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RESEARCH ARTICLE

Force control in the absence of visual and tactile feedback

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Abstract Motor control tasks like stance or object handling require sensory feedback from proprioception, vision and touch. The distinction between tactile and proprioceptive sensors is not frequently made in dynamic motor control tasks, and if so, mostly based on signal latency. We previously found that force control tasks entail more compliant behavior than a passive, relaxed condition and by neuromuscular modeling we were able to attribute this to adaptations in proprioceptive force feedback from Golgi tendon organs. This required the assumption that both tactile and visual feedback are too slow to explain the measured adaptations in face of unpredictable force perturbations. Although this assumption was shown to hold using model simulations, so far no experimental data is available to validate it. Here we applied a systematic approach using continuous perturbations and engineering analyses to provide experimental evidence for the hypothesis that motor control adaptation in force control tasks can be achieved using proprioceptive feedback only. Varying task instruction resulted in substantial adaptations in neuromuscular behavior, which persisted after eliminating visual and/or tactile feedback by a nerve block of the *nervus plantaris medialis*. It is concluded that proprioception adapts dynamic human ankle motor control even in the absence of visual and tactile feedback.

Keywords Motor control · Proprioception · Afferent feedback · Anesthesia · Tactile sense

Introduction

Our body provides us with redundant sensory information about forces: on the one hand tactile sensors or mechanoreceptors in the skin sense *external* forces (touch and pressure), while on the other hand proprioceptors in the muscles sense *internal* forces (as well as body posture). Most experimental studies isolate one of the sensing mechanisms, and as such much is known about individual properties of both the tactile sense (LaMotte and Mountcastle 1975; Marcus and Fuglevand 2009; Ribot-Ciscar et al. 1989; Van Lunteren and Stassen 1969) and proprioception (Benjaminse et al. 2009; Jones et al. 1992; Jones 1989; Van Beers et al. 1998). The experimental separation of individual contributions of the tactile sense and proprioception to functional tasks is difficult, while daily life activities require the use of both tactile and proprioceptive sensing (Tan 2000).

Previous work on separation of the contributions of the tactile sense and proprioception to motor control has been done using either modeling techniques or isolation of one of the senses (i.e. through anesthesia). The conclusions drawn from these studies range from explaining all the observed muscle activity solely with proprioception (in perturbation experiments) to synergy advantages of using both proprioception and the tactile sense (in non-perturbation

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experiments). Apparently the circumstances and the task at hand are of paramount importance for the required feedback pathways.

In non-perturbation experiments subjects assess a situation while a sense is excluded through carefully conditioning it not to contribute. For example, Voisin et al. (2002) conducted an experiment using several active and passive touch conditions with and without digital anesthesia that confirmed that both cutaneous feedback from the exploring digit and proprioceptive feedback from the shoulder contribute to angle discrimination. Performance was best with both modalities available, and diminished when either of the two sources of information was eliminated, indicating that this sensory task is an integrative task drawing on sensory information from two different (sub)modalities. In addition, John et al. (1989) reported that the ability to discriminate differences in the thickness of plates using a precision grip with both cutaneous and proprioceptive feedback available is far superior to what could have been expected from previous studies on proprioception, indicating a synergy advantage.

Perturbation experiments separating the tactile sense from proprioception isolate the reflexive contribution by studying electromyographical (EMG) and mechanical responses to perturbations (Akazawa et al. 1983; Dietz et al. 1994; Doemges and Rack 1992a, b; Kurtzer et al. 2010). Humans receive both tactile and proprioceptive feedback, which may both contribute to the responses as elicited in dynamic motor control experiments. Several dynamic motor control studies have used an anesthetic nerve block to eliminate feedback pathways. Clark et al. (1985) studied the position sense of the ankle plantar flexor muscles during a block of the common peroneal nerve, paralyzing the ankle dorsiflexor muscle. The authors argued that subjects lost position feedback from the plantar flexor muscles during slow displacements of the foot when the muscles were slackened. Grey et al. (2004) applied an anesthetic nerve block to assess the contribution of tactile feedback to the decline in the soleus EMG in response to a rapid plantar flexion perturbation during the stance phase during human walking. The authors concluded that proprioceptive afferents, rather than cutaneous afferents, contribute to the background soleus EMG during late stance phase.

Especially in the field of dynamic motor control the distinction between tactile and proprioceptive feedback is not always made, and if so mostly on the basis of time delays which are substantially higher for tactile (80–200 ms) than monosynaptic proprioceptive feedback (25–50 ms). However, the difference in time delay between the responses of slower, subcortical (50–150 ms) reflexive pathways and fast tactile feedback (such as cutaneous reflexes) is small, making isolation of proprioceptive contributions solely based on time delay questionable.

In dynamic motor control experiments using continuous perturbations the time delays are used to separate the contributions of tactile and proprioceptive feedback with the aid of modeling. One of our recent experiments (Mugge et al. 2010) in particular raised the question to what extent tactile and proprioceptive information contribute to functional motor tasks. Humans use and adapt neuromuscular feedback to perform a wide range of tasks (Crago et al. 1976; Doemges and Rack 1992a, b; Hammond 1956; Jaeger et al. 1982; Pruszynski et al. 2008; Rothwell et al. 1980; Shemmell et al. 2009). When comparing motor behavior during a "Force Task" (where subjects are instructed to give way to an unpredictable continuous force perturbation) to that during a "Relax Task" (in which subjects are instructed to relax and ignore the force perturbations), subjects showed increased admittance[1] (Abbink 2006; Abbink et al. 2011; Mugge et al. 2010). The neuromuscular model that was fitted to the experimental results attributed this change in admittance to inhibitory Golgi tendon organ activity, as it could not be explained by slower tactile and visual feedback. However contributions of tactile and visual feedback, especially at lower frequencies could not definitively be ruled out.

