Fusimotor Drive May Adjust Muscle Spindle Feedback to Task Requirements in Humans

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Submitted 17 September 2008; accepted in final form 24 November 2008

Fusimotor drive may adjust muscle spindle feedback to task requirements in humans. J Neurophysiol 101: 633–640, 2009. First published November 26, 2008; doi:10.1152/jn.91041.2008. The aim of the present study was to investigate whether the fusimotor control of muscle spindle sensitivity may depend on the movement parameter the task is focused on, either the velocity or the final position reached. The unitary activities of 18 muscle spindle afferents were recorded by microneurography at the common peroneal nerve. We compared in two situations the responses of muscle spindle afferents to ankle movements imposed while the subject was instructed not to pay attention to or to pay attention to the movement, both in the absence of visual cues. In the two situations, three ramp-and-hold movements were imposed in random order. In one situation, the three movements differed by their velocity and in the other by the final position reached. The task consisted in ranking the three movements according to the parameter under consideration (for example, slow, fast, and medium). The results showed that paying attention to movement velocity gave rise to a significant increase in the dynamic and static responses of muscle afferents. In contrast, focusing attention on the final position reached made the muscle spindle feedback better discriminate the different positions and depressed its capacity to discriminate movement velocities. Changes are interpreted as reflecting dynamic and static gamma activation, respectively. The present results support the view that the fusimotor drive depends on the parameter the task is focused on, so that the muscle afferent feedback is adjusted to the task requirements.

INTRODUCTION

Muscle proprioceptive feedback plays a predominant role in position and movement sense (see reviews by Gandevia and Burke 1992; Matthews 1982). This role is revealed by the ability of muscle proprioceptive inputs to code joint angles (Cordo et al. 2002; Ribot-Ciscar et al. 2003; Vallbo 1974) and movement velocities (Albert et al. 2005; Grill and Hallett 1995; Ribot-Ciscar et al. 2002). This feedback presents the particularity of originating from mechanoreceptors, the muscle spindles, the sensitivity of which may be directly and selectively changed by the CNS through activation of the γ-fusimotor system (see reviews by Hulliger 1984; Prochazka 1996).

For behaving animals, it has been suggested that by adjusting the activity of static and dynamic γ-motoneurons, the muscle spindle feedback is adapted to specific tasks (Prochazka et al. 1985). In humans, the role of the fusimotor system is most generally considered as more basic, i.e., it would prevent the silencing of muscle spindle endings during muscle shortenings (for reviews, see Prochazka 1996; Vallbo et al. 1979). This functional hypothesis was related to the fact that each time a change in muscle spindle sensitivity was observed, it seemed correlated with changes in muscle activity, the so-called α–γ linkage. Such a view has been now widened because it has been observed that this coupling between α and γ activities was not so obligatory. In particular, Jones and collaborators (2001) demonstrated, during adaptation to a visual perturbation, that in 83% of the trials, the spindle firing rates progressively decrease as the subjects progressively improve their visuomotor performance despite the fact that the muscular activity remained similar. These authors concluded “that gamma activity decreased without a concomitant change of the skeletomotor activity represents striking deviation from the dominant view on human fusimotor system control,” but “this would be a means of resolving the conflict between visual and proprioceptive feedback.” So the fusimotor drive seems to be adapted to the task; in this case, the muscle feedback is progressively given less importance because it is incongruent with visual inputs. Conversely, in the case in which muscle feedback is given importance, as during the performance of an attention task that relies only on proprioceptive cues, it may be enhanced. More precisely, we recently showed that the fusimotor control of human muscle spindle sensitivity changes when subjects’ attention is directed to the recognition of imposed two-dimensional movements in the form of written symbols (Hospod et al. 2007). Here again the observed effects seemed to agree with what could be expected for the muscle spindle feedback to be adapted to the ongoing task. That is, the assessment of the successive positions adopted in space that is necessary to recognize a complex movement trajectory was corroborated by a static sensitization of muscle spindle endings. Indeed the primary endings were shown to change their behavior by becoming secondary-like. This led us to suggest that the consequence of this fusimotor drive “might be to feed the brain movement trajectory information that is more accurate.” This proposal would be validated if it was demonstrated that the fusimotor drive changes depending on the movement parameters the task is focused on. Hence the aim of the present study was to investigate whether the fusimotor system may allow parametric control of muscle spindle feedback to fit the task requirements.

