RESEARCH ARTICLE

Gisa Aschersleben · Jörg Gehrke · Wolfgang Prinz

Tapping with peripheral nerve block

A role for tactile feedback in the timing of movements

Abstract This study examines the impact of peripheral nerve block, that is, the elimination of tactile feedback on synchronization performance. In a tapping experiment in which subjects were instructed to tap in synchrony with an auditory pacing signal, three different tasks were studied under conditions with and without peripheral nerve block: standard tapping with tactile contact, isometric tapping, and contact-free tapping. In addition, the maximum tapping rate was registered both with and without peripheral nerve block. It was found that the anticipatory error, usually observed in synchronization tasks, was affected by the peripheral nerve block in the standard tapping and the isometric tapping task. In both tasks, local anesthesia led to an increase in asynchrony between the pacing signal and the tap. Performance remained unimpaired in those tasks in which tactile information was assumed to play a minor role (maximum tapping rate and contact-free tapping). The results clearly demonstrate the importance of tactile feedback for the timing of movements. The predictions of a model assuming a strong correlation between the amount of sensory feedback and the size of the negative asynchrony in synchronization tasks were examined and discussed.

Keywords Sensorimotor synchronization · Tapping · Timing · Motor control · Peripheral nerve block · Human

Introduction

There are numerous scientific studies on planning and control of movements. Likewise, there are a number of sensory studies that address psychophysical issues pertaining to perception. However, there has been considerably less attention devoted to the nature of the interface between the input and output systems: how sensory inputs are used to create action programs, and how actions intervene in framing perceptual goals. This paper is concerned with the first question by studying the influence of afferent and reafferent information on the timing of movements.

The contribution of somatosensory information to movement control has always been a major concern of physiological studies and has recently been reappraised (Gandevia et al. 1992). In particular, the contribution of kinesthetic reafferences to the timing of movement sequences has been demonstrated in man (Cordo et al. 1994). Studies on deafferented patients suffering from polyneuropathy, affecting selectively the contingent of the large myelinated sensory fibers (thus suffering all cutaneous and proprioceptual information, but leaving the motor system intact), have shown that some reafferent signals generated in the moving body segment were mandatory to organize the precise timing of self-induced efferent commands required to synchronize the command with another event (Bard et al. 1991, 1992; Billon et al. 1996; LaRue et al. 1995; for a review on motor control in humans with large-fiber sensory neuropathy, see Sanes 1990).

In the present study, we examine the contribution of tactile afferent information to the timing of sequential finger movements by studying a sensorimotor synchronization task. In synchronization tasks, subjects are asked to tap with a finger in synchrony with a periodical sequence of auditory clicks, that is, to time their actions so as to coincide with certain events. It is commonly observed that people are not very exact in synchronizing; typically, the tap leads the click by approx. 20–50 ms (see Aschersleben and Prinz 1995, 1997; Aschersleben et al. 2000a; Fraisse 1980; Mates et al. 1992; O'Boyle 1997; Vos et al. 1995; for a recent overview, see Aschersleben 2000a). Recent accounts of this so-called negative asynchrony or anticipatory error have focused on the way people might cognitively control their performance in synchronization tasks. In particular, we have suggested that synchrony is not only controlled by, but also established at, a central representational level, where both stimuli and actions are represented in terms of their sensory effects (Aschersleben and Prinz 1995, 1997; Aschersleben et al. 2000a;

G. Aschersleben (✉) · J. Gehrke · W. Prinz
Max-Planck-Institut für psychologische Forschung,
Amalienstrasse 33, 80799 Munich, Germany
e-mail: aschersleben@mpipf-muenchen.mpg.de
Tel.: +49-89-38602250, Fax: +49-89-38602199

Prinz 1997). Therefore, action control in synchronization tasks in not so much concerned with the temporal relationship between the auditory input and the motor output but with realizing synchrony between perceived click and perceived tap. If so, the time it takes to perceive the click and the tap becomes crucial, the more so as auditory and kinesthetic-tactile stimulation can be assumed to differ in processing speed. In fact, as the temporal delay between actual and perceived click is shorter than the delay between actual and perceived tap, the actual tap must precede the actual click to achieve synchrony between the perceived events at a central level, hence the negative asynchrony between click onset and overt tap.

There are two models that are based on the assumptions (1) that the corresponding central representations of click and tap's sensory effects are brought to coincidence and (2) that the central representation of the tap is based on the somatosensory feedback arising from the finger movement and the touch of the key. However, these two accounts differ with respect to their assumptions on how differences in processing time are produced. According to the so-called Paillard-Fraisse hypothesis, differences in nerve conduction times between click and tap on their way to their central representation are responsible for the anticipatory error (Aschersleben and Prinz 1995, 1997), while the "sensory accumulator model" (SAM; J. Gehrke, unpublished work; Aschersleben et al. 2000a) assumes that clicks and taps differ with respect to the amount of sensory evidence required for central coding.

