MOTOR CONTROL AND PERCEPTION DURING HAPTIC SENSING: EFFECTS OF VARYING ATTENTIONAL DEMAND, STIMULI AND AGE

By

SABAH MASTER BSc

Thesis Supervisor: François Tremblay PT PhD

Thesis submitted as a partial fulfillment of the requirements for a doctoral degree in experimental psychology, specialization in behavioral neuroscience

School of Psychology, Faculty of Social Sciences

University of Ottawa

ACKNOWLEDGMENTS

I owe a great debt of gratitude to my supervisor and mentor, Dr. Francois Tremblay, for his true guidance, ready encouragement, and extreme generosity with his time throughout the completion of this thesis. Thank you to all participants for their time and patience during testing. Special thanks to Patricia Oliver, Francisca Avila-Ramirez, Liam Dessureault-Crawly, Sonia Hussain, Catherine Lebel, Roxanne Oetelaar, Sophie Richer, Caroline Rivard, Melissa Larue, and Caitlin Merritt for help with data collection and analysis. Thanks to FRSQ (Canada) and the Elisabeth Bruyere Research Institute for providing financial support. Part of this work was made possible through financial support for Dr. Francois Tremblay from a discovery grant from NSERC (Canada) and Research Development Funds, Faculty of Health Sciences, University of Ottawa. Finally, I am forever thankful to my parents Mohammed and Shaheena Master, husband Taha Rajabali and son Tummeem Rajabali for being a constant source of support and inspiration without whom I could not have started or completed this work.

SUMMARY

This thesis describes a series of experiments in human observers using neurophysiological and behavioural approaches to investigate the effects of varying haptic stimuli, attentional demand and age on motor control and perception during haptic sensing (i.e., using the hand to seek sensory information by touch). In Experiments I-IV, transcranial magnetic stimulation (TMS) was used to explore changes in corticomotor excitability when participants were actively engaged in haptic sensing tasks. These studies showed that corticospinal excitability, as reflected in motor evoked potential (MEP) amplitude, was greatly enhanced when participants were engaged in different forms of haptic sensing. Interestingly, this extra corticomotor facilitation was absent when participants performed finger movements without haptic sensing or when attention was diverted away from haptic input by a concurrent cognitive task (Exp I). This provided strong evidence that the observed corticomotor facilitation was likely central in origin and related to haptic attention. Neuroimaging has shown activation of the parieto-frontal network likely subserves this aspect of haptic perception. Further, this haptic-specific corticomotor facilitation was finely modulated depending on whether participants focused attention on identifying material (texture) as opposed to geometric properties of scanned surfaces (Exp II). With regards to aging effects, haptic-related corticomotor facilitation was associated with higher recognition accuracy in seniors (Exp III). In line with this, seniors exhibited similar levels of haptic-related corticomotor facilitation to young adults when task demands were adjusted for age (Exp IV). Interestingly, both young and senior adults also showed substantial corticomotor facilitation in the 'resting' hand when the ipsilateral hand was engaged in haptic sensing (Exp IV). Simply touching the stimulus without being required to identify its properties (no attentional task demands) produced no extra corticomotor facilitation in either hand or age group, attesting again to the specificity of the effects with regards to haptic attention. In Experiments V-VI, the ability to recognise 2-D letters by touch was investigated using kinematic and psychophysical measures. In Experiment V, we characterized how age affected contact forces deployed at the fingertip. This investigation showed that older adults exhibited lower normal force and increased letter-to-letter variability in normal force when compared to young adults. This difference in contact force likely contributed to longer contact times and lower recognition accuracy in older adults, suggesting a central contribution to age-related declines in haptic perception. Consistent with this interpretation, Experiment VI showed that haptic letter recognition in older adults was characterized not only by lower recognition accuracy but also by substantial increases in response times and specific patterns of confusion between letters. All in all, these investigations highlight the critical interaction of central factors such as attentional demand with aging effects on motor and perceptual aspects of haptic sensing. Of particular significance is the clear demonstration that corticomotor excitability is greatly enhanced when a haptic sensing component (i.e., attending to specific haptic features) is added to simple finger movements performed at minimal voluntary effort levels (typically <15 % of the maximal effort). These observations underline the therapeutic potential of active sensory training strategies based on haptic sensing tasks for the re-education of motor and perceptual deficits in hand function (e.g., subsequent to a stroke). The importance of adjusting attentional demands and stimuli is highlighted, particularly with regards to special considerations in the aging population.