To answer this question, it was necessary to access the indexes classically used to characterize afferent dynamic and static sensitivity and thus to go back to the usual ramp-and-
hold movements. We compared in two situations the response of muscle spindle afferents to movements imposed while the subject was instructed not to pay attention to or to pay attention to the movement, both in the absence of visual cues. In each situation, three ramp-and-hold movements were imposed in random order. In one situation, the movements differed by their velocities and in the other by their final position. The task consisted in ranking the three movements according to the parameter under consideration, either velocity or final position reached.

**METHODS**

Experiments were performed on eight healthy volunteers (6 men and 2 women) between 20 and 25 yr of age, all of whom gave their written informed consent to the experimental conditions, as required by the Declaration of Helsinki. The subjects were selected on the basis of their ability to relax. The activity of 18 single muscle spindle afferents originating from tibialis anterior (TA; n = 6), extensor digitorum longus (EDL; n = 8), extensor hallucis longus (EHL; n = 3), and peroneus lateralis (PL; n = 1) muscles was recorded at the common peroneal nerve by the microneurographic technique (Bergenheim et al. 1999; Valbo and Hagbarth 1968). Fifteen were classified as primary and three as secondary afferents (Edin and Vallbo 1990). This study was approved by the local ethics committee (Comité de Protection des Personnes Sud-Méditerranéenne I).

**Data recordings**

Muscle spindle afferent activity was recorded using an insulated tungsten microelectrode (Frederick Haer and Co. Bowdoinham, ME; impedance: 300 kΩ to 1 MΩ tested at 1 kHz, tip diameter: ~5–8 μm, length: 30 mm) inserted into the common peroneal nerve at the popliteal fossa level. Recordings were continuously monitored on an oscilloscope and a loudspeaker. Neural activity was amplified (200,000 times), using a band-pass of 300–3,000 Hz to ensure an optimal signal-to-noise ratio, and sampled at a 20-kHz frequency.

The absence of any muscle activity was controlled throughout the experiment by recording surface electromyographic (EMG) activity. Two pairs of surface electrodes were placed over the TA and the PL muscles. The interelectrode distance was 4 cm. The EMGs were recorded with high gain (10,000) and a band-pass of 3–3,000 Hz. They were sampled at 10 kHz. Contrary to our previous studies (Ribot et al. 1986; Ribot-Ciscar et al. 2000), the use of a highly sensitive photocell was not possible in the present one. Indeed, the movement amplitudes were incompatible with the very short distance (5 mm) between muscle tendon and transducer necessary for it to be sensitive to tiny displacements of the muscle tendon.

In addition, the subject’s level of arousal was monitored throughout the experiment by recording electrodermal activity (Critchley 2002). The movements were imposed in control trials only when the electrodermal activity recording was flat, to favor, as far as possible, a γ-free condition. This recording was performed using two surface electrodes placed on each side of the left hand (gain: 500; band-pass: 0.1–100 Hz; sampling frequency: 200 Hz).

**Experimental setup and protocol**

The subject was comfortably seated in an armchair with the legs positioned in cushioned grooves so that a standardized relaxed position could be maintained without any muscle activity occurring. The knee joint was at an angle of ~120–130°, and the feet were rested on supports. The right foot was laid on a stationary plate, and the left foot was attached to a rotating pedal connected to a computer-controlled machine. This movable machine allowed two-dimensional movements to be imposed (see Bergenheim et al. 2000). On the front plane of the machine (y, vertical axe), a downward (90°) or upward (270°) movement created a plantar flexion or dorsiflexion of the ankle joint, respectively. A sideward movement (x, horizontal axe) to the left (180°) or to the right (0°) resulted in an eversion or inversion of the foot, respectively. Here ramp-and-hold movements were imposed in the preferred sensory direction of the receptor-bearing muscle, i.e., 59, 73, 96, and 311° for afferents belonging to EDL, EHL, TA, and PL muscles, respectively (see Bergenheim et al. 2000). The components of each movement along the horizontal (x) and vertical (y) axes were sampled at 100 Hz.