Thus, unlike the SAM, according to the Paillard-Fraisse hypothesis the cause of asynchrony is to be found at a peripheral level. As it takes more time for sensory information (resulting from the tactile and kinesthetic feedback of the tap) to travel from the fingertip to the brain than from the ear to the brain, the tap has to lead the click to achieve temporal coincidence of the two central codes (Aschersleben and Prinz 1995, 1997; Fraisse 1980; Paillard 1949). Therefore, any change in the time between the tap and its central representation by manipulation of conduction delays should affect the asynchrony in a predictive manner: An increasing conduction time should lead to an increase in the amount of the anticipatory error. This view presupposes that the timing of the tap is not only determined by the first feedback component that is available at a central level. On the contrary, contributions from various feedback modalities are assumed to be integrated and to enter into a common gestalt. Only the timing of this gestalt as a whole determines the timing of the tap (see Fraisse et al. 1958 for a related notion).[1]

While the Paillard-Fraisse hypothesis stresses the role of delays derived from conduction times in afferent pathways, the SAM assumes that processing times needed to generate a central representation of peripheral events might also play a role in the observed asynchrony. The model assumes that an external event to be experienced and timed would necessitate its central representation as an experienced neural entity. The processing times necessary for generating this neural state would be threshold dependent, and this would change depending on the density of afferent neural signals generated by the physical events. Hence, the model is based on the assumption of an accumulation function whose steepness determines the time elapsed between an external event and its central representation. Consequently, the auditory pacing signal used in the synchronization task has a steeper accumulation function as compared to the tap; a negative asynchrony is obviously expected (Aschersleben et al. 2000a). A relevant factor influencing the size of the anticipatory error would then be the density of afferent signals arriving at a central level. The more afferent signals (in a unit of time) the earlier a threshold should be reached.

The aim of this study was, first of all, to demonstrate a contribution of somatosensory feedback to the timing of the tap in a sensorimotor synchronization task. The second aim of the study was to distinguish between the two hypotheses described above that make different assumptions concerning the processes influencing the timing of central representations. We can answer both questions by studying the influence of peripheral nerve block on the performance in a synchronization task. By anesthetizing the index finger that performed the tapping movement, we assumed that we suppressed tactile reafferent information without disturbing the reafferent discharge of the joint and muscle receptors.[2] Moreover, in terms of conduction times, by eliminating tactile feedback we supposed that the slower feedback component of the reafferent volley was eliminated, whereas the faster kinesthetic feedback component remained unimpaired (Strichartz 1976).

Figure 1 shows the predictions of the two models for digital nerve block. Two panels are shown for each model: activation volleys (upper panels) and accumulation functions reflecting their integrals (lower panels). According to the Paillard-Fraisse model, the critical computations are performed on the activation volleys (whereas the accumulation functions are irrelevant). Conversely, in the SAM model, the activation volleys play no role and the critical computations are performed on the accumulation functions. This difference is reflected in the breadth of the corresponding lines.

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[1] This view has gained empirical support from experiments in which additional auditory feedback was presented to the subjects each time the finger touched the key. As this feedback tone had the same conduction delay as the auditory pacing signal, the asynchrony should disappear under an assumption, assuming that the tap is represented by the first feedback component available. In a series of experiments, it has been shown that the asynchrony is significantly reduced under those conditions but still remains different from zero (Aschersleben and Prinz 1995, 1997; Mates and Aschersleben 2000; Mates et al. 1992; O'Boyle and Clarke 1996), supporting the assumption of a common gestalt.

[2] However, this does not mean that subjects do not have any information about their finger movement. First, information from the kinesthetic feedback is still available. In addition, Edin and Johansson (1995) have demonstrated that even after digital nerve block skin deformation related to digit movements could provide an excellent signal about finger movements.

Fig. 1a, b Predictions derived from the Paillard-Fraisse model (**a**) and the SAM model (**b**). *Upper panels* reflect hypothetical activation volleys for the control condition (*C*) and the nerve-block condition (*B*). *Lower panels* reflect the corresponding accumulation of activation over time
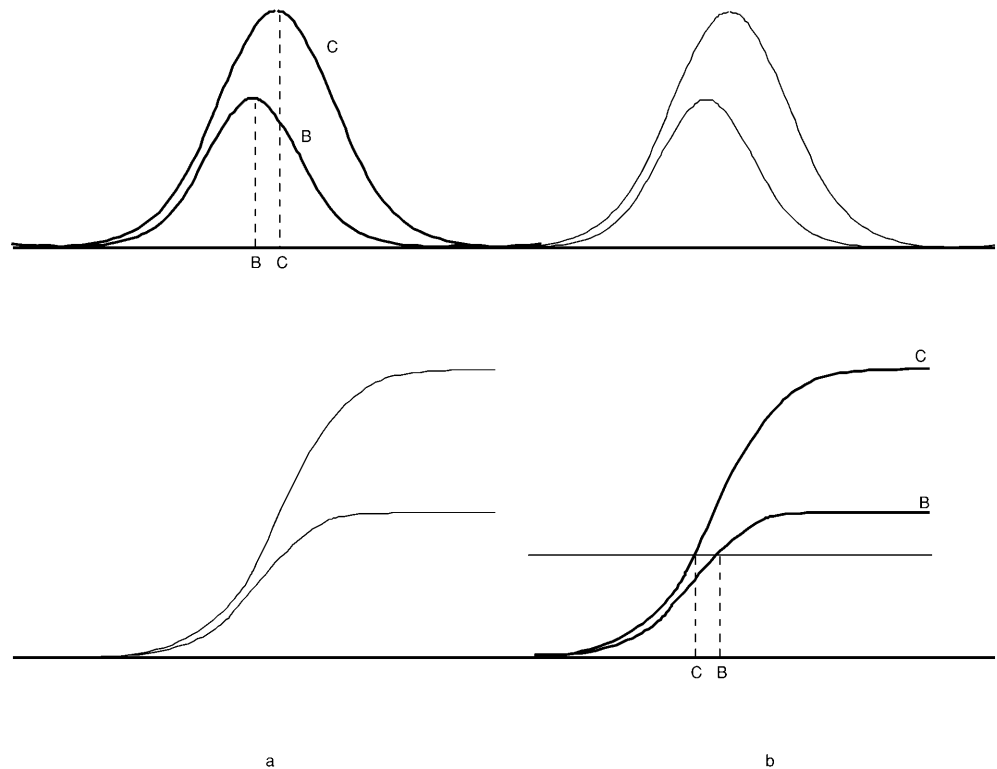
The Paillard-Fraisse model holds that the time of the tap is computed at an "early" brain site at which the arrival times of the sensory activation volleys still depend on the conduction velocities of the respective populations of afferent nerves. The upper panel of Fig. 1a shows two such hypothetical volleys: one for the control condition (C), and another for the digital nerve-block condition (B). The difference between the two volleys reflects the assumption that the nerve block acts to selectively attenuate, or block, the late components of the activation volleys (presumably reflecting cutaneous/tactile afferents) while leaving the early ones unaffected (presumably reflecting kinesthetic afferents from joints and muscles). Therefore, if one assumes that the effective times of taps are computed from the means (or medians) of these volleys, one would have to expect that the block acts to shift that time to an earlier point (relative to control). As a result, the amount of negative asynchrony should decrease.

