Video Article

Force and Position Control in Humans - The Role of Augmented Feedback

Benedikt Lauber[1,2], Martin Keller[2], Christian Leukel[1,3], Albert Gollhofer[1], Wolfgang Taube[2]

[1]Department of Sport Science, University of Freiburg

[2]Department of Medicine, Movement and Sport Science, University of Fribourg

[3]Bernsteincenter Freiburg

Correspondence to: Benedikt Lauber at Benedikt.Lauber@sport.uni-freiburg.de

URL: http://www.jove.com/video/53291
DOI: doi:10.3791/53291

Keywords: Behavior, Issue 112, Neurophysiology, Augmented Feedback, Force Control, Position Control, Motor Cortex, Trancranial Magnetic Stimulation, Intracortical Inhibition, EMG suppression

Date Published: 6/19/2016

Citation: Lauber, B., Keller, M., Leukel, C., Gollhofer, A., Taube, W. Force and Position Control in Humans - The Role of Augmented Feedback. *J. Vis. Exp.* (112), e53291, doi:10.3791/53291 (2016).

Abstract

During motor behaviour, humans interact with the environment by for example manipulating objects and this is only possible because sensory feedback is constantly integrated into the central nervous system and these sensory inputs need to be weighted in order meet the task specific goals. Additional feedback presented as augmented feedback was shown to have an impact on motor control and motor learning. A number of studies investigated whether force or position feedback has an influence on motor control and neural activation. However, as in the previous studies the presentation of the force and position feedback was always identical, a recent study assessed whether not only the content but also the interpretation of the feedback has an influence on the time to fatigue of a sustained submaximal contraction and the (inhibitory) activity of the primary motor cortex using subthreshold transcranial magnetic stimulation. This paper describes one possible way to investigate the influence of the interpretation of feedback on motor behaviour by investigating the time to fatigue of submaximal sustained contractions together with the neuromuscular adaptations that can be investigated using surface EMG. Furthermore, the current protocol also describes how motor cortical (inhibitory) activity can be investigated using subthreshold TMS, a method known to act solely on the cortical level. The results show that when participants interpret the feedback as position feedback, they display a significantly shorter time to fatigue of a submaximal sustained contraction. Furthermore, subjects also displayed an increased inhibitory activity of the primary cortex when they believed to receive position feedback compared when they believed to receive force feedback. Accordingly, the results show that interpretation of feedback results in differences on a behavioural level (time to fatigue) that is also reflected in interpretation-specific differences in the amount of inhibitory M1 activity.

Video Link

The video component of this article can be found at http://www.jove.com/video/53291/

Introduction

Sensory feedback is crucial to perform movements. Daily activities are hardly possible in the absence of proprioception [1]. Furthermore, motor learning is influenced by proprioceptive integration [2] or cutaneous perception [3]. Healthy humans with intact sensation are able to weight the sensory inputs arising from various sensory sources in order to meet situation-specific needs [4]. This sensory weighing enables humans to perform difficult tasks with high precision even when some aspects of the sensory information are unreliable or even absent (*e.g.*, walking in the dark or with eyes closed).

Additionally, various evidence suggests that providing augmented (or additional) feedback further improves motor control and/or motor learning. Augmented feedback provides additional information by an external source which can be added to the task intrinsic (sensory) feedback arising from the sensory system [5,6]. Especially the effect of the content of augmented feedback on motor control and learning has been of great interest in recent years. One of the questions addressed was how humans control force and position [7,8]. Initial investigations identified differences in time to fatigue of a sustained submaximal contraction using either position or force feedback and differences in load compliance (*e.g.,* [9-12]). When subjects were provided with force feedback, the time to fatigue of the sustained contraction was significantly longer compared to when position feedback was provided. The same phenomenon was observed for a variety of different muscles and limb positions and a number of neuromuscular mechanisms, including a greater rate of motor unit recruitment and a greater decrease in H-reflex area during the position controlled contraction (for review [13]). However, in these studies, not only the visual feedback but also the physical characteristics of the muscular contraction (*i.e.*, the compliance of the measurement device) was altered. Therefore, we recently conducted a study not altering compliance but only augmented feedback and provided evidence that provision of force and position feedback alone during a sustained submaximal contraction can cause differences in inhibitory activity within the primary motor cortex (M1). This was shown using a stimulation technique that is known to act solely at the cortical level [14], namely subthreshold transcranial magnetic stimulation (subTMS). Unlike suprathreshold TMS, the response evoked by subTMS, is not modulated by the excitability of spinal α-motoneurons and the excitability excitatory neurons and/or cortical cells [15-17] but solely by the excitability of inhibitory intracortical neurons. The postulated mechanism behind this stimulation technique is that it is applied at intensities below the threshold to evoke a motor evoked potential (MEP). It was shown in patients having electrodes implanted at the cervical level that this type of stimulation does not produce any descending activity but that it primarily activates inhibitory interneurons within the primary motor cortex [14,18,19]. This activation of inhibitory interneurons causes a decrease in the ongoing EMG activity and can be quantified by the amount of EMG suppression compared to the EMG activity obtained in trials without stimulation. In this respect, we showed that subjects displayed a significantly greater inhibitory activity in trials in which they received position feedback compared with trials in which force feedback was provided [20]. Furthermore, we also showed that not only the presentation of different feedback modalities (force *vs.* position control) but also the interpretation of feedback can have very similar effects on behavioural and neurophysiological data. More specifically, when we told the participants to receive position feedback (even though it was force feedback) they also not only displayed a shorter time to fatigue but also an increased level of inhibitory M1 activity [21]. Using an approach where the same feedback but with different information about its content is always provided has the advantage that the task constraints, *i.e.,* the presentation of the feedback, the gain of the feedback, or the compliance of the load are identical between conditions so that differences in performance and neural activity are clearly related to differences in the interpretation of the feedback and are not biased by different testing conditions. Thus, the current study investigated whether a different interpretation of one and the same feedback influences the duration of a sustained submaximal contraction and furthermore has an impact on the activation of inhibitory activity of the primary motor cortex.

