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Transfer of learned perception of sensorimotor simultaneity

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Abstract Synchronizing a motor response to a predictable sensory stimulus, like a periodic flash or click, relies on feedback (somesthetic, auditory, visual, or other) from the motor response. Practically, this results in a small (<50 ms) asynchrony in which the motor response leads the sensory event. Here we show that the perceived simultaneity in a coincidence-anticipation task (line crossing) is affected by changing the perceived simultaneity in a different task (pacing). In the pace task, human subjects were instructed to press a key in perfect synchrony with a red square flashed every second. In training sessions, feedback was provided by flashing a blue square with each key press, below the red square. There were two types of training pace sessions: one in which the feedback was provided with no delay, the other (adapting), in which the feedback was progressively delayed (up to 100 ms). Subjects' asynchrony was unchanged in the first case, but it was significantly increased in the pace task with delay. In the coincidence-anticipation task, a horizontally moving vertical bar crossed a vertical line in the middle of a screen. Subjects were instructed to press a key exactly when the bar crossed the line. They were given no feedback on their performance. Asynchrony on the line-crossing task was tested after the training pace task with feedback. We found that this asynchrony to be significantly increased even though there never was any feedback on the coincidence-anticipation task itself. Subjects were not aware that their sensorimotor asynchrony had been lengthened (sometimes doubled). We conclude that perception of

simultaneity in a sensorimotor task is learned. If this perception is caused by coincidence of signals in the brain, the timing of these signals depends on something—acquired by experience—more adaptable than physiological latencies.

Keywords Synchronization · Anticipation · Pacing · Perceptual timing · Coincidence detection

Introduction

The synchronization of an action (e.g., a tap) with a predictably occurring stimulus has to rely on information on the timing of this action provided by either the signal that initiates the action or its feedback from somesthetic, auditory, and visual modalities. Recent studies favor the use of feedback (Paillard 1949; Kolers and Brewster 1985; Aschersleben and Prinz 1997). However, it is found that the action usually precedes the predictable sensory event, a phenomenon known as *negative asynchrony* (Aschersleben 2002). Asynchrony has been shown to exist for all stimulus modalities with varying degrees of strength and variability among subjects. Auditory stimuli seem to produce the largest asynchrony with the least amount of variance while visual stimuli produce a smaller asynchrony with a greater amount of variance (Kolers and Brewster 1985; Chen et al. 2002). Much of the variance can be explained by the noise associated with processing time in each modality. However, the neural reason behind the asynchronous response time is still unclear.

The primary hypothesis proposed to describe asynchrony invokes the differences in latencies associated with the particular sensory events involved (Aschersleben and Prinz 1995, 1997; Mates and Aschersleben 2000; Aschersleben et al. 2001; Aschersleben 2002). For example, let us assume that the brain has to synchronize a motor response (e.g., finger tap) with a predictably occurring click. Let us assume also that the brain uses the

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kinesthetic feedback from the tap and, to determine event simultaneity, compares the timing of the received auditory and kinesthetic signals. If auditory processing takes less time than tactile and kinesthetic processing, then even though click and tap are rigorously simultaneous in the *physical* world, the tap would be experienced as leading the click. Subjects would likely attempt to compensate the perceived delay. If, in the same task, an additional feedback, such as the sound produced by pressing the key, is made available, subjects may use it to improve the synchrony of their action (given the probably equal auditory latencies, to click and key). In general, the timing of a subject's response to a stimulus should be found to depend on the delay of the feedback (Aschersleben and Prinz 1995, 1997). This has been shown experimentally by manipulating the delay of feedback and recording the timing of taps (Mates and Aschersleben 2000). Other procedures have been tested for modifying the neural transmission and central processing times: (1) removal of sensory feedback (e.g., via local anesthesia of the tapping finger) (Aschersleben et al. 2001), (2) increasing tapping force (Aschersleben 2002), (3) changing the duration of the pace stimulus (Vos et al. 1995), and (4) changing the interval duration between stimuli (Mates et al. 1992).