LIST OF ABBREVIATIONS

D wave	Direct wave
EMG	Electromyography
GABA	γ-Aminobutyric acid
I wave	Indirect wave
M1	Primary motor cortex
MEP	Motor evoked potential
MT	Motor threshold
NMDA	N-methyl-D-aspartic acid
RA1	Rapidly adapting type 1
RA2	Rapidly adapting type 2
RT	Response time
S1	Primary somatosensory cortex
SA1	Slowly adapting type 1
SA2	Slowly adapting type 2
SP	Silent period
TES	Transcranial electrical stimulation
TMS	Transcranial magnetic stimulation

TABLE OF CONTENTS

TABLE OF FIGURES

CHAPTER I. INTRODUCTION AND LITERATURE REVIEW

Introduction

The human hand is capable of exceptional manual dexterity. This is exemplified by the precisely controlled and highly skilled finger movements used to sense by touch. Indeed, the fingertip can be seen as the equivalent to the fovea for vison, due to its high density of sensory receptors. The activation of sensory afferent nerves in the skin, muscles, joints and tendons transmits a rich array of sensory information to the to somatosensory areas of the brain. Fine descending corticospinal motor control at the fingertip optimizes the extraction of this sensory information upon contact with a surface or an object. Research investigations on these mechanisms are required to design better interventions to re-educate hand function (e.g., after stroke).

Haptic sensing refers to this ability of human observers to actively seek sensory information through specific manipulative actions. Haptic sensing is cognitively demanding and attention-dependent, in addition to relying heavily on interconnections between parietal and frontal motor areas [3-5]. Thus, there is a need to consider the effects of task demands on both the sensory and motor systems when investigating aging effects on haptic sensing. However, there is still a dearth of literature examining the effects of task demands and normal aging on motor control and perception during haptic sensing. In the following sections, the anatomy and physiology of the corticospinal system controlling manual dexterity and its neurophysiological assessment using transcranial magnetic stimulation (TMS) will be described. Relevant literature examining the effects of behavioural context and aging on corticospinal excitability will then be briefly reviewed. Next, the anatomy and physiology of the somatosensory system and some common behavioural assessments of its function will be described, with a focus on the processing of haptic information acquired at the fingertip. Finally, a brief literature review of aging effects on haptic perception will be presented, and possible interactions between laterality or gender effects and aging will be considered.

1.0 Corticospinal Tract: Control of Manual Dexterity

1.1 Anatomy and physiology

The control of manipulative hand actions involved in haptic perception relies on the corticospinal tract [6]. Forty percent of the descending corticospinal tract axons originate in layer 5 of the primary motor cortex (M1) [6, 7]. As shown in Figure 1, the activity of these pyramidal cells is modulated by inputs from sensory and associative cortical areas [2, 6, 8-11].

