

The rhythm aftereffect: Support for time sensitive neurons with broad overlapping tuning curves

Mark W. Becker^{*}, Ian P. Rasmussen

Department of Psychology, Lewis & Clark College, 0615 SW Palatine Hill Road, Portland, OR 97219, USA

Accepted 28 March 2007

Available online 2 May 2007

Abstract

Ivry [Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, 6, 851–857.] proposed that explicit coding of brief time intervals is accomplished by neurons that are tuned to a preferred temporal interval and have broad overlapping tuning curves. This proposal is analogous to the orientation selective cells in visual area V1. To test this proposal, we used a temporal analog to the visual tilt aftereffect. After adapting to a fast auditory rhythm, a moderately fast test rhythm (400 ms between beats) seemed slow and vice versa. If the speed of the adapting rhythm was made too disparate from speed of the test rhythm the effect was diminished. The effect occurred whether the adapting and test stimuli were presented to the same or different ears, but did not occur when an auditory adapting rhythm was followed by a visual test rhythm. Results support the proposition that explicit time information is coded by neural units tuned to specific temporal intervals with broad overlapping tuning curves. In addition, it appears that there is a single timing mechanism for each incoming sensory mode, but distinct timers for different modes. © 2007 Elsevier Inc. All rights reserved.

Keywords: Time; Duration; Aftereffect; Interval timer; Cerebellum; Adaptation; Rhythm

1. Introduction

It is clear that human behavior is affected by time across many different time scales. Long time scales include circadian rhythms (Czeisler et al., 1999; Wever, 1986) that operate over the scale of days. Intermediate time scales involve intervals from minutes to several hours (Buhusi & Meck, 2005) and information in this time range may be important for sequencing behaviors in complex tasks (Sohn & Carlson, 2003) and decision making (Ivry & Spencer, 2004). Very fine time scales, on the order of milliseconds to several seconds, are important for coordinating motor movements, and speech perception (Mauk & Buonomano, 2004) and production (Schirmer, 2004). Research investigating behaviors associated with these different time scales suggests that independent processes and distinct brain areas are responsible

for processing time information for each time scale. While there is still some debate about whether timing information is explicitly coded for intermediate and longer time scales, there is growing consensus that there are structures which explicitly code time information for short time scales (Buhusi & Meck, 2005; Ivry & Spencer, 2004). In this paper we limit ourselves to the perception of short temporal durations, and investigate the organization of the neural units that explicitly code temporal information at this brief time scale.

Some of the earliest work indicating the existence of an independent neural mechanism for the encoding of brief temporal information came from Wing and Kristofferson (1973). In their experiments, subjects were asked to tap in unison with a metronome and to continue producing that rhythm after the metronome stopped. A careful examination of the variability between taps allowed Wing and Kristofferson to conclude that errors were caused by two independent sources of variability. One source was attributed to variability in executing a motor command, and a second source of variability was associated with a timing

^{*} Corresponding author. Present address: Michigan State University. Fax: +1 517 353 1652.

E-mail address: becker54@msu.edu (M.W. Becker).

mechanism. This initial demonstration of an independent timing mechanism led to further research investigating both the processes and brain areas involved in explicitly coding temporal information.

A combination of lesion studies (Gerwig et al., 2003, 2005; Perrett & Mauk, 1995; Perrett, Ruiz, & Mauk, 1993; Spencer & Ivry, 2005) and functional magnetic resonance imaging studies (for review see Lewis & Miall, 2003), contribute to a growing consensus that the cerebellum is instrumental in the explicit coding of short duration temporal information (Buhusi & Meck, 2005; Ivry, 1996; Ivry & Richardson, 2002; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). It is less clear whether the basal ganglia are also involved or only become involved when tasks require a less explicit coding of time associated with behaviors at intermediate time scales.

One model for how units within the cerebellum may code temporal information, the interval timer model (Keele, Nicoletti, Ivry, & Pokorny, 1989; Pashler, 2001), posits a bank of neural units each of which is tuned to a specific temporal duration. One indirect piece of evidence supporting this interval model comes from the observation of Fraisse (1963) who found that rhythm perception breaks down when the interval between beats exceeds a few seconds, suggesting that the precise timing associated with an explicit timing mechanism is limited in terms of the time frames to which it responds. In theory, the durations one could monitor under the interval timer model would be limited by the number of units within the bank and their tuning. The finding that rhythm perception breaks down when the interval between beats becomes too large is consistent with the interval timer model with temporally tuned units tuned to a limited set of durations.

Perhaps the best evidence supporting the existence of units tuned to specific durations comes from a study by Wright, Buonomano, Mahncke, and Merzenich (1997). In their study, participants were trained to discriminate whether a 1000 Hz tone was longer or shorter than 100 ms. During training, both the frequency of the tone and the time criterion were held constant and performance improved markedly. After training, either the time criterion was changed to a new interval (200 ms) or the tone was changed to a new frequency (4000 Hz). When the time interval was changed, the benefit due to training disappeared; however, when the tone's frequency changed and the time interval remained the same, the benefit of training transferred almost completely. These results suggest that the training was specific to a given temporal interval support the theory that there are different units specialized for encoding particular durations of time. Training one of these duration sensitive cells specifically affects temporal judgments at the trained interval without affecting duration judgments at untrained durations.