The latency hypothesis has recently been amended to incorporate a sensory accumulator model (Aschersleben et al. 2001; Aschersleben 2002), which takes into account processing times needed to generate a central representation of synchronous events. But, even this modified latency hypothesis explains sensorimotor synchronization as due to the hardware. If latency depends on the hardware, theoretically it should not be easily modifiable. Yet, it has been shown that trained musicians are able to reduce significantly the negative asynchrony associated with paced auditory stimuli, and, in some cases, individuals such as professional pianists even respond nearly exactly in time with the stimulus (Repp 1999). This suggests that the perception of simultaneity between sensory events (auditory, kinesthetic, and visual in any combination) may be adaptively recalibrated. Indeed, simultaneity between a paced auditory and visual event can be manipulated (Fujisaki et al. 2004). For this purpose, Fujisaki et al. introduced a delay in an adaptive training phase, such that one sensory event either lagged or led the other event. They found that their subjects shifted their point of subjective simultaneity in the direction of the adapted change, and such changes could be transferred to other types of stimuli. To show that sensorimotor adaptation occurs, Cunningham et al. (2001) used a paradigm in which subjects were asked to navigate an object (a toy plane), with a mouse, through an "obstacle field" on a computer screen. Then, a temporal delay (up to 200 ms) was introduced between the command from the mouse and the movement of the plane on the screen. Subjects were able to recalibrate their responses to adjust for the (known) delay introduced in the training phase. However, they were not able to perform nearly as accurately on the post-test (32% completion) as they were on the pre-test (84% completion).

Our point of inquiry was, first, whether perception of synchrony within a paced sensorimotor task can be adapted as in the experiments performed by Cunningham et al. (2001) and Fujisaki et al. (2004), and, second, most importantly, whether adaptation can be transferred to a separate task (line crossing). In order to induce adaptation, we introduced a delay between the key press and the presentation of a "visual feedback", in the pace task (and only in this task).

Methods

Seventeen naïve subjects and two non-naïve subjects (ages ranging from 18 to 37) participated in this experiment. All subjects responded with their dominant hand. A separate group of five naïve and one non-naïve subjects participated in a follow-up experiment.

Stimuli were generated in MATLAB (Mathworks) using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997), and run on an Apple Titanium Powerbook G4 attached to an external monitor (21 in. Dell Trinitron P260). The screen refresh rate was set to 75 Hz. Subjects' eyes were approximately 57 cm from the screen. White noise at a low volume was presented as a masking noise through headphones.

The experiment was divided into four tasks (see Fig. 1) to which all subjects participated. In this figure, letters (A–E) refer to each of the different tasks involved in the experiment. The tasks in C and D are identical except for their position in the experiment. For clarity, the same labels are used to report the results of the tasks in Fig. 2. The first task (50 trials) was a visual pace task (A in Fig. 1), in which a 3.5° red square was flashed for 50 ms in the center of a dark screen at a regular 1,000 ms interstimulus interval. Subjects were instructed to press a key synchronously with the flash. To give the subjects an initial estimate of the stimulus interval, the first stimulus of each set of trials was a green square of the same size and at the same location as the red square. Subjects were asked to begin responding with the first presentation of the red square. Time between the key press and the pace stimulus was recorded as asynchrony.

The second task (100 trials) was a coincidence anticipation task (line crossing, B in Fig. 1). A vertical blue bar (6° height, 0.5° width) and a white fixation point were presented at the center of the dark screen. A trial began when the fixation point was turned off and a vertical red bar (2° height, 0.5° width) appeared on the left or right side, 11° from the center, and horizontally traversed the screen at a speed of 8.2°s⁻¹. Subjects were instructed to press the key exactly when the moving red bar intersected the blue bar. Trial intervals were randomly varied between 1 and 3 s in order to avoid regular pacing. Time between the key press and the intersecting of the bars was recorded as asynchrony.

