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RESEARCH ARTICLE

Sleep-dependent consolidation benefits fast transfer of time interval training

Lihan Chen[1,2] · Lu Guo[3] · Ming Bao[3]

Abstract Previous study has shown that short training (15 min) for explicitly discriminating temporal intervals between two paired auditory beeps, or between two paired tactile taps, can significantly improve observers' ability to classify the perceptual states of visual Ternus apparent motion while the training of task-irrelevant sensory properties did not help to improve visual timing (Chen and Zhou in Exp Brain Res 232(6):1855–1864, 2014). The present study examined the role of 'consolidation' after training of temporal task-irrelevant properties, or whether a pure delay (i.e., blank consolidation) following pretest of the target task would give rise to improved ability of visual interval timing, typified in visual Ternus display. A procedure of pretest–training–posttest was adopted, with the probe of discriminating Ternus apparent motion. The extended implicit training of timing in which the time intervals between paired auditory beeps or paired tactile taps were manipulated but the task was discrimination of the auditory pitches or tactile intensities, did not lead to the training benefits (Exps 1 and 3); however, a delay of 24 h after implicit training of timing, including solving 'Sudoku puzzles,' made the otherwise absent training benefits observable (Exps 2, 4, 5 and 6). The above improvements in performance were not due to a practice effect of Ternus motion (Exp 7). A general 'blank' consolidation period of 24 h also made improvements of visual timing observable (Exp 8). Taken together, the current findings indicated that sleep-dependent consolidation imposed a general effect, by potentially triggering and maintaining neuroplastic changes in the intrinsic (timing) network to enhance the ability of time perception.

Keywords Crossmodal transfer · Perceptual training · Implicit · Consolidation · Ternus display

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Introduction

Perceptual learning is a process in which practice on a perceptual task (such as duration discrimination) improves the performance on that task. The time course and outcome of the perceptual learning can be affected by the task relevancy during the training, the time length and training regimen parameters as well as the potential role of 'sleep' (hence trigging a process of 'consolidation') (Atienza et al. 2004; Durrant et al. 2016; Fenn et al. 2003; Gottselig et al. 2004; Mednick et al. 2002; Molloy et al. 2012). In recent years, researchers have been interested in whether temporal training crossmodally (such as auditory and tactile modalities) leads to benefits for time perception in another modality (the visual modality). The accumulated evidence indicates that crossmodal temporal training does in fact benefit time perception in the visual modality (Bratzke et al. 2012, 2014; Chen and Zhou 2014; Meegan et al. 2000; Merchant et al. 2008; Stevenson et al. 2013; Wright et al. 1997). Much research indicates that a relatively long period of training with perceptual learning is necessary to produce

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this benefit. However, recent studies have shown that the transferred benefits may be acquired very quickly (Bratzke et al. 2014; Chen and Zhou 2014; Molloy et al. 2012). A previous study, using an 'explicit' time training protocol that required participants to compare the (variable) intervals between a pair of visual/auditory/tactile stimuli with a given fixed standard interval between the corresponding stimuli pair (Chen and Zhou 2014), showed that fast training of interval discrimination (about 15 min) was sufficient to improve performance on categorizing the visual apparent motion in Ternus displays (Shi et al. 2010; Ternus 1926), in which the categorization was indeed dependent on the perceived time interval between two Ternus visual frames. The significant observable benefits attained using the fast temporal training protocol, as well as the recent evidence from the rate perception adaptation between different sensory modalities (auditory vs. visual), indicate that our brain could flexibly exploit a 'central clock' to bind multiple modality-specific temporal representations into a cohesive one (Ivry and Schlerf 2008; Levitan et al. 2015).

Recent investigation in this line has also aimed to determine the effect size of the training benefits by manipulating the 'consolidation' interval after the training session. It is generally found that sleep-dependent consolidation facilitates the cognitive functions such as working memory (Diekelmann et al. 2009; Goerke et al. 2015; Stickgold 2005). To investigate the role of consolidation, Bratzke et al. (2014) assessed both auditory and visual discrimination performance (pretest vs. posttest) and provided interim auditory interval training. They found a general transfer benefit from extended consolidation following the training session, but differential effects for either short (5 min) or long (24 h) consolidation. The training effect for the trained auditory modality was independent of the consolidation interval, whereas the transfer effect for the visual modality was larger after 24 h than after 5 min (Bratzke et al. 2014).

The immediate transfer effect of crossmodal temporal training was recently explored in Chen and Zhou (2014), and the authors used visual Ternus display as probes, in which the perceptual classification of Ternus 'element motion' and 'group motion' was based on the perceived time interval between two visual frames that formed the visual Ternus display. In the interim task-relevant training session, a 15-min short task of discriminating the time intervals between two paired auditory beeps or two paired tactile taps improved the subsequent performance of Ternus task. However, this benefit was not observed in the task-irrelevant training protocol. In the task-irrelevant training session, the target time interval between the paired stimuli was manipulated to be varied randomly from 50 to 230 ms, compared to the reference interval of 140 ms within an auditory pair or a tactile pair. The participants received task of discriminating auditory pitches or tactile

intensities between two paired auditory beeps or two paired tactile taps and were ignorant of the time information, although they could implicitly perceive the difference in intervals. This type of implicit training of temporal perception between auditory and tactile events did not facilitate the discrimination of implicit visual timing (on the Ternus display).

As shown in previous studies, attention modulates our subjective perception of time (Coull et al. 2004), and performance on perceiving and producing a given sub-second interval increases with intensive training (Bartolo and Merchant 2009). For the implicit timing protocol in Chen and Zhou (2014), the relatively short (15 min) duration of training was possibly not substantial enough to produce the training benefits. Therefore, we hypothesize that the absence of benefits from the crossmodal implicit time training protocol, as shown in Chen and Zhou (2014), could be reactivated to improve visual timing by intensified training. Moreover, in the above most cited studies, the training transfer effect was only observed with direct training of temporal-related tasks. The further empirical question is whether the consolidation period for a delayed posttest could help implicit training (rather than explicit timing) and hence reactivate the crossmodal transfer benefit, giving that the consolidation could improve and strengthen the (working) memory, which shared partially the neural circuits and oscillatory properties of interval timing and would hence improve the timing ability as a by-product (Gu et al. 2015).