The subjects were asked to do two tasks with their eyes closed. In the “speed task,” three ramp-and-hold movements with constant amplitude (5°) were successively imposed, in random order, with three velocities (3.5, 4, and 4.5°/s for V1–V3, respectively). The hold phase lasted for 2 s, and the time between movements was 9 s (see Fig. 2A). During this task, the subject was asked to pay attention to the displacement phase and to give, at the end of the trial, the order in which the movements were imposed (for example, slow, fast, and medium).

In the “place task,” three ramp-and-hold movements were successively imposed, in random order, with three amplitudes (5, 6, and 7° for P1–P3, respectively). The hold phase lasted for 4 s, and the movements were 14 s apart (see Fig. 2B). During this task, the subject was asked to pay attention to the final position reached during the hold phase and to give, at the end of the trial, the order in which the movements were imposed (for example near, medium, and far). Note that these three positions could be attained either by maintaining a constant velocity and varying the time of displacement or by maintaining a constant time and varying the velocity. We chose a very short time of displacement (0.7 s), and we kept it constant so that the subjects did not perform the task by estimating neither the different movement velocities (i.e., 7, 8.5, and 10°/s for P1–P3, respectively) nor the different movement durations. It should be added that the choice of a constant rate and a longer static phase (example: 10 s) was not retained because lengthening time between first and third movement may have imposed a larger cognitive load on the subject, such that memory of the previous trial may have limited comparison with the current.

Throughout the recording sessions, the subjects wore white noise headphones to prevent them from executing the tasks with the help of differences in any slight noise of the working machine.

The two tasks were difficult since the differences between movements were small, with regard to the velocity in the speed task (0.5°/s) or the amplitude in the place task (1°). This choice was made to involve the subject’s attention regardless of the success rate.

The trials in which the subject executed the task were called the “rank” condition. The muscle afferent response recorded during this condition was compared with that recorded while the subject was asked not to pay attention to the imposed movements; it constituted the “control” condition.

At the beginning of the experiment, one of the two situations, speed or place, was randomly chosen. The subject was asked to be as relaxed as possible, as attested by EMG and flat electrodermal activity, and two successive control trials were recorded. Then the subject was informed about the task to be performed, speed or place, and two rank trials were executed. Afterwards, the same protocol was run with the other task, i.e., two control and two rank trials. If the afferent recording persisted, some pairs of control/rank trials in either one or both situations were conducted. Fourteen and 12 afferents were tested in the speed and place situations, respectively. The number of control and rank trials varied from two to four for each unit tested. In total, 64 rank trials were performed. The chance of correct ranking was 1/6 which leads to a significance level of 23.4% at P < 0.05 (15/64, binomial test).
Data processing

Data were stored on a digital tape recorder (DTR 1802, Biologic, Claix, France) and processed off-line by means of Spike 2 software (Cambridge Electronic Design).

To characterize how joint position and movement velocities are coded in the firing patterns of individual muscle afferents and to characterize the static and dynamic sensitivity of muscle spindle endings, two indexes were chosen. The first is the “hold rate,” defined as the average firing rate during the hold phase 0.5–1.5 s after the end of the ramp, which has a significant relationship with joint position (Cordo et al. 2002). The second is the dynamic index (DI), which is known because Matthews’s pioneering study (1963) to be linearly related to movement velocity (see also Grill and Hallett 1995). The dynamic index is usually defined in animals as the peak frequency before ramp completion minus the instantaneous frequency 0.5 s later (Jansen and Matthews 1962) (see Fig. 1A). Using these instantaneous frequencies gave rise to DI values that did not show a clear linear relation with movement velocities in the case of human muscle spindle afferents (see also Edin and Vallbo 1990). Herein, we defined the dynamic index as the average of the three shortest frequency intervals near the end of the ramp (PF₃) minus the hold rate; this adapted DI increased linearly with movement velocity (see Fig. 1B, —).

These two indexes were preferred to others in the literature, such as the “static difference,” the difference between the hold rate and the initial frequency just before movement, and the “dynamic difference,” the difference between the peak frequency and initial frequency (Roatta et al. 2002; Taylor et al. 1992). The two indexes were preferred because the short delay between two imposed movements, which was a prerequisite to make the ranking task possible, often did not allow the unit firing to totally adapt before the next movement was imposed, so that the initial frequency was not a relevant feature in the present experimental conditions.