The third task (250 trials) was a training task (C in Fig. 1) similar to the first pace task. The red square

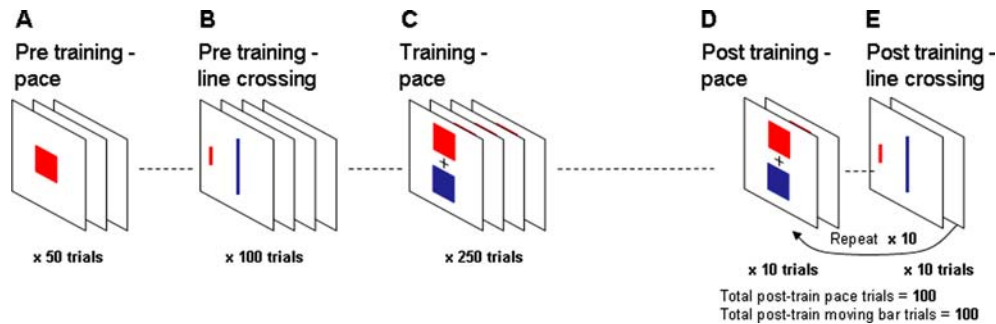


Fig. 1 Sequence of tasks. *A* Pace task before feedback training (50 trials). Subjects were instructed to press a key synchronously with a *red square* appearing on a *black background* at regular 1,000 ms intervals. *B* Line-crossing task before feedback training on the pace task (100 trials). Subjects were instructed to press a key synchronously with the crossing of a *stationary blue bar* by a *red bar* moving across the screen, from *right to left* or the *reverse*. *C* Pace task with

feedback training: a *blue square* appeared in response to each key press (250 trials). Feedback was either immediate (control, 10 subjects) or gradually delayed (test, 9 subjects). Blocks of ten trials of consolidating pace task with feedback (*D*) interleaved with blocks of ten trials of line-crossing task with no feedback (*E*). Total number of trials in both *D* and *E* is 200 train

flashed for 50 ms at a 1,000 ms interstimulus interval, but it was vertically offset so that the lower edge now was 1° above the center of the screen. The white fixation point was present in the center of the screen throughout the task. As before, a green square was presented at the same location as the red square to set the pace initially. In addition, a blue 3.5° square appeared 1° below the center of the screen for 50 ms in response to each key press. The instruction to the subjects was “to press the key synchronously with the presentation of the red square”. They were told that the blue square provided a feedback as to whether they pressed at the right time, too early or too late.

Subjects were divided into a control group and a test group for the training pace task. In training sessions (and post-training pace sessions, see below), the visual feedback for the control group ($n = 10$) was veridical, i.e. there was no delay introduced between key press and presentation of the blue square. In contrast, the visual feedback was systematically delayed in the test group ($n = 9$). To generate this delay, we took advantage of subjects’ natural tendency to press the key occasionally too soon. When this happened (and it did soon or later), the subject’s negative asynchrony on this trial was automatically measured, its value was halved, and from now on it was used as a delay to present the blue square. The effect was that subjects were led to press sooner and sooner if they attempted to synchronize the red and blue squares. However, it was important that subjects did not realize that they were “tricked”. Therefore, as mentioned above, we did not use the whole value of negative synchrony, but only half of that value to increment the feedback delay. And, second, delay changes were not introduced more often than once every five or more trials, until the final delay reached a maximum of 100 ms. For example, if, on a given trial, a subject pressed the key 50 ms before the appearance of the red pace stimulus and if there had been no delay increase within the last four trials, the feedback stimulus would thereafter appear

with an additional 25 ms delay after key presses. This procedure was tested and adjusted in preliminary experiments. It worked well because delays were not arbitrarily imposed on the subjects. Not knowingly, subjects increased the delays themselves. Furthermore, the rule of only one delay change per, at least, five trials made the changes so slowly progressive that they escaped attention. After completion of each session, subjects were asked if they “noticed anything unexpected” about the training and test sessions. For each trial, the time between key press and presentation of the pace stimulus was recorded, as well as the length of feedback delay.

The fourth and final task was made of ten identical blocks of trials. Each block consisted of ten trials of the training pace task described above (*D* in Fig. 1) followed, after a 1.5 s break, by ten trials of the line-crossing task (*E* in Fig. 1). For the group of subjects who had been trained with a feedback delay that progressively increased to 100 ms during the pace training task, a fixed delay of 120 ms between key press and feedback stimulus was used in the training trials of the last task. These groups of ten training trials were inserted within the test task to compensate for the possible decay of the effect of training.