Protocol

The protocol described here followed the guidelines of the ethics committee of the University of Freiburg and was in accordance with the declaration of Helsinki (1964).

1. Ethical Approval - Subject Instruction

1. Before the actual experiment, instruct all subjects about the purpose of the study and potential risk factors. When applying transcranial magnetic stimulation (TMS), there are some medical risks including any history of epileptic seizures, metal implants in eyes and/or head, diseases of the cardiovascular system and pregnancy. Exclude any subject affirming to one of these risk factors from the study.
2. Include only healthy individuals in the study. Exclude individuals with any neurological, mental and/or orthopaedic diseases.

2. Subject Preparation

1. Subject placement
    1. Throughout the entire experiment, seat subjects in a comfortable chair. Fix the head of the participant using a cast embracing the neck, ensuring a stable head position and avoiding any movements of the head relative the TMS coil.
    2. Place the right arm of the subjects in a custom-built arm rest to minimize movements of the wrist. Fix the subject's right index finger to a splint mounted to the arm of a robot. Align the axis of rotation of the robot arm with the metacarpophangeal joint of the right hand so that the joint centre matches the rotational centre of the robot.
2. Force recordings
    1. Measure the force applied by the subjects by a torquemeter mounted in the robot arm and measure the position of the robot arm (corresponding to the position of the index finger) by a potentiometer connected to the rotational axis of the robot [22].
3. Electromyography (EMG)
    1. Use a bipolar configuration of surface electrodes to measure electrophysiological responses elicited by TMS as well as muscular activation produced by the subjects.
        1. Before attaching the electrodes to the skin over the first dorsal interosseus muscle (FDI) and the abductor pollicis brevis (APB) of the right hand, shave the skin of the subjects, then slightly abrade it using sandpaper or abrading gel and disinfect it with propanol.
        2. Following this, attach self-adhesive EMG electrodes to the skin over the muscle bellies of the FDI and APB. Place an additional reference electrode on the olecranon of the same arm.
        3. Cable-connect all electrodes to an EMG amplifier and to an analogue-digital converter. Amplify the EMG signals (x 1,000), bandpass-filter (10 - 1,000 Hz) and sample at 4 kHz. Store the EMG signals for offline analysis.
4. TMS
    1. Use a figure of eight coil attached to a TMS stimulator to stimulate the contralateral motor cortical hand area.
    2. Find the optimal position of the coil relative to the scalp for eliciting motor evoked potentials (MEPs) in the FDI muscle by a mapping procedure:
        1. Place the coil approximately 0.5 cm anterior to the vertex and over the midline with the handle pointing at 45° anticlockwise relative to the sagittal plane, inducing a posterior-anterior flow of the current in the centre of the coil.
        2. At the beginning, choose a small stimulation (*e.g.,* below 30% maximum stimulator output, MSO) intensity to get the subjects accustomed to the magnetic pulses.
        3. Subsequently, increase the stimulation intensity in small steps, for example 2 - 3% maximum stimulator output (MSO) and move the coil in the frontal-rostral and medio-lateral direction in order to find the optimal site (hotspot) for stimulating the FDI muscle. The hotspot is defined as the place where the greatest MEP can be observed at a given stimulation intensity.
    3. After finding the FDI hotspot, determine resting motor threshold (MT) as the minimum intensity required to evoke MEP peak-to-peak amplitudes in the EMG larger than 50 µV in three out of five consecutive trials [18]. Inspect the size of the MEPs displayed online on the computer screen.
    4. After eliciting MEPs with 1.0*MT, constantly decrease the stimulation intensity of the TMS machine in steps of 2% MSO until the MEP can no longer be observed and an EMG suppression of the ongoing muscle activity becomes apparent.

Note: In order to depict the TMS induced EMG suppression it is necessary to apply a high number of stimulations (see section 5. "Data Processing")

3. Feedback Presentation

1. Divide the participants into three groups (pF, fF, CON).
2. Instruct subjects from the position feedback group (pF) in half of the trials to receive feedback about the position of the index finger (position feedback) when moving the index finger by pressing against the robotic device.
3. In the other half of the trials, instruct subjects to receive feedback about the applied force while moving the robotic device (force feedback).
   Note: In reality, however, they always receive the same feedback (position feedback).
4. Instruct subjects from the force feedback group (fF) to receive force feedback in half of the trials and receive position feedback in the other half.
   Note: In fact, this group is solely provided with force feedback.
5. Do not instruct the control group (CON) about the source of the feedback. Note: The control group receives force feedback in one half of their trials and position feedback in the other half.
6. Randomly alter the order of the sessions, that is, whether trials start with force or position feedback, in all groups.
7. Visually display the force and the position feedback on a computer screen placed 1 m in front of the subjects.
8. In each condition, present a target line corresponding to 30% of the subject's individual maximal voluntary force, or the finger angle of the index finger at 30% maximally voluntary contraction (MVC), on the computer screen and instruct the subject to match the target line as closely as possible.