To address the above research hypothesis, we used a pretest–training–posttest design similar to Chen and Zhou (2014) in the present study. In the pretest and posttest, we measured performance on discriminating Ternus motion, with the sensitivies of motion categorization, measured as just noticeable differences (JNDs), reflecting the training benefits. In the training session, implicit training of temporal information (auditory pitch or tactile intensity discrimination, Exps 1–4) or temporal-irrelevant problem-solving task (Exps 5–6—'Sudoku' task) was implemented. We used the Sudoku task as a typical mental exercise that trained working memory and relevant cognitive functions (Chang and Gibson 2011; Grabbe 2011), which could also serve as a manipulation of cognitive task (i.e., raw template) for later consolidation process. In addition, we carried out two control tests, in which either the posttest of Ternus task was launched after a short break of the pretest (Exp 7) or with a delay of 24 h (Exp 8). Note that the pretests and posttests of Ternus motion were implemented in all experiments. The logic underlying above experiments is that if extended task-irrelevant (implicit timing) duration is sufficient to make the training's efficacy tantamount to the one in short but explicit training protocol, we should observe the transfer benefits in visual timing for the type of prolonged, though implicit training protocol. Moreover, we

would expect to observe the benefits after a long period of delay in between the pretest and posttest, due to a consolidation period that would stabilize and enhance the ability of timing performance acquired during the period before the final probe test (i.e., discrimination of Ternus motion).

Methods

Participants

To avoid potential contamination of tasks, we adopted a between-participants design for different training protocols. One hundred and nine volunteers (55 females) took part in seven experiments. The participants were between the ages of 18 and 30, with a mean age of 24.3 years. Sixteen participants were tested for Experiment 1 (auditory pitch discrimination), 14 for Experiment 2 (auditory pitch discrimination, consolidation), 11 for Experiment 3 (tactile intensity discrimination), 16 for Experiment 4 (tactile intensity discrimination, consolidation), 11 for Experiment 5 ('Sudoku' task), 12 for Experiment 6 ('Sudoku' task, consolidation), 13 for Experiment 7 (Ternus baseline, i.e., short rest) and 17 for Experiment 8 (Ternus baseline, i.e., long rest with 24-h delay between pretest and posttest).

All participants reported normal hearing and somatosensory perception and were naïve to the purpose of the study. This study was carried out in accordance with the recommendations of institutional guidelines set by the Ethics Committee, Department of Psychology at Peking University. All experimental protocols were approved by Ethics Committee, Department of Psychology at Peking University. All participants signed informed consent in accordance with the Declaration of Helsinki. The participants were reimbursed on 20 CNY per hour for their time.

Pretest–training–posttest design

Participants received a pretest, then training, then a posttest. The pretest and posttest involved discriminations of Ternus apparent motion (Exps 1–7, no training session in Exp 8). The interim training protocols were task specific and addressed separately. They are described in more detail in the section on training protocols.

Prior to the formal experiment, participants practiced to become familiar with the Ternus displays of element motion (EM) and group motion (GM). A typical Ternus display contains two visual frames. Each frame had two disks, with the second disk of the first frame and the first disk of the second frame being presented at the same location. Observers could perceive either 'element motion,' in which the endmost disk is seen as moving back and forth while the middle disk at the central position remains
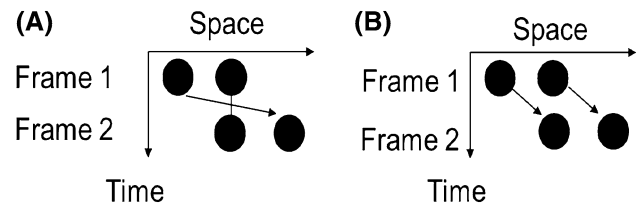

Fig. 1 Ternus display. Two possible motion percepts: **a** element motion (EM) for short ISIs with the middle disk being perceived as static and the outer disk being perceived as moving from one side to the other. **b** Group motion (GM) for long ISIs with the two disks being perceived moving together as a group

stationary, or 'group motion,' in which both disks appear to move laterally as a whole (Fig. 1).

Motion type was determined by the inter-stimulus interval (ISI). Participants saw either typical EM (ISI = 50 ms) or typical GM (ISI = 260 ms). They were asked to discriminate the two types of motions by pressing the left or right mouse button. The assignment of response button to type of motion was counterbalanced across participants. During practice, an incorrect response resulted in immediate feedback on the screen revealing the correct response (EM or GM). The practice session continued until all the participants could achieve an accuracy of 95% within 120 trials.

In Experiments 1–8, the pretests and posttests consisted of determining Ternus apparent motion as either element motion or group motion. The Ternus display was used to measure the implicitly perceived time interval for two Ternus frames in pretests and posttests, as shown in the reported perception of element motion or group motion. Each Ternus display was composed of two frames, with each frame presenting two black disks (12.50 cd/m² in luminance) horizontally for 30 ms on a gray background (which was 17.02 cd/m² in luminance). The two frames shared one disk location at the center of the screen and contained the other two disks on the horizontally opposite side of the center (Shi et al. 2010; Ternus 1926). The diameter of each black disk was 1.6° in visual angle, and the distance between the centers of the two adjacent disks was 3.1°, as shown in Fig. 1. The duration of each frame was 30 ms. For a given trial, the ISI between the two visual frames of the Ternus display was randomly selected from one of the following seven durations: 50, 80, 110, 140, 170, 200 or 230 ms. There were 40 trials for each level of ISI, with 20 trials for the leftward or rightward directions of apparent motion. The presentation order of the 280 trials was randomized for each participant. These trials were divided into four blocks, with 70 trials for each block. Participants took short breaks between blocks.

