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Changes in the Inhibitory Control Exerted by the Antagonist Ia Afferents on Human Wrist Extensor Motor Units During an Attention-Demanding Motor Task

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Nafati, Gilel, Annie Schmied, and Christiane Rossi-Durand. Changes in the inhibitory control exerted by the antagonist Ia afferents on human wrist extensor motor units during an attention-demanding motor task. J Neurophysiol 93: 2350–2353, 2005. First published November 24, 2004; doi:10.1152/jn.00996.2004. The aim of this study was to determine the extent to which an attention-demanding visuomotor task affects the strength of the inhibitory control exerted by the wrist flexor group Ia afferents on the wrist extensor motoneurons. Effects of median nerve stimulation on the tonic activity of wrist extensor single motor units were analyzed in terms of the interspike interval (ISI) lengthening. Results show that the inhibitory effects exerted by the antagonistic group Ia afferents were significantly enhanced when the wrist extensor motoneurons were involved in an attention-demanding task. Enhanced inhibition from antagonist afferents may reflect task-related changes in the excitability of the di- and polysynaptic pathways mediating reciprocal inhibition due to either the action of descending inputs and/or an increase in the efficiency of the Ia inputs to the premotoneuronal inhibitory interneurons. Modulation of the inhibition exerted by proprioceptive antagonist afferents may be one of the processes which contribute to the fine adjustment of the wrist muscle force output required in fine handling tasks.

INTRODUCTION

The motoneuron activity associated with voluntary muscle contractions is based on a balance between excitatory and inhibitory inputs. At the segmental level, group Ia afferents from the antagonist muscle constitute a major source of peripheral inhibitory inputs. These antagonist Ia afferents act on motoneurons via di- or polysynaptic pathways (see Crone 1993; Jankowska 1992). It has been established that the excitability of these inhibitory pathways depends on the subject’s posture (Kasai et al. 1998; Kido et al. 2004) and on whether agonist or antagonist muscles are contracted (Aimonetti et al. 2001; Cavallari et al. 1984; Kato and Kasai 2000). Even in the absence of any actual contractions, mental simulation of motor actions can affect the inhibitory effects of antagonist Ia afferents (Nielsen et al. 1995). In a previous study (Nafati et al. 2004), we observed that the homonymous Ia monosynaptic proprioceptive feedback acting on wrist extensor motoneurons was enhanced during an attention-demanding visuomotor task. The aim of the present study was therefore to examine the inhibitory control exerted by the antagonist Ia afferents from wrist flexor muscles under the same conditions. The hypothesis was put forward that this inhibitory control may increase during the performance of an attention-demanding task and thus maintain the balance between the excitatory and inhibitory inputs acting on the wrist extensor motoneurons.

METHODS

This study was performed on eight neurologically healthy subjects. All the subjects gave their written informed consent to the experimental procedure as required by the Helsinki Declaration (1964).

Procedure

Details of the experimental set-up, preparation of the subjects, data recordings, and the equipment used have been described previously (Nafati et al. 2004; Schmied et al. 2000). The subjects were seated in an adjustable armchair. Their right forearm was placed in a groove, and the distal end was immobilized. The hand was placed in a semi-prone position, with the wrist flexed at an angle of 10°, while the back of the hand was in permanent contact with an isometric force transducer device (DC gain, 0.25 V/N). The subjects had to selectively contract their wrist extensor muscles by pushing on the force transducer device with the back of their hand. The force was monitored on an oscilloscope screen (sweep rate: 0.5 ms/division), and the subjects were required to maintain the level of extension force as steady as possible by tracking a horizontal line located in the middle of the oscilloscope screen. Two gains in the force feedback were used alternately in two successive randomized recording sequences. The two gains differed by a factor of 50: a change of 0.1 N in the force output gave an oscilloscope trace deviation of 0.05 divisions at low gain and 2.5 divisions at high gain. The activity of single motor units (SMUs) was recorded in the extensor carpi radialis muscle (ECR) using tungsten microelectrodes. The subjects were asked to contract the ECR muscle and to maintain an extension force above the recruitment threshold (RT) of the motor unit under investigation so that its tonic firing rate was ~10 Hz. In these experiments, the level of the extension force was ~10% of the maximum voluntary contraction and only low-threshold SMUs were tested (RT < 1 N). The electromyographic activity of the extensor and flexor muscles was recorded using pairs of surface electrodes (surface EMG).

Stimulation paradigm

The effects of the median nerve electrical stimulation on the voluntary tonic discharge of extensor single motor units were investigated under the two feedback conditions in two successive recording

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sequences. Responses to 40–60 stimuli were collected throughout each sequence lasting ~2–3 min. Resting periods of 1–2 min were allowed to elapse between the sequences. Before each series of experiments, the median nerve stimulation was progressively increased in such way as to evoke a clear-cut H-wave (Hoffmann reflex, H-reflex) in the flexor carpi radialis muscle (FCR), which reflected the effectiveness of the group Ia afferent activation, just below the M-wave threshold. The FCR H-reflex was elicited by applying cathodic stimulation to the median nerve in the cubital fossa and the anode was placed opposite the cathode. The stimulus intensity was set at 0.8 the motor threshold. The cathodic stimulation (pulse duration: 0.5 ms) was delivered using a spike-triggered stimulation method (Jones and Bawa 1995; Nafati et al. 2004). The spikes produced by voluntarily activated motor units were discriminated on-line and the output TTL pulses were used to trigger the stimulator (Grass S88, USA) after a fixed delay with respect to the motor unit potential. In this study, a spike-to-stimulus delay of 40 ms was used. Stimuli were delivered with a minimum time interval of 3 s.