4. Maximal Isometric Force

1. After the subject is prepared (EMG), perform three isometric maximum voluntary contractions (MVC), consisting of a gradual increase in isometric force from zero to maximum over a 3 sec time span and the maximal force held for 2 sec [20,21].
2. Verbally encourage the subject to achieve maximal force. After each trial, allow the subjects to rest for 90 sec to avoid fatigue.

5. Experimental Procedure

1. Fatiguing Motor Task- Sustained contractions.
   Note: The fatiguing task consists of two sustained contractions executed on separate days.
    1. Instruct the subjects to match the target line of 30% MVC for as long as possible with a line corresponding to the applied force or the position of their finger corresponding to a force level of 30% MVC.
       Note: The target line during the position feedback condition (pF-group) therefore corresponds to the finger angle when subjects match the force level of 30% MVC.
    2. Ask the subjects to hold the contractions until task failure, which is defined as the point where the subjects are no longer able to hold the target force inside a 5% window of the target force over a period of 5 sec (fF-group). For the pF-group, define task failure as when the participants are unable to maintain the finger angle within 5 % of the required target angle for 5 sec [12,23].
    3. Ensure that the two sustained contractions are separated by at least 48 hr.

2. TMS-protocol
   Note: The subthreshold TMS experiment is carried out on separate day to the fatiguing contractions. This is important as fatigue has an influence on the EMG suppression evoked by subTMS [24,25] so differences between force and position cannot be clearly identified. Separating the fatiguing contractions from the TMS measurements has the advantage that differences in the EMG suppression can now be clearly be attributed to the different interpretation of the feedback but has the limitation that the results can not directly be linked to the differences in the time to fatigue of the sustained contractions.
    1. Conduct the part of the experiment using TMS (see also section 3. "Feedback presentation") on a separate occasion than the fatiguing experiments. Initially, follow the exact same procedure as for the fatiguing contraction (*e.g.,* MVC contractions) but this time, ask the subjects to hold the contractions only as long as the TMS stimulation lasts. Thus, the contractions are not fatigable and only held for approximately 100 sec during each TMS trial.
    2. Provide a break of 3 min between trials to minimize any bias of fatigue.

6. Data Processing

1. **TMS**
    1. Apply a total of 100 sweeps, 50 sweeps with and 50 sweeps without stimulation, with an inter-stimulus interval ranging from 0.8 to 1.1 s [20,21,25,26]. This short interstimulus interval makes sure that the subjects do not need to hold the contractions for too long so fatiguing effects can be minimized.
    2. To analyse if the TMS stimulation caused a facilitation (MEP) or an EMG suppression, subtract the rectified and then average 50 sweeps with stimulation (stimulated EMG) from the 50 sweeps without stimulation (control EMG) [20,21,25-27].
       Note: The onset of the EMG suppression is defined as the time point where the averaged EMG for the sweeps with the stimulation is less than the control EMG for at least 4 msec in a time frame of 20 to 50 msec after the TMS pulse. The end of the suppression is defined as the instant when the stimulated EMG is greater than the control EMG for at least 1 msec and the extent of the suppression is calculated as percentage change (control-stimulated/$mean_{control}$*100).

3. Use the sweeps without TMS stimulation for the calculation of the background EMG activation and average them over the same time window as the trials with stimulation [20,21,25,26].

2. **EMG**
    1. Determine the maximal EMG activity by calculating the root-mean-square value recorded in a 0.5s time window around the peak force measured during the MVC tests [20,21].
    2. For the sustained contractions, analyse the EMG by building 8 sec long bins where the root-mean-square of the rectified EMG is calculated and normalized to the EMG activity obtained during the MVC trials [20,21].

Representative Results

Interpretation of feedback

In procedure described here, subjects were instructed in a way that they believed in half of their trials to have received position feedback and in the other half of the trials to have received force feedback. In fact, they were tricked in half of their trials as they the pF-group always received position feedback and the fF-group always received force feedback.

Using this method has the advantage that any feedback specific differences (*e.g.,* gain of the signal, colour) can be excluded. Therefore, the results can be solely attributed to differences in the interpretation of the feedback and not to the presentation of the feedback itself. It is however theoretically possible that the subjects realized that the same feedback was presented without telling us. We therefore always asked at the end of the final test if they realized that the feedback was always the same. In the case of the present study, subjects reported that they did not recognize that they were tricked.

Sustained contractions

Irrespective of the group (fF or pF group), *i.e.,* irrespective whether subjects received force or position feedback, they always displayed the same pattern: when they thought to control force, the time to fatigue was significantly longer compared to when they believed they were receiving position feedback. The CON group displayed no differences between the two feedback conditions. An example of one subject from each of the three groups is represented in **Figure 1**. The FDI EMG activity increased in the course of the sustained contraction but was comparable between feedback conditions (**Figure 2**).

Force and position control in humans

The question of when and how humans use position or force information for motor control led to a large number of publications in this field with different results probably resulting from the different methodological approaches. Milner and Hinder [36] for example argued that position information rather than force information is used while adapting to new environmental dynamics (*i.e.,* perturbations of the hand path when moving from target A to B). A number of publications looking at behavioural and neural differences between position and force controlled sustained fatiguing contractions found that the time to fatigue is highly reduced when subjects are required to control position compared to force (for review please also see [13]). This reduced time to task failure was accompanied by a number of neural adaptations like a faster decrease in H-reflex area [12], a faster recruitment of motor units and differences in limb posture[23] as well as an enhanced level of perceived exertion during the position controlled contractions [12,37-40]. The paradigm of these studies was that subjects maintained position controlled contractions in a compliant system whereas the force controlled contractions were performed under rigid conditions. Thus, the latter studies and the study by Milner and Hinder [36] suggest that position or force control changes with differences in environmental dynamics and biomechanical demands. What remained unclear, however, was how position and force control is realized when the dynamics and biomechanics of the task remain constant. A recently conducted study showed when changing the feedback from force to position (or vice versa) but the task and thus the dynamics remained the same, that there are differences in time to fatigue [20]. The only difference between our tasks was the source of the feedback. Additionally, like in the current study Lauber *et al.* (2012) used subTMS to reveal differences in the amount of EMG suppression, and found a greater EMG suppression during the position controlled contractions.