A follow-up experiment, involving five new subjects, was virtually identical to the main experiment. However, instead of using the line-crossing task as the test task, we used the visual pace task itself in order to verify the effect of training on the same task and to use this control information for comparison.

As non-negligible delays are inherently involved in computer processing, we tried to estimate errors introduced in the data by these delays. We used electrical contacts placed directly on the key to measure the real time of key press, and a photocell over stimulus sites on the screen to measure the real time of stimulus presentation. We found that the error on the recorded time of key press was 8 ± 8 ms. This means that all the reported values of asynchrony should be increased by 8 ± 8 ms (i.e.,

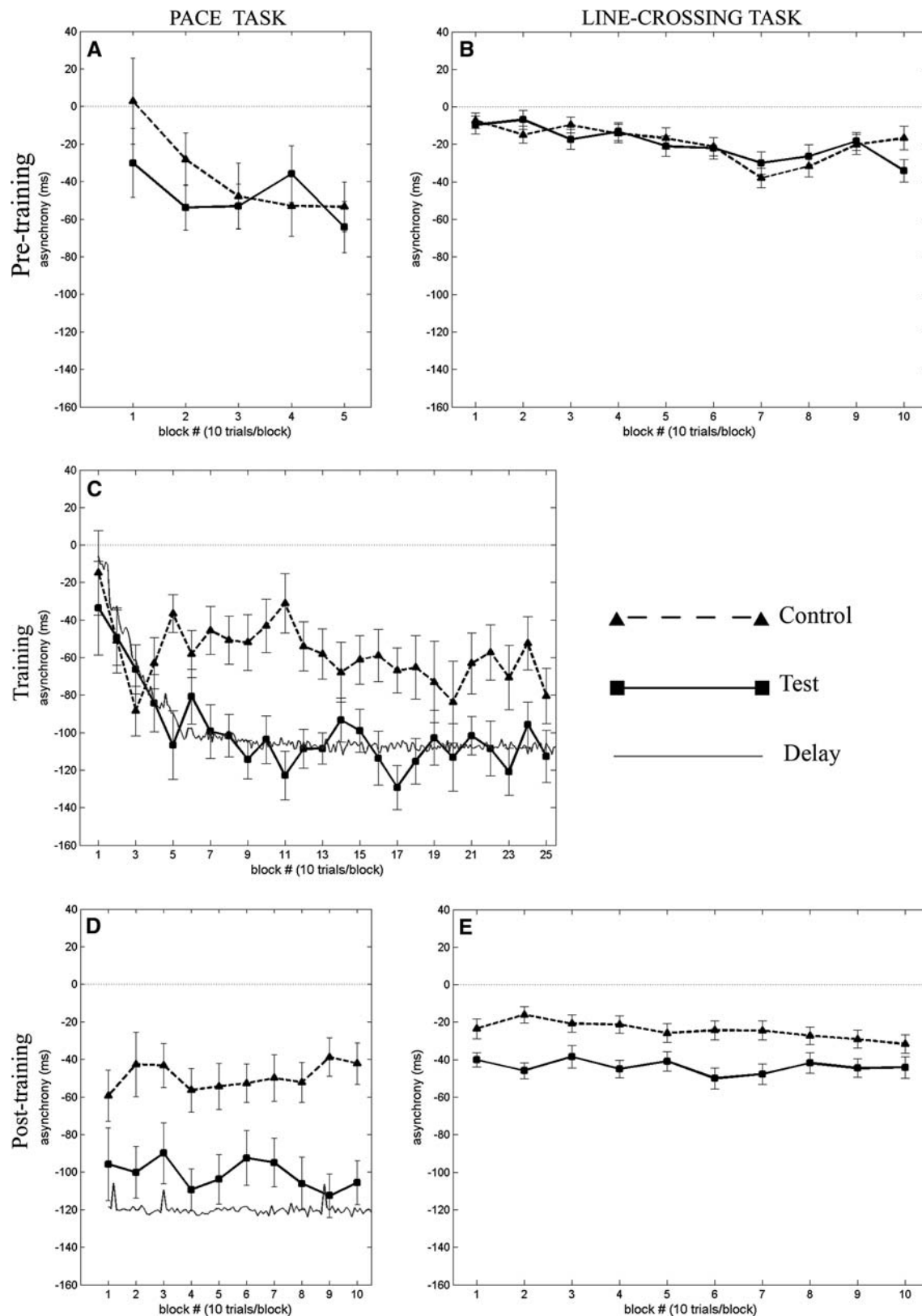


Fig. 2 Average asynchronies in successive pace tasks (*left*) and line-crossing tasks (*right*). **a, b** Pre-training. **c** Training. **d, e** Post-training. Control group (*triangles and dashed line*, $n = 10$) and test group (*squares and solid line*, $n = 9$). Asynchrony is the difference between the time of stimulus presentation and of key press (a negative value means key press precedes the stimulus). Each point is the average over ten trials per subject, across all subjects in a group. Error bars

are \pm SEM. In **c** control subjects (*dashed line*) received feedback with no injected delay whereas test subjects received feedback with gradually longer delay. *Fine dotted line* shows the time course of the mean delay injected. In **d**, feedback delay was fixed at 120 ms for the test group (*fine dotted line*). Trials of the post-training line-crossing task (**e**) were interleaved with trials of the consolidating pace task (**d**) as shown in Fig. 1

adding 0 to 16 ms to the reported data). Besides, whenever feedback was introduced in the pace task (i.e., by presenting the blue square in response to a key press) the minimum instrumental delay was around 10 ms. Therefore, all the reported values of feedback delay (including the so-called zero delay) should be increased by 10 ms. Although the reader should be aware of these intrinsic errors, we did not correct the reported results accordingly. It is not usual to correct data on account of computer delays and we thought preferable to conform to this practice, that is, to present our results in their raw form. This allows direct comparisons with results in the literature.