Conversely, the SAM model states that the time of the tap is computed at a "late" brain site, at which afferent nerve conduction times play no role in the resulting activation pattern. What counts, instead, is the amount of activation contained in the afferent volleys arising from the taps. The accumulation of this activation over time is reflected in the integral functions shown in the lower panel of Fig. 1b. Hence, if one assumes that the effective times of the taps are computed from a common activation threshold applied to these functions, one would have to expect that the block acts to shift that time to a later point (relative to control) and that, as a result, the amount of negative asynchrony should increase.

While the prediction derived from the SAM model is clear and distinct, the prediction derived from the Paillard-Fraisse model should perhaps be phrased in a somewhat more cautious form. This is because one cannot be sure how large the difference in mean conduction times between blocked and unblocked afferents really is. For instance, in a study by Macefield et al. (1989), no significant difference between the conduction velocities of low-threshold muscle and cutaneous afferents was found for upper and lower limb nerves. However, this result is still under discussion (Shefner and Logigian 1994). Therefore, a more cautious wording of what one has to expect under the Paillard-Fraisse hypothesis is that the nerve block should either act to reduce the negative asynchrony or leave it unaffected.

We tested two basic experimental conditions: the standard tapping task and an isometric tapping task (production of short-duration force pulses). In addition, two control tasks were introduced to examine whether the efferent signals and the kinesthetic feedback component remained indeed unaffected by the nerve block: contact-free tapping (free movement of the finger without any contact, i.e., without any important tactile component) and tapping at maximum rate.

Materials and methods

Subjects

Nine healthy right-handed subjects (five women and four men, mean age 31 years) participated in this study after giving their informed consent. None of them had signs or symptoms of disease

of any kind. The study was approved by the local ethics committee in accordance with the Helsinki Declaration. All subjects were unaware of the purpose of the study.

Apparatus and stimuli

Seated at a table in a quiet room, the subject was asked to tap with the index finger on a silent electrical contact switch that was equipped with a force transducer (Sensotec load cell) with a sample rate of 1 kHz. To eliminate visual feedback, subjects were blindfolded. The auditory pacing signal (400 Hz, 82 dB[A], duration 10 ms, interstimulus interval 800 ms) was presented binaurally through headphones (Sennheisser HD 250). To cover external sounds, white noise (53 dB[A]) was used under all conditions. The stimuli were produced by a personal computer (Pegasys 486/33) via a D/A converter and an amplifier (Phillips FA 630). The computer controlled the experimental procedure and registered the onset of keypresses (with a resolution of 1 ms). An optical marker system (Optotrak 3D measurement system, Northern Digital) was used to control and register the displacements of the finger. An LED marker, which signaled the position, was fixed laterally at the tip of the index finger. The kinematic data were collected at a sampling rate of 1 kHz.

Procedure

There were two experimental sessions run on the same day (one session in the morning and the second one in the afternoon). In the morning session, the control conditions without peripheral nerve block were administered to establish the baseline. In the afternoon session, identical tapping tasks were tested under conditions with peripheral nerve block. Each session comprised four parts: tapping at maximum rate, standard tapping, isometric tapping, and contact-free tapping task. In the first task, subjects were asked to tap as fast as possible with the index finger on a metal plate. Data from three trials each lasting 5 s were recorded. The remaining three tasks required subjects to tap in synchrony with an isochronous click sequence. In the standard tapping task, as well as in the isometric tapping task, subjects were asked to tap on a key. While subjects were instructed to lift the finger in the first one, the latter required the subjects to keep contact with the key during the whole trial and to produce short-duration force pulses. Finally, in the contact-free tapping task, subjects had to put their right arm on a wooden board and to move the index finger without any contact with other fingers or to the board.

Because we knew from previous studies that the finger amplitude and the maximum force applied to the key affected the size of the asynchrony (Aschersleben et al. 2000a; Gehrke 1995), we instructed subjects to keep this factor constant. At the beginning of each synchronization task, subjects were trained to perform movements with a fixed amplitude (in the range 20–40 mm in the standard and in the contact-free tapping task) or with a fixed maximum pressure (in the range 2–4 N in the isometric tapping task). At the end of each training trial, subjects received feedback about the mean amplitude or force, respectively. They were trained until they had performed two correct trials according to the criterion described above. Each experimental block after the training trials with the corresponding synchronization task comprised seven trials. A trial consisted of the following sequence of events: First, a warning tone signaled that the trial was started. After an interval of 1,000 ms, the subject was continuously exposed to white noise and the sequence of 36 pacing signals was started. The next trial was started automatically after a pause of about 10 s. Instructions required the subject to start tapping within the first three signals and then to tap along with the signal as precisely as possible using the index finger only, that is, they were not allowed to move the other fingers or the wrist. In the standard tapping task, the instruction stressed onset synchronization in the sense that it was the finger's initial contact with the response key that had to be synchronized with the appearance of the click. In the isometric tapping

task, subjects were asked to synchronize the force peak with the onset of the click and, finally, in the contact-free tapping task, subjects were instructed to synchronize the lowest point of the movement.