Neural control of force and position in humans

The primary motor cortex seems a worthwhile target as it is not only part of the transcortical reflex loop [41,42] but also because it plays a key role during voluntary movement control [43,44]. The results of the present study further highlight the role of M1 during force and position controlled contractions as the greater EMG suppression during the position controlled contraction indicates a greater susceptibility of intracortical inhibitory interneurons as soon as the subjects interpreted the feedback as position feedback. This is supported by the finding that when no information about the source of the feedback is provided, no difference in the EMG suppression could be observed. Recent observations suggest that a great amount of EMG suppression caused by the magnetic stimulation indicates a greater contribution of the cortex (*i.e.,* M1) [24]. This increased M1 activity in position controlled movements could derive from interpretation specific changes in integrating proprioceptive signals [21]. The modified proprioceptive signal could then be differently processed in other cortical areas (*e.g.,* supplementary motor areas (SMA)) which than modify the activity of M1 via their synaptic input. This would be in line with the finding that changes in proprioceptive feedback have the potential to modify intracortical and corticospinal excitability [45].

Taken together, the current findings highlight that depending on the interpretation, augmented feedback can be differently integrated, leading to distinct behavioural and neural adaptations within the central nervous system.

EMG suppression by subTMS:

The subthreshold stimulation resulted in a suppression in the EMG activity during all feedback conditions. The EMG suppression was, however, greater when the subjects thought to receive position feedback compared to when they believed to receive force feedback; again this was independent which kind of feedback they really perceived. Thus, subjects of the pF and the fF group behaved the same kind of way (**Figure 3A&B**). The CON group (**Figure 3C**) displayed no differences in the EMG suppression between conditions. **Figure 3** shows representative results from individual subjects of all groups that participated in the study and **Figure 4** group mean data. Background EMG activation was not different between groups and conditions.

Subthreshold TMS

The principle of subthreshold transcranial magnetic stimulus is that at this low intensities (*i.e.,* below the threshold to evoke MEPs), intracortical inhibitory interneurons are activated which then synaptically reduce the excitability of corticospinal cells [14,27,31]. This results in a reduction of the excitatory drive from the cortex down to the muscle during a submaximal sustained contraction and can be quantified by the reduction of the ongoing EMG activity. The reduction in EMG activity represents inhibitory activity acting onto M1 and is most commonly analysed by the size (area) of the suppression.

There exist some evidence that this EMG suppression is solely the result of an increased intracortical inhibition because subthreshold stimulation at a subcortical level failed to induce changes in the EMG [31] and also because subTMS causes a simultaneous inhibition of the agonist and antagonist excluding the influence of spinal reciprocal inhibition [25,27,32]. Additionally, recordings from epidural electrodes implanted in the cervical spine showed no responses after subTMS stimulation [14]. Finally, direct corticospinal projections seem to play an important role when using subthreshold TMS as Butler *et al.*[33] demonstrated that the onset of the EMG suppression can be observed already after only 20 ms after the TMS stimulation.

Together with the results of the current study it seems very likely that force and position information are differently integrated within the central nervous system leading to a different activation of the primary motor cortex. This is further supported by the findings of the current study showing a shorter time to fatigue of the sustained contraction when interpreting the feedback as position feedback compared to force feedback conditions and to the control where no instruction about the source of the feedback was given resulting in no difference in the time to fatigue.

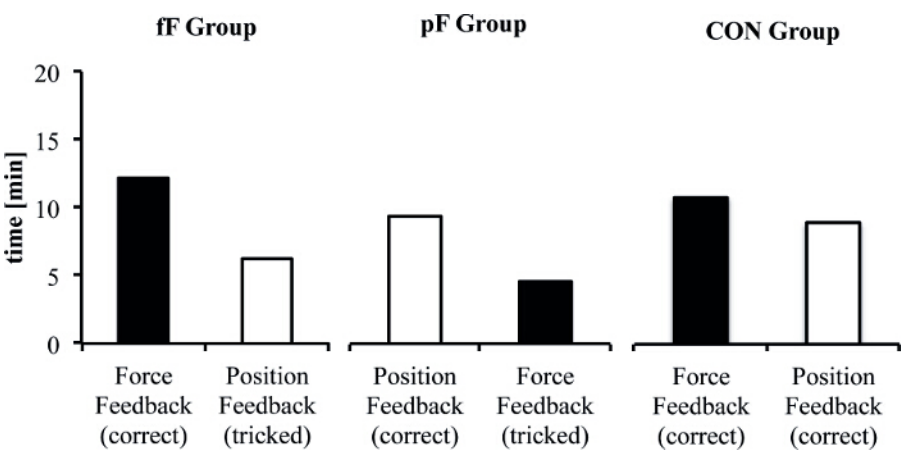

Figure 1. Time to Fatigue of Sustained Contractions. Representative data from one subject from each group (fF-pF and CON group) displaying their time to fatigue of the sustained contractions. From left to right the figure shows that as soon as the subject from the fF group received force feedback, the time to fatigue was longer compared to when the subject believed he/she was receiving position feedback (tricked). The second graph from a subject of the pF group shows that as soon as the subject interpreted the feedback as force feedback (tricked), the time to fatigue was longer compared to when the subject received position feedback. The last graph shows that without any instruction about the source of the feedback, the subject from the CON group displayed no difference in the time to fatigue. Please click here to view a larger version of this figure.

