptible and subliminal shifts in auditory stimuli for bilateral phase changes. Third, all participants were able to maintain a reasonable accuracy when modulating their finger tapping despite increased variability, suggesting similar operating characteristics across all participants and a basic common mechanism for subliminal response modulation. Fourth, the only difference between the two threshold groups was that the higher threshold group was less well-tuned (more variable) in the gradual conditions. Finally, both abrupt and gradual conditions necessitated adjustment in synchronization strategies, but the subliminal change was mainly compensated by the dominant finger alone.

One limitation of our study is that our approach focuses on trial block means, and ignores dynamical and transient phase changes of the tapping responses, which likely takes away useful information about possible nonlinear responses during the first five seconds that were not recorded. Sampling rate could also be considered to be a limitation, since time intervals shorter than 10ms were not captured, due to our sampling rate; at the same time, since the data show that the mean relative phase values correspond to time intervals that are in most cases larger than 18–20ms, the fidelity of the response data should be high. Finally, the sampling period of 25 seconds could be considered as low; we had to find a good balance between collecting more data, and, given that the experiment already lasted for an hour, detrimental effects of fatigue. In addition, we wanted a comparison to future work with children who do not tap in a focused manner for long time periods.

Acknowledgments

The National Institute of Health supported this work with an award (RO1 HD 42527) to J. E. Clark and sub-contract to J. Whitall. We thank an anonymous reviewer and Bruno Repp for helpful comments on an earlier version.

References

- Aschersleben G. Temporal control of movements in sensorimotor synchronization. *Brain Cogn.* 2002; 48:66–79. [PubMed: 11812033]
- Drake C, Botte MC. Tempo Sensitivity in Auditory Sequences - Evidence for a Multiple-Look Model. *Perception & Psychophysics.* 1993; 54:277–286. [PubMed: 8414886]
- Forrester L, Whitall J. Bimanual finger tapping: effects of frequency and auditory information on timing consistency and coordination. *J Mot Behav.* 2000; 32:176–191. [PubMed: 11005947]

- Fraisse P. Anticipation of rhythmic stimuli. Speed of establishment and accuracy of synchronization. *Annee Psychol.* 1966; 66:15–36. [PubMed: 5921119]
- Fraisse P. Relationship between the duration of perceptual identification and verbal reaction time. *Annee Psychol.* 1980; 80:433–447. [PubMed: 7235644]
- Haken H, Kelso JA, Bunz H. A theoretical model of phase transitions in human hand movements. *Biol Cybern.* 1985; 51:347–356. [PubMed: 3978150]
- Hary D, Moore GP. Temporal tracking and synchronization strategies. *Hum Neurobiol.* 1985; 4:73–79. [PubMed: 4030426]
- Kagerer FA, Ilmberger J, Poeppel E, Mates J, Radil T. Auditory motor synchronization: timing in incremental and decremental rhythmic tapping. *Act Nerv Super.* 1990; 32(2):145–46.
- Kagerer FA, Contreras-Vidal JL, Stelmach GE. Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp Brain Res.* 1997; 115:557–561. [PubMed: 9262212]
- Mates J, Radil T, Poppel E. Cooperative tapping: time control under different feedback conditions. *Percept Psychophys.* 1992; 52:691–704. [PubMed: 1287574]
- Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia.* 1971; 9:97–113. [PubMed: 5146491]
- Peters M. The Relationship between Variability of Intertap Intervals and Interval Duration. *Psychological Research-Psychologische Forschung.* 1989; 51:38–42.
- Repp BH. Detecting deviations from metronomic timing in music: Effects of perceptual structure on the mental timekeeper. *Perception & Psychophysics.* 1999; 61:529–548. [PubMed: 10334099]
- Repp BH. Compensation for subliminal timing perturbations in perceptual-motor synchronization. *Psychol Res.* 2000; 63:106–128. [PubMed: 10946585]
- Repp BH. Processes underlying adaptation to tempo changes in sensorimotor synchronization. *Hum Mov Sci.* 2001a; 20:277–312. [PubMed: 11517673]
- Repp BH. Phase correction, phase resetting, and phase shifts after subliminal timing perturbations in sensorimotor synchronization. *J Exp Psychol Hum Percept Perform.* 2001b; 27:600–621. [PubMed: 11424648]
- Repp BH. Automaticity and voluntary control of phase correction following event onset shifts in sensorimotor synchronization. *J Exp Psychol Hum Percept Perform.* 2002a; 28:410–430. [PubMed: 11999863]
- Repp BH. Phase correction in sensorimotor synchronization: nonlinearities in voluntary and involuntary responses to perturbations. *Hum Mov Sci.* 2002b; 21:1–37. [PubMed: 11983432]
- Schoner G, Haken H, Kelso JA. A stochastic theory of phase transitions in human hand movement. *Biol Cybern.* 1986; 53:247–257. [PubMed: 3955100]
- Semjen A, Ivry RB. The coupled oscillator model of between-hand coordination in alternate-hand tapping: a reappraisal. *J Exp Psychol Hum Percept Perform.* 2001; 27:251–265. [PubMed: 11318046]
- Summers JJ, Rosenbaum DA, Burns BD, Ford SK. Production of polyrhythms. *J Exp Psychol Hum Percept Perform.* 1993; 19:416–428. [PubMed: 8473848]
- Tecchio F, Salustri C, Thaut MH, Paswqualetti P, Rossini PM. Conscious and preconscious adaptation to rhythmic auditory stimuli: a magnetoencephalographic study of human brain responses. *Exp Brain Res.* 2000; 135:222–30. [PubMed: 11131507]
- Thaut MH, Kenyon GP. Rapid motor adaptations to subliminal frequency shifts during syncopated rhythmic sensorimotor synchronization. *Hum Mov Sci.* 2003; 22:321–338. [PubMed: 12967761]
- Thaut MH, Miller RA, Schauer LM. Multiple synchronization strategies in rhythmic sensorimotor tasks: phase vs period correction. *Biol Cybern.* 1998; 79:241–250. [PubMed: 9810681]
- Treffner PJ, Turvey MT. Symmetry, broken symmetry, and handedness in bimanual coordination dynamics. *Exp Brain Res.* 1996; 107:463–478. [PubMed: 8821386]
- Treutwein B. Adaptive psychophysical procedures. *Vision Res.* 1995; 35:2503–2522. [PubMed: 8594817]
- Whitall J, Forrester L, Song S. Dual-Finger Preferred-Speed Tapping: Effects of Coordination Mode and Anatomical Finger and Limb Pairings. *J Mot Behav.* 1999; 31:325–339. [PubMed: 11177641]