Given this evidence in favor of units that are tuned to specific temporal durations and the evidence suggesting that the cerebellum is the most likely site of these units, Ivry (1996) proposed a model of how these temporally sen-

sitive units might be organized within the cerebellum. Ivry based this interval timing model on visual area V1. In area V1 there are cells which are tuned to lines of particular orientations. But, across these orientation tuned cells, there are a relatively limited number of preferred orientations with roughly 15 deg separating the preferred orientations between cells. Cells tuned to different orientations have broad tuning curves which overlap with the tuning curves of cells tuned to nearby orientations (Hubel & Wiesel, 1962). These tuning curves allow the precise orientation of lines to be determined by using distributed coding across a number of cells tuned to nearby orientations. This method of extracting orientation is extremely efficient, allowing a relatively small set of orientation selective cells to code a nearly infinite number of possible orientations.

Given the efficiency of this type of distributed coding and its prevalence for coding visual features (orientation, color, motion direction), Ivry speculated that a similar coding scheme could be used by the interval timer. Thus he suggested that the time sensitive units would be optimally tuned to a specific temporal delay but would have broad tuning curves that overlapped with other temporally sensitive neurons. Although Ivry's extension of the structure of V1 to the structure of the temporally sensitive cells in the cerebellum is logical, there is little direct evidence supporting this type of architecture within the cerebellum.

In the present experiments, we attempted to provide evidence for the broad overlapping tuning curves posited by Ivry. To do so we adopted a psychophysical technique that has been used to support the existence of broad tuning curves in area V1 and altered the method so that it was appropriate for investigating the structure of temporally tuned units in the cerebellum.

The broad overlapping tuning of orientation selective cells in area V1 is thought to cause the tilt aftereffect (TAE) in vision (Gibson & Radner, 1937; Jin, Dragoi, Sur, & Seung, 2005; Mitchell & Muir, 1976; Paradiso, Shimojo, & Nakayama, 1989). To produce the TAE, an observer stares for a number of seconds at an adapting display consisting of lines of a particular orientation and then views a test pattern that consists of lines of a nearby orientation. The effect is that the test pattern will be perceived as tilting away from the orientation of the adapting stimulus. For example, if one adapts to lines tilted just left of vertical, and then views a vertical test pattern, the lines of the test pattern will appear to be tilted to the right of vertical. The explanation of this effect is that adapting to a left tilting pattern will selectively reduce the firing rate of cells tuned to the left (Coltheart, 1971; Wainwright, 1999). When subsequently viewing a vertical pattern, the dampened response of the leftward tuned cells will result in a rightward shift in the overall pattern of activity, so that the vertical lines will appear to tilt rightward. This tilt aftereffect is a direct result of having a bank of orientation selective cells with broad overlapping tuning curves and distributed coding across those cells.

In addition, the effect should be largest when the orientation of the adapting and test patterns are similar enough such that the cells tuned to the adapting pattern are part of the distributed code for the test pattern. If the orientations of the adapting and test patterns are too disparate, lowering the firing rate of cells tuned to the adapting pattern should not influence coding for the test pattern, since these orientation selective cells are not part of the distributed code.

If the interval timing model is correct and there is a bank of broadly tuned time-selective units, a similar type of adaptation should occur in the temporal domain. Adapting a person to a slightly faster train of beats should make a subsequent moderate train of beats seem artificially slower. But adapting a person to an extremely fast train of beats should have little influence on the subsequent judgment of a moderate train of beats. Conversely, adapting a person to a slightly slower train of beats should make a moderate train of beats seem slightly faster. But adapting a person to an extremely slow train of beats should have little influence on their subsequent perception of a moderate train of beats. Thus, the interval timing model makes fairly clear and precise predictions about how adaptation should influence perception, predicting differential effects of adaptation depending on the relationship between the speed of the adapting train and the test train of beats.

To test these predictions, in Experiment 1 a binaural standard rhythm was preceded by a binaural adapting train of beats that could either be much faster, slightly faster, slightly slower, or much slower than the standard rhythm. To foreshadow our results, we found that the adapting beats caused significant negative aftereffects but only if the adapting and test beats were sufficiently similar in tempo. In Experiment 2, we used monaural stimuli to demonstrate that the aftereffect occurs when the test and adapting trains are presented to opposite ears, suggesting that adaptation was occurring to a central timing mechanism that received binaural input. In Experiment 3, we used a cross-modal paradigm to demonstrate that an auditory rhythm did not influence the subsequent perception of a visually presented rhythm, suggesting that the adaptation was occurring to a modality specific timing mechanism and not to the timing mechanism controlling the motor command required for the production of the timing responses.