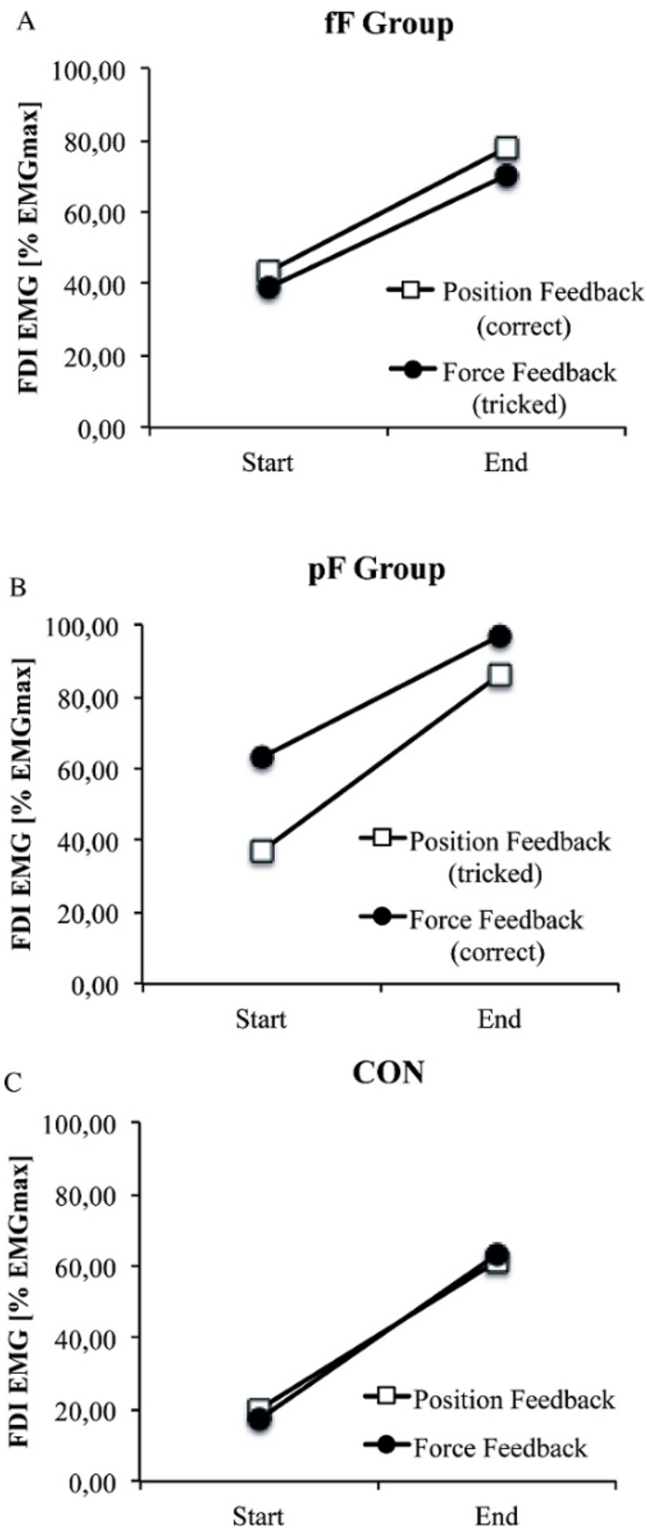

Figure 2. EMG Activity in the Course of the Sustained Contractions. Representative data from one subject from each group (fF-pF and CON group) displaying an increase in the EMG activity from the start to the end of the contraction. This was independent whether the subjects always received force feedback (fF group, **A**) and believed in half of the trials that they were receiving position feedback, or if the subjects always received position feedback (pF group, **B**) and believed in half of their trials that they were receiving force feedback or when they were not informed about the nature of the signal (CON group, **C**). Please click here to view a larger version of this figure.