Data analysis

The inhibitory effects of the median nerve stimulation on the tonic activity of ECR motor units were analyzed in terms of the interspike interval (ISI) lengthening. The spike trains were displayed in the form of trial-by-trial rasters, and peristimulus time histograms (PSTH) of the motor unit discharge were drawn up using Spike 2 software (CED Cambridge, UK). The durations of the ISIs around each stimulation were computed, including the ISI during which the stimulus occurred (stimulus ISI, ISI 0), the following ISI (poststimulus ISI, ISI +1), and the prestimulus ISI (ISI –1), which was obtained by averaging the three preceding ISIs (Fig. 1). The value of ISI –1 was taken as an estimate of the motor unit’s instantaneous background activity. The mean durations of ISI –1, ISI 0, ISI +1 were calculated for each SMU.

Statistical analysis

The mean ISI –1, mean ISI 0, mean ISI +1, the mean forces, and the mean EMGs were compared between the two conditions, using a paired sample Wilcoxon test. The condition-related changes in the ISI durations were assessed in each single motor unit by performing a Mann and Whitney test on the absolute values. The significance level was set at \( P < 0.05 \).

RESULTS

No significant differences were detected in the overall motor output depending on whether the level of motor accuracy was low or high. The mean force at which the motor units were tested (0.27 ± 0.13 N above the recruitment threshold) did not differ consistently between the two visual force feedback conditions [0.93 ± 0.43 (SD) N and 0.93 ± 0.49 N, low and high gains, respectively]. The background EMG activity of the ECR muscles was similar in both cases (0.12 ± 0.026 and 0.11 ± 0.024 mV/s low and high gain, respectively). No detectable EMG activity was observed in the wrist flexor muscles whether the gain was high or low. No statistical changes were detected in the motoneuronal discharge frequency throughout the recording sequences between low- and high-gain conditions in any of the SMUs tested. In the SMU population as a whole, the mean value of the prestimulus ISI (ISI –1) was 87.3 ± 4.5 and 87.5 ± 4.2 ms, at low and high gain, respectively.

The visual force feedback-related changes in the ISI duration were assessed by examining the tonic firing activity of 31 wrist extensor motor units. Figure 2 shows a typical example of the changes observed in a single motor unit. In this example, no differences were detected between the prestimulus ISI (ISI –1) tested under low- and high-gain force feedback conditions (86.9 ± 7.2 and 86.1 ± 7.6 ms, respectively). The stimulus ISI (ISI 0) was significantly longer than the prestimulus ISI (ISI –1) in both conditions (90.8 ± 4.9 and 99.3 ± 5.4 ms, low and high gain, respectively; \( P < 0.05 \)), in keeping with the inhibitory effects of the median nerve stimulation in both situations. The main result illustrated by this example was that the lengthening of the stimulus ISI (ISI 0) was significantly greater under high-gain than low-gain conditions (\( P < 0.05 \)). The median nerve stimulation did not affect the duration of the poststimulus ISI (ISI +1) in either of the conditions (85.5 ± 9.1 and 84.2 ± 10.8 ms, low and high gain, respectively).

Figure 3A shows the task-related changes in stimulus ISI (ISI 0) duration associated with each SMU recorded. In the case of 24 of the 31 motor units tested, the duration of ISI 0 was longer under high-gain than low-gain conditions and the difference was significant with 18 of them (black symbols; \( P < 0.05 \)).

To investigate the extent of the task-related changes, we pooled the data on the eight subjects, including 31 SMUs in all (Fig. 3B). The median nerve stimulation lengthened the mean duration of ISI 0 by 7.6% under low-gain (\( P < 0.05 \)) and by 13.3% under high-gain conditions (\( P < 0.01 \)), expressed as percentages of ISI –1. The lengthening of the stimulus ISI (ISI 0) was therefore significantly longer under high- than low-gain conditions (\( P < 0.01 \)). The lack of change in both the pre- and poststimulus ISI (ISI –1 and ISI +1) between the two force feedback conditions was confirmed by the data based on the SMU population as a whole.