Visual feedback is a relatively slow feedback path (>200 ms) that may elicit responses to mechanical perturbation of a limb. Vision is the dominant sense, but has been suggested to be subordinate to haptics during specific motor tasks like doing up a button. Also in size estimation experiments it is suggested that subjects only rely on one sense (either vision or touch) when they are required to self-generate more precise judgments. Thus, task requirements influence sensory dominance; and vision does not invariably prevail over touch (Heller et al. 1999).

Reflex modulation manifests even without the contribution of visual and tactile feedback as established by a wide range of dynamic motor control studies (e.g. Bawa and McKenzie 1981; Cody et al. 1987; Colebatch and McCloskey 1987; Lewis et al. 2006; Loo and McCloskey 1985; Soechting et al. 1981). In fact these studies show that excluding visual or tactile feedback had no significant impact on reflex activity. On the other hand, psychophysical studies show integration of sensory feedback and deteriorated performance in case one of the feedback pathways is eliminated. If removal of tactile and visual feedback does not affect the motor control behavior during dynamic motor control tasks, then the task is performed

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[1] The admittance is a frequency response function, that captures the causal dynamic relationship between force (input) and position (output), essentially describing the mass-spring-damper characteristics of a limb (Hogan 1985; De Vlugt et al. 2002). It is the mathematical inverse of impedance, used in other studies.

using reflexes only. Whereas, if the motor control behavior does adapt, then the motor task is integrative in nature and the extent of the adaptation will reveal the separate contributions of these pathways. The role of visual and haptic feedback may therefore be different for different tasks: does a force task draw upon other feedback pathways as well?

The goal of the present study was to separate the contributions of visual, tactile and proprioceptive feedback in so-called maximal tasks (resist, relax and give way to force perturbations) as commonly used in dynamic motor control experiments; and to investigate to what extent, adaptation to the task is possible using proprioceptive feedback pathways only. We used continuous perturbations, engineering analyses, and several instructions, setting the present study apart from previous studies with step perturbations and just one instructional set. We applied a previously published experimental protocol by our group (Mugge et al. 2010) and manipulated visual and tactile feedback. Tactile sensation of the foot sole was eliminated by applying a nerve block to the *nervus plantaris medialis*. We hypothesize that maximal tasks will mainly evoke activity of the fast proprioceptive pathways and that visual and tactile feedback are not essential for ankle admittance control. In other words, performing a task without visual or tactile feedback will not bring about substantial changes in motor control behavior.

Materials and methods

Subjects

Seven healthy subjects (6 male, 1 female, age 28.3 SD 6.4 years, range 22–42 years) participated in the experiment. Subjects were excluded when having a known allergy to local anesthetics, low blood pressure, a history of cardiac, neurological or vascular diseases, diabetes mellitus, orthopedic or other diseases of the right foot/ankle or prior surgery of the right foot/ankle. Subjects gave their informed consent prior to participation and the local ethics committee approved the experimental protocol.

Experimental setup

The subjects were comfortably seated in a car driving posture (Fig. 1) and their right foot was firmly strapped to a pedal connected to a haptic manipulator using Velcro. The pedal system was based on a commercially available force-controlled actuator (Moog, Nieuw-Vennep, The Netherlands) by which a virtual mass-spring-damper system can be simulated. The pedal applies torque perturbations to the ankle, which result in small ankle rotations (SD ~1.0°) enabling linear analysis. This study was performed using a pedal stiffness of 17.5 Nm/rad ($\approx$1.6 N/° force at foot contact). The pedal damping ($7.5 \cdot 10^{-4}$ Nms/rad) and virtual inertia ($5.1 \cdot 10^{-3}$ kg m^2) were set to low values. A bias force (12 N) together with the pedal stiffness compensated for the weight of the foot at a pedal depression of about 10° ($\approx$90° ankle flexion angle). This allowed the subject to relax the lower leg muscles in the desired configuration (90° ankle flexion).

Perturbation signals

The perturbation signals were designed in frequency domain to have rectangular spectra containing dominant power from 0.1 up to 0.7, 1.2 and 2.0 Hz. Power was applied to two adjacent frequency points to enable frequency averaging to reduce estimator variance (Jenkins and Watts 1968; Pintelon and Schoukens 2001). All perturbations were supplemented with a reduced level of power up to 40 Hz, according to the Reduced Power Method (Mugge et al. 2007) enabling system identification at higher frequencies, while still evoking behavior adapted to low-frequency perturbations. Inverse Fourier transform yielded unpredictable time signals with 37.0 s duration. To prevent possible non-linear effects due to amplitude variability, the standard deviation of pedal depression was equalized by individual scaling of the torque perturbation magnitudes (the correct scaling was determined during training).

Experiment design

Figure 1 presents a flow chart of the experiment. The experiment comprised two measurement sessions. In each session, the subjects performed three task instructions in face of unpredictable continuous torque perturbations (Fig. 2) in two conditions (with and without visual feedback). The subjects received written and oral instructions as to how to perform the three tasks:

- Force task (FT), i.e. maintain force, minimize force deviations by giving way to the perturbation.
- Relax task (RT), i.e. passive behavior, minimize muscle activity (relax).
- Position task (PT), i.e. maintain position, minimize position deviations by resisting the perturbation.