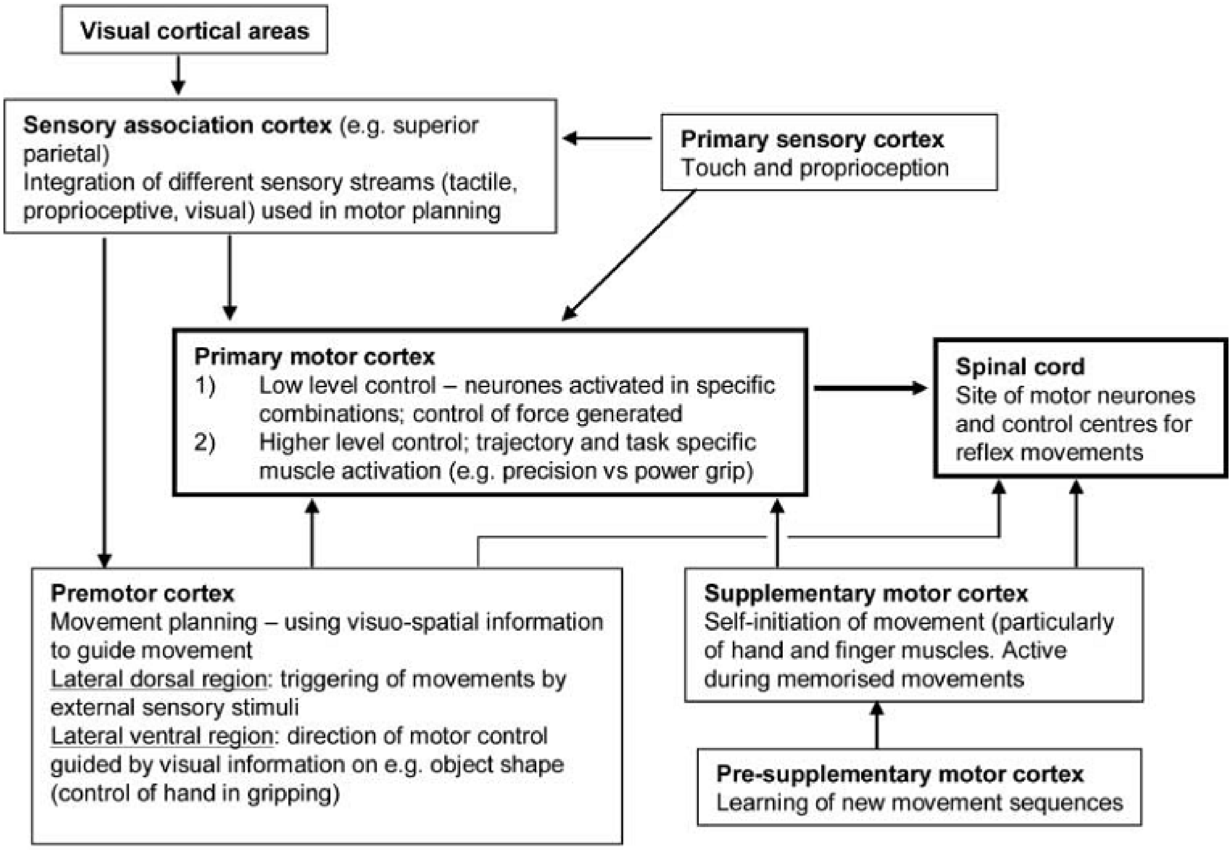

Figure 1: Layer 5 pyramidal cells in M1 are modulated by cortico-cortical inputs from many sensory and motor association areas. Figure used with permission from Dr Alan H. D. Watson [2].

These cortical inputs to M1 layer 3 are especially important in higher primates, as indicated by the relatively large size of layer 3 in humans relative to other animals [12]. It is important to note that about two thirds of corticospinal axonal fibers also come directly from other neocortical somatosensory and voluntary motor areas, such as S1, the premotor cortex and the supplementary motor area [6, 8, 13]. These sensorimotor corticospinal projections descend in the anterior portion of the posterior limb of the internal capsule to the lower ventral medulla, where they form the pyramidal decussation. They then descend in the dorsolateral funiculus of spinal cord white matter onto spinal interneurons and motorneurons in the ventral horn [14].

Although in humans the vast majority of corticospinal projections innervate spinal interneurons, a significant percentage do directly contact spinal motor neurons and provide a strong synaptic drive for their control [8, 14]. The corticospinal pathway thus contributes substantially to controlling skilled and precise manual dexterity, with cortical inputs playing an important role in the production of fine finger movements in particular [6, 8, 13]. The hands are thus ideally suited for object manipulation and detailed haptic exploration, allowing precise control over extraction of surface features at the fingertip by the employment of specific finger exploratory patterns [3, 15, 16]. Note that the fingers, tongue, and lips are represented over disproportionally large regions of M1. The excitability of the corticospinal cells in M1 is the net result of facilitatory and inhibitory sensory and motor cortical inputs. These vary depending on the behavioural context. The study of these variations has become accessible in human subjects with the advent of non-invasive, safe and virtually painless brain stimulation [17-20].

1.2 Neurophysiological assessment

As shown in Figure 2, the physical basis of TMS consists of passing a brief strong electrical current through a coil, which will induce a strong time-varying magnetic field (1-2 Tesla lasting 100-200μs) below it [18, 21]. The induced magnetic field in turn induces an electrical current that directly depolarizes axons in layers 2-3 of the cerebral cortex [17, 22].

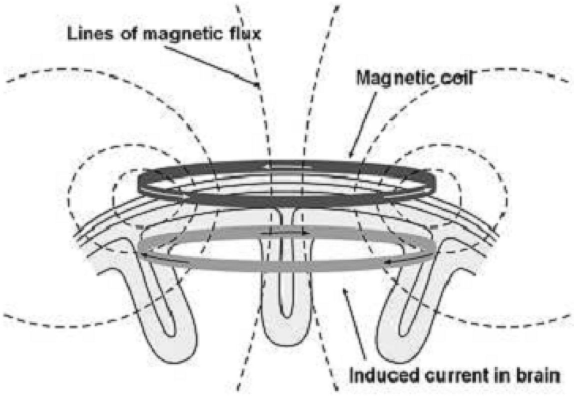

Figure 2: Transcranial magnetic stimulation (TMS) generates an electric field within the brain. A very strong transient current is run through the TMS coil, inducing a time-varying magnetic field focused under the coil. This magnetic field in un-attenuated by the scalp and skull and painlessly passes through these structures, inducing electrical currents within the brain. Figure used with permission from Dr M. Hallett [1]

The induced electrical current within the brain generated by TMS penetrates at an effective field strength to a maximal depth of ~2 cm [21, 23]. Magnetic field and induced current strength decrease exponentially with distance from the coil. Stimulation is optimally effective when the coil position is tangential to the scalp, maximizing induced current density in the cortex [24]. The focality of TMS depends on the shape of the coil. The center of the figure-of-eight coil is an area where the current's intensity is maximised, approximately double that of other points along the figure-of-eight coil [20, 25]. A single TMS pulse from a figure-of-eight coil can cause localized depolarization of neurons ~2-3 cm^2 around this point of intersection [21, 23].

