Electrical or mechanical stimulation of the perioral receptors has been known to generate short lasting reflex inhibition of the jaw closing muscle electromyogram (EMG) (reviewed in Lund et al., 1983; Türker, 2002). The intensity of the stimulation does not need to be painful (Yu et al., 1973) and its pathway is thought to be Aβ fibres, as innocuous stimulus, such as a fine jet of saline directed to the lips of healthy humans, can generate this inhibitory reflex (Cruccu et al., 1989). This inhibitory reflex is often referred to as ‘exteroceptive suppression’ to distinguish it from the ‘exteroceptive silent period’ that is associated with muscle shortening and unloading of spindles (Godaux and Desmedt, 1975). Exteroceptive suppression of the jaw muscle activity has been the focus of large number of studies. There are three main reasons for this interest: first, that it illustrates the existence of a protective inhibitory pathway that connects perioral receptors to the motoneurons of the jaw closing muscles (Türker, 1988, 2002). Second, it has been used as an experimental tool to scrutinize conditioning effects of other peripheral or central pathways on this pathway and vice versa, highlighting the details of the network that forms the neurological basis for jaw movement (Dubner et al., 1978; Sessle and Hu, 1981). Third, it can be used as a diagnostic tool for many neurological disorders in the trigeminal system (De Laat et al., 1998; Türker et al., 1989; Romaniello et al., 2003).

The article in this issue by Torisu and colleagues (Torisu et al., 2007) adds important new information on the properties of the exteroceptive suppression of jaw muscles. Their findings suggest that muscle fatigue influences the jaw closing muscle inhibitory pathway both directly and also via the pain pathway. They also provide evidence that muscle fatigue increases resting EMG activity which is further increased by the injection of glutamate. There are however several methodological questions that have arisen during the review of that article. In this editorial, we would like to remind the readers of these important questions and suggest some possible solutions.

What level of background excitation to use and why?

It is necessary to control the excitability of the motoneuronal pool during a reflex experiment since changes in the background excitability significantly influence the expression, duration and strength of the inhibitory reflex response (Türker, 1988). This phenomenon known as the ‘frequency principle of inhibition’ (Miles and Türker, 1986) and illustrates that inhibitory reflex responses are largely determined by the discharge rates of motor units. For example, if a motor unit is discharging at 10 Hz, the inhibitory reflex response will be stronger and longer lasting to an identical stimulation than the response when it is discharging at a frequency of 15 Hz (Türker and Miles, 1989). Similarly, it has also been shown that the inhibitory reflex is more easily obtained when the level of excitation of the muscle is low (5–10% MVC) (van der Glas and van Steenbergh, 1989; Türker and Miles, 1989). Since, the expression of the stimulus induced inhibitory postsynaptic potential (IPSP) on the surface EMG is estimated indirectly in human studies, it is ideal to use low levels of background activity in order to obtain the full characteristics of the IPSP developed on the motoneurons that innervate the muscle of interest. Using a very high level of background excitation is likely to reduce the expression of the IPSP on the surface EMG and hence can underestimate the incidence and the level of inhibitory connection of the trigeminal afferents to the motoneuronal pool that innervate the jaw closing muscles.

Besides the importance of a low level of background activity, it is also important to keep the level of activity constant throughout any reflex study. Although at a high level, Torisu et al. (2007) used a constant level of activity (50% MVC) in their article during their entire study and hence their results are valuable and relevant.
Does the same level of surface EMG represent the same level of motor unit discharge?

Even if the same motor units are active in fresh and fatigued muscles, it is expected that the discharge rates of the motor units will be lower post fatigue than in the pre fatigue condition. It has been reported by several researchers that the expression of fatigue can be recognized by an increase in the amplitude of the EMG and a reduction in the discharge rate of the underlying motor units (Bigland Ritchie et al., 1986; Gandevia, 2001). Therefore, when the level of surface EMG is kept constant during a fatiguing contraction, the fatigued muscle will reach the same level of surface EMG by motoneurons that are discharging at lower rates. As mentioned above, lower discharging units have a distinct advantage in expressing the underlying IPSP more accurately. Therefore, even if the IPSP does not change during fatigue, the expression of the IPSP on the surface EMG will be more prominent in the fatigued muscle. When studying the effect of fatigue on reflexes, it is perhaps best to use single motor units and control their discharge rates in all experimental conditions. This will allow experimenters to be sure that the fatigue effect observed in the reflex response is genuine and not caused by the recruitment of different motoneurons with different characteristics, and/or the same motoneurons discharging at reduced rates in the fatigued state.

How can we overcome the errors that are inherent in the classics techniques for determining reflex responses?

The most common classical techniques are full-wave rectification and averaging of the surface EMG record around the time of stimulation and/or compiling peristimulus time histograms (PSTHs) from the single motor unit records (Türker et al., 1997). These techniques are used to estimate the reflex response, which is an indirect consequence of the effects of the postsynaptic potentials that develop on motoneurons after the stimuli. The profile of the postsynaptic potential is then used to assess the sign, number and length of periods of less or more spikes in the probabilistic analysis (count-related errors) of the classical methods. However, probability-based records also contain secondary and tertiary peaks and troughs that are not directly related to the time course of the underlying postsynaptic potential. These errors are caused by phase-advanced or delayed spikes that generate periods of less or more spikes in the probabilistic analysis (count-related errors), and are followed by secondary and tertiary peaks and troughs due to synchronous discharge of the spikes lined up in relation to the stimulus (synchronization-related errors).

At present these peaks and troughs are often still taken to indicate excitatory and inhibitory post synaptic potentials and associated neuronal pathways, respectively (e.g., Bastiaanse et al., 2006). Türker and Powers (2003) have proposed an analysis based on the cumulative sum (CUSUM; Ellaway, 1978) calculation, to overcome the delay or advance related (i.e., the count-related) errors of the classical methods. However, probability-based records also induced secondary and tertiary peaks and troughs due to synchronization of the spikes in relation to the stimulus (i.e., the synchronization-related errors) that could not be overcome even with the special CUSUM approach.

We therefore suggest the following strategy for the reflex studies in the future:

1. When possible, utilize single motor units to ensure that the same motoneurons are examined, and maintain a sustained low frequency discharge rate of the selected unit (~10 Hz), using auditory and visual feedback, under all experimental conditions to ensure that the expression of prestimulus motoneuronal postsynaptic potential will be stable.
2. Utilize peristimulus frequencygram technique to assess the characteristics of peristimulus postsynaptic potential and hence the net effects of the stimulated afferents on the motoneurons under study, and use CUSUM records to determine significant poststimulus deflections (Türker and Powers, 2003, 2005).
3. If single unit approach is not possible as is often the case for the clinical settings, use surface EMG to assess the reflex responses and make sure that CUSUM of the EMG is utilized not only to determine the existence of a significant deflection in the poststimulus record but also to determine its latency, duration and strength (Türker et al., 1997; Brinkworth and Türker, 2003). However, even doing so, beware that this analysis can only illustrate the very first postsynaptic event on the
motoneuron pool (i.e., the shortest pathway between the stimulated afferent and the motoneuron pool) and that secondary peaks and troughs can be due to synchronization type error and hence may not indicate genuine neural pathways.

References


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