The first session (baseline A) was used to determine the subject's ability to perform the three required tasks with tactile feedback available. The second session (after nerve block B) served to determine the subject's ability to perform the tasks without tactile feedback. Only if baseline A showed that the subject could change the low-frequency admittance by at least a factor of two between the relax

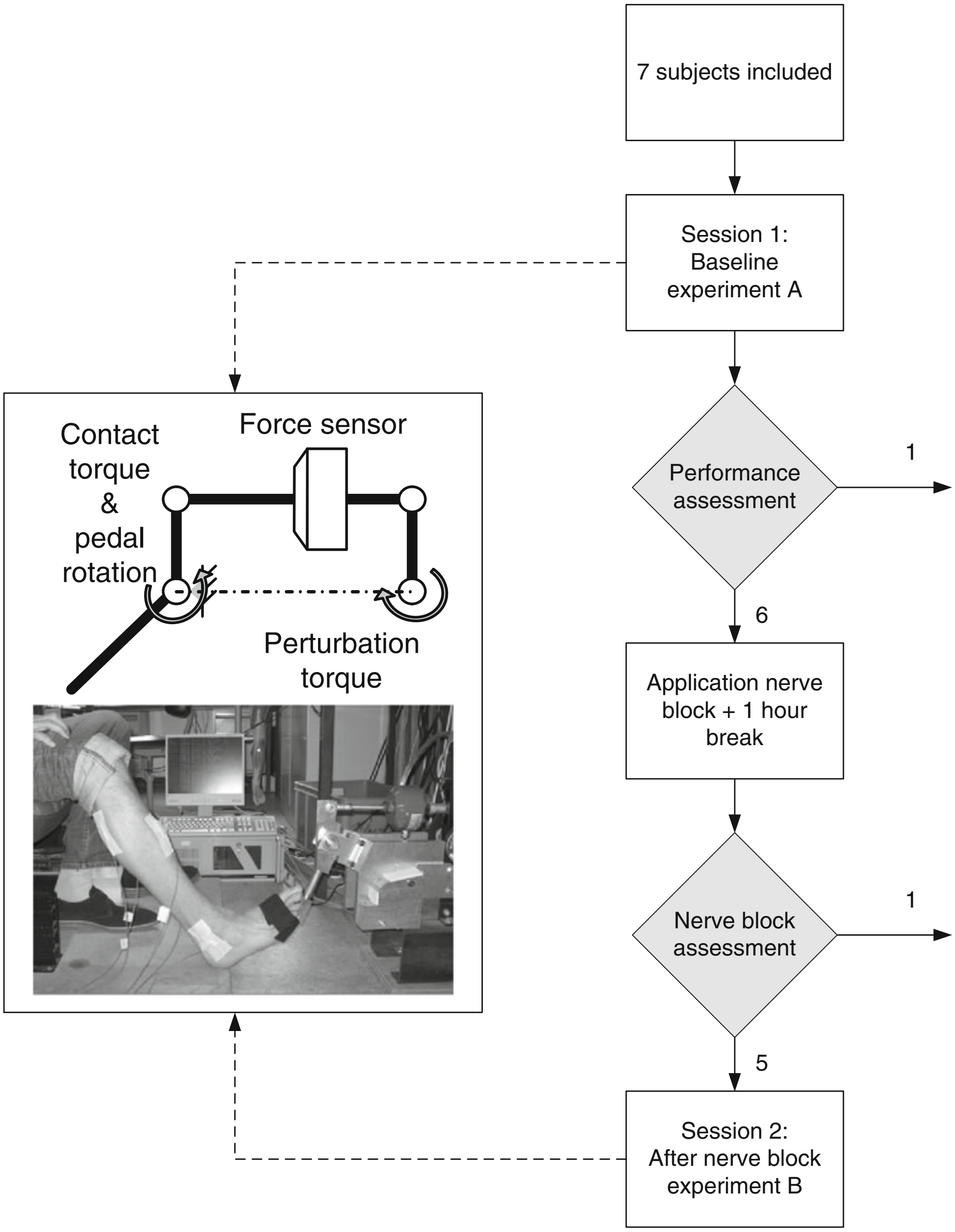


Fig. 1 Experiment design and setup. The *flow chart* shows the subsequent steps of the experiment. Each subject performed two sessions (baseline and anesthetized) of three tasks (force task, relax task and position task) in face of force perturbations with three perturbation bandwidths (0.1–0.7, 0.1–1.2 and 0.1–2.0 Hz). The force and position task were performed with visual feedback and blindfolded and each perturbation bandwidth was applied 4 times. The relax task was performed blindfolded only and each perturbation bandwidth was applied 2 times. The order of the tasks, perturbation bandwidths and conditions were randomized. The experimental design allowed for prevention of application of the nerve block to subjects with little motor control adaptation to begin with and for exclusion of incompletely anesthetized subjects. The *panel to the left* shows a close-up of the lower limb, with the foot strapped to the pedal and a schematic representation of the setup with indicated measured signals: perturbation torque, contact torque and pedal rotation

task and the other tasks, we proceeded with the nerve block (B). As a result, one male subject was excluded. Table 1 shows the conditions and abbreviations as defined in the experiment.

For each of the tasks, three torque perturbation signals with different bandwidth were designed yielding nine combinations of perturbation bandwidths and task instructions. For averaging purposes, all trials were repeated four times, except during RT at which only two repetitions were required due to its high repeatability. In total 24 trials during FT and PT and 6 trials during RT were performed (54 trials) both before and after the nerve block. The order in which subjects had to perform the three tasks was randomized for each subject. The order of the trials and whether visual feedback was available was randomized as well, but all trials within a task were performed consecutively to improve overall task perception. Every task instruction was accompanied by a 5-min break to prevent fatigue and 10 min of training to get acquainted with the task. The whole experiment was conducted within 1 day and took about 5 h, including the medical intervention, breaks and training.