Statistical analysis

In each condition, control and rank, and during each task, speed and place, the muscle afferent response was characterized by a dynamic index and a hold rate, corresponding respectively to the average of dynamic indexes and hold rates measured for all trials (from 2 to 4).

The statistical analysis of the whole population of afferent responses was done using a two-way variance analysis with repeated measures [condition (control, rank) × speed (V1–V3); condition (control, rank) × place (P1–P3)]. Data obtained with the two types of afferents were pooled in the present study because the very few secondary endings exhibited similar changes in their responses.

FIG. 1. Indexes characterizing the afferent patterns of discharge. A: response to a 96° ramp-and-hold movement of a primary muscle spindle afferent from tibialis anterior (TA) muscle. Are illustrated from top to bottom: the instantaneous frequency curve, the spike train, and the displacement of the machine along the horizontal (x) and vertical (y) axes. Two values were extracted from the afferent responses: the average of the 3 latest frequency intervals before ramp completion (i.e., the peak frequency 3 points, PF₃) and the average firing rate during the hold phase 0.5–1.5 s after the end of the ramp (hold rate). B: relation between movement velocities and dynamic index (DI) calculated for the whole sample of afferents in the control condition (velocities are 3.5, 4, and 4.5°/s for V1–V3, respectively). Both the dynamic index defined here as PF₃ minus hold rate (adapted DI, —) and the classical Matthews’s DI (· · ·) defined as the instantaneous peak frequency (PF) before ramp completion minus the instantaneous frequency 0.5 s later are shown. Imp, impulse.
RESULTS

Indexes as indicators of the movement parameters

As examples of the whole population of afferents, Fig. 2, C and D, gives the variations in the dynamic index (—) and of the hold rate (•) calculated from three control responses of the unit illustrated above (Fig. 2, A and B). As expected, the dynamic index increased with movement velocities both in the speed (Fig. 2C) and place (Fig. 2D) situations with a general level higher in the latter situation. For the whole population of afferents, the dynamic index significantly discriminated the different movement velocities in the speed \[F(2,26) = 3.87, P = 0.03\] and place \[F(2,22) = 4.28, P = 0.03\] situations.

The hold rate was unchanged for the three movements imposed in the speed situation because these movements had the same amplitude (Fig. 2C). Conversely, in the place situation, the hold rate linearly increased with movement amplitude (Fig. 2D). In the whole population of afferents, the hold rate was significantly different for the three final positions reached \[F(2,22) = 12.4, P = 0.0002\].

Comparison of muscle spindle activities between control and ranking conditions

Figure 3 illustrates some of the changes observed in the muscle afferent responses when the subject paid attention to the movements to rank them (bottom) as compared with control (top). The movement is here the fastest and the largest in the speed and place situations, respectively.

Paying attention to the movements induced clear changes in the unit responses as compared with control. More specifically, during the speed task (left), these changes were characterized...
by an increase in the initial burst and in the discharge frequency at the end of the ramp (PF$_3$) together with an increase in the activity during the muscle shortening phase. During the place task (right), the changes in afferent response were the opposite, i.e., the initial burst and the peak frequency decreased. These changes in the afferent response appear clearly even in the lowest histograms, which give the difference between control and rank responses in both situations. This mode of representation also shows that the spontaneous activity and the activity during the hold phase tend to increase in both situations and more specifically during the speed task. Note that the initial burst was independent of the imposition order of the movement, i.e., when absent at V3 (top left), it was also absent at V1 and V2; when present (top right and middle left and right), it was also present during the two other movements of each trial (data not shown).

Figure 4 gives the mean results obtained for the whole set of afferents by means of the indexes chosen to characterize the
dynamic and static muscle spindle ending sensitivity: the dynamic index (left) and the hold rate (right) in control (■) and rank (■) conditions, during the speed (top) and place (bottom) situations. The large variability observed is explained by the fact that each afferent presents its own discharge rate which ranges from 4 to 28 imp/s during the hold phase, for example.

