Is proprioception important for the timing of motor activities?¹

Jacques LaRue, Chantal Bard, Michelle Fleury, Normand Teasdale, Jacques Paillard, Robert Forget, and Yves Lamarre

Abstract: This study tested whether a deafferented patient demonstrates impaired timing ability compared with four control subjects. By comparing normal subjects with the deafferented patient, some insight was expected on the importance of proprioception in timing of motor behavior. The protocol was set to enhance the strategy of the subjects in using feedbacks. Subjects had to synchronize finger taps with a sound produced at regular intervals. Once synchronized, the bips were muted and the subjects had to continue the tapping at the same pace. Interresponse interval (IRI) variability was measured under two feedback conditions: with and without vision and auditory feedback. The Wing and Kristofferson model (A.M. Wing and A.B. Kristofferson. Percept. Psychophys. 13(3): 455-460. 1973) was used to segment IRI variance into separate components: a central clock and a peripheral motor delay. When the deafferented patient saw and heard the outcome of her tapping movements, there was a greater variability in successive intervals between taps than when vision and hearing were blocked. We interpret this variability as indicating that the subject used auditory and visual feedback to maintain a correct overall rhythm. The patient may easily substitute visual and (or) auditory feedback for her defective proprioception for movement timing. However, this substitution proved to be inefficient in the limited training period provided in this experiment. The results suggest that the proprioceptive contribution to the time-keeping mechanism presumably depends on the presence of an efference copy signal.

Key words: tapping, Wing and Kristofferson model, repetitive movements, synchronization, efference copy.

Résumé: Dans cette étude, on a comparé la capacité rythmique d'un patient déafferenté à celle de quatre témoins normaux, dans le but de mieux comprendre le rôle de la proprioception dans la synchronisation du comportement moteur. On a établi le protocole de manière à améliorer la stratégie adoptée par les sujets pour utiliser des boucles de rétroaction. Les sujets devaient synchroniser des tapements de doigts avec un son produit à intervalles réguliers. Une fois la synchronisation obtenue, les bips ont été éliminés et les sujets ont continué les tapements au même rythme. On a mesuré la variabilité des intervalles inter-réponses (IIR) dans deux conditions de rétroaction : avec et sans rétroaction auditive et visuelle. On a utilisé le modèle de Wing et Kristofferson (A.M. Wing and A.B. Kristofferson. Percept. Psychophys. 13(3): 455-460. 1973) pour segmenter la variance IIR en deux composantes : une horloge centrale et un délai moteur périphérique. Lorsque la patiente déafferentée a visualisé les mouvements de ses doigts et entendu les tapements, la variabilité des intervalles successifs entre les tapements a été plus grande qu'en l'absence de vision et d'audition. On interprète cette variabilité comme une indication que le sujet utilise une rétroaction visuelle et auditive pour maintenir un rythme global approprié. La patiente pourrait facilement substituer la rétroaction visuelle ou auditive à sa proprioception déficiente pour établir le rythme de ses mouvements. Toutefois, cette substitution s'est avérée inefficace durant la période d'apprentissage limitée allouée à cette expérience. Les résultats suggèrent que la contribution proprioceptive au mécanisme de rythmicité dépend probablement de la présence d'un signal de copie d'efférence.

Mots clés : tapement, modèle de Wing et Kristofferson, mouvements répétitifs, synchronisation, copie d'efférence.

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**Introduction**

More than 150 years after Charles Bell's description of the spinal reflex pathways, the importance of somatosensory afferent input remains a matter of debate. Deafferentation has been recognized as a strong model to test the importance of proprioception in motor control (for a review see Sanes et al. 1985). In the present study, we compared a deafferented patient with normal subjects to assess the contribution of proprioceptive feedbacks to the timing process of repetitive movements.