![FIG. 1. Methods of data analysis used. The effects of median nerve stimulation (n = 40) on the motor-unit tonic discharge were displayed in standard peristimulus time histograms (PSTH; bin duration, 0.5 ms) and the rasters giving the results of individual trials. The stimulation, occurring at time 0, was triggered at a specific time in relation to the preceding spike (40 ms later). ISI, the ISI in which the stimulation occurred (ISI 0). Top: a schematic representation of the interspike intervals (ISIs) analyzed. The value of the prestimulus ISI (ISI –1) was obtained by averaging the 3 preceding ISIs. The durations of ISI –1, ISI 0, and ISI +1 in response to each stimulus applied to the median nerve were calculated.](http://jn.physiology.org/Downloadedfrom)
DISCUSSION

Methodological considerations

When the activity of single motor units was being recorded in humans, the effects of stimulating the antagonist Ia group afferents were previously assessed in terms of the firing probability in poststimulus time histograms, which showed a decrease (Aimontetti et al. 2000, 2001; Ashby and Label 1977; Nielsen and Kagamihara 1992). In the present study, the effects of median nerve stimulation on the tonic firing pattern of voluntarily activated wrist extensor motor units were analyzed in terms of the interspike interval duration. Analyses of this kind are particularly helpful means of assessing the inhibitory effects of a stimulation-elicited afferent volley on the spike trains of individual motor units (Garland and Miles 1997). Here we observed a lengthening of the ISI in which the Ia afferent volley occurred, in keeping with the expected inhibitory effects of the antagonist primary afferent stimulation.

The stimulation was elicited 40 ms after the triggering spike. The earliest inhibitory processes induced by the antagonist Ia afferent volleys can therefore be expected to reach the motoneuron ~60 ms after the triggering spike was generated (40 ms + mean FCR H-reflex latency). Consequently, the inhibitory processes observed in the present study should last from ~20 to 40 ms at least to be able to affect the next spike, which can be expected to occur 80–100 ms after the triggering one in the absence of stimulation (minimum ISI −1: 77.6 ms and maximum ISI −1: 96.1 ms).

Besides the disynaptic reciprocal inhibition lasting <10 ms (Aimonetti et al. 2001; Crone 1993), later and/or longer lasting synaptic effects are liable to contribute to the inhibitory responses observed. This contribution includes the late inhibitory response (latency: 30–40 ms) that follows the disynaptic one (Aimonetti et al. 2001; Crone 1993). It is therefore quite likely that under the present experimental conditions, part of the ISI 0 lengthening induced by median nerve stimulation may have involved polysynaptic pathways in addition to the disynaptic one. On the other hand, the possible contribution of the recurrent inhibition pathway cannot be excluded, given its specific pattern of organization in the motor nuclei of the wrist extensor and flexor muscles (Aymard et al. 1997). However, the strength of this possible recurrent interaction would probably be weaker than that of the reciprocal inhibition (Windhorst 1996).

Possible mechanisms involved in changes in antagonist inhibition

The present results show that the efficiency of the inhibitory pathways fed by the antagonist Ia muscle afferent is enhanced when the wrist extensor motoneurons are involved in an attention-demanding task. These changes in inhibitory strength cannot be due to changes in the level of extensor motoneuron excitability as no significant differences were detected between the mean prestimulus ISIs analyzed under low- and high-gain conditions, and the effects of the antagonist afferent sensory burst were tested at a specific time during the interspike interval. In addition, a previous study using the same experimental procedure, we obtained convincing findings showing the consistency of the motor output between the two visual force feedback conditions (Nafati et al. 2004).

The fact that the ISI during which the stimulation was delivered showed a greater lengthening under high-gain con-
conditions may reflect an increase and/or a lengthening of the composite IPSPs generated by the median nerve stimulation. These changes may have resulted from the action of descending inputs on the Ia inhibitory interneurons from flexor to extensor muscles (Crone and Nielsen 1994; Jankowska et al. 1976; Nielsen et al. 1992), which would facilitate transmission in the reciprocal inhibitory pathways when special attention was required by the motor task. This central modulation of the group Ia inhibitory interneurons may be exerted via propriospinal neuron relays (Alstermark et al. 1984; Pierrot-Deseilligny 1989). Enhanced excitability in the neural pathways mediating antagonist inhibition might also result from an increase in the Ia afferent inputs to premotorneuronal inhibitory interneurons, resulting either from an attention-related decrease in presynaptic inhibition of flexor Ia afferent terminals on Ia inhibitory interneurons (Enriquez-Denton et al. 2000) and/or from an increased on-going spinal discharge rate. The latter assumption is in keeping with the data obtained in our former study, suggesting that a fusimotor-drive activation occurs under high-gain visual force feedback conditions (Nafati et al. 2004). This activation would therefore be likely to increase the resting discharge of the flexor muscle spindles (cf. Rossi-Durand 2002). This may result in either the facilitation of premotorneuronal inhibitory interneurons, making them more responsive to the median nerve stimulation, or the activation of alternative polysynaptic pathways, such as propriospinal pathways, that were inactive under low gain conditions (cf. Crone 1993).

Functional implications

The increase in the reciprocal inhibitory control exerted by the antagonist flexor afferents during attention-demanding tasks would compensate for the increase in the autogenic excitatory control exerted by the homonymous muscle spindle afferents that we previously observed under the same conditions and would thus contribute to maintaining the balance between excitatory and inhibitory inputs to the wrist extensor motoneurons.

This modulation of the antagonist propriospinal inhibitory control depending on the level of attentiveness required by the task may be one of the processes involved in the fine adjustment of the wrist muscle force output required in accurate handling tasks.

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