During the speed task, both the dynamic and static sensitivities of muscle afferents increased, as shown by a significant increase in both the dynamic index \( F(1,13) = 10.7, P = 0.006 \) and the hold rate \( F(1,13) = 10.44, P = 0.007 \) during the rank condition as compared with control. During the place task, these indexes did not change significantly \( F(1,11) = 0.37 \) and \( F(1,11) = 0.98 \), for DI and HR, respectively. However, there is a significant interaction between the factors condition and place \( F(2,22) = 6.2, P = 0.008 \) and \( F(2,22) = 3.8, P = 0.04 \), for DI and HR, respectively. This means that changing the condition from control to rank influences the relation between indexes and movements. More precisely, in the rank condition the afferents have significantly depressed capacity to discriminate movement velocities, and conversely they have improved capacity to discriminate the final positions reached as compared with control.

**DISCUSSION**

By setting the tension of intrafusal muscle fibers, the fusimotor system modifies the static and dynamic sensitivity of muscle spindle endings (for a review, see Hulliger 1984; Prochazka 1996). That such a complex system of sensitivity control exists makes one naturally think that its role would be to adjust the proprioceptive feedback to the changing behavioral context. Yet this role has long been debated concerning humans because when a change in muscle spindle sensitivity occurred, it was often coupled with a change in muscle activity, the so-called \( \alpha-\gamma \) linkage. Such a coupling led the fusimotor system to be considered as a simple system that prevents muscle spindle silencing during muscle shortenings (for a
review, see Prochazka 1996; Vallbo et al. 1979). Yet this role is already devoted to the β-skeletofusimotor system (Gandevia et al. 1986; Kakuda et al. 1998; Rothwell et al. 1990). To claim that the fusimotor system presents a functional interest by itself, it is necessary to demonstrate that the CNS is able to control muscle spindle sensitivity both specifically, that is, independently of any alpha activity, and differentially, that is, in terms of static and/or dynamic sensitivity. The present study follows a set of previous ones we conducted that aims at analyzing whether this ability exists in humans.

By recording unitary γ-fusimotor neurons, we showed that γ activity might be triggered in the completely relaxed subject by means of various factors that are cognitive, behavioral, or environmental (Ribot et al. 1986). These data suggested, for the first time in humans, that muscle spindle sensitivity might be controlled by the CNS independently of muscle activity. Later we showed that this γ-induced activity expressed itself at the level of muscle spindles by selectively changing their sensitivity to movements (Ribot-Ciscar et al. 2000). Finally, we suggested that the fusimotor drive might be adapted to the ongoing task (Hospod et al. 2007). Indeed when the subject is asked to focus attention on an imposed two-dimensional movement (letter or number) to name it, the primary endings tend to become secondary-like, with a depressed dynamic and an enhanced static sensitivity, as compared with a no-attention situation. These changes in muscle spindle sensitivity seemed to be particularly suited to the task of recognizing a trajectory shape (see DISCUSSION in Hospod et al. 2007), and this led us to suggest that the fusimotor drive would be helpful “to feed the brain movement trajectory information that is more accurate.” However, another assumption could have been that the changes in muscle spindle sensitivity observed when the subject is involved in such an attention task would have resulted from an unspecific sensitization of the whole muscle sensory apparatus, i.e., a sort of arousal or alertness effect. Thus here we split the task and asked the subjects to deal with the movement velocity or with the final position reached. The hypothesis was that the fusimotor drive in both situations should be qualitatively either the same, if it is unspecified, or different, if it is specific to the task.