Within the various tasks, some trials were rejected from the data analysis, either because no tap occurred or it occurred more than 350 ms before or after the stimulus presentation, indicating either an anticipatory error or a late reaction to the stimulus, instead of an attempt to synchronize.

Results

Mean performance across subjects per blocks of trials in the successive pre-training, training, and post-training tasks are presented in Fig. 2. In the initial pace task (a), all subjects tended to tap before the presentation of the pace stimulus (red square). As expected, there was no significant difference between the asynchronies of the control and test groups ($t(17) = 0.69$, $P > 0.05$). The mean asynchrony was -36.3 ms (tap preceding red square) for the control group, and -47.9 ms for the test group.

The training pace task was used to alter subjects' response asynchrony by introducing a feedback (blue square) and by progressively increasing the delay of this feedback (Fig. 2c). The test group took approximately ten blocks (i.e., 100 trials) to adapt to the maximum feedback delay of 100 ms; accordingly, all means and comparisons for the training task were taken from the data of the last 150 trials. The control group, which was given veridical feedback (theoretically, 0-ms delay), showed a mean asynchrony of -62.9 ms, whereas the test group (delayed feedback) showed a mean asynchrony of -109.7 ms. As seen in Fig. 2c, the response asynchronies from the test group on the pace task closely followed the timing of the introduced feedback delay. There was no significant difference between the test group's asynchrony and the value of this feedback delay (pairwise, $t(8) = -0.41$, $P > 0.05$). There was a significant difference between the asynchronies of the control and test groups ($t(17) = 3.75$, $P = 0.002$).

The post-training pace task (that we call consolidating pace task, Fig. 2d) was identical to the training pace task; therefore, as expected, there continues to be a difference between the response asynchronies of the control and test groups ($t(17) = 4.33$, $P < 0.001$).