All subjects started with tapping at maximum rate. A set of three different orders was used for the three synchronization tasks (the same order of tasks was used in the control session as well as in the session with peripheral nerve block). Subjects were assigned to one order at random. Each session lasted about half an hour.

At the beginning of the second session, the peripheral nerve block was applied to achieve complete anesthesia of the moving index finger. The right hand was injected with 3–10 ml of xylocaine 2% (w/v; Xylonest). Skin punctures were made distal to the metacarpophalangeal joint of the index finger and approximately 2 ml of the anesthetic dispersed subcutaneously on either side of the median and ulnar nerves (local anesthesia; Oberst). Sensibility to touch, pinprick and squeezing of the finger was tested 10 min later, and if there was any residual sensation a further injection of xylocaine up to a maximum of 10 ml was given as necessary. Thus, tests were not run until a complete clinical anesthesia of the right index finger to light and heavy touch, pinprick, and powerful squeezing was obtained.

Data analysis

In the synchronization tasks, data analysis started with the seventh signal in each trial. The first taps were not included because a minimum of three to five signals were required to pick up the beat. Hence, the means and standard deviations reported here always refer to the taps matching the remaining 30 signals in each trial. To control whether subjects followed the instructions, means of the maximum amplitudes (in the standard and contact-free tapping tasks) and of the peak forces (in the isometric tapping task) were computed per trial.

Usually, the asynchrony between tap and click is computed as the temporal delay between the two onsets, with the tap onset being defined as the onset of the keypress. For the isometric and the contact-free tapping task, the problem of parameter identification occurs because there isn't such a "tap onset" in these two tapping tasks. Therefore, asynchronies were computed between click onsets and the instructed parameter (the maximum force peaks in the isometric tapping task and the lowest points of the movement trajectory in the contact-free tapping task). Still this selection of parameters remains arbitrary. To ensure that the results do not depend on the parameters, we also computed the asynchronies between the click onset and an additional parameter for each task. As a second parameter, the one was chosen at which the highest amount of sensory feedback is supposed to be available to the system (the maximum force peak for the standard tapping task and the maximum deceleration for the isometric tapping task as well as for the contact-free tapping task; for a detailed discussion of the parameter selection problem, see J. Gehrke, unpublished work).

The means and standard deviations of asynchronies between the selected parameter and click onsets were computed per trial. Negative asynchronies indicate that taps come first. Trials were eliminated when they contained fewer than ten productions or when the standard deviation of the asynchrony exceeded a criterion of 100 ms.

Results

To check, on the basis of behavioral data, whether efferent signals were impaired by the peripheral nerve block, the mean number of taps per seconds (hertz) in the tapping-at-maximum-rate task was computed per trial and subsequently analyzed with a repeated-measurement analysis of variance (ANOVA), with the between-subject factors Condition and Trial. No source of variance
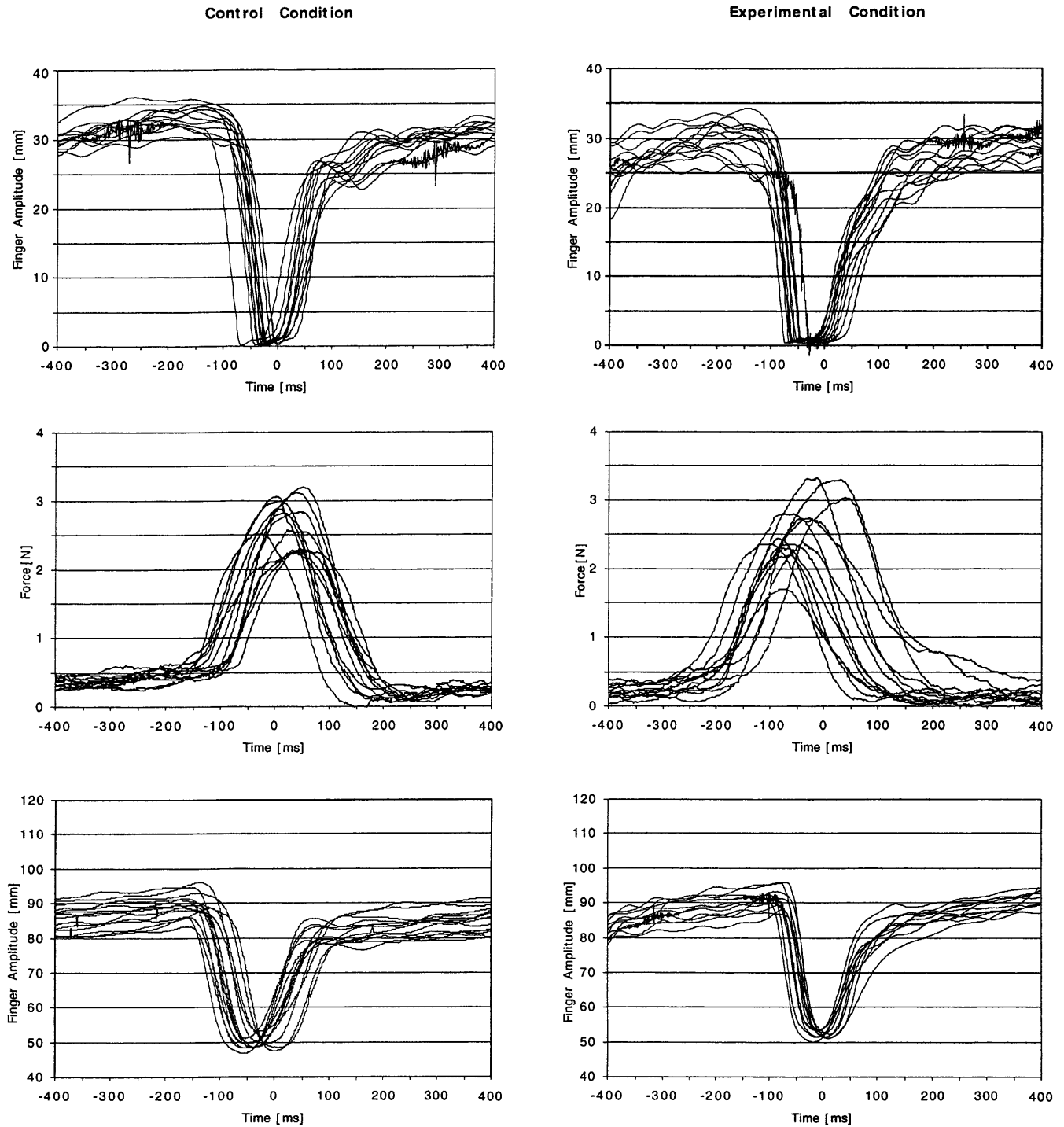
Control Condition