A single TMS pulse may be delivered over a specific muscle representation in M1 [17-19, 26]. As shown in **Figure 3**A, orienting a figure-of-eight coil so that the induced current is running in a posterior-to-anterior (antero-lateral-postero-medial) direction is optimal for targeting hand muscles [18, 27, 28]. At low intensities such as those used in the studies comprising this thesis, TMS directly activates axons in layers 2-3 of M1. This leads to indirect trans-synaptic activation of layer 5 pyramidal tract neurons in M1. The activation of these corticospinal cells generates descending volleys along the spinal cord in the corticospinal tract. The corresponding electrical fluctuations at the cervical level are termed indirect or I waves. The number and size of I-waves depends on the excitability of layer 5 pyramidal tract neurons in M1. Voluntary contraction increases the size and number of I-wave volleys [e.g., 29]. These descending I wave volleys then depolarize the motoneurons at the spinal level, leading to an evoked response in the target muscle that may result in a visible muscle twitch [18, 30, 31]. Commonly the FDI, a hand muscle which controls index finger adduction, is recorded. Surface electrodes placed on the hand can capture its electromyographic (EMG) activity. The belly-tendon montage used in the present studies shown in **Figure 3**B.

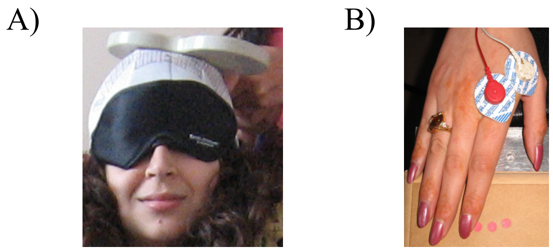

Figure 3: A) Optimal position for TMS stimulation of the contralateral primary motor cortex with a figure-of-eight coil to generate motor evoked potentials (MEPs) in the first dorsal interosseous (FDI) muscle. B) Right hand showing the belly-tendon montage used to record from the FDI in the present studies.

These EMG responses evoked by TMS over M1 are known as motor evoked potentials (MEPs), shown in **Figure 4**. As described in several recent reviews, the size of the MEP can be used as an index of corticospinal excitability [1, 17-19, 25, 26, 29, 31-35]. Briefly, a TMS pulse is applied to the hotspot (e.g., for the FDI) at a constant intensity (e.g., 110% MT), resulting in a larger MEP when corticospinal excitability is high and a smaller MEP when corticospinal excitability is low. It is important to note that the size of the MEP can be influenced by many physical factors such as the orientation of axons with respect to coil, and the distance of neuronal elements from the coil. However, when these factors are constant (e.g., stimulating the same individual participant and holding the coil in the same position), the size of the MEP may reflect the balance of excitatory and inhibitory neurotransmitters which influence membrane excitability of spinal interneurons, motor neurons, and corticospinal cells in M1. The excitability of corticospinal cells in M1, in particular, is in turn affected by modulatory inputs from sensory, premotor and associative cortical areas.

MEP amplitude is the peak-to-peak distance in microvolts. MEP latency also reflects corticospinal excitability. It is the time in milliseconds between TMS application (the stimulus artefact) and MEP onset. Greater MEP amplitudes and shorter MEP latencies indicate increased corticospinal excitability.

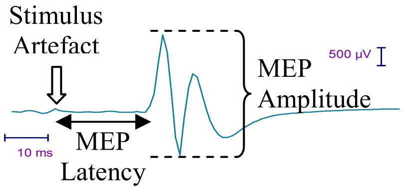

Figure 4: Characteristic shape of a typical MEP recorded in the FDI. Depolarization is followed by hyper-polarization and repolarization. Phases reflect the detection of polarity changes in muscle membrane conduction under the two electrodes.

One factor increasing the size of MEP amplitudes is active muscle contraction. Indeed, even slight contractions of the small hand muscles facilitate corticospinal excitability. TMS delivered before and after muscle contractions showed that corticospinal excitability started to increase about 100 ms before EMG onset and remained elevated for about 160 ms after EMG offset but was depressed from about 500 to 1,000 ms after the offset of EMG [36].