The effect of delayed feedback in the pace training on the coincidence-anticipation task was clear (Fig. 2,

compare b to e). The difference in response asynchrony for trials before and after the pace training task was analyzed by a repeated measures analysis of variance (ANOVA). There was a significant effect of the training within individual subjects (pre-, post-training, $F(1,17) = 34.52$, $P < 0.001$), as well as a significant interaction between group membership and task ($F(1,17) = 13.89$, $P < 0.01$). There was no significant effect of group membership (control or test; $F(1,17) = 0.46$, $P > 0.05$).

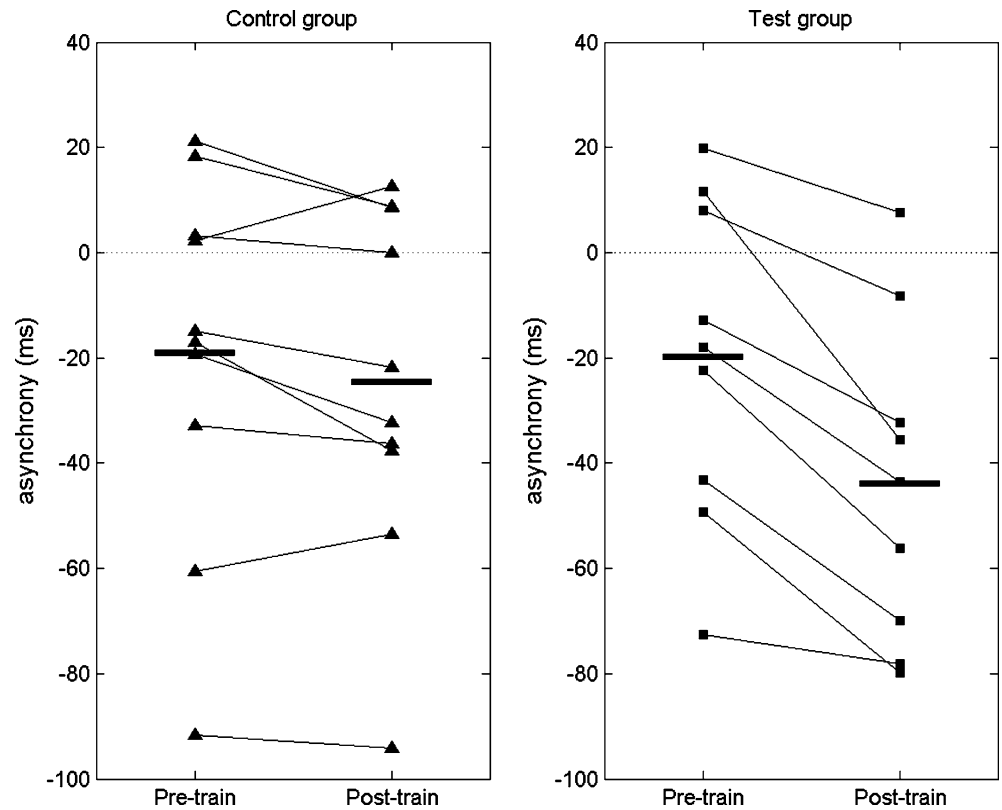
To explain the significance of the estimated marginal means in the line-crossing task, pairwise t tests were performed on each group (control and test) comparing the conditions (pre- and post-training). The control group did not show a significant change in asynchrony ($t(9) = 1.8$, $P > 0.05$; Fig. 2b, e, triangles), with a 5.4 ms change in asynchrony from pre-training (mean = -19.1 ms) to post-training (mean = -24.5 ms). Such a small difference is not surprising. It would be expected given the instrumental delay (approximately 10 ms, see Methods) introduced between the time recording of the key press and the time recording of the feedback stimulus in the pace task when the delay supposedly was zero.

Subjects in the test group showed a significant change in asynchrony ($t(8) = 5.78$, $P < 0.001$; Fig. 2 b, e, squares), with a 24.1 ms change from pre-training (mean = -19.8 ms) to post-training (mean = -44.0 ms). Figure 3 illustrates the differences in individual pre- and post-training asynchronies on the line-crossing task. A comparison between the control group and the test group shows that the transfer of training affected the asynchronies of the test group in the same manner for all subjects.

