Muscle Spindle Afferent Input to Motoneurons in Human Masseter

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Scutter, Sheila D. and Kemal S. Türker. Muscle spindle afferent input to motoneurons in human masseter. J. Neurophysiol. 82: 505–507, 1999. The H-reflex response in large and small single motor units in human deep anterior masseter was studied to investigate the distribution of muscle spindle afferents onto masseter motoneurons. We found that only the larger units displayed H-reflex responses. This indicates preferential distribution of muscle spindle input onto large motoneurons or a skewed distribution of tonic presynaptic inhibitory mechanisms.

INTRODUCTION

The H-reflex is notoriously difficult to elicit in masseter (Macaluso and De Laat 1995) even though this muscle contains large numbers of muscle spindles (Rowlerson 1990). H reflexes are also difficult to elicit in the small muscles of the hand, possibly due to a skewed distribution of Ia afferent input onto the large motoneurons (Mazzocchio et al. 1995). This distribution makes it difficult to evoke an H reflex as it is blocked in the large motor axons by antidromic impulses. The same explanation may apply to the difficulty of producing H reflexes in the jaw-closing muscles. Thus the aim of the current study is to compare the H-reflex size in simultaneously active large and small motoneurons in masseter to indicate the effectiveness of the afferent input from the muscle spindles.

METHODS

Seventeen healthy consenting volunteers (10 females, 7 males, age range 21–38 yr) participated in the experiments. Details of the experimental methodology have been published previously (Scutter et al. 1997) and are summarized here. The stimulating electrodes consisted of an anode and a cathode incorporated into a U-shaped frame. The anode was fixed inside the mouth, posterosuperior to the left third upper molar. This arrangement allowed for transmuscular stimulation of the left masseteric nerve. The frame was held in position by a bite plate, which incorporated an impression of the subject’s teeth (Formasil). To record intramuscular activity, two Teflon-insulated bipolar single motor unit (SMU) wire electrodes and a single Macro wire electrode were inserted to a depth of ~2 cm into the anterior portion of left masseter. One or two SMUs were selected and analyzed from each SMU electrode. Macro electromyography (EMG) was used in preference to surface EMG for recording reflex responses, as the M wave and H reflex are difficult to separate in surface EMG recordings (Scutter et al. 1997). The Macro EMG was recorded using the Macro wire in the muscle against an indifferent electrode on the right ear lobe. The SMU signal was filtered at 200 Hz to 5 kHz and Macro at 50 Hz to 5 kHz, and both were recorded on tape for off-line analysis.

The subjects were asked to control the discharge of one SMU at a steady frequency of ~15 Hz with the help of audio feedback. While the SMU was firing steadily, the masseteric nerve was stimulated (Digitimer Isolated Stimulator) using the transmuscular stimulating frame. Stimulus pulse width was 1 ms, applied at random intervals of between 2 and 5 s. The stimulus was increased until an H reflex was present in the Macro EMG. The H reflex was differentiated from the M wave in the Macro EMG by the latency (~6 ms) and by the increase in H-reflex amplitude, which occurred with an increase in biting level. The intensity of the stimulus and position of the cathode were then adjusted until an H reflex was present with the smallest possible M wave. This stimulation then was applied, and the firing of the SMUs recorded until the subject was no longer able to continue to fire the SMU regularly. The subject then rested for ≥10 min before commencing another run. Data from SMUs that did not run for ≥20 stimuli was discarded. Within a run, the contraction level, stimulus intensity and stimulus position were stable.

To investigate H reflexes at different contraction levels, subjects were asked to contract the masseter muscle at ~5, 10, 15, and 20% of their maximum contraction level during different runs. The rectified, smoothed surface EMG record of the left masseter was used to determine contraction level at the beginning of each run: after a SMU was identified, the audio feedback of its firing was used by the subject to maintain the drive to the muscle (Türker and Miles 1989). To eliminate any possible fatigue effects, the order of contraction levels was randomized. The shape of the SMU action potential was recognized using a template-matching algorithm (SPS-8701). Peristimulus time histograms (PSTHs) were built for the identified SMUs. Cumulative sum (CUSUM) (Ellaway 1978) was calculated from the PSTH to determine the presence of a reflex response. To determine whether the deviations in CUSUM indicated a significant reflex response, significance curves were constructed according to the methods of Davey et al. (1986). To ensure that responses in SMUs were not obscured by other units firing at the H-reflex latency, the occurrence of action potentials at H-reflex latency was inspected. Any runs where the existence of superimposition could not be corrected, using an off-line program in SPS-8701, were discarded. As SMU firing frequency may affect the size of the reflex response (Jones and Bawa 1995), a two-way ANOVA for unbalanced data was used to investigate whether there was a difference in firing frequencies of the units with and without significant H reflexes.

The amplitude of the representation of the SMU in the Macro EMG (MacroRep) (Scutter and Türker 1998; Stålberg 1983) was used in the current study for determining the relative sizes of the SMUs in a run. The characteristic shape of the MacroRep was used to identify any SMUs that occurred several times in different runs.