2. Experiment 1

2.1. Method

2.1.1. Participants

Thirty-three undergraduates (aged 18–21) participated for course credit or monetary compensation. All participants reported normal audition and all were able to hear the stimuli.

2.1.2. Procedure

Participants were instructed that the experiment would evaluate people's ability to reproduce a given rhythm. They were told that the experiment would be run on the computer and that they would hear a longer train of beats, followed by a brief pause, and a shorter train of six additional beats. Subjects were instructed that their task was to ignore the longer first train of beats and replicate the rhythm of the second set of six beats by pressing a game controller button at the same rate as the second train of beats. After being instructed on the procedure of the experiment, participants were sat in front of a computer screen and were fitted with a pair of stereo headphones. The testing chamber was a small, quiet, dimly lit room that was free of visual distractions. The use of headphones also helped limited any extraneous noise from the environment.

A given trial began with the word "Ready?" which stayed on the screen for 1000 ms. The screen then went blank (500 ms) and a randomly selected adapting train played for 10 s. The adapting train was followed by a 1300 ms pause after which the test rhythm of six beats was presented. Immediately following the test train, the computer screen said "Begin Tapping" instructing the participants to tap out six beats mimicking the test train. Participants tapped out their responses by using their right index figure to tap the button on a video game controller. After they had tapped the game control six times, the screen changed to "Stop Tapping" for 1500 ms, then went blank for 3000 ms, and another trial began with the "Ready?" screen.

2.1.3. Design and stimuli

The experiment was within subjects design. Participants completed a total of 20 trials comprised of four trials in each of five randomly interleaved conditions. Six sound files were created using Sony's Sound Forge software. Five of these files were adapting trains and the sixth was the test train that subjects were asked to replicate. Each adapting train was 10 s long and each beat was a 10 ms presentation of a 2000 Hz tone. The adapting trains differed in terms of the speed of the beats. The very slow adapting condition consisted of one beat every 700 ms, the slow adapting condition consisted of one beat every 500 ms, the control condition consisted of one beat every 400 ms, the fast adapting train consisted of one beat every 300 ms, and the very fast condition consisted of one beat every 100 ms. These timings were chosen to allow for a range of timings that were within the range that the cerebellum is thought to process (Buhsu & Meck, 2005). Regardless of the adapting train, the test train that the subjects were asked to replicate was always a train of six beats that occurred once every 400 ms. For both the adapting trains and test train, the beats were presented in stereo.

2.1.4. Apparatus

To obtain good temporal resolution, the experiment was programmed using SR-Research's Experiment Builder

software and presented in the Eye Link II eye tracking environment. Although eye movements were not recorded, this environment's precise temporal control (<2 ms temporal variability) allowed for good temporal control of the stimulus presentation and data collection. In addition, a Microsoft SideWinder Game Pad game controller with good temporal response was used to collect button presses.

2.2. Results

Each participant produced a total of 100 intervals between button presses (5 intervals for each trial \times 4 trials for each condition \times 5 conditions) with 20 intervals for each condition. The mean and standard deviation for the 20 intervals in each condition were calculated individually for each subject. Any intervals that were more than three standard deviations away from the mean for that subject in that particular condition were eliminated from further analysis. This trimming procedure resulted in the elimination of 11 of the 3300 total intervals (.3%). After this trimming, we calculated the mean time between button presses for each subject for each condition by averaging the remaining intervals. These subject means were then used for further analysis.

Fig. 1 plots the mean elapsed time between button presses for each adapting condition across subjects. Note that since the ordinate contains the number of milliseconds that passed between button presses, higher values represent slower tapping. Error bars indicate the within subjects error as suggested by Loftus and Masson (1994). It is clear from the figure that adaptation produced a negative aftereffect; adapting to a slow train of beats resulted in perceiving the test train as faster while adapting to a fast train of beats resulted in perceiving the test train as slower.

To verify this interpretation, we ran two repeated measures ANOVAs. One ANOVA consisted of a single factor with the five adapting trains as separate levels. This

ANOVA verified that the speed of tapping was dependant on the adapting conditions, $F(4, 166) = 12.70$, $p < .001$. This analysis was followed with paired t -test contrasts between various conditions. A second ANOVA was performed on the four conditions that had adapting trains that did not match the test train. This resulted in a 2×2 repeated measures ANOVA with two levels of speed (faster than the test train, slower than the test train) and two levels of distance (near the test train's speed, far from the test train's speed). The main effect of speed was significant, $F(1, 29) = 18.49$, $p < .001$, verifying that fast adapting trains resulted in a slower perception of the test train than slow adapting trains. The main effect of distance from the adapting train's speed was not significant, $F(1, 29) = 2.44$, $p = .129$. However, there was a significant speed by distance interaction, $F(1, 29) = 9.87$, $p = .004$.