Experimental Condition

Fig. 2 Kinetic and kinematic data for samples of individual taps performed in the three tapping tasks. The interstimulus interval between two clicks was 800 ms (see *abscissa*); the zero value corresponds to the click onset. *Left:* control condition without peripheral nerve block. *Right:* experimental condition with peripheral nerve block. *Top:* typical individual movement trajectories in the standard tapping task (the zero value in the finger amplitude, *ordinate*, corresponding to the surface of the key). *Middle:* typical individual trajectories in the isometric tapping task (the zero value of the force, *ordinate*, corresponding to a slight touch of the key). *Bottom:* typical individual movement trajectories in the contact-free tapping task

reached significance ($F<1.1$).[3] The mean tap rate (averaged over the three trials per condition) was almost identical under conditions without and with peripheral nerve block (5.82 Hz and 5.94 Hz, respectively). Furthermore, the observed values fitted to the usual range for young adults described in the normative tables for the finger-tapping test (see Shimoyama et al. 1990).

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[3] In order to avoid the risk of violating statistical assumptions in repeated-measures designs owing to the inhomogeneity of the variance-covariance matrix, P-values were corrected according to Geisser and Greenhouse (1958).

Standard Tapping Task

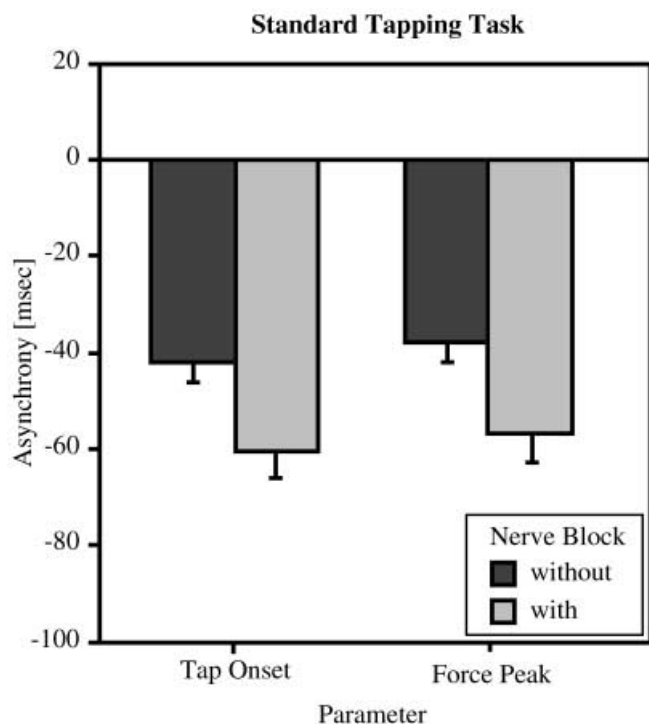

Isometric Tapping Task

Fig. 3 Means and between-subject standard errors of the mean asynchronies in the standard tapping task under the two tested conditions without and with peripheral nerve block for the two analyzed parameters

Fig. 4 Means and between-subject standard errors of the mean asynchronies in the isometric tapping task under the two tested conditions without and with peripheral nerve block for the two analyzed parameters

Before analyzing the performance in the synchronization tasks, we had to make sure that the subjects fulfilled the desired demands. For each task separately, mean forces or mean amplitudes per trial were entered into a repeated-measurement ANOVA with two within-subject factors: Condition (without and with peripheral nerve block) and Trial (three trials). To ensure that the nerve block was still effective, we analyzed the first three trials per condition only. One source of variance was significant: the main effect of Trial in the standard tapping task ($F_{2,16}$=9.50, $P<0.05$) indicating an increase in amplitude from 24 mm in the first trial to 29 mm in the third trial. No main effects of Condition and no interactions involving this factor were observed in any of the three tasks. Mean values for the amplitude and the force corresponded to the instructed values (standard tapping, 27 mm; contact-free tapping, 33 mm; isometric tapping, 2.6 N). A sample of individual trajectories from taps performed in each tapping task obtained in the two conditions (without and with peripheral nerve block) is illustrated in Fig. 2.