In Experiments 1–8, for the pretest and posttest of Ternus motion discrimination task, each trial began with a fixation crosspresented at the center of the screen for 300 ms.

A blank display (with a gray background) was then shown for a random duration of 300–500 ms, followed by a Ternus display with a variable ISI (50, 80, 110, 140, 170, 200 or 230 ms) between the two frames. After a blank screen of 300 ms, a question mark appeared to prompt participants to make a two-alternative forced-choice response, indicating whether they had perceived EM or GM. The next trial began 500 ms after the participant pressed the button.

Training protocols and procedures

Experiments 1 and 2: Extended (and implicit) auditory empty-interval training and consolidation

In Experiments 1 and 2, temporal intervals (from 50 to 230 ms) were implicitly perceived and were task-irrelevant. They were the same as those in Experiment 6 (auditory pitch discrimination) conducted by Chen and Zhou (2014), with a fixed standard interval of 140 ms and random comparison interval from 50 to 230 ms. In our study, however, the number of trials was doubled (336 trials), which participants took about 30 min (including the break during experiment) to complete, to compensate for the decreased attention in implicit training when the number of trials were reduced (Coull et al. 2004). In Experiment 1, two paired auditory beeps were presented in each trial. The beeps were delivered through binaural headphones, with one pair having a standard pitch frequency of 1000 Hz and the other pair having a frequency from 850 to 1150 Hz (with 50 Hz as a step size). One paired auditory beeps have a fixed time interval of 140 ms in between, while the interval between another paired auditory beeps varied randomly from 50 to 230 ms. The order of the presentation with reference auditory pair (with interval as 140 ms) and the comparison pair was randomized and counterbalanced. Participants were asked to discriminate which tone pair had a higher frequency, but were ignorant of the perceived differences in intervals.

In Experiment 2, we reduced the trials to make the experimental conditions comparable with those explicit temporal training protocols used in Chen and Zhou (2014). Secondly, we tried to implement the experimental logic that a consolidation period following the 'short' interim training could still help to observe the benefits of crossmodal transfer. After the training of discrimination of auditory pitches, participants did not attend the posttest immediately. Instead, there was a time delay of 24 h after the training session.

Experiments 3 and 4: Extended (and implicit) tactile empty-interval training and consolidation

In Experiment 3, two paired tactile taps were given to the tip of the left middle finger. The tactile stimuli were produced using solenoid actuators with embedded cylinder metal tips tapped to the tip of the left middle finger (Heijo Box, Heijo Research Electronics, UK). The Heijo Box which we used for presenting tactile stimuli had a controller panel for setting the intensity of the tap, in which the maximum of intensity is 60 (setting range of intensity from 1 to 60). In the experiment, we used the setting values of 6, 12, 24, 30, 42, 54 and 60 as the seven ascending levels. The value 60 (largest intensity) corresponds to 3.06 watt for tactile output. Before the formal experiment, in a pilot test, the intensity of the tactile tap was calibrated and a medium intensity was set as the standard stimulus (Level 4). The seven intensity levels were then set accordingly, with Level 1 being the weakest in intensity and Level 7 being the greatest in intensity. In Experiment 2, one pair of taps were of standard intensity (medium: Level 4) and the other pair of variable intensities, from Level 1 (the weakest) to Level 7 (the strongest). As in Experiment 1, the reference interval was fixed 140 ms between two taps and the comparison intervals were from 50 to 230 ms. Participants were asked to discriminate which tactile pair had a stronger intensity and were ignorant of the perceived differences in intervals.

Experiment 4 (intensity discrimination) utilized the same training tasks as Experiment 3; however, the number of trials was reduced to 168. The training tasks were not followed immediately by the posttest. Instead, there was a time delay of 24 h after the training test. When that time delay ended, the posttest took place.

Experiment 5 and 6: Sudoku puzzles solving

In this training session, the participants were required to work on five Sudoku puzzles within 15 min, and each puzzle had a total of 9 by 9 cells, with 49 blank cells for filling in Arabic numbers from 1 to 9. Each row/column/diagonal axis must contain all the numbers from 1 to 9 without misses or duplications. Those five puzzles were selected by a screen test of medium level of difficulty. The order of presenting the five Sudoku puzzles was arranged in a Latin square sequence. Each correct answer would receive one point in scoring. The Sudoku task served as a manipulation of cognitive task that helps to improve function of working memory, and the task-triggered brain states which are indirectly relevant with the timing circuits and could be exploited by later consolidation process (Gu et al. 2015). In Experiment 5, the Sudoku task was followed immediately by the posttest of Ternus motion, while in Experiment 6 the time delay between the Sudoku task and the posttest of Ternus motion is 24 h.

Experiment 7 was a control test in which the pretest and posttest of Ternus motion were implemented, with a short break in between.

Experiment 8 was also a control test in which the pretest and posttest of Ternus motion were separated by a time delay of 24 h.

The test room was dimly lit with an average ambient luminance of 0.12 cd/m^2. Visual stimuli were presented on a 22-in. CRT monitor (1024 × 768 pixels; 100 Hz), positioned at eye level. Viewing distance was set to 57 cm, maintained with a chin rest. A headset (Philips, SHM 1900) was used to emit sound stimuli as well as to prevent participants from hearing the faint noise produced by tactile taps. Stimulus presentation and data collection were implemented with computer programs developed with MATLAB 7.1 (MathWorks Inc., Natick, MA) and Psychophysics Toolbox (Brainard 1997; Pelli 1997).

The seven data points (one for each ISI) were fitted to the psychometric curve using a logistic function (Treutwein and Strasburger 1999). The transitional ISI, point of subjective equality (PSE) at which the participant was equally likely to report the two percepts of apparent motion, was calculated by estimating 50% of reporting of group motion on the fitted curve. The just noticeable difference (JND), indicating the resolution of apparent motion discrimination, was calculated as half of the difference between the lower (25%) and upper (75%) bounds of the thresholds in the psychometric curve.