Visual feedback—blindfolding

A 17″ monitor mounted in front of the subject presented the pedal angle against a horizontal reference line indicating the target angle (90° ankle flexion) during PT,

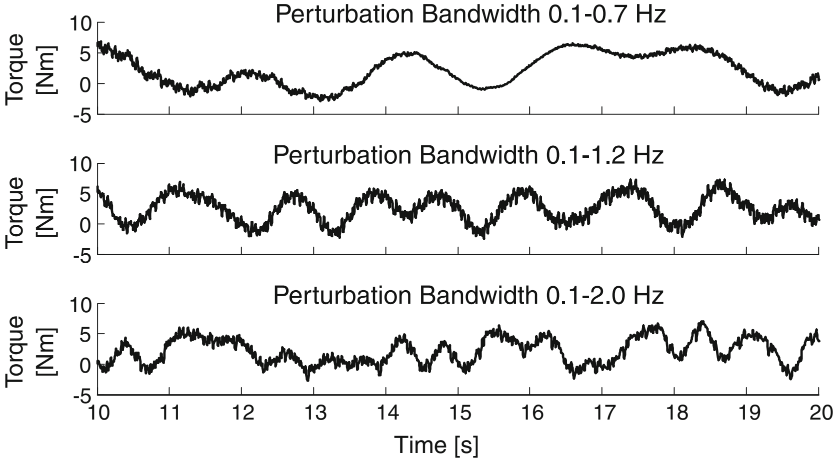


Fig. 2 The torque perturbation signals as used during the relax task. All signals were designed according to the Reduced Power Method and scaled to equalize the standard deviation of pedal depression to prevent non-linear effects. The *windows* show 10-s time segments of the three full-power bandwidths: 0.1–0.7 Hz (*top window*), 0.1–1.2 Hz (*center window*), 0.1–2.0 Hz (*bottom window*). All signals contained additional reduced power up to 40 Hz for identification purposes

whereas it presented the torque exerted on the pedal against a horizontal reference line indicating the target torque during FT. The target torque was equal to the weight of the foot at the desired position (approximately 28 N at foot contact). During the blind trials, the subjects had eyes closed and the monitor was turned off.

Tactile feedback—nerve block

In the second part of the experiment, a nerve block was applied to the *nervus plantaris medialis* about 5 cm above the malleolus medialis of the ankle. Echoscopic guidance with Doppler was used to identify nearby blood vessels during insertion of the needle. Low current electrical stimulation was used to establish proper placement of the needle in relation to the nerve. The needle was repositioned until the subject experienced tactile sensations in the foot sole in response to the pulse stimulation. Positional fine-tuning was performed by finding the spot where tactile sensations were felt in the entire foot-sole in response to minimal stimulation current. Subsequently, 1 cc of a 0.5 % bupivacaine solution was injected via the stimulation needle. Bupivacaine effectively blocks initiation and conduction of nerve impulses for about 4 till 8 h, which was sufficient to perform the second part of the experiment.

The effectiveness of the nerve block was checked by comparison of pre- and post-nerve-block sensibility using Semmes–Weinstein mono-filament tests (Sosenko et al. 1999). A successful block resulted in complete absence of tactile sensation in the foot sole. One male subject was excluded as the Semmes–Weinstein monofilament test revealed incomplete anesthetization.

Table 1 Experiment conditions and annotations

Task and condition	Description	Task			Condition			
					Blind?		Anesthetized?	
		FT	RT	PT	Yes	No	Yes	No
F	Force task with visual and tactile feedback	X				X		X
F-B	Blindfolded force task with tactile feedback	X			X			X
F-A	Anesthetized force task with visual feedback	X				X	X	
F-BA	Blindfolded and anesthetized force task	X			X		X	
R	Relax task with tactile feedback		X		X			X
R-A	Relax task without tactile feedback		X		X		X	
P	Position task with visual and tactile feedback			X		X		X
P-B	Blindfolded position task with tactile feedback			X	X			X
P-A	Anesthetized position task with visual feedback			X		X	X	
P-BA	Blindfolded and anesthetized position task			X	X		X	

Data recording and analysis

Recordings

The torque on the pedal $T_c(t)$ was measured by a force sensor (Interface, 1210BXH-300, positioned at a moment arm (d_1) of 76.2 mm). The pedal angle θ_{pedal} was measured by an angle encoder. The signals were recorded via analog-to-digital conversion at 250 Hz sample frequency and digitally stored. Furthermore, differential surface electrodes (Delsys) recorded EMG of four muscles: ankle plantarflexors (pushing down) Gastrocnemius Medialis (GM), Gastrocnemius Lateralis (GL) and Soleus (SOL), and dorsiflexor (pulling up) Tibialis Anterior (TA). The EMG signals were pre-amplified, band-pass filtered (20–450 Hz), before digitization at 2,500 Hz. All recorded EMG signals were notch-filtered with an anti-causal filter (between 49 and 51 Hz and its higher harmonics), then high-pass filtered (20 Hz) to remove small offsets due to filtering, rectified, low-pass filtered at 3 Hz, and subsequently digitally resampled at 250 Hz. All EMG signals were then normalized to the identically processed EMG during maximum voluntary contraction (MVC), and finally averaged over time to get an indication of activation level. Note that the EMG during MVC was obtained by averaging several repetitions of a maximum contraction of several seconds, measured in both directions (plantar and dorsiflexion), both before and after the experiment (to check for fatigue, which was not found). The EMG normalization allowed for inter-subject comparison. We will subsequently distinguish dorsiflexor EMG (consisting of EMG of TA only), and plantar flexor EMG (the average of EMG of GM, GL, and SOL muscles). One subject (male) was excluded from EMG analysis only due to a bad signal-to-noise ratio.