While corticospinal cells in M1 are usually activated transynaptically by TMS, they are activated directly by another brain stimulation technique, transcranial electrical stimulation (TES). This difference between the mechanism of action of these two techniques allows an inference regarding how much of the change in MEP amplitude during muscle contraction relies on differences in excitability at the cortical vs. the spinal level. With TES, the layer 5 corticospinal neurons in M1 are activated directly by the stimulus and there is no difference between rest and active muscle contraction at the level of recorded corticospinal volleys at the medullary pyramids. However, TES induced MEPs at the muscle belly are larger during active muscle contraction vs. rest and MEP latency is also shorter. In the case of TES, these changes in MEP amplitude and latency with active contraction can be explained by changes in the excitability of the spinal motor neuron pool. During active contraction, this pool is close to firing threshold and there is the greatest opportunity for the earliest descending corticospinal volley to cause a discharge. With a given stimulus intensity and contraction of 10–20% maximum voluntary contraction (MVC), latency variation is much less than amplitude variation. Critically, the difference in MEP amplitudes evoked by TMS at rest and during even slight active contraction are greater than those seen with TES because they reflect the contribution of the I waves and the enhancement in cortical as well as spinal excitability.

The cortical silent period (SP) is another index of corticospinal excitability (shown in Figure 4 below). The SP is the period of EMG suppression that occurs after an MEP is evoked during muscle contraction. Inhibition in the initial portion of the SP (~50 ms) is due in part to spinal cord refractoriness. However, for the most part the SP reflects the activation of inhibitory cortical interneurons and seems to be mediated by $GABA_B$ receptors. Pharmacological studies using benzodiazepines provided evidence that the SP reflects a long-lasting cortical inhibition mediated by $GABA_B$ receptors. Dopaminergic drugs lengthened the SP in normal subjects and the SP was found to be abnormal in Parkinson's disease as well as stroke and dystonia patients. SP duration has also been shown to be modulated by physiological phenomena that change cortical excitability, such as hyperventilation, sleep deprivation and muscle fatigue, or after high-frequency rTMS.

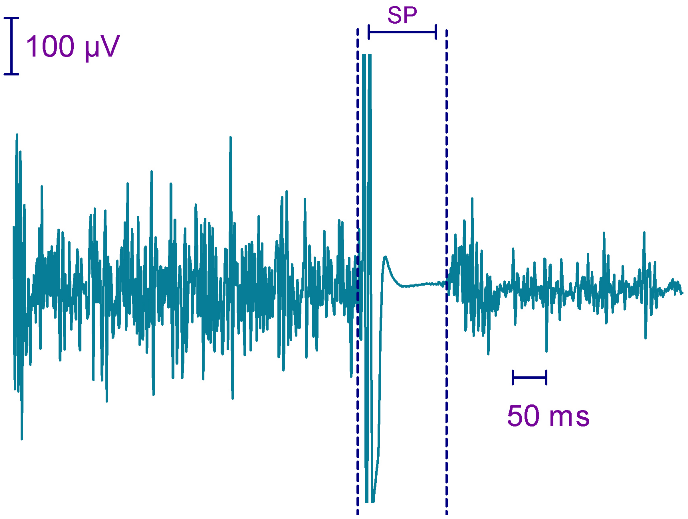

Figure 5: MEP produced in the FDI hand muscle during active contraction. It is followed by a silent period (SP) characterized by the absence of electrical activity. The SP is measured from MEP onset to the return of EMG activity.

The motor threshold (MT) refers to the lowest TMS intensity capable of eliciting reliable MEPs. This threshold for producing an MEP reflects the excitability of a central core of neurons in the muscle representation in the motor cortex. The minimum size of MEP required to be produced at threshold is 50 µV in amplitude in muscles at rest or 200 µV in active muscles, and this must be observed in at least five out of 10 trials. The method of limits is a rapid and reproducible means of determining the MT [37]. This method calculates MT as the median number between the lower and upper thresholds. The lower threshold is the highest stimulus intensity at which no responses are evoked to ten stimulations in a row. The upper threshold is the lowest stimulus intensity at which a response is evoked after 10 consecutive stimulations. The MT is lower for the activation of intrinsic hand muscles compared with proximal arm, lower limb, and truncal muscles, likely reflecting the presence of stronger corticospinal projections to the hand muscles. At the cellular level, MT likely reflects neuronal membrane excitability. It is decreased by non-NMDA glutamatergic agents and influenced by drugs that affect sodium and calcium channels, but not drugs that alter γ-aminobutyric acid (GABA) or N-methyl-D-aspartic acid (NMDA) glutamate transmission.

TMS intensity may be adjusted so that an MEP is evoked in a given muscle by stimulation of a certain brain region but not by stimulation of the surrounding regions. Thus TMS may focally stimulate the somatotopic region of M1 which sends corticospinal projections to a target muscle. This process is commonly termed *finding the hot spot* in TMS literature. Given that M1 is organized somatotopically, with the legs represented most medially, the arms and hands more laterally, and the oral cavity and face even more so, moving the coil over the surface of the scalp and recording MEPs from different muscles is also a means of mapping the motor cortex.

By applying TMS to M1 and observing changes in indices of corticospinal excitability such as MEP amplitude, latency and SP durations, researchers have been able to gain new insights into the neural mechanisms that influence corticospinal excitability, such as drugs, disease, aging, and task-dependent effects [31]. In all TMS experiments described in this thesis, single pulse stimulations were used to probe changes in corticospinal excitability related to haptic attention, task demands and age, using the FDI as the target muscle.