Results

Pretests

For each level of ISI between the two frames, the percentage of GM responses was collapsed over two motion directions.

A one-way analysis of variance (ANOVA) was conducted for the PSEs derived for the eight groups of participants in pretest (Exps 1–8, using Ternus motion as probes). There were no significant differences between PSEs in the eight experiments, $F(7, 109) = 1.716$, $p = 0.114$. The PSEs were 140.9 ± 2.1 ms (associated standard error) for Experiment 1, 128.6 ± 4.6 ms for Experiment 2, 139.9 ± 2.0 ms for Experiment 3, 135.8 ± 4.3 ms for Experiment 4, 139.6 ± 4.6 ms for Experiment 5, 130.4 ± 5.6 ms for Experiment 6, 132.5 ± 4.1 ms for Experiment 7 and 129.8 ± 2.6 ms for Experiment 8.

Comparisons were also made for the JNDs in pretest, which measured the task difficulty and participants' sensitivity in discriminating the two possible percepts of the visual Ternus display. Again, there were no significant differences between the eight experiments, $F(7, 109) = 1.824$, $p = 0.091$. The JNDs were 29.2 ± 1.8 ms for Experiment 1, 31.6 ± 4.9 ms for Experiment 2, 36.9 ± 3.2 ms for Experiment 3, 32.4 ± 2.8 ms for Experiment 4,

28.4 ± 1.8 ms for Experiment 5, 24.2 ± 2.5 ms for Experiment 6, 24.5 ± 2.5 ms for Experiment 7 and 28.1 ± 2.6 ms for Experiment 8. The absence of significant differences between the eight experiments suggests that the participants in them were generally well matched in their ability to discriminate visual apparent motion and to implicitly process time intervals between visual frames.

Training performance

For the probability data from the training session, we first checked if the data from all stimuli levels followed the normal distribution. The nonparametric of one-sample K–S method showed that only the data pattern of middle levels (950 and 1050 Hz in auditory pitches and L3, L4 in tactile intensities) followed normal distribution across the participants. Therefore, we conducted nonparametric K-related sample tests for the training data. The statistics showed that for Experiments 1–4, the trainings were effective and there were significant differences among the proportions across different levels; Chi-square values and p values were 18.47 ($p < 0.01$), 38.08 ($p < 0.001$), 32.31 ($p < 0.001$) and 39.59 ($p < 0.001$) for Experiments 1–4, respectively. Moreover, the K-related sample tests with Kendall's W method showed there was significant difference among the four experiments, with Chi-square values and p values 16.71 ($p < 0.01$). It is clear from Fig. 2 that performance was worse when the pitch frequency or intensity level was close to that of the standard stimuli. The correct rates were lowest in tactile 'consolidation' condition (Exp 4, i.e., with less trials).

The average scores for Sudoku tasks in Experiments 5 and 6 were 56.3 ± 13.4(SE) and 53.4 ± 8.5(SE), and there was no difference between the training scores of the two groups in Experiments 5 and 6, $F(1, 22) = 0.032$, $p = 0.860$, showing the task difficulty was generally equivalent during the two tests.

Pretests versus posttests

To rule out a potential participant-by-participant bias, we calculated the index of the change in PSEs and JNDs across pretest and posttest. The indices are defined as (PSEinital-PSEfinal)/PSEinitial and (JNDinital-JNDfinal)/JNDinitial. Across Experiments 1–8, one-way ANOVAs with PSEs and JNDs as dependent variables and experiments as independent variable showed the main effect of JND was significant, $F(7, 109) = 3.140$, $p < 0.01$; however, the main effect of PSE was not significant, $F(7, 109) = 0.837$, $p = 0.559$. We therefore tested the effects separately for each experiment, as shown in Table 1.

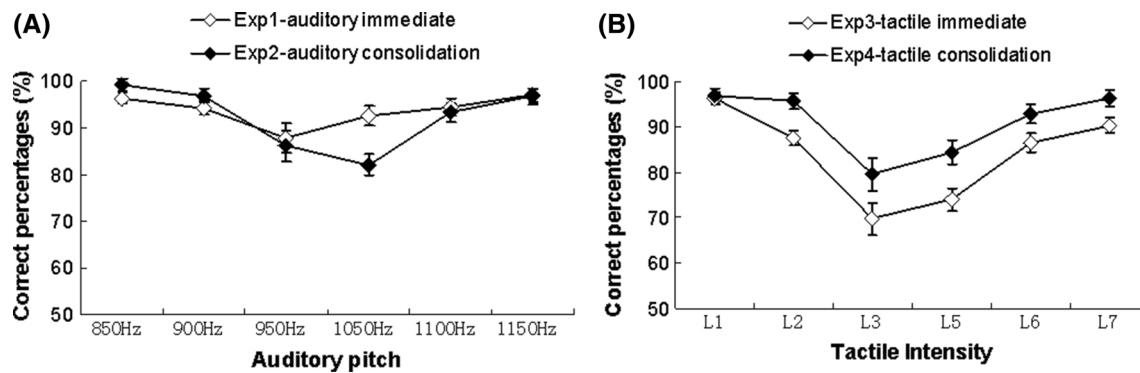Figure 3 illustrates the PSEs and JNDs for the pretest and posttest of Ternus motion for a typical subject in

Fig. 2 Correct response percentages for pitch/intensity discriminations as a function of the pitch frequency (850, 900, 950, 1050, 1100 and 1150 Hz) versus standard pitch (1000 Hz) or as a function of tactile intensity levels (from L1 to L7 except L4) versus standard intensity (Level 4). **a** The *solid line with blank diamonds* depicts the correct percentages in pitch discrimination with immediate posttest of Ternus motion (Exp 1). The *solid line with filled diamonds* depicts the correct percentages in pitch discrimination with a long rest period of 24 h before the posttest of Ternus motion (Exp 2). **b** The *solid line with blank diamonds* the correct percentages in tactile intensity discrimination (Exp 3). The *solid line with filled diamonds* the correct percentages in intensity discrimination with a long rest period of 24 h before the posttest (Exp 4). The *error bars* denote standard error of the mean (SE)