The significant interaction resulted because the adaptation effect was strongest for the adapting trains that were nearest to the test train's speed. This was particularly true for the fast adapting beats. With a much faster adapting train ($M = 379.32$, $SD = 7.21$), people did not tap significantly slower, $t(29) = .932$, $p = .359$, than they did with an adapting train that matched the test train ($M = 376.99$, $SD = 6.01$); but with a slightly faster adapting train ($M = 387.17$, $SD = 7.97$), they tapped much more slowly than they did in either the much fast condition, $t(29) = 3.282$, $p = .003$, or the condition in which the adapting train matched the test train, $t(29) = 3.064$, $p = .005$. With the slowest adapting train ($M = 368.34$, $SD = 6.22$), subjects tapped more quickly, $t(29) = 2.89$, $p = .007$, than they tapped with an adapting train that matched the test train ($M = 376.99$, $SD = 6.01$), but they tapped even more quickly when the adapting train was only slightly slower ($M = 366.62$, $SD = 6.07$) than the adapting train. This slightly slower adapting train condition produced taps that were significantly faster than the condition in which the adapting train matched the test train, $t(29) = 4.01$, $p < .001$, but was not significantly different from the very slow condition, $t(29) = .67$, $p = .51$.

In summary, the data points are fit well by a cubic function. This was verified by a follow-up contrast testing for a cubic trend, $F(1, 29) = 21.61$, $p < .001$. This pattern of results matches the predictions of an interval model which consists of time sensitive neurons with broad, overlapping tuning curves. The aftereffect should be strongest when the adapting trains are similar to the test train and the effect should diminish as the speed difference between the adapting train and the test train increases.

Most adaptation effects are rather short lived; thus one might expect that the effect of the adaptation would diminish during the production of multiple responses. Fig. 2 plots the mean time between button presses for the first and last interval produced within a single trial. Separate lines indicated the different speeds of adapting trains. Consistent with the adaptation hypothesis, the size of the aftereffect diminished during the response phase, as the adaptation faded. A 2 (first interval/last interval) \times 5 (very

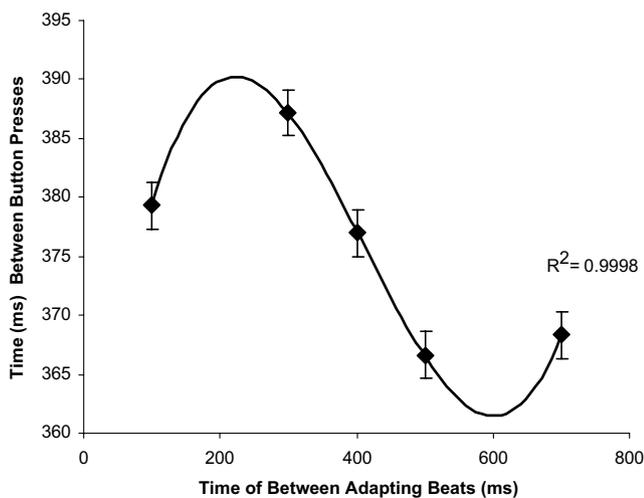


Fig. 1. The mean time between button presses is plotted as a function of the speed of the adapting train for Experiment 1.

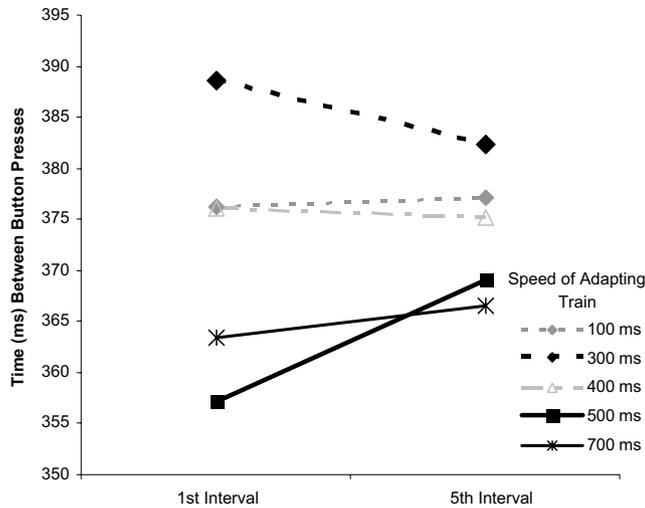


Fig. 2. The mean time between button presses for the 1st and 5th intervals is plotted for each adapting train speed of Experiment 1.

fast, fast, control, slow, and very slow adapting train) repeated measures ANOVA confirmed that there was a main effect of speed of adapting train, $F(4, 116) = 8.730$, $p < .01$. There was no main effect of interval, $F(1, 29) = .347$, $p > .3$, but there was an interval by adapting train interaction, $F(4, 116) = 3.624$, $p < .01$. The interaction results because the adaptation effect diminishes from the first to the fifth interval, with the artificially short intervals produced after adapting to a slow train of beats becoming longer and the artificially long intervals caused by adapting to a fast train of beats becoming shorter.