Timing is generally known as an important function of motor coordination. The capacity to synchronize movements to external events and to regulate the time spacing of self-paced movements has been studied for more than a century. Still, whether timing is an open-loop or a closed-loop process remains a controversial issue. If it is a closed-loop process, what sources of feedback are used and what is the importance of proprioception in this process?

Many studies on "timing" used a common methodology including a repetitive external stimulus (usually a sound) and a simple response (typically a finger tap). The mean and variance of interresponse intervals (IRIs) were recorded as the dependent variables. Over the years, very sophisticated analyses have been developed to delineate timing mechanisms. The main discussion concerns the sources of variance in the timing process. Keele et al. (1988) suggested that the timing mechanism is distributed over several neural systems rather than forming a single oscillator located in a small area of the nervous system. Yet, the specific circuitry has not been identified, and timing processes still have to be inferred. Visual and auditory feedbacks were often manipulated, but kinesthetic and cutaneous feedbacks were usually left uncontrolled. A comparison between normal subjects and a deafferented patient should provide some answers about the importance of proprioception in timing.

**Timing as a closed-loop process**

Stevens (1886) developed the continuation paradigm, which is still in use today. In this paradigm, the subject hears a sound at a regular interval and synchronizes a motor response with the sound. When he feels that his tapping is synchronized, the sound is turned off. This is the beginning of the continuation (self-paced) phase, where the subject attempts to maintain the same rhythm as in the synchronization phase. Without any external cue, it is assumed that subjects rely on an internalized model of the rhythm.

During the continuation phase, Stevens noted a "zigzag" in the length of immediately successive IRIs that looks like a correction process. He assumed that any discrepancy with the remembered standard is used as a basis for adjusting the next IRI. Stevens also identified two sources of variation in the timing process, the "will" and the "hand" or, in more modern terms, a central and a peripheral process. However, the feedback modalities used to detect the error were not assessed.

Fraisse et al. (1958) observed that subjects are more similar in their synchronization errors when they have access to unequivocal feedback than when such feedback is not available. However, kinesthetic feedbacks were adequate to stabilize their response variability. When provided with different synchronization cues (kinesthetic, end of movement; auditory feedback), the subjects' strategy consisted in searching a stable pattern rather than in trying

to synchronize the stimulus with a given cue. The kinesthetic feedback, better controlled by the subject, was the most efficient.

Support to feedback monitoring was provided by Fraisse and Voillaume (1971). They examined how subjects synchronized their responses with an external sound produced at regular intervals of 400, 800, 1600, and 3200 ms. Two conditions were tested: (i) real synchronization, when the sound was produced by an external device, and (ii) pseudosynchronization, when the sound coincided with the subject's tap. No subject detected a difference between pseudosynchronization and the real synchronization situation; they tended to increase their response rate up to the tapping frequency. The authors explained this effect by the tendency to anticipate the sound and the corrections made for each response in anticipation. However, the subjects behaved as if they were in the real synchronization condition (i.e., they maintained their rhythm) when they knew that the sounds were produced by their own responses. This suggests that the IRI is continually monitored and that a correction is made when an IRI differs from the external criteria. Moreover, this process is unconscious, although it can be consciously reversed.

In agreement with Stevens' (1886) explanation of the zigzag pattern in successive IRIs, Fraisse and Voillaume (1971) obtained negative autocorrelations between successive IRIs that they attributed to corrections of perceived errors. Testing different frequencies allowed them to infer conclusions about the correction process. The difference between the tap and the sound was the criterion against which the response was compared to determine if there is an error. In high frequency tapping, few errors were detected because most of the responses occurred within the perceptual threshold of synchronization (60 ms) (Hirsh and Fraisse 1964). In low frequency tapping, the errors were larger, more easily detectable and, therefore, more corrections were made.

There are some observations showing that sensory feedback contributes to tapping regularity. Chase et al. (1961) reported decreased performance under a decreased sensory feedback condition. Barratt et al. (1988) observed faster rates and less intrasubject variability when auditory feedback was provided compared with a no-feedback condition.