Table 1 Summary of results

Experiment	N	Pre-PSE (ms ± SE)	Post-PSE (ms ± SE)	t	p	Pre-JND (ms ± SE)	Post-JND (ms ± SE)	t	p
Exp 1: auditory pitch training	16	140.9 ± 2.1	141.7 ± 2.5	−0.378	0.710	29.2 ± 1.8	32.2 ± 3.1	−1.407	0.180
Exp 2: auditory pitch consolidation	14	128.6 ± 4.6	129.5 ± 5.4	−0.182	0.859	31.6 ± 4.9	23.8 ± 4.3	2.909	*
Exp 3: tactile intensity training	11	139.9.1 ± 2.0	140.7 ± 2.6	−0.265	0.796	36.9 ± 3.2	42.8 ± 4.7	−1.053	0.317
Exp 4: tactile intensity consolidation	16	135.8 ± 4.3	132.8 ± 5.3	0.695	0.498	32.4 ± 2.8	28.0 ± 2.8	2.206	*
Exp 5: Sudoku task	11	139.6 ± 4.6	143.8 ± 5.9	−0.938	0.370	28.4 ± 1.8	24.6 ± 1.5	1.742	0.112
Exp 6: Sudoku task consolidation	12	130.4 ± 5.6	126.3 ± 4.9	1.381	0.195	24.2 ± 2.5	19.6 ± 2.1	3.105	*
Exp 7: Ternus control	13	132.5 ± 4.1	138.9 ± 3.5	−1.947	0.075	24.6 ± 2.5	24.1 ± 2.0	0.181	0.859
Exp 8: Ternus consolidation	17	129.8 ± 2.6	132.4 ± 4.4	−0.750	0.464	28.1 ± 2.6	21.2 ± 1.4	3.896	**

The table shows the mean values of PSEs and JNDs and the standard errors of the mean (SE) across pretest and posttest in the eight experiments. A single star indicates the statistical significance at $p = 0.05$ level and two stars $p = 0.01$ level

Experiment 3. We obtained the PSEs and JNDs for each experiment and plot the bars as shown in Fig. 4.

Experiments 1 and 2 The mean PSEs in Experiment 1 were 140.9 ± 2.1 and 141.7 ± 2.5 ms for the pretest and posttest, respectively. The difference between them was not significant, $t(15) = −0.378$, $p = 0.710$. The difference between the mean JNDs for the pretest (29.2 ± 1.8 ms) and posttest (32.2 ± 3.1 ms) was also not significant, $t(15) = −1.407$, $p = 0.180$. Thus, auditory pitch intensive training seemed unable to improve the participants' performance on discriminating the apparent motion in Ternus display.

In Experiment 2, the PSEs showed no significant difference between the pretest (128.6 ± 4.6 ms) and the posttest (129.5 ± 5.4 ms), $t(13) = −0.182$, $p = 0.859$, but the JNDs did have an effect (31.6 ± 4.9 vs. 23.8 ± 4.3 ms), $t(13) = 2.909$, $p = 0.012$. Therefore, the consolidation period after the training of discrimination of auditory pitch improves the sensitivity of classifying Ternus motion.

Experiments 3 and 4 Again, in Experiment 3, the extensive tactile intensity training imposed no influence on the performance for discriminating visual apparent motion in Ternus display. T tests showed no significant differences
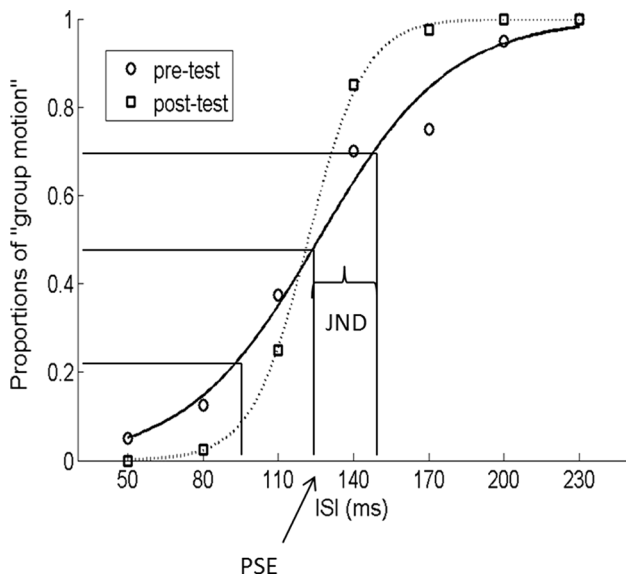
Fig. 3 Psychometric curves for a typical participant in Experiment 3. The *solid curve with circles* represents the proportion of GM responses as a function of the ISI between the two Ternus frames in the pretest. The *dotted curve with squares* represents GM responses in the posttest. PSE refers to the ISI value that corresponds to the 50% point of *Y*-axis, while JND is equal to the half of ISI difference between the two ISI values which correspond to 75 and 25% points on *Y*-axis, respectively

between them, $t(10) = -0.265$, $p = 0.796$ for PSE and $t(10) = -1.053$, $p = 0.317$ for JND.

In Experiment 4, a consolidation period after training of discrimination of tactile intensity improved the sensitivity of judging Ternus apparent motion. *T* tests showed no significant differences between pre-PSE and post-PSE, $t(15) = 0.695$, $p = 0.498$ for PSE, but significant difference between pre-JND and post-JND, $t(15) = 2.206$, $p < 0.05$ for JND.

Experiments 5 and 6 In Experiment 5, the PSEs were 139.6 ± 4.6 and 143.8 ± 5.9 ms for the pretest and posttest, $t(10) = -0.938$, $p = 0.370$. The JNDs were 28.4 ± 1.8 and 24.6 ± 1.5 ms for the pretest and posttest, $t(10) = 1.742$, $p = 0.112$.