3. Experiment 2

In Experiment 2, we attempted to replicate the aftereffect from Experiment 1 and investigated whether the aftereffect would remain when the adapting train and the test train were presented to different ears. There is evidence that there are independent timing mechanisms for different efferent connections. This cross ear manipulation should allow us to determine whether there are separate timing mechanisms for independent afferent connections, or whether the two ears impinge on a common timing mechanism.

3.1. Methods

3.1.1. Participants

Fifteen undergraduates (aged 18–21) who had not participated in Experiment 1 participated for course credit or monetary compensation. All participants reported normal audition and all were able to hear the stimuli.

3.1.2. Procedure

Experiment 2 was similar to Experiment 1 except for two changes. We used only the two adapting trains that produced the greatest adaptation effect in Experiment 1

(300 ms between beats and 500 ms between beats) and the control adapting train (400 ms between beats). We also made each sound file monaural so that we could vary which ear received the adapting beats and which ear received the test beats. For each adaptation condition, half of the trials presented the adapting and test beats to the same ear and half of the trials presented them to different ears. We also counterbalanced which ear (right or left) received the adapting train across all conditions. This manipulation resulted in a 2 (same ear/different ears) \times 3 (300 ms, 400 ms, 500 ms adapting train) repeated measures design. Each participant completed four trials in each cell for a total of 24 trials. In all other respects the experiment was identical to Experiment 1.

3.2. Results

The trimming procedure describe for Experiment 1 was used to eliminate outliers that were more than three standard deviations away from a given subject's mean for a given condition. This trimming resulted in the elimination of 10 out of a total of 1800 intervals (.6%). After trimming each subject's average was calculated for each condition and subjected to additional analysis.

Fig. 3 plots the mean elapsed time between button presses for each adapting condition as a function of whether the adapting train and test train were presented to the same or different ears. The data replicate the findings from Experiment 1; the test train was perceived as fast after a slow adapting train and vice versa. In addition, it appears that the effect is due to a central process; it occurs whether the adapting and test train are presented to the same or different ear. A 2 (same ear/different ears) \times 3 (slow, control, fast) repeated measures ANOVA verified this interpreta-

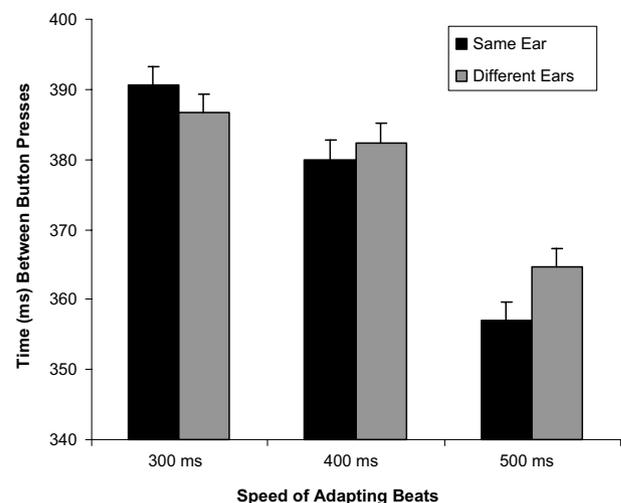


Fig. 3. The mean time between button presses is plotted as a function of the speed of the adapting train for Experiment 2. Black bars represent trials in which the adapting train test train were presented to the same ear. Gray bars represent trials in which the adapting train and test train were presented to different ears.

tion. There was a main effect of the speed of the adapting train, $F(2, 28) = 34.369$, $p < .001$, but no main effect of same vs. different ears, $F(1, 14) = .468$, $p = .505$, and no ear by speed interaction, $F(2, 28) = 2.314$, $p = .117$. A follow-up contrast that collapsed across the same and different ear conditions demonstrated that fast adapting trains resulted in slower button pressing than the control condition, $F(1, 14) = 5.706$, $p = .032$, and that slow adapting trains resulted in faster button pressing than the control condition, $F(1, 14) = 58.982$, $p < .001$.

3.3. Discussion

We still found an aftereffect even when the adapting train and test train were presented to different ears. This finding suggests that there are not separate timing mechanisms for the two afferent connections from the ears. Although there maybe separate timing mechanisms for different efferent connections controlling outgoing motor commands, it seems that incoming perceptual information about time affects a common timer regardless of which ear receives the auditory input. In addition, the fact that the aftereffect maintained across ears is consistent with the interpretation that the site of adaptation is a central location where information from the two ears has been combined rather than an effect of adapting peripheral neurons in the cochlea.

4. Experiment 3

The results from Experiment 2 open the possibility that incoming perceptual information may affect a universal amodal timing mechanism. To test this possibility, in Experiment 3 we presented auditory adapting beats and determined whether they would influence the perceived tempo of a blinking visual stimulus. If afferent sensory connections influence a universal timer, we would expect the adaptation to maintain. If, however, there were separate timing mechanisms for each modality, we would expect the effect to be eliminated.