The first 3 s and the last second of all measured signals were excluded from analysis to reduce the influence of possible transient effects (due to the onset of the perturbation or an imminent stop).

Analysis

The experiment results are analyzed in time and frequency domain. In time domain, torque and angle signals are compared in a specific time window to assess the response to perturbations and EMG signals are compared over the total measurement time to assess the average muscle activity, a measure of the level of co-contraction. In the frequency domain, the admittance was estimated, using a closed-loop frequency-domain identification procedure (Van der Helm et al. 2002). The cross-spectral density of torque perturbation and pedal angle was divided by the cross-spectral density of torque perturbation and pedal torque to estimate the admittance, as a function of frequency. The admittance consists of a magnitude and a phase, where magnitude represents the frequency-dependent ratio of angular displacement and torque, and the phase incorporates the effects of time delays in the system, reflected in a frequency-dependent phase lag. The coherence, a measure for linearity ranging from 0 to 1, was determined by dividing the squared modulus of the cross-spectral density of torque perturbation and pedal angle by the product of the autospectra of torque perturbation and pedal angle (Mugge et al. 2010). Averaging was done over all repetitions and subsequently over all the subjects.

As a second step, the low-frequency impedance (the inverse of admittance) was determined to enable easy interpretation of the task performance. All frequency points below 0.7 Hz were averaged and inverted to attain an estimate of effective stiffness (combined passive and active components) for each task and condition.

Statistical analysis

Statistical testing was performed using a Linear Mixed Model analysis on the data from the 1.2 Hz perturbation bandwidth. Basically, two analyses were carried out. First, the effects of FT and PT were tested per frequency over all four conditions as for RT data were only available for the conditions blind and blind & anesthetized. The second analysis comprised the comparison of the conditions blind and blind & anesthetized) per frequency for all three tasks. Main effects and interactions were included in the model. A diagonal covariance model was applied.

We considered our hypothesis that tactile information is required for modulation of the joint admittance to be untrue when the effect of task instruction on joint admittance, was still significant during the anesthetized condition (absence of tactile feedback) and additionally the interaction between task instruction and condition was not significant.

Additionally, paired *t* tests compared EMG and log-transformed effective stiffness of FT and PT with the subsequent RT and bandwidth effects within tasks. Statistical testing was performed using SPSS 16.0, with the significance level set at 0.05.

Results

Time domain analysis

Figure 3 shows a typical time segment of a subject performing the force task in the blind (F-B) and blind & anesthetized conditions (F-BA). The subject is giving way to the perturbation as can be seen from the slightly delayed dorsiflexor muscle activity while the ankle was moved into dorsiflexion by the perturbation. EMG activity in phase with the perturbations indicates that subjects actively used muscle activation strategies that give way to the perturbations, as found in Mugge et al. 2010. Table 2 shows the mean EMG levels and the standard deviation of ankle rotation for all tasks and conditions. During all PTs significantly more EMG activity was found compared to RTs, indicating increased muscle co-contraction (all P: $p < 0.05$; all P-B, P-A and P-BA: $p < 0.01$). Within the tasks and conditions no significant effect of perturbation bandwidth on the mean EMG level was found, indicating any changes in admittance are due to feedback mechanisms, other than co-contraction.

Table 2 Mean and standard deviation of normalized EMG

Task and condition	Perturbation bandwidth		
	0.1–0.7 Hz	0.1–1.2 Hz	0.1–2.0 Hz
F	0.154 (0.066)	0.152 (0.061)	0.200 (0.099)
F-B	0.170 (0.088)	0.180 (0.062)	0.166 (0.052)
F-A	0.190 (0.085)	0.188 (0.106)	0.210 (0.108)
F-BA	0.202 (0.095)	0.155 (0.085)	0.165 (0.082)
R	0.150 (0.120)	0.101 (0.089)	0.105 (0.084)
R-A	0.094 (0.080)	0.088 (0.070)	0.090 (0.071)
P	0.578 (0.156)	0.607 (0.044)	0.686 (0.157)
P-B	0.581 (0.129)	0.592 (0.040)	0.601 (0.109)
P-A	0.635 (0.124)	0.646 (0.116)	0.666 (0.164)
P-BA	0.550 (0.151)	0.554 (0.111)	0.514 (0.107)

EMG was normalized to maximum voluntary contraction

Frequency domain identification

Figure 4 presents the gain and phase of the admittance of one typical subject performing the three tasks in two conditions, i.e. left panel: both visual and tactile feedback available; right panel: neither visual nor tactile feedback available. Task instruction substantially influenced the admittance. The largest admittance occurs during FT (i.e. minimize force deviations), a smaller, but still relatively large, admittance during RT (i.e. minimize muscle activity), and a small admittance during PT (i.e. minimize position deviations). The bottom panels show the coherence, which is generally high, indicating that the input–output behavior during the experiment can be considered to be linear with low levels of noise.

Figure 5 shows the averaged admittance over all subjects per task. The figure illustrates that all subjects exhibited more or less the same behavior and the task effect on admittance is similar in all conditions: top left, with visual and tactile feedback; top right, with tactile feedback, but without visual feedback; bottom left, with visual feedback, but without tactile feedback; bottom right, without visual and tactile feedback.