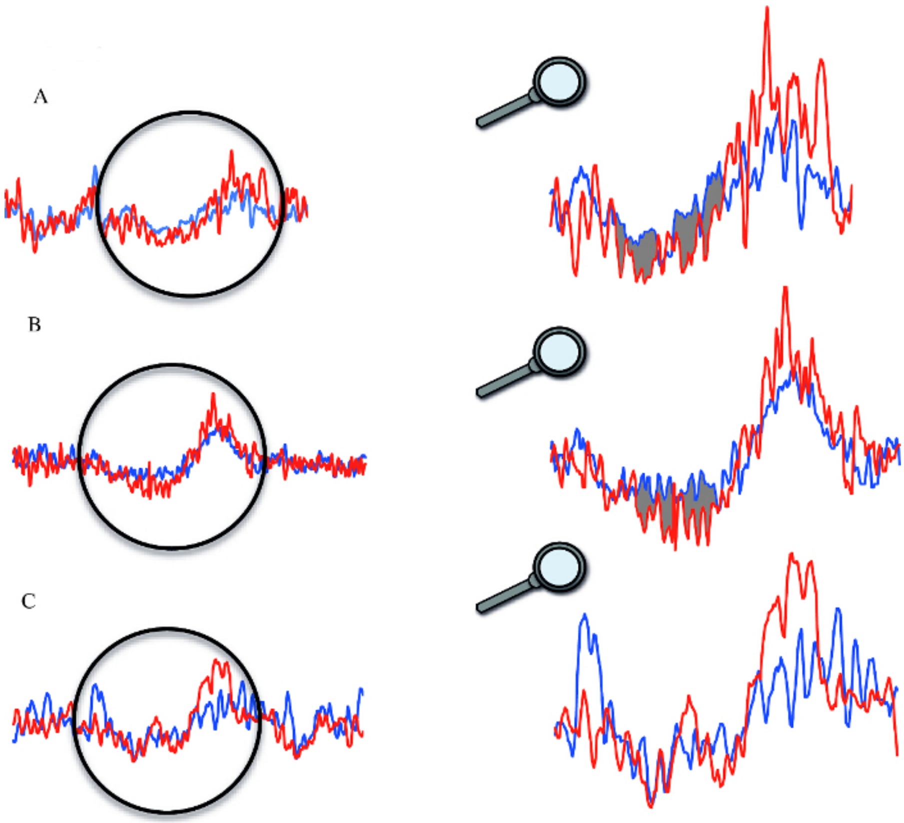

Figure 3. TMS evoked EMG suppression. The right panels show the EMG suppression during the force and the position controlled contraction for the fF group **(A)**, the pF group **(B)** and the CON group **(C)**. In all three representative subjects, the stimulation with subTMS resulted in a suppression of the EMG activity which was greater when the subject from the fF group believed that they were receiving position feedback (red line) compared to the trail where the subjects received force feedback (**A**, blue line), when the subject from the pF group actually received position feedback (red line) compared to when the subject believed that he/she was receiving force feedback (**B**, blue line). When no information was given there was no difference (blue force control, red position control) between the EMG suppression in the subjects from the CON group (**C**). The right panel are enlarged images of the same EMG traces as in the left side of the figure highlighting the difference in EMG suppression by the grey shaded area. Please click here to view a larger version of this figure.

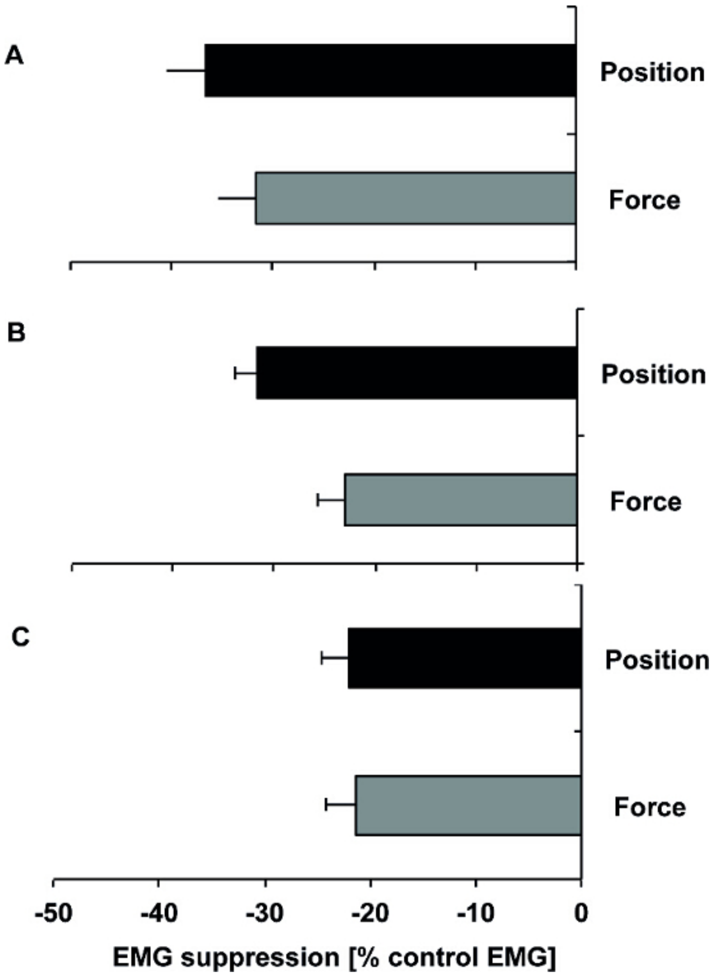

Figure 4. TMS Evoked EMG Suppression - Group Data. In the pf- **(A)** and the fF- **(B)** groups, the stimulation with subTMS resulted in a greater suppression during the position controlled task compared to the force controlled task. When no information was given there was no difference in the EMG suppression **(C)**. Error bars indicate standard error of the mean. Please click here to view a larger version of this figure.

Discussion

The present study investigated if the interpretation of augmented feedback influences the time to fatigue of a sustained submaximal contraction and the neural processing of the primary motor cortex. The results show that as soon as the participants interpreted the feedback as position feedback (compared to force feedback), the time to fatigue was significantly shorter and the inhibitory activity of the motor cortex (measured as the amount of EMG suppression caused by subTMS) is greater. As the task did not change between conditions, the current findings indicate differences in force and position control strategies depending on the interpretation of the source of the feedback. Most previous experiments focused on feedback specific aspects such as the timing [28] or the frequency [29,30] of the feedback whereas the present study evaluated whether information about the content of the feedback signal and thus the interpretation about it can affect motor behaviour.

One limitation of this method is that it is not always possible to cause a TMS evoked EMG suppression in every subject without prior facilitation. Some studies reported that it was only possible in 50% of the subjects to cause the EMG suppression in the absence of an initial facilitation but that the method is nevertheless accepted as a valid tool for quantifying intracortical inhibition [24,26,34]. This is probably the case when the thresholds for the activation of inhibitory and excitatory interneurons are very similar [25,35].