Overall, 0.2% of the synchronization trials had to be rejected because they failed to meet the criteria presented above. Subsequently, for each of the three tapping tasks, two identical ANOVAs were applied to the mean asynchronies: a repeated-measurement ANOVA with two within-subject factors: Condition (without and with peripheral nerve block) and Trial (three trials). For the standard tapping task for both parameters (tap onset and force peak), only one source of variance was significant,
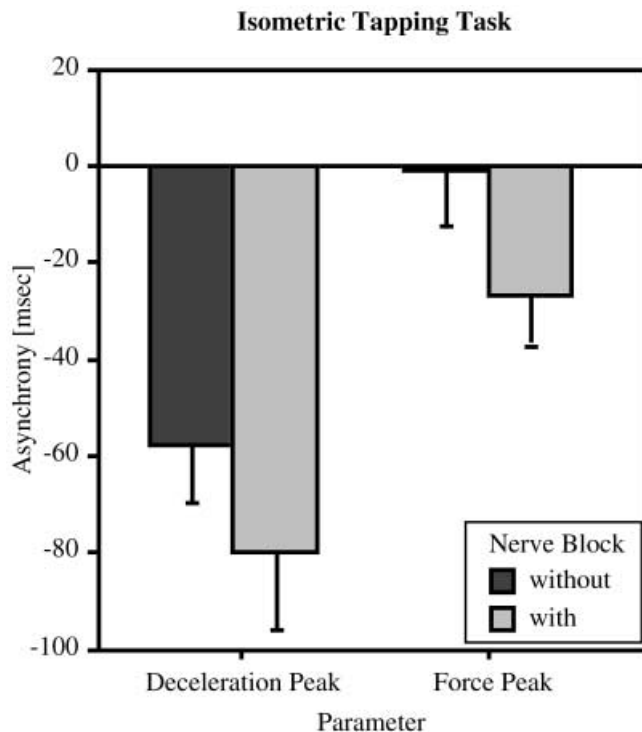
the main effect of Condition ($F_{1,8}$=9.23, $P<0.05$ and $F_{1,8}$=9.77, $P<0.05$, respectively). The amount of the asynchrony between tap onset and click onset was enlarged from –42 ms in the control condition to –60 ms under conditions with peripheral nerve block (–38 ms and –57 ms for the force peak; see Fig. 3).

A similar result was observed in the isometric tapping task: the asynchrony between deceleration peak and click onset increased from –58 ms in the control condition to –80 ms with anesthesia (–1 ms and –27 ms for the force peak; see Fig. 4). The corresponding ANOVAs supported this tendency by revealing at least almost significant effects of Condition ($F_{1,8}$=3.89, $P=0.08$ and $F_{1,8}$=4.27, $P=0.07$, respectively (see Fig. 3).

For the contact-free tapping task, no significant effects were observed for either of the two parameters ($P>0.20$). These results are supported by the individual subject data. In the standard tapping task, each of the nine subjects showed an increase in the amount of asynchrony under conditions with peripheral nerve block. In the isometric tapping task, the effect was observable in seven out of nine subjects, while in the contact-free tapping task four subjects showed a decrease in the anticipatory error and five subjects an increase.

To test the influence of the peripheral nerve block on the variability of tapping, standard deviations of the mean asynchronies per trial were analyzed in the same way as the mean asynchronies. No source of variance reached significance in any of the three tasks; that is, the

variability of tapping did not change under conditions with peripheral nerve block.

Discussion

Our major findings can be summarized as follows: Under conditions in which tactile feedback was assumed to play an important role in the timing of the synchronization movement, this timing was affected by local anesthesia, that is, the elimination of the tactile feedback component disturbed the timing of the movement. In both the standard tapping task and in the isometric tapping task, the asynchrony between the pacing signal and the tap was increased under conditions with peripheral nerve block. To be able to relate this change in asynchrony directly to the introduced experimental conditions, we first had to check several control variables. First of all, it is known from previous studies that the kind of the finger movement (mainly the amplitude of the finger movement and the force applied to the key) deeply influences the amount of the asynchrony (see Aschersleben et al. 2000a; Gehrke 1995). Therefore, to control for the role of finger movements, both amplitudes and forces were recorded throughout the experiment. However, these control variables showed no significant differences between conditions for any of the tasks. Thus, differences in the asynchronies cannot be attributed to changes in the finger movements or forces applied to the key.

Second, in applying local anesthesia to the right index finger of the subjects, we aimed at establishing conditions that were different concerning the feedback available to the subject. To be able to interpret the data in such a way, we had to make sure that the efferent fibers remained unimpaired, that is, that no change in the delivery and execution of the motor command to the finger occurred. On the basis of behavioral data, the intactness of the efferent fibers could be examined by analyzing the maximum tapping speed of the subjects. The results obtained in this task revealed no difference between conditions with and without peripheral nerve block, indicating that the execution of a pure motor task was unimpaired. A further indicator for motor impairment would be an increase in the variability of the taps. Kelso and coworkers reported that subjects were even unable to perform a tapping task at all under conditions with nerve compression block, leading to kinesthetic as well as motor impairment (Kelso et al. 1974, 1975). In the present experiment, the analysis of the standard deviations of the asynchronies revealed no change resulting from the application of the peripheral nerve block. Therefore, the results obtained in the maximum tapping task as well as those from the analysis of the standard deviations of the asynchronies indicated that the efferent fibers were not impaired by the local anesthesia.