Hary and Moore (1985) presented a model for feedback in timing. Subjects were free to use visual, proprioceptive, tactile, or other sensations to regulate their synchronization. Subjects were unaware that the pulse sequence alternated between 30 intervals of 705 ms and 30 intervals of 695 ms (for a total of 240 intervals). Correlograms showed which strategy a subject used when he synchronized his taps with metronome sequences. Several theoretical strategies were simulated on a computer and compared with experimental data; both data sets closely matched. The results provided the first evidence of error correction in the temporal tracking process.

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3 An autocorrelation is a correlation between one observation of a variable and another observation of the same variable. Thus, for a measure repeated 55 times it is possible to create 54 pairs of score. This is called a lag 1 autocorrelation. The autocorrelation obtained from these pairs evaluates the relationship between a given measure and the immediately following measure. The general idea is to test whether an event is linked to the one preceding it.
and strongly implicated the synchronization error as the base of the corrective action, with subjects being unaware of the phenomenon. Because of inherent instability in the results of the simulation, the authors rejected a simple response reset model. In this model (Michon and Van der Valk 1967; Fraisse and Voillaume 1971), the subject detected the occurrence of the metronome event and produced his next response after a fixed central delay plus a peripheral delay; the central delay was not modified by the resulting error. One model, fitting closely to the laboratory data, included (i) the subject evaluation of the synchronization error; (ii) using that evaluation, a correction of the internal (stored) delay during which he waits before executing his next response; (iii) an internal source of variability (noise) in the error evaluation process; and (iv) a peripheral (motor) delay variability.

However, what could be used by the subject to evaluate his synchronization error? Schmidt (1971) suggested that proprioceptive feedback arising from a movement completed earlier in a sequence may serve as a cue for initiating the next response. Adams (1977) noted that, lacking an organ of time, it must be assumed that timing is governed by an undiscovered brain mechanism or a derived function of one or more of the senses. He proposed that the firing of slowly adapting joint receptors was the source of information about limb position and that the time-varying function was the basis of timing. McClosky et al. (1983) showed that subjects could time when a muscle contracts by using either of two signals: one central, generated prior to neural activity in motoneurons, and the other peripheral, due to movement-evokedafferent activity.

Al-Falahe et al. (1990) showed that spindle afferents provide stretch response with passive and active movements of the index finger (such as a tapping task). The impulse rate was slightly higher and the interspike interval variability much larger during active movement. Tendon organs were totally unmodulated by an imposed stretch in the relaxed muscle. However, their impulse rate was highly modulated during active movement (see also Gandevia and Burke (1992) for a review of the contribution of kinesthesias to movement control).

Timing as an open-loop process

Some studies recently reported used the presence of a negative autocorrelation between successive taps to support the idea that feedback is used to correct errors in timing. However, Wing and Kristofferson (1973) showed that a negative autocorrelation between two successive taps might be produced not by a correction of error but by simple random variations in the timing of response. In a series of successive finger taps, a given IRI that was longer than the criterion tended to be followed by a shorter IRI, and vice versa. However, nonadjacent taps tended to be uncorrelated. Two processes served to model this phenomenon: (i) a central clock emitting a pulse (timekeeper) and (ii) an overt response produced after a delay (MD) required by the motor implementation process.4