4.1. Methods

4.1.1. Participants

Twenty-one undergraduates (aged 18–21) who had not participated in the previous experiments participated for course credit or monetary compensation. All participants reported normal audition and all were able to hear the stimuli. In addition all participants reported normal or corrected to normal vision.

4.1.2. Procedure

Like Experiment 2, Experiment 3 only used three speeds (300 ms, 400 ms, and 500 ms between beats) of adapting trains; however, they were presented in stereo. The main difference was that the test beats the participant was to replicate were no longer presented auditorily. Instead, after

the auditory adapting train, a single white dot blinked off and on six times in the center of a black computer screen. The dot was approximately .5 deg of visual angle. The timing of these blinks was identical to the auditory beats from Experiments 1 and 2; the dot onset for 10 ms every 400 ms. The monitor for this experiment was a 20 in. ViewSonic Professional Series P90f running at 100 Hz; thus the dot was drawn on a single monitor refresh and then replaced on the next monitor refresh. The design was a within subjects design and each subject performed five randomly interleaved trials in each condition for a total of 15 trials.

4.2. Results

The same method of trimming as used in the earlier experiments resulted in the elimination of 13 out of a total of 1575 intervals (.8%). After trimming, each subject's average was calculated for each condition and subjected to additional analysis. Fig. 4 plots the mean elapsed time between button presses for each adapting condition. As is clear from the figure, adapting to an auditory set of beats does not systematically affect the subsequent speed judgment of a blinking light. A repeated measures ANOVA comparing the three adapting conditions confirms that there was no significant effect of adapting condition, $F(2, 40) = .159$, $p = .854$.

4.3. Discussion

The fact that the aftereffect disappeared in Experiment 3 suggests the existence of a different timing mechanism for incoming visual and auditory signals rather than an amodal universal timing mechanism. It is possible, however, that our failure to find a cross-modal aftereffect may be explained by attention. Presenting the adapting stream and the test stream in different modes may have made it easier for the participants to selectively filter out the adapting train. There is evidence that attention can modulate the size of an aftereffect (Festman & Ahissar, 2004; Montaser-Kouhsari & Rajimehr, 2004). Although we cannot rule out

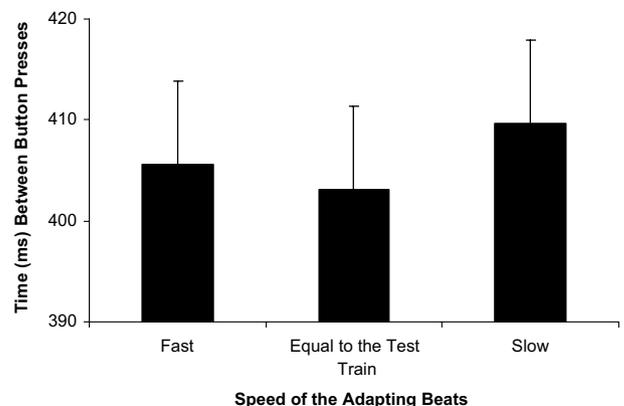


Fig. 4. The mean time between button presses is plotted as a function of the speed of the adapting train for Experiment 3.

this possibility, it seems unlikely. The adapting train was presented auditorily while no other stimuli were present. It seems unlikely that participants could have completely ignored the auditory stimuli without having some other stimulus to attend to.

5. General discussion

We have provided evidence of a negative aftereffect in the perception of rhythm; after adapting to a fast train of beats, the perception of a subsequent train of slower beats is shifted such that it is perceived as being slower than it actually is, and vice versa. In addition, the size of this effect diminishes as the speed discrepancy between the adapting trains of beats and the test trains became more extreme.

This pattern of results is analogous to the tilt aftereffect in vision, and strongly supports the theory that time perception is achieved by a bank of neural units that have broad tuning curves centered on a specific temporal duration. During the adaptation phase of a trial, the presence of a fast train of beats should diminish the response of cells tuned to those fast beats. When a slightly slower train of beats is then presented during the test phase of the trial, the overall output from the bank of time sensitive cells will be shifted towards the slow end of the spectrum given the depressed firing rate of the adapted cells responsible for coding fast temporal durations. The aftereffect should, however, depend critically on the size of the temporal discrepancy between the adapting train and the test train; if the two times are too disparate then the output from the adapted neurons would not contribute to the distributed code of the test train and thus should have no effect.