For the tasks FT and PT a significant effect of task instruction ($df = 1$, $F = 126$, $p < 0.001$), frequency ($df = 17$, $F = 172$, $p < 0.001$) and condition ($df = 3$, $F = 17$, $p < 0.001$) was found, but no significant interaction effect of condition and task ($df = 3$, $F = 2.42$, $p = 0.119$). Likewise for the conditions blind and blind & anesthetized a significant effect of task instruction ($df = 2$, $F = 89.4$, $p < 0.001$), frequency ($df = 17$, $F = 631$, $p < 0.001$) and condition ($df = 1$, $F = 24.9$, $p < 0.01$) was found, but no significant interaction effect of condition and task ($df = 2$, $F = 2.43$, $p = 0.096$). Apparently, subjects still adapted their motor behaviour to task instruction after blindfolding and anesthetizing.

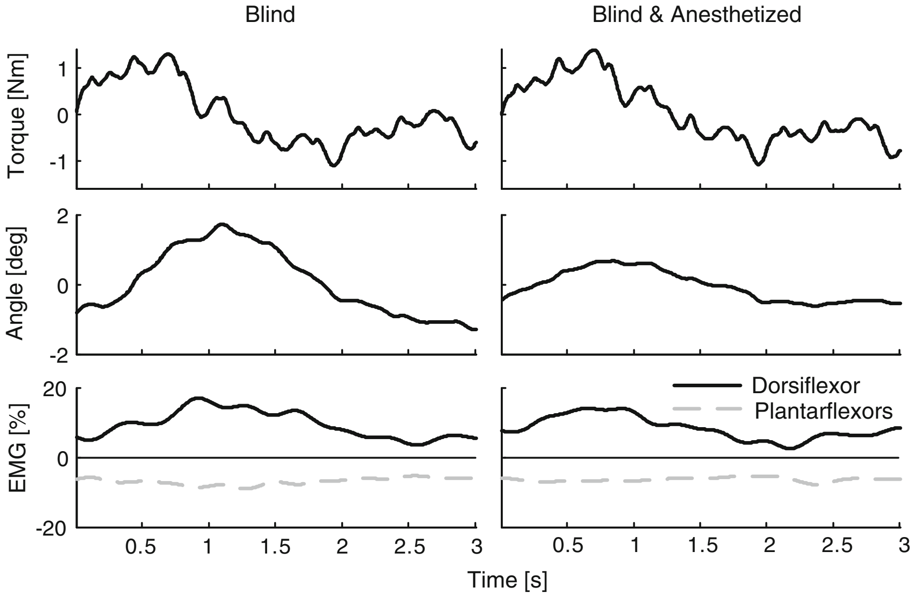


Fig. 3 Time domain results for a typical subject during FT when blindfolded (F-B, *left*) and when blindfolded & anesthetized (F-BA, *right*). The *top panels* show the perturbation torque at the ankle. The *middle panels* show the pedal angle (dorsiflexion is defined as positive). For this plot, all signals are filtered with a 3rd-order Butterworth filter at 3 Hz. The *bottom panels* show the EMG activity of plantarflexors (averaged) and the dorsiflexor, scaled to a percentage of maximal EMG activity. EMG activity is in phase with the perturbation, indicating that the subject is actively giving way to the perturbation

Fig. 4 Task effect on admittance of a typical subject when blindfolded and when blindfolded & anesthetized. For each of the four repetitions, the magnitude (*top panel*), phase (*middle panel*) and coherence (*lower panel*) are shown for FT (*small dash*), RT (*solid*), and PT (*large dash*). Note that RT comprises only two repetitions, which suffices due to its high repeatability. The shown admittance is the response to a perturbation with a bandwidth of 1.2 Hz (supplemented with reduced power up to 40 Hz)