Four predictions emerged from this model: (i) IRIs sharing a common boundary (i.e., immediately adjacent IRIs) are negatively correlated; (ii) IRIs that do not share a common boundary (i.e., IRIs separated by one or more intervening IRIs) are not correlated; (iii) in a completely periodic time-keeper (which would imply that any IRI variance is entirely due to motor variance), the correlation is -0.5; (iv) when motor variance is much smaller than that of the timekeeper variance, the correlation approaches 0. As most studies using this kind of analysis showed various degrees of violation of these predictions, it is not clear if the model is totally valid. To verify the contribution of feedback to timing, Wing (1977) applied the continuation paradigm combined with a “perturbed auditory feedback” (PAF) method, which modifies the time of production of auditory feedback for some taps. Before the insertion of PAF, a negative autocorrelation between adjacent responses was found, supporting an open-loop control as hypothesized by Wing and Kristofferson (1973). However, the existence of an effect of PAF on the immediately subsequent interval showed that subjects did process auditory feedback. Thus, the control of timing is not totally an open-loop process. Wing (1977) modified the original model accordingly: feedback is used to define internal intervals that are compared with a central “clock” output so that the timekeeper can be monitored. This view differs from the closed-loop view consisting of a response triggered by the sensory information provided by the previous response. Instead of the response itself, it is the rate of response of the timekeeper that the feedback loop regulates. As pointed out by Wing, this processing presents some violations of the original predictions. For example, if corrections are applied throughout the entire series, the predicted correlation between adjacent IRI drops to zero.

Repetitive movements and timing in deafferented subjects

Data issued from a deafferented population are scarce and do very little in resolving the controversy. A patient with sensory loss following a parietal lesion (Jeannerod et al. 1984) and subjects suffering from peripheral sensory neuropathy (Rothwell et al. 1982) showed a rapid deterioration in the rate of tapping when vision of their deafferented tapping arm was not allowed. Sanes et al. (1985) attributed the difficulty of his patients in performing rapid successive movements to the appearance of cocontraction at high movement frequency. However, Ivry and Keele (1989) compared several groups who suffered from different neurological deficits and obtained results consistent with the Wing and Kristofferson model. Two patients presenting a sensory loss and an age-matched

4 The duration \( l_i \) of any IRI is the sum of the intervals between two successive clock pulses \((C_i)\) and the difference between the current MD \((MD)\) and the immediately preceding response \((MD_{i-1})\).

\[
l_i = C_i + MD_i - MD_{i-1}
\]

Because this is assumed to occur in an open-loop process, it follows that a randomly longer MD lengthens the current IRI and shortens the next one; however, a long or short clock pulse affects only the current IRI. Thus a negative lag 1 autocorrelation provides an estimate of the MD variance. Under these conditions, Wing and Kristofferson (1973) showed that the central clock variance \((\text{VAR}(C))\) might be estimated using the following equation:

\[
\text{VAR}(C) = \text{VAR}(I) - 2\text{VAR}(MD)
\]

where \(\text{VAR}(I)\) is obtained directly from the IRI series and \(\text{VAR}(MD)\) is given by lag 1 autocovariance.
control group displayed nearly identical results; their performance was unchanged following the elimination of visual information. This finding supported the assumption of the Wing and Kristofferson model that feedback from a given response interval should not affect subsequent intervals.

Therefore, our study investigated the ability of a subject suffering from total sensory loss and neurologically normal subjects, matched for sex and age, to produce regularly timed intervals. The role of feedback (visual-auditory and (or) proprioceptive) in the timing of a motor response was analyzed.

Materials and methods

A deafferented patient and four control subjects voluntarily participated in this study. The patient suffered from two episodes of polyneuropathy resulting in a permanent loss of the large myelinated fibres of the four limbs. Intensive clinical investigations of the subject showed a total loss of sensory modalities, except pain and temperature, but a normal efferent neuromotor system (Cooke et al. 1985; Forget and Lamarre 1987; Forget and Lamarre 1990).

The experimental task consisted of the continuation paradigm previously described. The subjects were seated with the right arm (dominant) resting palm down on a table. The index finger established a contact on a metal plate, and each contact produced by a tap was recorded by the computer with a time resolution of 0.5 ms. Each trial began with a series of tones produced by a piezoelectric buzzer (50 ms in duration, 1000-ms intertone interval). The subjects started tapping along with the tones. Once they had internally established the target pace (after 12-15 taps), the tones ended. Subjects were instructed to continue at the same pace when the tone disappeared. The computer stopped after 60 s, which allowed the recording of approximately 55 taps per trial.