1.3 Behavioural context

As mentioned earlier, corticospinal drive to the intrinsic hand muscles can be modulated depending on the behavioural context, i.e., task conditions. When TMS is applied in the active state, MEP's are facilitated (i.e., increased size and reduced onset latency) in the target contracting muscles. This facilitation is particularly prominent in intrinsic hand muscles, where even slight voluntary muscle contraction can lead to a substantial increase in MEP amplitude and reductions in onset latency [38]. At these very low-level contractions, MEP facilitation is thought to reflect mainly an increase in excitability at the cortical level (i.e., increase in the size and number of I-waves) with further contribution of spinal mechanisms as the level of contraction increases above 30% of the maximum voluntary contraction [19, 30].

Research on task-dependent modulation of corticospinal drive to the hand has generally focused on changes in motor cortical output during precision grip tasks. Single-unit and population recordings in the monkey have shown that the excitability of specific motor cortical cells and populations of pyramidal neurons varies in a task-dependent manner [39, 40]. These task-dependent variations in corticomotor excitability have been confirmed in human TMS research showing MEP amplitude changes as a function of the task being performed, even when the strength of voluntary muscle contraction demanded by the two tasks is equivalent [41, 42].

Previous work aimed at discovering the impact of afferent input on corticospinal excitability [see 19, 43] used electrical stimulation of the afferent nerves and described two periods of facilitation interrupted by a period of inhibition following a single electrical input. Whole-hand afferent electrical stimulation elicited lasting changes in motor cortical excitability including decreased motor threshold and reduced intra-cortical inhibition [44]. In another key experiment investigating changes in corticospinal excitability during somatosensory discrimination, Rosenkranz & Rothwell [45] investigated how attention could change the ability of vibratory inputs to condition corticospinal excitability to subsequent vibratory stimulation. This work suggests that changes (lasting ~30min) in corticospinal drive brought on by vibratory stimulation can be prevented if the stimulus is being attended. Corticospinal excitability during imagery of squeezing a foam ball was enhanced by somatosensory input generated by passively holding the ball, only when the holding hand and the imagined hand were on the same side [46].

Hess et al. [47] used TMS to compare corticospinal drive to the intrinsic hand muscles during active haptic exploration with the fingers and voluntary muscle contractions requiring up to 20% of the maximum force an individual could produce. They found that the period of EMG silence following the MEP was longer during haptic exploration than during voluntary muscle contractions, though no changes in MEP amplitude were detected. However, these results could be attributed to differences between isometric and dynamic contractions, hand and arm position, the phase of muscle contraction (concentric or eccentric) and finger position, or the level of prestimulus EMG at the time of pulse delivery. Oliver and Tremblay [48] compared corticospinal excitability during a haptic letter-recognition task and a control task requiring similar finger exploratory movements, finding MEP facilitation during the haptic exploration task. Further work is needed in which finger position is constant at the time of TMS pulse delivery. Finally, it is would be interesting to investigate if these findings would extend to various different haptic sensing behaviours, ipsilateral activity in the resting hand, and aging.

1.4 Aging effects

Aging is associated with a greater than two-fold decrease in excitability of the corticospinal system, and with decreased task-specific facilitation of corticospinal excitability [49-54]. Significant increases in motor threshold, decreases in MEP amplitude, and shortening of the SP have also been reported with healthy aging [49-51, 55-57]. These observations are likely related to anatomical findings showing that the level of organization of spinal white matter in the lateral corticospinal tract decreases with aging in a manner that correlates with decreases in grip force control, and that the cortical sensorimotor areas and frontal regions in humans lose both white matter and gray matter between the ages of 20 and 50 [58-62]. Complementary evidence from neuroimaging of healthy young and old rhesus macaques also showed loss in the prefrontal areas and around the superior temporal sulcus [63]. In healthy human aging, decreased blood flow to brain association areas and reduced anterior-to-posterior coordination was observed [64, 65].

These changes in brain structure, function, and the neurophysiology of the corticospinal system could be responsible for the decreased manual dexterity, and perhaps also cutaneous sensation, observed in healthy aging [66-71]. Indeed, increased activation in sensory, motor and frontal cortical regions has been reported in good performers in conjunction with decreased central activation in poor manual dexterity [72]. Interestingly, such deficits are often improved with practice [51, 73-75]. Indeed, fine motor skills such as typing and piano-playing are often retained with age while other motor skills deteriorate, possibly due to strengthened cortical networks and larger motor cortical representations for the hand that may occur when these fine motor tasks are practiced regularly [51, 73, 76]. This idea of compensation fits with the theory of a posterior-anterior shift in brain activity with aging (PASA) [68, 77-80].