As the aim of the study was to examine the influence of tactile feedback on the timing of movements, we have to control for the other feedback components remaining constant across conditions. Auditory as well as visual feedback was eliminated throughout the experiment by presenting white noise through headphones and by blindfolding the subjects. To control for the kinesthetic feedback, we analyzed the results obtained in the contact-free tapping task. In this task, subjects were asked to tap free in the air without any contact to the board or to other fingers at any time of the finger movement. This instruction ensured that (almost) no tactile feedback was available to the subjects to control the finger movement. The only remaining part of the tactile component was the information coming from the skin stretch of the finger, which was assumed to play a minor role as compared to the kinesthetic feedback resulting from the joint receptors and the muscle spindles. The results obtained in the contact-free tapping task revealed no significant difference between the two conditions. Therefore, we can conclude that the kinesthetic fibers remained unimpaired by the peripheral nerve block; no change in the availability of kinesthetic feedback occurred throughout the experiment.

One final argument against the interpretation of the present findings in terms of feedback manipulation is a methodological one. As we used a fixed order of conditions (first control condition, second condition with peripheral nerve block), one might argue that the increase in asynchrony is due to order or learning effects. The main reason for this design was that we wanted to make sure that our control condition was not affected by a residual influence of the nerve block. This could first be a remaining influence of the xylocaine being not completely catabolized. Second, subjects might develop a strategy to handle the experimental situation without tactile feedback and transfer this strategy to the control condition. The only way to avoid such problems is to present the control condition first. On the other hand, there is evidence that there are no learning effects under usual tapping conditions as long as subjects are not informed about their asynchrony, that is, presented with knowledge of results. Aschersleben (2000b) had subjects tap for 10,000 taps (under conditions similar to the control condition in the present study) and still could not demonstrate a change in asynchrony at all.

After excluding alternative explanations of the observed results, we first of all can conclude from the present study that sensory feedback plays an important role in the timing of repetitive movements. Further support for this notion comes from a recent study with a deafferented subject who suffered a purely sensory neuropathy leading to a total loss of kinesthetic and tactile sensibility for the whole body below the neck but leaving the motor system intact (Aschersleben et al. 2000b). In this study, the amount of sensory feedback from the tap was manipulated and the results clearly indicated that the presentation of feedback had a great influence on the performance of the deafferented subject in that it considerably improved his performance.

Moreover, we now can draw conclusions concerning the two to-be-tested hypotheses. The SAM assumes that the accumulation of afferent signals at a cortical level is

necessary to establish a central representation with the negative asynchrony arising from the different accumulation functions for clicks and taps. According to this model, the number of afferent signals was reduced under conditions with peripheral nerve block because one feedback component was eliminated. This should lead to a less steeper accumulation function; therefore, an increase in asynchrony was predicted (see Fig. 1). Conversely, according to the Paillard-Fraisse hypothesis, the anticipation arises from differences in nerve conduction times between click and tap and their corresponding central representations, thus, putting it on a peripheral level. The Paillard-Fraisse hypothesis predicted a decrease in the amount of asynchrony because the slower feedback component was eliminated, whereas the faster kinesthetic feedback component remained unimpaired, which means that the time between the tap and its central representation should be reduced. (A somewhat more cautious form of the hypothesis predicted no effect of the nerve block on the asynchrony under the assumption that the difference in mean conduction times between blocked and unblocked afferents would be too small to be effective.) The results clearly ruled out (both versions of) the Paillard-Fraisse hypothesis, while the predictions of the SAM were fully confirmed. In both the standard tapping task and the isometric tapping task, the amount of asynchrony was increased under conditions with peripheral nerve block.

Converging evidence in favor of the SAM comes from experiments in which the feedback arising from the tap was manipulated by changing the movement of the finger (Aschersleben et al. 2000a). In these experiments, subjects were instructed to produce finger movements with either small or large amplitudes. As conditions with large finger amplitudes were assumed to produce enhanced somatosensory feedback, the SAM predicted a reduction in the amount of asynchrony under those conditions. This prediction was fully confirmed. Furthermore, the results are in line with experiments in which isometric force pulses were examined. Here, subjects had to produce either weak or strong forces and, again, the predictions of the SAM were verified: The asynchrony between click and tap was significantly enlarged if subjects had to produce weak forces rather than strong forces.

The sensibility of the asynchrony on the peripheral nerve block indicated that the timing of a single movement within a sequence of movements is affected. Contrary to our results, Gordon and Soechting (1995) reported that in typing the normal rhythm was unaffected by digital anesthesia. At first sight, this seems to contradict the findings of the present study, which revealed a disruption in the timing of the tap. However, the tasks were distinctly different, since during normal typing the time between successive keypresses is typically between 100 and 140 ms for a skilled typist. That is, the movements overlap by several hundred milliseconds. These short intervals indicate that the initiation of a movement segment in a sequence cannot be triggered by the sensory information derived from the immediately preceding movement. Thus, the typing task studied by Gordon and Soechting (1995) is rather different to the tapping task examined in the present study. Here, intertap intervals comprised 800 ms, thus leaving enough time to evaluate the feedback from the preceding tap in order to correct the timing of the next one.

In conclusion, the present study clearly demonstrates the important role of tactile feedback in the timing of movements. Moreover, it provides further supporting evidence for the more general view that (anticipated or perceived) action effects play a critical role in the control of actions. Empirical support for such an approach came not only from our studies in sensory motor synchronization (Aschersleben and Prinz 1995, 1997; Aschersleben et al. 2000b) but also from studies on compatibility effects and sequence learning (Elsner and Hommel, in press; Kunde, in press).