As a control, a follow-up experiment was performed to verify that training with a delay of visual feedback had an effect on the pace task itself (data not illustrated). All five participating subjects received delayed feedback in the training pace task (C). There was no significant difference between the group's asynchrony and the value of the introduced feedback delay (pairwise, $t(7) = -0.90$, $P > 0.05$). As in the case of the other 19 subjects, the measurements of asynchrony and the actual delay values were taken for the last 150 trials of the training session. There was a significant difference of asynchrony between the pre-training and post-training pace tasks ($t(12) = 2.43$, $P = 0.03$), with a 45.6 ms change from pre-training (mean = -49.9 ms) to post-training (mean = -95.5 ms).

When questioned after completion of the task, seven of the nine subjects in the test condition stated that they did not notice anything unexpected about the task. The two other subjects answered that they felt that "something was off in the timing," but they said that they were not sure what that might be. As expected, none of the subjects in the control group (i.e. with no delay) found anything unusual. Thus, subjects in the test group appear to have been unaware that a delay had been introduced between action and visual feedback, and that, finally, this delay was 120 ms during the test task. Subjects did not realize either that they were pressing the key too early in the line-crossing test.

Fig. 3 Changes in individual asynchronies on the coincidence line-crossing task after training with delayed feedback on the pace task. Data from individual subjects are connected by a line showing the change from pre- to post-training. *Black bars* indicate means over all subjects. *Left panel* Control group subjects; *Right panel* test group subjects



Discussion

In the initial pre-training visual pace task for both control and test groups, the asynchrony observed was in accordance with the expected value from previous visual pace experiments (Kolars and Brewster 1985). When a delayed feedback was introduced in the pace task and progressively increased, we found that the asynchrony was significantly shifted negatively (Fig. 2c). With no delay in visual feedback (control group), the asynchrony remained unchanged. Intentionally, the delay between key press and visual feedback was introduced very gradually in the hope that the subjects would remain unaware that the timing conditions were manipulated. This seems to have been successful since subjects did not report having “noticed anything unexpected”. Previous studies have shown that the perception threshold for temporal discrimination, often known as the Weber fraction, is approximately 5% of the interstimulus interval (Killeen and Weiss 1987; Ivry and Hazeltine 1995). In our pace experiment with an interstimulus interval of 1,000 ms, the threshold would be approximately 50 ms before subjects perceive a difference in timing of stimuli. In a preliminary study, we found that randomly inserted delays between key press and feedback stimulus that were larger than 50 ms were perceived as delays, while delays less than 50 ms were not (data not shown). But, as we gradually increased the delay between key press and feedback stimulus, subjects appeared not to perceive that a delay was introduced. We may thus assume that adap-

tation of perception of synchrony had occurred. If our subjects had been able to perceive the run-away of their asynchrony, would not this perception have forced them to correct the timing of their key press?

In the literature, asynchronous responses in a pace task have been attributed to differences in latencies (Mates et al. 1992; Aschersleben and Prinz 1995, 1997; Mates and Aschersleben 2000; Aschersleben et al. 2001; Aschersleben 2002). An important contribution to latencies is nerve conduction times, potentially modifiable by sensory accumulation (Aschersleben et al. 2001). However, an explanation of asynchrony in terms of different latencies associated with different sensory modalities has difficulties. King and Palmer (1985) showed that the latency associated with visual processing is longer than that with auditory processing by 30–50 ms. If this is indeed the case, then one would normally expect that in a visual pace task the tap will come 30–50 ms later than if the stimulus were auditory. Taps in an auditory paced task lead the stimulus by approximately 60 ms (Aschersleben and Prinz 1995). One would then predict that, in a model based on conductance latencies, a visual pace task would result in tap times close to the time of stimulus presentation. However, experimental findings (Kolars and Brewster 1985; Aschersleben and Prinz 1997) have shown just the opposite, with a slightly reduced but still distinct negative asynchrony in a visual pace task. The current study confirms this observation.

In addition, it has been claimed that, in judging the simultaneity of a visual stimulus and an auditory stimulus, subjects take into account the distance of the source

of these stimuli (Sugita and Suzuki 2003; but also see Lewald and Guski 2004). If automatically subjects can introduce corrections by dynamic recalibration, their judgments were not strictly based on neural latencies.