In theory, one might be able to map the width of the tuning curves of these temporally sensitive neurons using a similar paradigm. To do so would, of course, require a far more detailed sampling of test and adapting train speeds. However, our results provide preliminary data to suggest that the width of a tuning curve may get wider as the preferred duration of a cell gets longer. We found that an extremely fast adapting beat (100 ms between beats) did not influence the subsequent perception of the test train (400 ms between beats), suggesting little overlap between the units coding for the adapting train and the test train. By contrast, an extremely slow adapting train (700 ms between beats) still influenced the perception of the test train, suggesting that the units coding the slow beats overlapped with those coding the test train. This finding suggests that temporal units tuned to beats occurring every 700 ms have wide tuning curves that overlap with the tuning curves of cells tuned to beats occurring every 400 ms, but that units tuned to beats occurring every 100 ms have a narrower tuning curves that did not overlap with 400 ms units' tuning curves. This finding suggests that the width of a temporal unit's tuning curve may scale relative to the preferred tempo; however, additional research investigating the width of tuning curves for various timings is needed to verify this relationship.

In addition, we found that within the auditory modality the effect transferred across ears, suggesting that input from both ears impinge on a common time mechanism. Finally, in Experiment 3 we found that an auditory adapting stream had no effect on the subsequent judgment of the speed of a visual presented rhythm. This cross-modal finding supports two theoretically important conclusions.

First, Experiment 3 suggests that adapting to an auditory rhythm influences a perceptual mechanism rather than a motor mechanism. If the effect was caused by motor adaptation, there should have been little difference in the results for Experiments 1 and 3, since both experiments consisted of identical adapting trains and motor responses. The finding that there was an effect for Experiment 1 but not for Experiment 3, in which the input modality between the adapting train and test train changed, suggests that adaptation affects the perception of subsequent stimuli in the same modality, rather than affecting the motor timing device used to produce the button taps. The conclusion that our task adapted a perceptual rather than a motor mechanism may also explain why our results differ dramatically from a similar experiment performed in the motor domain. [Vaughan, Mattson, and Rosenbaum \(1998\)](#) previously demonstrated that preceding a series of moderately fast finger taps, with a series of fast or slow finger taps produced a hysteresis rather than the type of negative aftereffect we have reported here.

Second, Experiment 3 suggests that different input modalities may affect different timing mechanisms. This finding is interesting in light of claims that visual rhythm information is actually recoded into the auditory domain. [Guttman, Gilroy, and Blake \(2005\)](#) have argued that the perception of visual rhythms is recoded into an auditory signal. Our results seem inconsistent with this finding. In Experiments 1 and 2 we found that adapting to auditory sequences influenced the subsequent perception of an auditory test beat. If the visual test rhythms presented in Experiment 3 were recoded into an auditory signal, one would have expected the same aftereffect as occurred with auditory tests beats, but that did not happen.

Finally, we should note that in Experiments 1 and 2 there was a bias towards speeding up overall responses. That is, the actual temporal delay in the test stimulus was 400 ms, and yet we found that the control conditions (which contained a 400 ms adapting train) were perceived as significantly faster than 400 ms. It is worth noting that others ([Penton-Voak, Edwards, Percival, & Wearden, 1996](#); [Treisman, Faulkner, & Naish, 1992](#); [Wearden & Philippot, 1999](#)) have found that presenting auditory stimuli speeds up the perceived timing of subsequent events. For instance, if one is presented with an 800 ms tone, a train of clicks, and a second 800 ms tone, the duration of the second tone will be judged as lasting longer than the first. The explanation that has been offered for this finding is that the auditory stimuli speeds an internal clock, and thus the second tone appears to take longer since more time has elapsed on the sped up clock. Although our study was not directly designed to investigate the speeding up of an

internal clock, if the clock were running more quickly during the production of beats than during the initial encoding of them one would find the type of speed up we found in Experiments 1 and 2. Additional research would be needed to determine the precise source of this bias.