In Experiment 6, the PSEs were 130.4 ± 5.6 and 126.3 ± 4.9 ms for the pretest and posttest, $t(11) = 1.381$, $p = 0.195$. The JNDs were 24.2 ± 2.5 and 19.6 ± 2.1 ms for the pretest and posttest, $t(11) = 3.105$, $p < 0.05$. These results indicate that after receiving the task of temporal-irrelevant task ('Sudoku' puzzle solving), a consolidation period of 24 h (i.e., rest) played an important role to improve the sensitivities of perceiving Ternus motion.

Experiments 7 and 8 Both the two control tests showed there was no significant difference between the pretest and posttest in the PSEs. However, JND was reduced across pretest and posttest in Experiment 8, $t(16) = 3.896$

$p < 0.01$. The JND was not changed in Experiment 7, $t(12) = 0.181$, $p = 0.859$.

Moreover, we selected all the 'consolidation' experiments and carried out between-experiments analysis. The main effect of experiments was not significant, $F(3, 55) = 0.410$, $p = 0.746$. For the PSEs across pretest and posttest, there was no significant main effect, $F(1, 55) = 0.176$, $p = 0.677$. The interaction effect between PSEs and experimental conditions was also not significant, $F(3, 55) = 0.588$, $p = 0.625$.

For the JNDs, the main effect of experimental conditions was not significant, $F(3, 55) = 1.490$, $p = 0.227$. However, there were significant differences across the pretest and posttest, $F(1, 55) = 32.830$, $p < 0.001$. The interaction effect between factors of experiments and JNDs was not significant, $F(3, 55) = 0.657$, $p = 0.582$.

Therefore, the data pattern of JND changes showed that in all consolidation conditions no matter in the 'crossmodal' case where in the interim training session the task was from a third modality—auditory and tactile modality (Exps 2, 4), or in the 'unimodal' situation, where stimuli from the same modality (visual modality) were given (Exps 6, 8), unified benefits for improving Ternus task after a consolidation (rest) period of 24 h, was observed.

Discussion

Timing in the ranges from tens to hundreds of milliseconds subserves a wide range of sensory and motor tasks, including speech perception, motion perception, motor coordination and crossmodal interaction. Evidence has shown that improvements in temporal discrimination generalize across sensory modalities (Bratzke et al. 2012, 2014; Nagarajan et al. 1998; Stevenson et al. 2013; Westheimer 1999; Wright et al. 1997), and even from a sensory modality to a motor task (Karmarkar and Buonomano 2003; Meegan et al. 2000). But the crossmodal transfer between different sensory modalities was asymmetric. This asymmetry is reflected in the specific direction of transfer between different types of modalities (such as from the auditory modality to the visual modality, but not from the visual modality to the auditory modality). Importantly, for the crossmodal temporal transfer to take effect, the stimuli for learning should be in the temporal domain and be task-relevant (Bratzke et al. 2012, 2014; Karmarkar and Buonomano 2003; Meegan et al. 2000; Nagarajan et al. 1998; Stevenson et al. 2013; Westheimer 1999; Wright et al. 1997).

However, previous studies usually employed an intensive training protocol, with the length of training lasting from days to approximately 2 weeks. Further, the training task was of explicit one, in which participants either made perceptual discrimination of temporal intervals (or
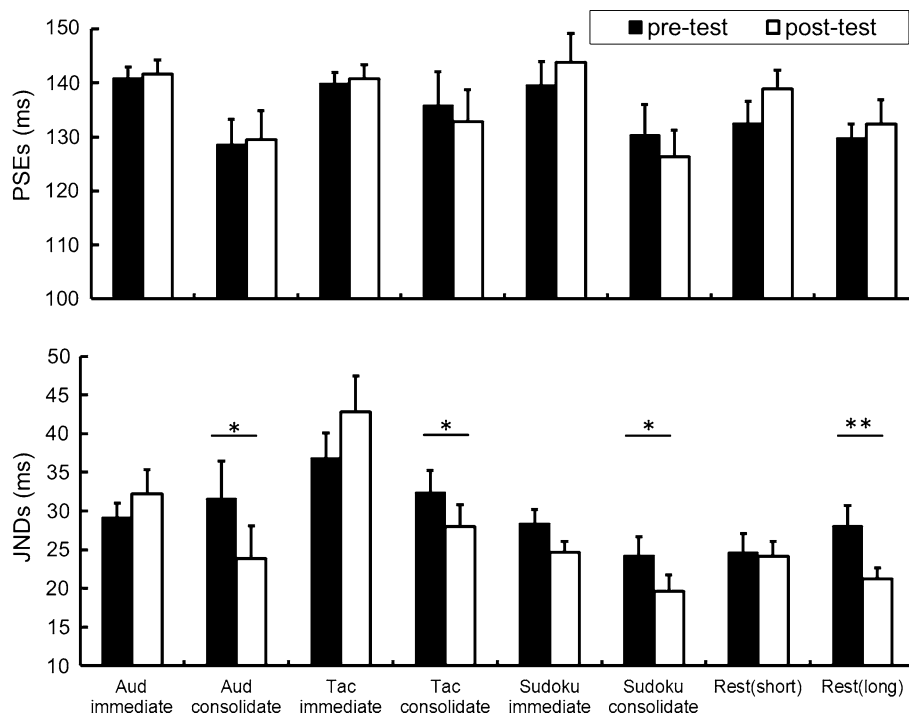
Fig. 4 PSEs and JNDs for pretests and posttests of discriminating the Ternus apparent motion in the eight experiments. The *black bars* indicate values of PSEs or JNDs in the pretests, and the *white bars* indicate values of PSEs and JNDs in the posttests. The *error bars* represent the standard errors of mean. 'Aud Immediate'—extensive trials for auditory pitch training followed by immediate posttest of Ternus motion; 'Aud consolidate'—consolidation period of 24 h after auditory pitch training; 'Tac immediate'—extensive trials for tactile intensity training followed by immediate posttest of Ternus motion; 'Tac consolidate'—consolidation period of 24 h after tactile intensity