Obviously one cannot be sure the subjects really attend to the movement parameter they were asked to deal with. In particular, in the place situation, even if the duration of the ramp displacement was very short (0.7 s), we cannot exclude the possibility that some of the subjects may have used velocity cues. Moreover, some subjects may have encountered problems in recalling the order of movements. However, the tasks seem to have been correctly performed because, despite their great difficulty, the percentage of correct ranking was 49.2% for the whole trials. This value is largely above chance set at 23.4% for \( P < 0.05 \) (see METHODS). As regards the muscle afferent activities, it cannot be excluded that some thixotropic changes in the muscle spindles (Proske et al. 1993), due to previous movements and/or previous fusimotor drive, may have led to changes in the following trial. Even if these introduced variability in the data, they did not impair the significance of the results at the population level. Finally, one cannot be sure that muscle activity was totally absent because the surface EMG may remain flat despite the presence of deep muscle activity as revealed by the use of indwelling electrodes in the muscle (Gandevia et al. 1997). Inserting such wire electrodes around the recorded spindle ending would have stressed the subject, and this is incompatible with the experiment requirements. The use of a highly sensitive photocell was not possible in the present experimental conditions (see METHODS). However, if changes in muscle activity had occurred, one would expect similar changes in muscle spindle responses whatever the attention task, yet our results show that these differed. More precisely, focusing attention on movement velocities gave rise to a significant increase in both static and dynamic components of the afferent response. Conversely, focusing attention on the final position reached altered the relation between movement parameters and afferent discharge, i.e., the capacity of the population of afferents to discriminate the different movement velocities was depressed and conversely its capacity to discriminate the different final positions was improved in the rank condition as compared with control.

As usual in humans, it is not certain to infer the nature of the fusimotor neurons involved from the responses of muscle spindles. The increase in dynamic and static sensitivities during the speed task may be seen as the result of a mixed activation of γ dynamic (γd) and γ static (γs) fusimotor neurons. But, thanks to animal studies, it is known that purely dynamic actions are very rare because most γd-axons make contact not only on bag1 but also on bag2 and/or chain intrafusal muscle fibers (Banks et al. 1978; Durbaba et al. 2001; Emonet-Dénand et al. 1977). Therefore it is probable that the simultaneous increase in the afferent static and dynamic sensitivity observed in the present task was related to the involvement of such γd neurons in humans. Conversely, in the place task, the fact that movement velocities became less discriminated while positions became better discriminated by muscle spindle feedback seems to account for the involvement of γs-fusimotor neurons (Brown et al. 1965; Crowe and Matthews 1964). Referring to animal data, one may have expected stronger effects and in particular a biasing effect, but it has always been an intriguing observation that the muscle spindle firing rates are much lower in humans than in animals, and thus it is probable that the fusimotor-induced effects are relatively weaker in humans.

So whether the subject’s attention was directed toward movement velocity or final position reached, the nature of the fusimotor drive differed and seems to adapt the muscle afferent feedback to the task requirements. We should add that, interestingly, in the place and the speed tasks, we only rarely observed changes in the variability of the instantaneous firing rates of muscle afferents, whereas these were relatively frequent during a task consisting in recognizing complex two-dimensional movements in the shape of writing movements (Hospod et al. 2007). The different natures of the movements where only one or two parameters varied at the same time may account for these different observations.

Finally, the present work follows two studies by our group, all conducted in the frame of the contentious issue of whether fusimotor-independent control of alpha activity exists in humans (see discussion in Ribot-Ciscar et al. 2000 and reviews in Prochazka 1996; Vallbo et al. 1979). In the former studies, we showed that only some afferents underwent changes in their response to movement in the relaxed subject (Hospod et al. 2007; Ribot-Ciscar et al. 2000). This is in line with the observation by other groups that some independent control of fusimotor activity might also occur in humans (Burg et al. 2001). Indeed in humans, it is not certain to infer the nature of the fusimotor neurons involved from the responses of muscle spindles. The increase in dynamic and static sensitivities during the speed task may be seen as the result of a mixed activation of γ dynamic (γd) and γ static (γs) fusimotor neurons. But, thanks to animal studies, it is known that purely dynamic actions are very rare because most γd-axons make contact not only on bag1 but also on bag2 and/or chain intrafusal muscle fibers (Banks et al. 1978; Durbaba et al. 2001; Emonet-Dénand et al. 1977). Therefore it is probable that the simultaneous increase in the afferent static and dynamic sensitivity observed in the present task was related to the involvement of such γd neurons in humans. Conversely, in the place task, the fact that movement velocities became less discriminated while positions became better discriminated by muscle spindle feedback seems to account for the involvement of γs-fusimotor neurons (Brown et al. 1965; Crowe and Matthews 1964). Referring to animal data, one may have expected stronger effects and in particular a biasing effect, but it has always been an intriguing observation that the muscle spindle firing rates are much lower in humans than in animals, and thus it is probable that the fusimotor-induced effects are relatively weaker in humans.

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