Further, it has been shown that passive tactile and electrical stimulation improved the sensorimotor aspects of hand function and functional sensorimotor connectivity in older adults [81-83]. However, it remains to be seen whether the behavioural context in haptic sensing can be designed to elicit such compensatory motor mechanisms to engender greater task-related facilitation of corticospinal excitability in older adults. The first goal of this thesis is to characterize the interaction between the effect of varying haptic stimuli and attentional demand and aging on corticospinal excitability during haptic sensing and recognition accuracy. The second is to investigate the interaction of age, gender and laterality effects on fingertip contact forces, response times and patterns of confusion using raised letters as stimuli. The role of the somatosensory system in processing haptic information acquired at the fingertip is thus described in the following section.

2.0 Somatosensory System: Processing Haptic Information Acquired at Fingertip

2.1 Anatomy and physiology

The somatosensory system processes haptic information acquired at the fingertip, allowing observers to identify features of surfaces and objects by touch. Acquiring haptic information at the fingertip usually involves manual exploration, i.e., actively moving the hand and fingertips to feel by touch [3, 84, 85]. The most critical input representing haptic surface features is transmitted by the cutaneous mechanoreceptors and their associated afferent nerve fibers which respond to pressure applied to the skin [3, 86-90]. The properties of these fibers have been described in recent reviews, which form the basis for this section [3, 86, 91-97].

The large myelinated (Aβ class) afferent fibers associated with the cutaneous mechanoreceptors are differentially sensitive to physical pressure. Type 1 afferents are located superficially in the dermis, have small receptive fields, and are densely distributed at the fingertips. The Merkel cell mechanoreceptors are associated with type 1 afferents with firing rates that reflect slow adaptation (SA1) to a constant pressure applied to the skin. This sensitivity makes them critically important for the spatial discrimination of pressure, raised lines and forms, corners and curvature. Meissner corpuscle mechanoreceptors are associated with type 1 afferents with firing rates reflecting rapid adaptation (RA1) to a constant pressure. This property makes them sensitive to lower frequency vibrations contributing to the sensation of flutter on the skin, in addition to allowing them to signal the direction of movement.

Type 2 afferents are located more deeply in the dermis, and have larger receptive fields and a sparser innervation density than type 1 afferents. The Ruffini endings are slowly adapting type 2 (SA2) afferents associated with connective tissue. SA2 fibers contribute to the perception of hand shape and finger position. Pacinian corpuscle mechanoreceptors are associated with rapidly adapting type 2 (RA2) afferents. These RA2 afferents are sensitive to higher-frequency vibrations, and contribute to the sensation of vibration.

These cutaneous afferents transmit their sensory inputs to the spinal cord forming ascending projections in the ipsilateral spinal cord white matter, the dorsal columns. The dorsal columns are somatotopically organized. At the cervical level the gracile fasciculus contains fibers from the lower body and ascends medially, while the cuneate fasciculus ascends laterally and consists of axons from the upper body. In the gracile and cuneate nuclei in the lower medulla the fibers synapse on 2nd order neurons. Projections from these 2nd order neurons ascend contra-laterally in the medial lemniscus to the ventral posterolateral nuclei of the thalamus. This pathway for discriminative touch is the dorsal column medial-lemniscus tract.

Third-order neurons from the thalamus ascend in the posterior portion of the posterior limb of the internal capsule and project in a topographically precise manner to the primary somatosensory cortex (S1) in the postcentral gyrus. These projections terminate mainly in cortical layer 4, one of the most prominent cell layers in S1, reflecting the importance of these sensory inputs to processing in S1 [98-101]. In the somatosensory system the hand (along with the lips and tongue) is one of the primary organs of use, having a high density of afferent innervation and great sensory acuity [3, 102-104]. A large region of the primary somatosensory cortical surface is devoted to processing inputs from the fingertips, lips and tongue [104-107].

The primary somatosensory cortex is also divided up in columnar fashion into four somatotopic maps [108]. Area 3a has mosaics of inputs from deep afferents in the joints and muscle spindles [109]. Somatosensory area 3b receives input from SA1, RA1, and RA2 afferents [110, 111]. The organization of area 1 is similar to 3b except that the segregation between receptor types is more refined [112]. Functionally, area 3b has been shown to be important in processing of single digit input that allows for haptic discrimination, roughness discrimination and changes in movement velocity [110, 113-115]. Area 1, in contrast, integrates input across digits and is more sensitive to stimulus movement direction [110, 113-115]. Area 2 is important for haptic discrimination of angles, and discrimination of 3D properties [110, 113-115]. Cutaneous afferent input is processed hierarchically starting in areas 3a and 3b, followed by further processing in area 1 then 2, the secondary somatosensory cortex, and the parietal and frontal multisensory and motor association areas [110, 111, 115, 116].