training; 'Sudoku-immediate'—Sudoku puzzle solving followed by immediate posttest of Ternus motion. 'Sudoku consolidate'—Sudoku puzzle solving in between the pretest and posttest of Ternus motion (with 24-h delay in between the pre- and posttests). 'Rest (short)'—posttest of Ternus motion follows immediately after pretest of Ternus motion; 'Rest (long)'—posttest of Ternus motion follows after pretest of Ternus motion, with a delay period of 24 h. The *stars* showed the statistical significance of $p = 0.05$ (*single star*) or $p = 0.01$ level (*double stars*)

durations) or produced a given duration. In temporal tasks, explicit and implicit time trainings take different forms. Tasks that require explicit training or perception were duration discrimination, tapping and even motor-related tasks, such as intermittent circle drawing (Zelaznik et al. 2002). In contrast, tasks that require implicit time training/perception involve either of two situations. In one, it is an emergent property of the control process that is relatively independent of an explicit temporal representation. This is seen in the current visual Ternus apparent motion, in which one observer can discriminate the state of perceived element motion versus group motion based on the implicitly perceived interval between two visual Ternus frames. In the other, implicit time training/perception refers to a situation in which attention is not directed to the temporal task, such as discrimination of pitch differences toward paired auditory beeps with variable intervals. While it is of note that explicit and implicit time perceptions mobilize different neural mechanisms (Coull and Nobre 2008; Wiener et al. 2010), this has not been examined in crossmodal transfer tasks. There remains the possibility that training of

the non-temporal factors might contribute to improve the implicit time perception.

Recently, using visual Ternus motion, Chen and Zhou (2014) have shown a fast crossmodal temporal transfer effect. After 15 min of explicit training using auditory/tactile intervals of 50–230 ms discrimination (task-relevant, time-dependent training), participants improved their ability to categorize visual Ternus apparent motion (with decreased JNDs). However, no such benefits occurred for implicit interval training protocols, in which the task involved auditory pitch/tactile intensity discrimination (i.e., discrimination of non-temporal information) and the empty intervals between paired auditory/tactile stimuli were implicitly perceived (Chen and Zhou 2014).

One might argue the non-observable of training benefits in task-irrelevant auditory pitch/tactile intensity discrimination task in Chen and Zhou (2014) is probably due to the insufficient time for training. However, the current dataset did not largely favor this possibility. The extended training of discriminations for auditory pitch (Exp 1) and tactile intensity (Exp 3) did not help improve performance on

Ternus motion discrimination. This was true even though the differences of empty intervals between two paired tones and two paired taps during the training session were manipulated and according to post hoc interviews, could be implicitly perceived by the participants. This finding indicates that the cues of implicit training are inertia in changing the perceived (visual) sensory timing, due to the potential biological constraints. Indeed, evidence has shown that explicit timing and implicit timing mobilize different neural circuits. This differentiation should be taken into account in addressing the role of implicit time training upon the target task with timing factor explicitly involved. Wiener et al. (2010) used data from a meta-analysis to support the idea that there is a left-hemispheric bias (left supramarginal gyrus of the inferior parietal cortex) for implicit time perception, while there is dominant right supramarginal gyrus activation for processing explicit timing. Furthermore, distinct neural representations and biological constraints in implicit time perception have limited the neural coupling between different types of time-related processing, especially within short temporal scales of training (Coull and Nobre 2008; Wiener et al. 2010). Therefore, even for a relatively long duration of implicit training, it was likely not ready to form a stable representation of the time information from modalities with higher temporal resolution to calibrate the visual timing in Ternus display (Eagleman 2008; Eagleman and Pariyadath 2009). Thus, this renders the transfer benefits for implicit time training unobservable. With that said, currently we cannot rule out the possibility of any quantitative improvement when more trials during training of implicit timing are implemented.

Interestingly, the critical finding here is that the benefits missing from implicit interval training seemed to be reactivated by a consolidation period of 24 h after the task-irrelevant (implicit time and incongruent to probe stimuli in time property) training/perceptual learning (Exps 2 and 4). This finding replicates that of Bratzke et al. (2014) and extends the exploration of the explicit training domain to an implicit one. It has been revealed that the time course of perceptual learning can be divided into two stages: (a) a fast within-session improvement, such as in Chen and Zhou (2014) and (b) a slowly developing improvement that occurs during a consolidation phase lasting at least 6–8 h (Atienza et al. 2002; Karni and Bertini 1997). Bratzke et al. (2014) found that consolidation is important for the cross-modal transfer of perceptual learning. Further, they found that the transfer of perceptual learning from the auditory to the visual modality benefits more from an extended consolidation interval (24 h) than from a short interval (5 min). Indeed, fast perceptual learning has been observed in perceptual learning of spatial discrimination long time ago (Fahle 2005). In Fahle (2005), an asymptote of perceptual learning for vernier detection was reached fastly during a training session. Moreover, training again a day after led to a new asymptotic level, which suggested a role of consolidation in securing/improving the learning effect. Analogously, the time course of learning in Fahle (2005) might be materialized in current study, although the current data are not sufficiently enough to reveal the fine-tuned course within about 15 min of training. The current findings suggest that after a consolidation of 1 day, the training perhaps again lead to a new (putative) asymptotic level and that is why we observed the transfer benefits even with implicit training protocol. With the protocol of interim crossmodal training task, the information of boosted (higher) temporal resolution in either auditory or tactile could be strongly rewired or connected that might be exploited to serve as an amodal temporal reference by a centralized timing mechanism and contribute to improve the visual interval perception (in Ternus display) (Allman et al. 2014; Buhusi and Meck 2005; Durrant et al. 2016; Dyjas et al. 2012; Ivry and Schlerf 2008; Chklovskii et al. 2004).