- Yamanishi J, Kawato M, Suzuki R. Two coupled oscillators as a model for the coordinated finger tapping by both hands. *Biol Cybern.* 1980; 37:219–225. [PubMed: 7448245]
- Zanone PG, Kelso JA. Coordination dynamics of learning and transfer: collective and component levels. *J Exp Psychol Hum Percept Perform.* 1997; 23:1454–1480. [PubMed: 9336961]

Figure 1.

Experimental design. The top panel (A) illustrates the phase relationship during baseline and the phase shift, and shows a graphical explanation of the main variables. The bottom panel (B) shows the details of the sequence of the different trial blocks as they were presented during the experiment.

Figure 2.

Individual perceptual thresholds, defined as the highest phase change that could not be perceived as different from the 180° phase relationship, whereas the next higher change could be perceived (e.g., participant 10 could not detect 5° , but needed a minimum of 10° for detection: the threshold would be 5°). The y-axis represents the auditory thresholds in degrees, and the x-axis the individual participants. The dashed line demarcates the boundary between high threshold group (light bars), and the low threshold group (dark bars).

Figure 3. Abrupt condition: Mean relative phase (MRP) for the low threshold group (top panel) and high threshold group (bottom panel). The empty circles represent the 'ideal' relative phase values, reflecting the stimulus phase, and the filled circles represent the participants' response.

Figure 4.
 Gradual condition: Combined relative phase (MRP) for the low and high threshold group. The empty squares represent the 'ideal' relative phase (=stimulus phase), and the filled squares represent the participants' response.

Figure 5. Variability of mean relative phase for the low and high threshold groups in the abrupt condition (top panel), and the gradual condition (bottom panel). The asterisks denote a significant difference between the respective trial block and baseline (trial blocks 1&6); *** $p=0.001$, * $p=0.04$.

Figure 6. Absolute error for the low and high threshold groups in the abrupt condition (top panel), and the gradual condition (bottom panel). The asterisks denote a significant difference between the respective trial block and baseline (trial blocks 1&6); *** $p=0.001$, * $p=0.04$.

Table 1

Mean relative phase (MRP, in %), variability of MRP (MRPV, in %), and absolute error (AE, in %) for the low and high threshold group in the abrupt condition, and across the two groups in the gradual condition. The asterisks mark significant differences between averaged baseline blocks (blocks 1 & 6) and the respective middle blocks (blocks 2–5). CI denotes the 95% confidence intervals.