Each subject performed five trials under each experimental condition. In the feedback condition, vision and hearing of the taps was possible. In the no-feedback condition, the subjects repeated the task without vision and hearing, i.e., blindfolded and wearing ear muffs during the self-paced tapping.

It is important to note that the subjects did not receive additional knowledge of results (KR) in terms of IRI variability or IRI errors. Thus, leaving the subjects without external performance criteria should force them to rely on their own proprioceptive feedbacks.

The order of presentation of the experimental conditions was fully counterbalanced within a subject. Two subjects and the patient had their first trial with feedback followed by one trial without feedback. Feedback conditions were alternated up to a total of five trials in each condition. The next two subjects were tested in the reverse order (no feedback, feedback).

Results

The IRI was measured (in milliseconds) as the time elapsed from the first contact of the finger on the plate and the next contact. Means and variances were computed for each trial. Clock and motor delay standard deviations were estimated according to the Wing and Kristofferson model (see footnote 3).

Verification of the predictions of the Wing and Kristofferson model

Prediction 1: Temporally abutting cycles are negatively correlated (lag 1 autocorrelation) with an average lower bound of -0.5

The observed negative correlations were low (ranging from 0.1 to 0.25). Of the 49 trials recorded in this experiment, 23 did not correlate negatively and thus violated the first prediction. The amount of violation was similar for the patient and control subjects.

A positive autocorrelation is problematic since it yields a "nonsensical" negative motor delay variance and inflates clock variance. In such a case, it was suggested to substitute a value of zero to the motor delay variance and the total IRI SD to the clock variance (Ivry and Keele 1989; Greene and Williams 1993). A comparison of the results involving only the negatively autocorrelated trials and all the trials after substitution revealed no modification for the normal subjects variance estimates. However, the patient's results were largely affected; normal subjects' IRI SDs were in the same range as the estimate of clock SD, whereas the patient's IRI SDs were 2-3 times larger than her clock SD. Therefore, and because of the high rate of violation, it was decided to adopt a more conservative approach by rejecting the positively

### Table 1. Comparisons between the patient and the control group in each feedback condition using t-tests of a sample (the patient) from a population (control group).

<table>
<thead>
<tr>
<th>Variable, condition</th>
<th>Patient (Mean)</th>
<th>Control group (Mean)</th>
<th>Control group (SD)</th>
<th>t, df = 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>IRI, no feedback</td>
<td>1029.50</td>
<td>924.56</td>
<td>49.50</td>
<td>1.98</td>
</tr>
<tr>
<td>IRI, feedback</td>
<td>1189.40</td>
<td>916.65</td>
<td>40.30</td>
<td>3.38</td>
</tr>
<tr>
<td>SD, no feedback</td>
<td>70.90</td>
<td>53.34</td>
<td>14.11</td>
<td>0.62</td>
</tr>
<tr>
<td>SD, feedback</td>
<td>109.74</td>
<td>43.11</td>
<td>2.33</td>
<td>14.32*</td>
</tr>
<tr>
<td>Clock, no feedback</td>
<td>45.00</td>
<td>43.12</td>
<td>13.50</td>
<td>0.07</td>
</tr>
<tr>
<td>Clock, feedback</td>
<td>82.50</td>
<td>34.91</td>
<td>2.20</td>
<td>10.72*</td>
</tr>
<tr>
<td>Motor delay, no feedback</td>
<td>39.15</td>
<td>21.24</td>
<td>4.09</td>
<td>2.19</td>
</tr>
<tr>
<td>Motor delay, feedback</td>
<td>53.17</td>
<td>17.17</td>
<td>1.15</td>
<td>15.72*</td>
</tr>
</tbody>
</table>

* IRI, mean of interresponse intervals; SD, standard deviation of IRIs; Clock, estimation of clock standard deviation; Motor delay, estimation of motor delay standard deviation.