As the masseteric nerve stimulation used in this study also would have caused stimulation of cutaneous receptors, the effect of a similar cutaneous stimulation on the firing of masseter SMUs was investigated. Thus in two subjects (4 runs; 8 SMUs) the cathode was moved anteriorly so that the stimulus was applied within the distribution of the maxillary branch of the trigeminal nerve but was not over the masseteric nerve. The stimulation and recording procedures were repeated with the stimulus in this position, using the same stimulus current as was applied over the masseteric nerve.
RESULTS

Masseter H-reflexes could not be elicited from 5 of the 17 subjects. In the 12 subjects in whom H reflexes could be produced, an H reflex was identified in the Macro EMG in 23 runs. H reflexes were recorded only when the contraction level was >10% of maximum masseter contraction. Within each of the 23 successful runs, two to four SMUs were identified. Sixty-six different SMUs thus were identified and H-reflex responses were recorded in 26 (39%) of these. Eleven runs had two voluntarily activated units, one of which demonstrated the H reflex and one that did not. Of these 11 pairs, in 10 cases the larger unit was the one demonstrating the H reflex. In 12 runs, three to four units were identified, some with and some without the H reflex present. In 11 of these runs, the unit(s) with the largest MacroReps was that which demonstrated an H reflex. There was no significant difference between the firing rates of the units with and without H reflexes ($F = 0.12$, $P = 0.73$). When the cathode was moved anteriorly to provide cutaneous stimulation only, no short-latency excitatory reflex responses were observed in any of the eight SMUs followed, even though an H reflex had been present in four of these SMUs when the stimulus was applied over the masseteric nerve.

On nine occasions, it was possible to identify the same unit at different contraction levels with the same stimulus position and intensity. This enabled the effect of contraction level on H reflexes in the same SMUs to be determined. Figure 1 shows an example from one subject. When contraction level was 19%, three SMUs were followed. The larger two SMUs demonstrated an H reflex and the smaller one did not. When the contraction level was decreased to 15%, two large SMUs were followed, one of which was the same as followed previously. Again, the two large SMUs demonstrated the H reflex, whereas the smallest SMU did not. When contraction was decreased to 5%, two small SMUs were followed. There was no H reflex in the Macro EMG nor in either of the SMUs at this contraction level. This figure clearly shows that the larger units demonstrated an H reflex irrespective of the contraction level and that at higher contraction levels the smaller units still did not produce an H reflex. The same pattern was observed on the other eight occasions where the same SMUs were identified at different contraction levels.

DISCUSSION

Masseter H reflexes were difficult to elicit in this study, and even when present in the Macro EMG were only present in 39% of the SMUs recorded, suggesting a limited distribution of the muscle spindle input to masseter motoneurons. A similar finding was reported by Miles et al. (1995) when studying the masseter stretch reflex: 35% of SMUs did not demonstrate a short-latency response. These authors could not demonstrate a relationship between motor unit size (as indicated by discharge frequency) and the absence of a stretch reflex response. Using the MacroRep as an indicator of motor unit size, in the current study we found that it was nearly always the larger units that demonstrated a reflex response. This may have been due to a limited distribution of Ia inputs, preferentially distributed onto the larger motoneurons, or to tonic presynaptic inhibition (PSI) of the input onto the smaller motoneurons.

There are opposing findings concerning Ia distribution in human subjects. Awiszus and Feistner (1993) and Schmeid et al. (1997) found that monosynaptic Ia excitatory postsynaptic potential size was greater in smaller motoneurons and concluded that Ia input supported the size principle in the soleus and wrist muscles, respectively. However, Semmler and Türker...
(1994) found that the H reflex was larger in larger SMUs in human tibialis anterior. Furthermore Mazzocchio et al. (1995) demonstrated that Ia input was ineffective on small motoneurons within the motoneuron pool of the hand. Although these authors concluded that preferential Ia distribution onto large motoneurons was responsible for their findings, uneven distribution of PSI equally may have been the cause. PSI of human masseter Ia input has been demonstrated (Lobbezoo et al. 1993) although the source is not clear. In animals, PSI has been shown to be equally distributed to large and small motoneurons (Zengel et al. 1983), so a biased distribution of PSI could be specific to the masticatory system. At this stage, it is not possible to state which mechanism, limited and preferential Ia excitatory input to large motoneurons or tonic PSI of Ia input onto small motoneurons, may have produced the findings of our study.

Previous explanations for the difficulty of producing H reflexes in masseter have included the low projection of single masseter Ia afferents onto masseter motoneurons (10%) (Appenteng 1990) and the thickness of the motor fibers in the masseteric nerve (Morimoto et al. 1982). As we have used stimulation of the whole masseteric nerve, we should have overcome the problem of limited distribution of individual afferent fibers if all motoneurons receive Ia input. The motor fibers are thicker than the Ia fibers in the masseteric nerve of the cat (Morimoto et al. 1982). If this is the case in humans, this could make it difficult to produce H reflexes, but it cannot explain why H reflexes are present more often in large motor units. A more effective muscle spindle input onto large motoneurons, as found in this study, can provide an explanation for the difficulty of eliciting H reflexes in masseter. The need for increased levels of voluntary masseter activity noted in this study and previously (De Laat and Macaluso 1995) reflects the need to recruit the larger SMUs that can participate in the H reflex.

What might be the benefits of preferential distribution of Ia input onto large motoneurons in masseter? Dessem (1995) suggested that when the jaw muscles are used in aggressive biting behavior, such as during defense or prey capture, the “fusimotor set” will be high. This would make jaw muscle spindle afferents readily activated and would provide a short-latency pathway to the masseter motoneurons. If the Ia input is more effective on the large motoneurons, as suggested by the findings of this study, then it will be the large, strong and fast SMUs that are recruited preferentially during such activities, providing the capacity to produce very large bite forces with the minimum effort.

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