An explanation of asynchrony based on latency is insufficient, very likely because asynchrony can easily be modified by adaptation. Earlier experiments (Bennett and Westheimer 1985; Shimojo and Shams 2001; Stone et al. 2001; Watanabe and Shimojo 2001; Fujisaki et al. 2004) have shown that the perception of simultaneity across sensory modalities is modifiable. In a recent example, Fujisaki et al. (2004) trained subjects to perceive simultaneity between visual and auditory stimuli with variable intervals between the stimuli (up to 100 ms). They proposed that the perceived point of simultaneity between a visual event and an auditory event is adaptively calibrated based on prior experience.

There are numerous examples of the use of a motor response to determine adaptation of sensorimotor coordination (Aschersleben and Prinz 1997; Thaut et al. 1998; Foulkes and Miall 2000; Meegan et al. 2000; Repp 2000; Cunningham et al. 2001; Ceux et al. 2003). Most of these experiments concerned the auditory modality because of its greater temporal resolution. Aschersleben and Prinz (1997) showed an increase in the negative asynchrony when an auditory stimulus was added as a delayed feedback of key press, thus increasing the asynchrony of a response to a paced auditory stimulus. Adaptation of a motor response has also been shown when the delayed feedback was visual (Cunningham et al. 2001). When the delay was removed, subjects had difficulty in readjusting to the task with no feedback delay. These results suggest that internal delay inherent in multisensory integration can be altered.

Meegan et al. (2000) suggested that perceptual learning of timing intervals, based on a discrimination task, is able to transfer to a motor response by reducing the variability of the estimation of an interval. Discrimination of simultaneity between stimuli of different modalities, such as auditory and visual stimuli, has been shown to transfer to a different perceptual task (Fujisaki et al. 2004).

We asked whether the effects of adaptation could be transferred from one task (visual pacing) to a separate task (coincidence anticipation). As shown in Fig. 3, subjects who experienced a delayed feedback in the visual pace task responded significantly earlier in the line-crossing task than they did originally. A change of asynchrony of over 50 ms in the visual pace task apparently caused an increased asynchrony (> 20 ms) in the coincidence-anticipation task. Although clear and significant, the absolute amount of change in one task did not equal the absolute change achieved in the other task. This may be explained by the difference in task, already evident in the pre-training results (compare Fig. 2a to b). For instance, the initial negative asynchrony and its variance were much smaller (about half) for the line crossing than for the pace task. There is no a priori good reason for asynchrony to have the same value for all tasks. The line-

crossing task appears to have been easier than the pace task. However, the effect of training—or its transfer—has been similar in both tasks: more than doubling the asynchrony.

This raises the question of what could be the cause of the initial adaptation that creates an asynchrony, specifically when the motor response leads a predictable sensory event, as it generally does. One compelling explanation would be taking into account the prior experience in sensorimotor synchrony of the participant. Throughout one's lifetime, it is likely that one learns that the effect of an action such as a tap is not always immediate. Besides, one needs not necessarily to be right on time but surely ready in advance as for catching a ball. Due to the long history of natural feedback that one receives for a variety of sensorimotor events throughout life, it is possible that one adopts a convenient, average, "default" asynchrony to which one tends to return automatically. This would explain the temporary duration of adaptation that we saw: although we were able to train subjects to respond up to 100 ms early, this effect disappeared rapidly if there was no continuing feedback to maintain the effect.

There is a mental correlation between voluntary action and awareness of one's action. Haggard et al. (2002) asked subjects to judge the timing of either a key press or a tone resulting from the key press. They found that subjects perceive the tone occurring closer in time to the key press than it actually occurred; likewise, the key press was judged to occur closer to the tone than the physical time of action. This causal link between motor action and perception is described as being a shift in perception of the timing of the events. By the transfer of an increased negative asynchrony from one task to another, the phenomenon of temporal attraction may occur in the case of anticipation as well as causation (Haggard's intentional binding, 2002).

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