* Significantly different at p < 0.02.
autocorrelated trials. Twenty-one trials were then rejected, and the remaining 28 trials were analyzed.

*Prediction 2: Non abutting cycles (lag 2, 3, ...; see footnote 5) are uncorrelated*

This condition was verified for all of the 28 trials showing a negative autocorrelation.

**Comparisons between the patient and control subjects**

This study was designed to compare the timing behavior of deafferented patient with the behavior of normal subjects. Significance level was set at $p < 0.02$ to account for the number of comparisons; a $t$ test of a sample from a population (Table 1) showed that SD of IRI and clock and motor delay standard deviation estimates of the patient differ significantly from those of control subjects in the feedback condition, but not in the no-feedback condition (Fig. 1).

**Discussion**

This study examined whether proprioception is important in timing of motor behavior by comparing a deafferented subject to four control subjects. The main result is observed when the deafferented patient saw and heard the outcome of her tapping movements; there was a greater variability in successive intervals between taps than when vision and hearing were blocked. This result might seem surprising. It is usually expected that the absence of vision or hearing impairs performance and, conversely, that the addition of vision and hearing improves it. In fact, the improvement of performance when vision and hearing are allowed is not a general law. In a postural task, Teasdale et al. (1993) observed an increased sway amplitude during the transition between darkness (no vision) and light (vision) conditions; since there is still an increase in sway amplitude when the conditions are reversed, the authors concluded that vestibular, proprioceptive, and visual information must be integrated for a better performance. Adding vision momentarily degraded performance. Proteau et al. (1992) observed a decrease of accuracy in pointing movements when vision was provided after an extensive training period without vision. This could be due to a lack of integration of sensory output or to a resetting of the learned strategy including the new sensory inputs. This phenomenon may also be present for other sensory modalities; Clark et al. (1985) observed that the variance of estimates of knee position may be reduced by cutaneous anesthesia as if this removed noise from detection. These researches exemplify the need for convergence within the nervous system.

Experiments in which all sensory input had been eliminated by dorsal root section (in monkeys, Polit and...
Bizzi 1979) or afferent polyneuropathy (in man, Rothwell et al. 1982; Sanes et al. 1985) showed that well-trained movements can be performed adequately. However, unfamiliar movements were completely disrupted when sensory information was lacking.

As is probably the case for the tapping task, there are conditions where a performance might be controlled by many interrelated subsystems. For a particular task some subsystems might be better suited for an optimal performance. The relative contribution of each subsystem is what we will call here a strategy. This idea of a strategy agrees with McCloskey et al. (1983), who stated that subjects often show a preference for peripheral or central signals to control the timing of movement, but can attend to either signal without training.

The control subjects may always rely on proprioception, and rely on vision or hearing when they are available. In this group, the absence of difference between feedback conditions suggests three possible strategies. (i) Proprioception provides enough information, and vision or hearing provides redundant or integrated information. (ii) Proprioception is the only system used. (iii) None of these feedback systems is used and the tapping regularity is totally maintained by a central clock. The results suggest that the first strategy was adopted since there is a slight decrease (not significant) in response variability when vision and hearing are provided.

Since the patient could not rely on proprioception, her augmented variability when vision and hearing are provided leaves only one possible strategy. Vision and (or) hearing are used somehow to control tapping regularity. Obviously, the results showed that this strategy was not very successful for the patient. The patient was trying to maintain her rhythm by consciously focusing on the visual and auditory information. This is consistent with the overall behavior of the subject since her accident. Given the short training and the novelty of the task the subject was unable to adjust. However, it is expected that more extensive training would significantly improve her performance.

This experiment was questioning whether proprioception is used in timing. It appears that proprioception is involved in timing of motor activity. Moreover, in comparison with proprioception, the data suggest that vision and (or) hearing are less important for the timing in a tapping task.