Furthermore, it is important to conduct the subthreshold TMS experiment on a separate occasion than the fatiguing contractions. The reason is that fatigue can have and influence on the EMG suppression meaning that differences between force and position might be hard to interpret. On the one hand this has the advantage that by separating the measurements, it is possible to link potential differences in the EMG suppression with the interpretation of the feedback but on the other hand has the limitation that the results can not directly be linked to the differences in the time to fatigue of the sustained contractions.

It is also very important that the same experimenter is conducting the individual experiments so subjects do not become aware that they might be cheated in the sense that they receive a different kind of feedback than they were told.

What the current approach does not reveal is what exactly caused the differences in time to fatigue and the differences in EMG suppression between the force and the position controlled contraction. During fatigue, a number peripheral, subcortical and cortical mechanism could play a role. For the differences in the EMG suppression evoked with subTMS, it is very likely that an altered inhibitory activity is responsible for the observed results. One way to test this would be to use a modified TMS protocol such as short intracortical inhibition (SICI) being a potential future application.

Disclosures

The authors have nothing to disclose.

Acknowledgements

The authors have no acknowledgements.

References

1. Rothwell, J. C., Traub, M. M., Day, B. L., Obeso, J. A., Thomas, P. K., & Marsden, C. D. Manual motor performance in a deafferented man. *Brain : a journal of neurology.* **105** (Pt 3), 515-542 (1982).
2. Rosenkranz, K., & Rothwell, J. C. Modulation of proprioceptive integration in the motor cortex shapes human motor learning. *The J Neurosci.* **32** (26), 9000-9006 (2012).
3. Choi, J. T., Lundbye-Jensen, J., Leukel, C., & Nielsen, J. B. Cutaneous mechanisms of isometric ankle force control. *Ex Brain Res.* **228** (3), 377-384 (2013).
4. Peterka, R. J., & Loughlin, P. J. Dynamic regulation of sensorimotor integration in human postural control. *J Neurophys.* **91** (1), 410-423 (2004).
5. Schmidt, R. A., & Lee, T. D. *Motor Control and Learning: A Behavioral Emphasis.* Human Kinetics: Champaign, (2011).
6. Lauber, B., & Keller, M. Improving motor performance: Selected aspects of augmented feedback in exercise and health. *Eur J Sport Sci.* **14** (1), 36-42 (2014).
7. Antfolk, C., D'Alonzo, M., Rosén, B., Lundborg, G., Sebelius, F., & Cipriani, C. Sensory feedback in upper limb prosthetics. *Exp rev med dev.* **10** (1), 45-54 (2013).
8. Lundborg, G., & Rosén, B. Sensory substitution in prosthetics. *Hand clinics.* **17** (3), 481-488, (2001).
9. Maluf, K. S., Shinohara, A. M., Stephenson, J. L., & Enoka,. R. M. Muscle activation and time to task failure differ with load type and contraction intensity for a human hand muscle. *Ex Brain Res.* **167**(2), 165-177 (2005).
10. Mottram, C. J., Jakobi, J. M., Semmler, J. G., & Enoka, R. M. Motor-Unit Activity Differs With Load Type During a Fatiguing Contraction. *J Neurophys.* **93**(3), 1381-1392 (2005).
11. Baudry, S., Maerz, A. H., & Enoka, R. M. Presynaptic Modulation of Ia Afferents in Young and Old Adults When Performing Force and Position Control. *J Neurophys.* **103**(2), 623-631 (2010).
12. Klass, M., Lévénez, M., Enoka, R. M., Duchateau, J., & Le, M. Spinal Mechanisms Contribute to Differences in the Time to Failure of Submaximal Fatiguing Contractions Performed With Different Loads. *J Neurophys.* **99**, 1096-1104 (2008).
13. Enoka, R. M., Baudry, S., Rudroff, T., Farina, D., Klass, M., & Duchateau, J. Unraveling the neurophysiology of muscle fatigue. *J Electromyogr Kinesiol.* **21** (2), 208-219 (2011).
14. Di Lazzaro, V., Oliviero, D. R. A., Ferrara, P. P. L., Mazzone, A. I. P., & Rothwell, P. T. J. C. Magnetic transcranial stimulation at intensities below active motor threshold activates intracortical inhibitory circuits. *Ex Brain Res.* **119**(2), 265-268 (1998).
15. Nielsen, J. B., & Petersen, N. Evidence favouring different descending pathways to soleus motoneurones activated by magnetic brain stimulation in man. *J Physiol.* **486** (Pt 3), 779-788 (1995).
16. Ugawa, Y., Terao, Y., Hanajima, R., Sakai, K., & Kanazawa, I. Facilitatory effect of tonic voluntary contraction on responses to motor cortex stimulation. *Electroen Clin Neuro.* **97** (6), 451-454 (1995).
17. Morita, H., Olivier, E., Baumgarten, J., Petersen, N. C., Institut, P., & Kiel, È. Differential changes in corticospinal and Ia input to tibialis anterior and soleus motor neurones during voluntary contraction in man. *Acta Physiol Scand.* **70**(1), 65-76 (2000).
18. Kujirai, T., *et al.* Corticocortical inhibition in human motor cortex. *The J Physiol.* **471**, 501-519 (1993).
19. Di Lazzaro, V., & Rothwell, J. C. Cortico-spinal activity evoked and modulated by non-invasive stimulation of the intact human motor cortex. *J Physiol.* **19**, 4115-4128 (2014).
20. Lauber, B., Leukel, C., Gollhofer, A., & Taube, W. Time to Task Failure and Motor Cortical Activity Depend on the Type of Feedback in Visuomotor Tasks. *PLoS ONE.* **7** (3), e32433 (2012).
21. Lauber, B., Keller, M., Leukel, C., Gollhofer, A., & Taube, W. Specific interpretation of augmented feedback changes motor performance and cortical processing. *Ex Brain Res.* **227** (1), 31-41 (2013).
22. Lauber, B., Lundbye-Jensen, J., Keller, M., Gollhofer, A., Taube, W., & Leukel, C. Cross-limb interference during motor learning. *PLoS ONE.* e81038 (2013).
23. Rudroff, T., Jordan, K., Enoka, J. A., & Matthews, S. D. Discharge of biceps brachii motor units is modulated by load compliance and forearm posture. *Ex Brain Res.* **202**(1), 111-120 (2010).
24. Seifert, T., & Petersen, N. C. Changes in presumed motor cortical activity during fatiguing muscle contraction in humans. *Acta Physiol.* **199**, 317-325 (2010).
25. Sidhu, S. K., Lauber, B., Cresswell, A. G., & Carroll, T. Sustained cycling exercise increases intracortical inhibition. *Med Sci Spo Exerc.* **45** (4), 654-662 (2013).
26. Zuur, A. T., *et al.* Contribution of afferent feedback and descending drive to human hopping. *J Physiol.* **5**, 799-807 (2010).
27. Petersen, N. C., *et al.* Suppression of EMG activity by transcranial magnetic stimulation in human subjects during walking. *J Physiol.* **537** (Pt2), 651-656 (2001).
28. Molier, B. I., Van Asseldonk, E. H. F., Hermens, H. J., & Jannink, M. J. A. Nature, timing, frequency and type of augmented feedback; does it influence motor relearning of the hemiparetic arm after stroke? A systematic review. *Disabil Rehabil.* **32** (22), 1799-1809 (2010).
29. Moran, K. A., Murphy, C., & Marshall, B. The need and benefit of augmented feedback on service speed in tennis. *Med Sci Sports Exerc.* **44** (4), 754-760 (2012).