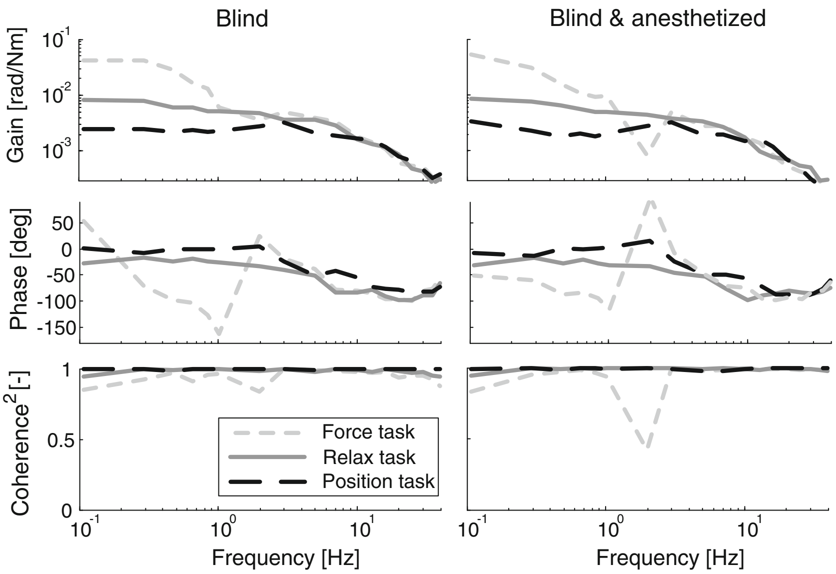
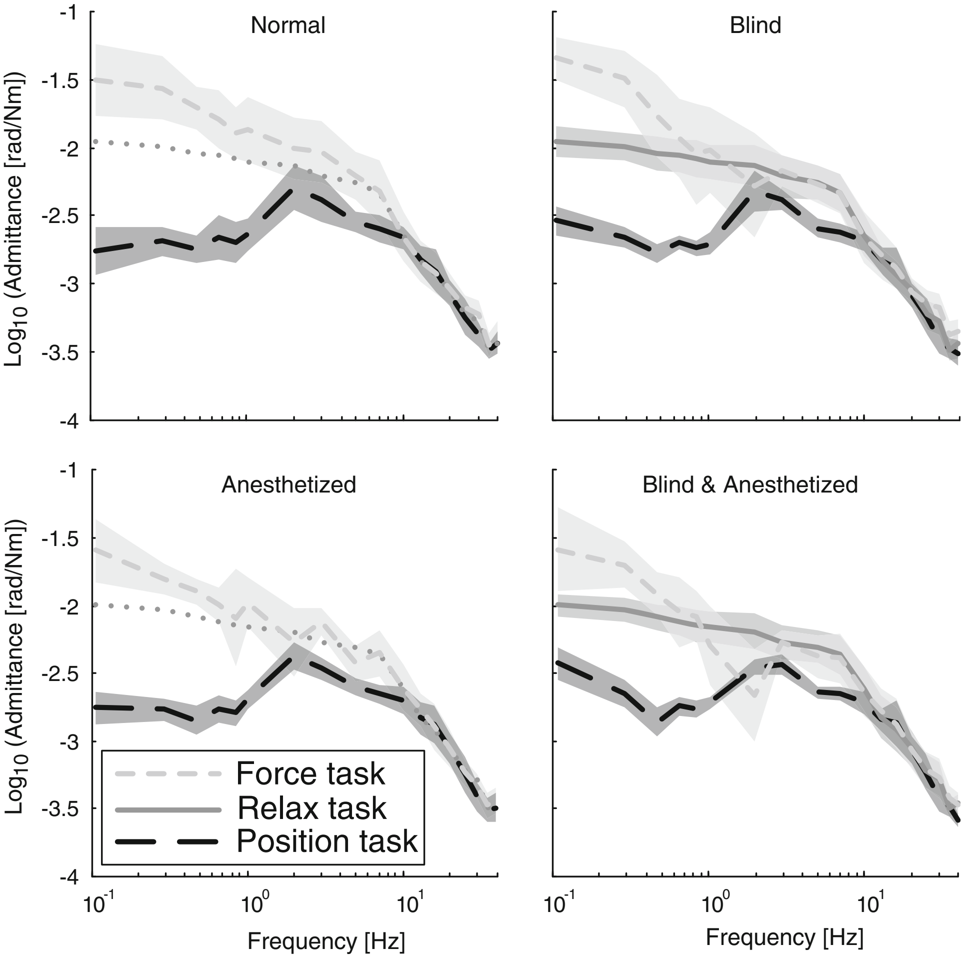


Fig. 5 Task effect on admittance averaged over all subjects ($n = 5$) for the four conditions: with visual and tactile feedback, blindfolded, anesthetized and blindfolded & anesthetized. The *plot* shows log-transformed magnitudes of the admittances with subsequent standard deviations as indicated by the *colored areas*. *Left* with visual feedback, *right* without; *top* with tactile feedback and *bottom* without. Note that RT was only performed blindfolded to accomplish best performance; the blindfolded results were copied to the visual conditions as a reference to facilitate visual task comparison indicated by a *dotted line*. The effects of blindfolding and anesthetizing are small, indicating the motor adaptations are due to proprioception



To further illustrate how the experimental conditions influenced the low-frequency admittance, Fig. 6 presents the bar plot of the effective stiffness (the inverse of low-frequency admittance) for all tasks and conditions. During P, subjects were significantly stiffer than during R for all perturbation bandwidths (all $p < 0.01$). With the subjects blindfolded & anesthetized (P-BA) the increase in effective stiffness persisted (0.7 and 2.0 Hz: both $p < 0.01$; 1.2 Hz:

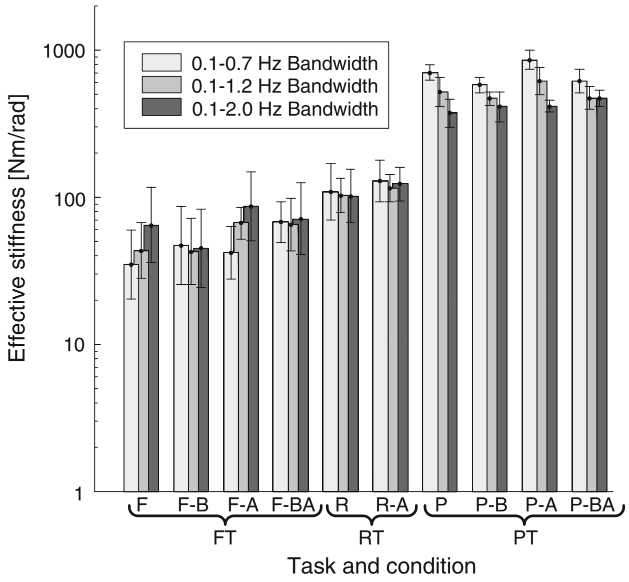


Fig. 6 Results of the effective stiffness estimates based on the low-frequency impedance for all tasks and conditions. Mean and standard deviations over all subjects are shown ($n = 5$). For each condition *three bars* present the results for the three perturbation bandwidths: 0.7 (*left*), 1.2 (*middle*), and 2.0 Hz (*right*). During RT, subjects were significantly less stiff than during PT and significantly stiffer than during FT. This task effect on stiffness persisted after blindfolding and anesthetizing

$p < 0.001$). During F, subjects were significantly less stiff than during R for perturbation bandwidths 0.7 and 1.2 Hz (both $p < 0.05$). With the subjects blindfolded & anesthetized (F-BA) the decrease in effective stiffness persisted (both $p < 0.05$).