These results were consensus with a memory-related account for perceptual learning in temporal discrimination (Bratzke et al. 2012). Indeed, the encoding of interval timing in terms of oscillatory activities (such as theta and delta oscillations) has been shared by the memory mechanism in general (Gu et al. 2015; Moon and Anderson 2013). There are some striking similarities in the shared neuroanatomical features between interval timing and (working) memory, and the electrophysiological evidence from rodents and primates provided similar firing rates of neural spikes during timing task (Gu et al. 2015; Lisman 2010). Therefore, functionally, interval timing reflects a specialized form of (working) memory in that an internal representation of time needs to be maintained so as to control temporal processing even in the absence of an external stimulus (Taatgen et al. 2007).

In Experiment 6, Sudoku task plus a consolidation period of 24 h improved the performance of Ternus task. Sudoku puzzle solving requires a combination of critical cognitive functions such as attention and memory and contrasts to the cognitive states of mind wanders (Chang and Gibson 2011; Grabbe 2011). In addition to preventing aging and potentially exercise/improve the intelligence, a by-product of Sudoku puzzle solving is the elevated attention, and a concomitant of perceived expansion of time interval (Terhune et al. 2014; Tse et al. 2004). The cognitive faculties including the Sudoku task, even seemingly no connection with timing, could result in a change in the current memory state or by updating the problem-specific memory representations and hence indirectly activates the shared neural circuits of interval timing (Lisman 2010; Lisman and Idiart 1995). In this means, this integrative nature between interval timing and other cognitive process provides a venue in which training of non-temporal tasks

could help to improve the time perception, when a delay period of (memory) consolidation is given (Taatgen et al. 2007). This reasoning was also supported by the unimodal test of Ternus motion with a blank consolidation period of 24 h (Exp 8). For the pure 'rest' manipulation, even in the absence of an ongoing stimulus, neural oscillations in the brain continue in time, oscillatory fluctuations (say, after the pretest of Ternus motion) that reside in the recurrent networks continue to be sustained over the course of time, regardless of the existence of an external stimulus. The shared cortical representations from memory-related activities enhanced the subsequent, delayed performance of visual Ternus task. Alternatively, a moderate and tantamount level of 'cognitive training' even during the pure 'rest' session could improve the sensitivities of perceiving Ternus motion. Since we did not control the participants' activity during the long rest of 24 h (Exp 8), they might well perform various cognitive tasks such as exploiting their working memory. Therefore, those activities during the rest would serve as a kind of 'cognitive training' and we obtained the similar results as with those conditions of carrying out specific tasks (Exps 2, 4 and 6).

Despite the utility of the current study, it has some limitations. In the experiments here, we used a trial-by-trial training protocol. In order to reduce potential response bias, a between-participants design was adopted. This poses some difficulty in pinpointing the exact time course of the training/learning efficacy due to the randomized trial sequence, as well as to the potential variances between participants. Moreover, the training benefits we observed might mobilize a suite of complex information processing stages. In the experiments presented here, we used classical psychophysics procedures with a standard stimulus and comparison stimuli in each experimental trial. This theoretically requires a decision process based on the reference to standard stimulus and the updated comparison stimulus (Shi et al. 2013). Even the presentation order of standard stimulus and comparison stimulus was randomized, there is a possibility of memory mixing during the experimental procedure that had introduced and emphasized the role of memory. Moreover, how attention resources are redistributed to a different temporal domain (Coull et al. 2004) after time-relevant (such as in implicit timing tasks for pitch/intensity discrimination) or time-irrelevant (such as in Sudoku task) and how the plastic changes in brain activities are involved, i.e., what exactly is learned (Bueti et al. 2012) remains a topic for further exploration.

Together with the study of Chen and Zhou (2014), with visual Ternus display as probes, there exists a dissociation between time-dependent and time-independent factors in achieving the training benefits. First, for explicitly training,

the interval discrimination task from a third modality (auditory or tactile modality) helps to enhance the timing sensitivities of visual events in Ternus display. Second, we have shown a general benefit arising from a period of long rest (24 h) even without specific interim cognitive training tasks between the pretest and posttest sessions. This indicates a pivotal role of sleep-dependent consolidation process in obtaining the benefits of fast transfer of interval timing. The present results also echo the findings from a large body of literature showing sleep-dependent benefits concerning mainly memory functions (Born and Wilhelm 2012; Censor et al. 2006; Diekelmann et al. 2009; Durrant et al. 2016; Goerke et al. 2015; Stickgold 2005). As we discussed above, the shared neural underpinnings between interval timing and memory make the improvement of interval timing possible. In the case of implicit training, since the time interval (in Ternus display) was not directly targeted, hence all the relevant improvement essentially relies on non-temporal factors. To substantiate the role of non-temporal factors and the emergent role of consolidation in improving the implicit visual timing, in future studies, we should formulate a testable hypothesis with more cognitive training paradigms and examine whether an interim 24-h consolidation period would produce observable improvements in the posttest with respect to the pretest in the Ternus training/test experiment. Alternatively, we could also consider setting up a control test by depriving sleep (for 1 day) to examine rigorously the role of sleep-dependent consolidation.

In conclusion, the current findings indicate that the benefits of fast training were visible when a sleep-dependent consolidation period was implemented after either implicit temporal training or temporal-irrelevant task training. The benefits of consolidation process were robust and span over either interim training session of unimodal or crossmodal tasks, across either temporal-relevant or temporal-irrelevant domains. Though the exact mechanisms of the consolidation are far from clear, the results showed that perception of implicit visual timing is plastic and is an incidental process along with many perceptual and cognitive tasks.

Author contributions L.C. and M.B. designed the experiments, and L.C. wrote the main manuscript. L.C. and L.G. performed the experiments and did data analysis. All authors reviewed the manuscript.

Compliance with ethical standards

Conflict of interest There are no competing financial interests.

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