References

- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 6(10), 755–765.
- Coltheart, M. (1971). Visual feature-analyzers and aftereffects of tilt and curvature. *Psychological Review*, 78(2), 114–121.
- Czeisler, C., Duffy, J., Shanahan, T., Brown, E., Mitchell, J., Rimmer, D., et al. (1999). Stability, precision, and near-24-hour period of the human circadian pacemaker. *Science*, 284(5423), 2177–2181.
- Festman, Y., & Ahissar, M. (2004). Attentional states and the degree of visual adaptation to gratings. *Neural Networks*, 17(5–6), 849–860.
- Fraisse, P. (1963). *The Psychology of time*. New York: Harper and Row.
- Gerwig, M., Dimitrova, A., Kolb, F. P., Maschke, M., Brol, B., Kunnel, A., et al. (2003). Comparison of eyeblink conditioning in patients with superior and posterior inferior cerebellar lesions. *Brain: A Journal of Neurology*, 126(1), 71–94.
- Gerwig, M., Hajjar, K., Dimitrova, A., Maschke, M., Kolb, F. P., Frings, M., et al. (2005). Timing of conditioned eyeblink responses is impaired in cerebellar patients. *Journal of Neuroscience*, 25(15), 3919–3931.
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. *Journal of Experimental Psychology*, 20, 453–467.
- Guttman, S. E., Gilroy, L. A., & Blake, R. (2005). Hearing what the eyes see: Auditory encoding of visual temporal sequences. *Psychological Science*, 16(3), 228–235.
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, 160, 106–154.
- Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, 6, 851–857.
- Ivry, R. B., & Richardson, T. C. (2002). Temporal control and coordination: The multiple timer model. *Brain and Cognition*, 48(1), 117–132. [Special issue: Human movement timing and coordination].
- Ivry, R., Spencer, R. M., Zelaznik, H. N., & Diedrichsen, J. (2002). The cerebellum and event timing. In S. M. Highstein & W. T. Thach (Eds.), *The cerebellum: Recent developments in cerebellar research* (Vol. 978, pp. 302–317). New York: New York Academy of Sciences.
- Ivry, R. B., & Spencer, R. M. C. (2004). The neural representation of time. *Current Opinion in Neurobiology*, 14(2), 225–232.
- Jin, D. Z., Dragoi, V., Sur, M., & Seung, H. S. (2005). Tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex. *Journal of Neurophysiology*, 94(6), 4038–4050.
- Keele, S. W., Nicoletti, R., Ivry, R. I., & Pokorny, R. A. (1989). Mechanisms of perceptual timing: Beat-based or interval-based judgements? *Psychological Research*, 50(4), 251–256.
- Lewis, P., & Miall, R. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Current Opinion in Neurobiology*, 13(2), 250–255.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, 1(4), 476–490.
- Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience*, 27, 307–340.
- Mitchell, D. E., & Muir, D. W. (1976). Does the tilt aftereffect occur in the oblique meridian? *Vision Research*, 16(6), 609–613.
- Montaser-Kouhsari, L., & Rajimehr, R. (2004). Attentional modulation of adaptation to illusory lines. *Journal of Vision*, 4(6), 434–444.
- Paradiso, M. A., Shimojo, S., & Nakayama, K. (1989). Subjective contours, tilt aftereffects, and visual cortical organization. *Vision Research*, 29(9), 1205–1213.
- Pashler, H. (2001). Perception and production of brief durations: Beat-based versus interval-based timing. *Journal of Experimental Psychology: Human Perception and Performance*, 27(2), 485–493.
- Penton-Voak, I. S., Edwards, H., Percival, A., & Wearden, J. H. (1996). Speeding up an internal clock in humans? Effects of click trains on subjective duration. *Journal of Experimental Psychology: Animal Behavior Processes*, 22(3), 307–320.
- Perrett, S. P., & Mauk, M. D. (1995). Extinction of conditioned eyelid responses requires the anterior lobe of cerebellar cortex. *Journal of Neuroscience*, 15(3, Pt 1), 2074–2080.
- Perrett, S. P., Ruiz, B. P., & Mauk, M. D. (1993). Cerebellar cortex lesions disrupt learning-dependent timing of conditioned eyelid responses. *Journal of Neuroscience*, 13(4), 1708–1718.
- Schirmer, A. (2004). Timing speech: A review of lesion and neuroimaging findings. *Cognitive Brain Research*, 21(2), 269–287. [Special issue: Neuroimaging of interval timing].
- Sohn, M.-H., & Carlson, R. A. (2003). Implicit temporal tuning of working memory strategy during cognitive skill acquisition. *American Journal of Psychology*, 116(2), 239–256.
- Spencer, R. M. C., & Ivry, R. B. (2005). Comparison of patients with Parkinson's disease or cerebellar lesions in the production of periodic movements involving event-based or emergent timing. *Brain and Cognition*, 58(1), 84–93.
- Treisman, M., Faulkner, A., & Naish, P. L. (1992). On the relation between time perception and the timing of motor action: Evidence for a temporal oscillator controlling the timing of movement. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, 45A(2), 235–263.
- Vaughan, J., Mattson, T. R., & Rosenbaum, D. A. (1998). The regulation of contact in rhythmic tapping. In D. A. Rosenbaum & C. E. Collyer (Eds.), *Timing of behavior: Neural, psychological, and computational perspectives* (pp. 195–211). Cambridge, MA, USA: The MIT Press.
- Wainwright, M. J. (1999). Visual adaptation as optimal information transmission. *Vision Research*, 39(23), 3960–3974.
- Wearden, J. H., & Philpott, T. (1999). Speeding up and (...relatively...) slowing down and internal clock in humans. *Behavioural Processes*, 46, 63–73.
- Wever, R. (1986). Characteristics of circadian rhythms in human functions. *Journal of Neural Transmission. Supplementum*, 21, 323–373.
- Wing, A. M., & Kristofferson, A. B. (1973). Response delays and the timing of discrete motor responses. *Perception & Psychophysics*, 14(1), 5–12.
- Wright, B. A., Buonomano, D. V., Mahncke, H. W., & Merzenich, M. M. (1997). Learning and generalization of auditory temporal-interval discrimination in humans. *Journal of Neuroscience*, 17(10), 3956–3963.