References

Aschersleben G (2000a) Temporal control of movements in sensorimotor synchronization. Brain Cogn (in press)

Aschersleben G (2000b) Knowledge of results and the timing of actions (paper 1/2000). Max Planck Inst Psychol Forsch, Munich

Aschersleben G, Prinz W (1995) Synchronizing actions with events: The role of sensory information. Percept Psychophys 57:305–317

Aschersleben G, Prinz W (1997) Delayed auditory feedback in synchronization. J Mot Behav 29:35–46

Aschersleben G, Gehrke J, Prinz W (2000a) A psychophysical approach to action timing. In: Kaernbach C, Schröger E, Müller H (eds) Psychophysics beyond sensation: laws and invariants in human cognition. Hillsdale, NJ: Erlbaum (in press)

Aschersleben G, Stenneken P, Cole J, Prinz W (2000b) Timing mechanisms in sensorimotor synchronization: intersensory integration of action effects. In: Prinz W, Hommel B (eds) Attention and performance XIX. Common mechanisms in perception and action. Oxford University Press, Oxford (in press)

Bard C, Paillard J, Teasdale N, Fleury M, Lajoie Y (1991) Self-induced versus reactive triggering of synchronous hand and heel movement in young and old subjects. In: Requin J, Stelmach GE (eds) Tutorials in motor neuroscience. Kluwer, Amsterdam, pp 189–196

Bard C, Paillard J, Lajoie Y, Fleury M, Teasdale N, Forget R, Lamarre Y (1992) Role of the afferent information in the timing of motor commands: a comparative study with a deafferented patient. Neuropsychologia 30:201–206

Billon M, Semjen A, Cole J, Gauthier G (1996) The role of sensory information in the production of periodic finger-tapping sequences. Exp Brain Res 110:117–130

Cordo P, Carlton L, Bevan L, Carlton M, Kerr GK (1994) Proprioceptive coordination of movement sequences: role of velocity and position information. J Neurophysiol 71:1848–1861

Edin BB, Johansson N (1995) Skin strain patterns provide kinaesthetic information to the human central nervous system. J Physiol (Lond) 487:243–251

Elsner B, Hommel B (2000) Effect anticipation and action control. J Exp Psychol Hum (in press)

Fraisse P (1980) Les synchronisations sensori-motrices aux rythmes. In: Requin J (ed) Anticipation et comportement. Centre National, Paris, pp 233–257

Fraisse P, Oléron G, Paillard J (1958) Sur les repères sensoriels qui permettent de contrôler les mouvements d'accompagnement de stimuli périodiques. Ann Psychol 58:322–338

Gandevia SC, McCloskey DI, Burke D (1992) Kinaesthetic signals and muscle contraction. Trends Neurosci 15:62–5

Gehrke J (1995) Sensorimotor synchronization: the intensity of afferent feedback affects the timing of movements (paper 15/95). Max Planck Inst Psychol Res, Munich

Geisser S, Greenhouse SW (1958) An extension of Box's results on the use of F-distribution in multivariate analysis. Ann Math Stat 29:885–891

Gordon AM Soechting, JF (1995) Use of tactile afferent information in sequential finger movements. Exp Brain Res 107:281–292

Kelso JAS, Stelmach GE, Wanamaker WM (1974) Behavioral and neurological parameters of the nerve compression block. J Mot Behav 6:179–190

Kelso JAS, Wallace SA, Stelmach GE, Weitz GA (1975) Sensory and motor impairment in the nerve compression block. Q J Exp Psychol 27:123–129

Kunde W (2000) Response-effect compatibility in manual choice reaction tasks. J Exp Psychol Hum (in press)

LaRue J, Bard C, Fleury M, Teasdale M, Paillard J, Forget R, Lamarre Y (1995) Is proprioception important for the timing of motor activities? Can J Physiol Pharmacol 73:255–261

Macefield G, Gandevia SC, Burke D (1989) Conduction velocities of muscle and cutaneous afferents in the upper and lower limbs of human subjects. Brain 112:1519–1532

Mates J, Aschersleben G (2000) Sensorimotor synchronization: the influence of temporally displaced auditory feedback. Acta Psychol 104:29–44

Mates J, Radil T, Pöppel E (1992) Cooperative tapping: time control under different feedback conditions. Percept Psychophys 52:691–704

O'Boyle D (1997) On the human neuropsychology of timing of simple, repetitive movements. In: Bradshaw CM, Szabadi E (eds) Time and behaviour. Psychological and neuro-behavioural analyses. Elsevier, Amsterdam, pp 459–515

O'Boyle DJ, Clarke VL (1996) On the source of the negative synchronization error during temporal-tracking performance. BRA Abstr 13:40

Paillard J (1949) Quelques données psychophysiologiques relatives au déclenchement de la commande motrice. Ann Psychol 48:28–47

Prinz W (1997) Perception and action planning. Eur J Cogn Psychol 9:129–154

Sanes JN (1990) Motor representations in deafferented humans: a mechanism for disordered movement performance. In: Jeannerod E (ed) Attention and performance XIII. Erlbaum, Hillsdale, NJ, pp 714–735

Shefner JM, Logigian EL (1994) Conduction-velocity in motor, cutaneous afferent, and muscle afferent-fibres within the same mixed nerve. Muscle Nerve 17:773–778

Shimoyama I, Ninchoji T, Uemura K (1990) The finger-tapping test. Arch Neurol 47:681–684

Strichartz G (1976) Molecular mechanisms of nerve block by local anesthetics. Anesthesiology 45:421–441

Vos PG, Mates J, Kruysbergen NW van (1995) The perceptual centre of a stimulus as the cue for synchronization to a metronome. Q J Exp Psychol 48:1024–1040