**Does proprioception modulate the central clock or the motor delay?**

The only tool available to answer this question is the Wing and Kristofferson model. Since we observed a high violation rate (47%) of this model, we might question the validity of this procedure. First note that violation of the model is often observed: Greene and Williams (1993) reported a 2.25% violation rate; Irvy and Keele (1989) and Turvey et al. (1989) reported rejection rates of 12.8 and 14%, respectively.

Differences in methods might explain the higher violation rate. (i) The beep interval of 1000 ms used in the present study is two times longer than in other studies (400-550 ms). This factor can be rejected since an interval of 500 ms was previously tested in the patient and produced the same rate of violation. (ii) While subjects performed from 12 to over 100 trials in the mentioned studies, our subjects performed five trials per condition only. Wing and Kristofferson (1973) clearly acknowledged the existence of a practice effect on interresponse delay variance; more practice reduces the response variance, yet this effect was not quantified. It is important to recall that the Wing and Kristofferson model is suited for an open-loop control of tapping. An open-loop control is most likely to occur after a large amount of practice. However, in the first trials, the subject might be in an adjustment process using some feedback. Thus, testing the first trials or testing after hundreds of trials might involve two different processes and modify the behavior of the model accordingly. Since it is most likely that the subjects rely on feedback more at the beginning of practice than after long training, the first trials should be the most powerful procedure to detect whether feedback is used. (iii) Finally, the absence of knowledge of results (KR) is another important factor. In other studies, KR was usually provided after each trial, stating how far the responses were from the criteria IRI, whereas in our study, we deliberately choose not to provide KR. According to the Input Hypothesis (Schmidt 1971) KR is used to error label the proprioceptive feedback from the mediating limb, ultimately informing the performer as to the appropriate velocity-proprioceptive cue combination that will lead to effective time-keeping mediation. The absence of KR might prevent the automatization of the response, forcing subjects to use intrinsic feedback.

Our point is that the high rate of violation of the model does not necessarily come from a noisy system characterized by high intra-individual variability: instead, it may reflect the adjustment process to the feedbacks. Considering that the proper procedure was applied to correct the problems faced by the violation of the model (see Results), we attempted to ascertain whether the clock or the motor variance is affected by proprioceptive feedback.

The patient was more variable than normal subjects. The increase of motor delay estimates was expected because of a slight spasticity in the patient's hand. However, the observed lag 1 autocorrelations were close to zero in all subjects. Since a low autocorrelation reflects a greater relative contribution of the clock variance (Wing 1977), then the relative peripheral variability of the deafferented patient might be considered similar to that of normal subjects. On the other hand, nothing made us expect that the subject would have a higher clock variance estimate than normal subjects. This suggests that proprioception could be used in the regulation of the central clock.

In the feedback condition, the differences between the patient and controls suggest that vision and (or) hearing interfered with the timing process of the patient. Such perturbation affected only the central clock. In the no-feedback condition, the patient could not adjust the central clock, whereas the controls could always rely on their proprioception. Fraisse et al. (1958) also reported that kinesthetic feedback was sufficient to control synchronization.

**How could proprioception be used by the central lock?**

The efference copy theory may give an answer. A system is provided with some model corresponding to the expected...
pattern of afferent information on an ongoing movement. Ivy and Keele (1989) and Keele and Ivy (1991) suggested that an efference copy is made available to the cerebellum. The efference copy presumably incorporates some form of prediction of delay since the afferent signal is continuously changing over time. According to Gellman et al. (1985), in active movement, an efferent copy of the motor commands elicits the expectation of a particular feedback. If that feedback occurs, no error signal is generated. Furthermore, it seems that the efference copy involves not only the activation of an expected feedback, but explicit timing of the anticipated feedback. If the feedback signal comes too early or too late, an error signal occurs. Feedback occurring at the correct time does not produce an error signal.

Our results support the idea that, without proprioception and knowledge of results, the effectiveness of the efference copy is jeopardized. Proprioception appears to be more useful to the central clock process than to the peripheral motor component of the response.

References