Perturbations with dominant power up to a lower frequency result in improved task performance: an increased admittance during FTs and a decreased admittance during PTs. During PT, modulation due to perturbation bandwidth is evident for all conditions (P: all $p < 0.01$; P-B: 0.7 vs 1.2 Hz $p < 0.01$ and 0.7 vs 2.0 Hz $p < 0.05$; P-A: 0.7 vs 1.2 Hz and 1.2 vs 2.0 Hz both $p < 0.05$ and 0.7 vs 2.0 Hz $p < 0.001$; P-BA: 0.7 vs 1.2 Hz and 0.7 vs 2.0 Hz both $p < 0.01$). Remarkably, modulation due to perturbation bandwidth during FT seems present only in conditions with visual feedback (F-A: 0.7 vs 1.2 Hz $p < 0.05$ and 0.7 vs 2.0 Hz $p < 0.01$).

Discussion

In accordance with previous research, a substantial effect of task instruction on joint admittance was found (Abbink et al. 2011; Crago et al. 1976; Doemges and Rack 1992a, b; Hammond 1956; Mugge et al. 2010; Jaeger et al. 1982; Pruszynski et al. 2008; Rothwell et al. 1980; Shemmell et al. 2009). All subjects switched to a small admittance when resisting force perturbations (PTs), and to a large admittance when trying to give way (FTs), even when blindfolded and anesthetized.

The perturbation bandwidth affected the admittance for both PTs (Van der Helm et al. 2002) and FTs (Mugge et al. 2010): the lower the perturbation bandwidth, the better the subjects performed their task. The found motor adaptations to changing perturbation bandwidth in the blindfolded and anesthetized condition can only be explained by proprioceptive feedback since visual and tactile feedback were blocked and EMG measurements indicated no changes in co-contraction within the same task. The observation that perturbation bandwidth did not seem to change the effective stiffness during FT in conditions that excluded visual feedback, suggests that the change in effective stiffness during FT is due to modulation of visual feedback. Such modulation occurs according to established principles like the cross-over model of McRuer and Jex (1967). Yet, FT does not show largely increased effective stiffness when visual feedback is excluded, which implies that the contribution of visual feedback to the effective stiffness is relatively small during FT. The data suggests a notable difference between the tasks: during FT tactile feedback affects the behavior more than visual feedback, while during PT this effect is reversed.

We previously showed that contributions of feedback pathways to motor control can be identified using computational models (Schouten et al. 2008). Convergence of model fits to experiment data relies on the key assumption that longer latency feedback paths such as tactile or visual feedback do not significantly contribute to the measured behavior. This assumption was based on the indirect evidence of measured responses which the model could only attribute to short-latency feedback paths (Abbink 2006; Mugge et al. 2010). Results of previous model studies were supportive of the aforementioned assumption in three ways: (1) experimental results *could* accurately be described with a model with proprioceptive feedback only (2) experimental results *could not* be described with a model with visual and tactile feedback only (3) adding visual and tactile pathways did not improve the model fit but caused unreliability of the results due to over-parameterization. Nevertheless, by model studies alone the presence of visual and tactile feedback cannot be definitively excluded. The results of the present study confirm the validity of our assumption and of our current experimental and modeling approach to explain deficiencies in pathological motion control.

It was previously concluded (Mugge et al. 2010) that the low-frequency motor control adaptations could only be accurately described with modulating force feedback. In the current study we reproduced the results with exclusion of visual and tactile feedback, which means the force feedback is indeed proprioceptive.

Several recent studies on human locomotion support our finding that proprioceptive force feedback can modulate. Grey et al. (2007) found a decline in soleus activity after plantar flexion perturbation. This suggests load-dependent activity. In fact, since then several studies on the involvement of positive muscle force feedback and its modulation during human locomotion have been published (Af Klint et al. 2009, 2010). These studies support the hypothesis that the force feedback originates from Golgi tendon organs by excluding ankle rotation and tactile feedback. Using modeling studies, Geyer has shown the augmented capability to cope with perturbations like slopes and steps with muscle force feedback in the locomotor system (Geyer et al. 2003; Geyer and Herr 2010). Mugge et al. (2010) reported adaptation of muscle force feedback during motor control tasks other than locomotion. The experimental results in this study support the measurement technique and model fit described in that paper, and proves that substantial motor adaptations can be realized without visual or tactile feedback. The findings of this study are in line with previous studies like Grey et al. (2007) and Bawa and McKenzie (1981). In contrast to those studies, here task instructions in face of continuous perturbations were used instead of transient perturbations, which unambiguously prescribe the most effective behavior during dynamic motor tasks and allows identification of the full dynamic range of the limb.

Conclusion

We studied the dynamic human ankle response to unpredictable force perturbations, resulting in strong motor adaptations due to task instruction, which persisted after eliminating visual feedback and tactile feedback by applying a nerve block to the *nervus plantaris medialis*. Even when both visual and tactile feedback were eliminated during force tasks, significantly less effective stiffness was found compared to a relaxed condition. This can only be attributed to proprioceptive activity, as the level of co-contraction (averaged EMG activity) was constant. Likewise, during position tasks, significantly more effective stiffness was found compared to a relaxed condition. Although the substantially increased stiffness is partly due to more co-contraction, persisting bandwidth adaptations at equal levels of co-contraction indicate the contribution of proprioceptive reflexes.

Apparently, proprioception is a major contributor to the reported motor adaptations, although exclusion of visual and tactile feedback did deteriorate task performance. It is vital to assess the role of visual and tactile feedback in every experimental condition as the contribution of cutaneous reflexes change, for instance as a function of walking phase (Bouyer and Rossignol 1998). Our study implies that information from sensory feedback channels (visual, tactile, proprioceptive) is adaptively integrated to achieve optimal task performance. Consequently, when investigating relative contributions of sensory feedback channels to motor control tasks, possible adaptations in all of them should be taken into account.

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