Abrupt condition, low threshold group					
MRP		MRPV		AE	
Mean (std)	CI	Mean (std)	CI	Mean (std)	CI
Baseline	2.26 (0.59)	2.17 (0.75)		1.06 (0.73)	
Block 2	9.06 (3.45) ***	3.78 (1.69) *	0.54–2.86	4.25 (2.69) *	1.01–5.39
Block 3	9.11 (3.31) ***	4.33 (1.23) ***	1.45–2.87	4.07 (1.98) ***	1.57–4.47
Block 4	7.70 (2.62) ***	3.75 (0.76) ***	0.96–2.21	3.22 (1.91) *	0.65–3.68
Block 5	6.58 (2.80) *	3.37 (0.77) *	0.46–1.81	3.07 (1.82)	0.22–3.64
Abrupt condition, high threshold group					
Baseline	2.57 (0.60)	2.53 (0.69)		1.38 (0.86)	
Block 2	16.63 (5.03) ***	4.04 (0.98) ***	0.87–2.14	4.72 (4.29)	0.35–6.34
Block 3	15.55 (3.68) ***	3.85 (1.05) ***	0.64–1.99	3.16 (3.19)	0.48–4.05
Block 4	15.37 (2.73) ***	4.03 (0.63) ***	0.91–2.10	3.37 (3.34)	0.48–4.46
Block 5	14.45 (3.17) ***	3.69 (0.85) ***	0.70–1.62	2.90 (2.58)	0.45–3.51
Gradual condition, both groups					
Baseline	2.68 (0.93)	2.39 (0.68)		1.37 (1.05)	
Block 2	2.72 (0.97)	2.52 (0.48)	–0.49–0.25	0.98 (0.47)	–0.03–0.98
Block 3	3.57 (1.50)	2.93 (0.82)	0.08–1.00	1.69 (1.10)	0.36–1.00
Block 4	5.04 (2.59) ***	3.30 (0.90) ***	0.39–1.44	2.77 (1.45) ***	0.54–2.25
Block 5	8.06 (3.66) ***	3.54 (0.86) ***	0.63–1.68	3.78 (2.29) ***	1.29–3.54

* p=0.04

*** p=0.001

Table 2

Mean relative synchrony values (MRS, in % phase) between fingers and respective signal for the low and high threshold group in the abrupt condition, and across the two groups in the gradual condition. A phase relationship <100% indicates a response lead with respect to the stimuli, a values >100% indicate a response lag. The asterisks mark significant differences between averaged baseline blocks (blocks 1 & 6) and the respective middle blocks (blocks 2–5).

Abrupt condition, low threshold group				
	Non-dominant finger		Dominant finger	
	Mean (std)	CI	Mean (std)	CI
Baseline	89.29 (5.20)		89.22 (5.33)	
Block 2	96.38 (11.06)	−1.72–13.90	85.94 (8.08)	−2.58–9.15
Block 3	97.34 (5.34)	1.99–14.10	87.47 (9.15)	−7.46–10.97
Block 4	95.34 (6.40)	−0.16–12.24	85.47 (6.57)	−19.11–12.41
Block 5	91.06 (4.99)	−5.01–7.90	83.53 (7.10)	−3.06–14.88
Abrupt condition, high threshold group				
Baseline	90.10 (2.30)		89.70 (2.41)	
Block 2	103.14 (11.49)*	4.20–21.87	80.93 (10.05)	0.52–17.03
Block 3	100.09 (10.38)	2.19–17.78	79.11 (8.79)*	3.71–17.47
Block 4	102.12 (10.87)*	3.33–20.71	83.06 (10.32)	−1.61–14.91
Block 5	99.63 (11.56)	0.37–18.69	78.80 (9.00)*	3.08–18.72
Gradual condition, both groups				
Baseline	88.76 (4.40)		88.43 (4.43)	
Block 2	90.19 (6.12)	−5.07–1.63	89.29 (5.93)	−4.62–2.38
Block 3	90.93 (5.52)	−5.52–1.17	88.95 (7.16)	−4.61–3.57
Block 4	88.93 (4.50)	−3.03–2.69	83.20 (5.30)***	1.82–8.64
Block 5	92.13 (4.42)	0.38–6.36	84.31 (9.00)	−0.80–9.04

*
p=0.04

p=0.001