30. Keller, M., Lauber, B., Gehring, D., Leukel, C., & Taube, W. Jump performance and augmented feedback : Immediate benefits and long-term training effects. *Hum Mov Sci.* **36**, 177-189 (2014).
31. Davey, N. J., Romaiguere, P., Maskill, D. W., & Ellaway, P. H. Suppression of voluntary motor activity revealed using transcranial magnetic stimulation of the motor cortex in man. *J Physiol.* **477** (Pt 2), 223-235 (1994).
32. Leukel, C., Lundbye-jensen, J., Gruber, M., Zuur, A. T., Gollhofer, A., & Taube, W. Short-term pressure induced suppression of the short-latency response : a new methodology for investigating stretch reflexes. *J Appl Phys.* **107**(4), 1051-1058 (2010).
33. Butler, J. E., Larsen, T. S., Gandevia, S. C., & Petersen, N. C. The nature of corticospinal paths driving human motoneurons during voluntary contractions. *J Physiol.* **584**(Pt 2), 651-659 (2007).
34. Bentley, D. J., Smith, P. A., Davie, A. J., & Zhou, S. Muscle activation of the knee extensors following high intensity endurance exercise in cyclists. *Eur J Appl Physiol.* **81** (4), 297-302 (2000).
35. Sidhu, S. K., Cresswell, A. G., & Carroll, T. Motor cortex excitability does not increase during sustained cycling exercise to volitional exhaustion. *J Appl Physiol.* **113** (3), 401-409 (2012).
36. Milner, T. E., & Hinder, M. R. Position information but not force information is used in adapting to changes in environmental dynamics. *J Neurophys.* **96** (2), 526-534 (2006).
37. Rudroff, T., Justice, J. N., Matthews, S., Zuo, R., & Enoka, R. M. Muscle activity differs with load compliance during fatiguing contractions with the knee extensor muscles. *Ex Brain Res.* **203**(2), 307-316 (2010).
38. Rudroff, T., Justice, J. N., Holmes, M. R., Matthews, S. D., & Enoka, R. M. Muscle activity and time to task failure differ with load compliance and target force for elbow flexor muscles. *J Appl Physiol.* **110**(1), 125-136 (2013).
39. Griffith, E. E., Yoon, T., & Hunter, S. K. Age and Load Compliance Alter Time to Task Failure for a Submaximal Fatiguing Contraction with the Lower Leg. *J Appl Physiol.* **108**(6), 1510-1519 (2010).
40. Maluf, K. S., *et al.* Task failure during fatiguing contractions performed by humans Task failure during fatiguing contractions performed by humans. *J Appl Physiol.* **99**(2), 389-396 (2011).
41. Porter, R., & Lemon, R. N. *Corticospinal Function and Voluntary Movement.* Oxford Univ. Press: (1993).
42. Scott, S. H. The role of primary motor cortex in goal-directed movements: insights from neurophysiological studies on non-human primates. *Cur Neurobio.* **13**(6), 671-677 (2003).
43. Evarts, E. V & Tanji, J. Reflex and intended responses in motor cortex pyramidal tract neurons of monkey. *J Neurophys.* **39** (5), 1069-1080 (1976).
44. Cheney, P. D., & Fetz, E. E. Corticomotoneuronal cells contribute to long-latency stretch reflexes in the rhesus monkey. *J Physiol.* **349**, 249-272 (1984).
45. Kobayashi, M., Ng, J., Théoret, H., & Pascual-Leone, A. Modulation of intracortical neuronal circuits in human hand motor area by digit stimulation. *Ex Brain Res.* **149** (1), 1-8 (2003).