2.2 Behavioural assessment

Three commonly used psychophysical tasks for testing the integrity of the peripheral sensory innervation at the fingertip are the Rydel-Seifel Tuning Fork test for vibration detection threshold which demonstrates integrity of the pacinian afferent system, and the grating orientation discrimination (see APPENDIX A. TESTS FOR VIBRATION DETECTION AND TACTILE ACUITY on page xiii for copies of these two tests) and two-point discriminations (TPD) which rely more on the SA1afferent system [117-120]. The goal in all of these tasks is to find stimuli near participants' perceptual threshold. The accuracy of responses to a given task is often measured as the percentage of correct responses on a task, and response time is usually defined as the time taken to produce a correct response from the time of stimulus presentation. In the context of haptic pattern recognition, the exploration strategy used by an individual to feel by touch can be characterized using the biomechanical variable of force output. The active control exerted by individuals over both the normal and tangential contact forces deployed at the fingertip during scanning can be measured using a force plate.

2.3 Aging effects

Many researchers have observed an age-related decline in tactile spatial acuity at the fingertip [121-128]. Older individuals often vary widely in their ability to perform spatial discriminations at the fingertip [126, 128, 129], suggesting that individuals may have different degrees of impairment at different levels, that is, peripherally and/or centrally. In some though not all cases this decline is related to decreased peripheral innervation at the fingertip [70]. Other age-related alterations at the central level (e.g., motor control, attention, working memory) could also be involved[121]. Control of grip force has been robustly shown to decrease with increasing age [66]. Older adults show more variability in force output during the maintenance of an isometric contraction [130, 131]. Seniors also have difficulty completing fine precision variable force tracking tasks accurately [132]. This may be because fine dynamic precision force control results in increased activation of M1 even when very low forces are generated [132, 133]. Indeed, age-related changes in brain morphology affect associative areas, primary sensory and motor areas [59, 64, 123, 134]. Scialfa [135] demonstrated a robust association between cognitive and sensory aging, and concluded that sensory factors may impede cognition. Indeed, haptic perception declines with aging and this is correlated with cognitive declines [121]. Complementary work showed an age-related decline in more attentionally demanding sensory tasks even when stimuli were presented well above threshold [136-138].

There are two alternative views as to how aging affects functional asymmetries in the brain [80, 139, 140]. The right hemi-aging hypothesis holds that processes engaging the right hemisphere are subject to a greater decline than those engaging the left hemisphere. Hemispheric asymmetry reduction in old adults proposes that frontal activity tends to be less lateralized as people age. The two models have emerged largely from assessment of cognitive and memory functions in visual or auditory-verbal tasks [80, 139, 140]. So far, very few studies have tested these models in the haptic modality [e.g., 141]. Temporal order tactile judgments and force matching have been shown to remain symmetrical with aging [142, 143].

2.4 Right vs. left and gender differences

Several authors have observed that spatial acuity tasks are relatively impervious to laterality effects [144, 145]. A left hand advantage has been reported in tactile spatial acuity measured using TPD but not tactile detection [146]. Others have found mixed results, observing a left hand advantage in texture discrimination with one set of task demands and a right hand advantage with other demands [147]. However, Borgo et al. [148] found a right hand advantage in accuracy when participants used a semantic strategy to tactually identify letters rather than a spatial one. Brain imaging studies during haptic pattern recognition at the fingertip have also produced mixed results, with some authors reporting right asymmetric activation [149-151], and others reporting selective activation on the left side [149, 151]. Sadato, Ibañez, Deiber, & Hallett [152] noted that dorsal premotor cortex activation was bilateral in women and unilateral in men. The greater degree of bilateral activation in women might have contributed to their improved performance. Indeed, laterality effects on haptic performance are often related to gender.

Gender effects were not observed during haptic letter exploration and roughness discrimination [148, 153]. Indeed, an observed female advantage in haptic grating orientation discrimination was later explained by fingertip size rather than gender [154, 155]. In contrast, improved haptic orientation perception was found in males [156]. The higher spatial resolution exhibited by females might also be due to males having less compliant skin than females [157, 158]. However, central cortical factors could also play a role as suggested by Zuidhoek et al. [156] who speculated more efficient right hemisphere processing in males. More recently, females were found to have better tactile detection and better preserved tactile acuity with aging, while males had better haptic object recognition performance with aging [121, 146].

Objectives and Hypotheses

The goals of this thesis are two-fold: first, to explore how varying stimuli, attentional demand and age impact recognition accuracy and corticospinal excitability during haptic sensing. Second, to characterize aging effects on fingertip contact forces, response times, recognition accuracy and patterns of confusion during haptic letter recognition. Both goals are related by their common focus on central cortical mechanisms affecting motor control and perception during haptic sensing in young and older adults. The focus is on how aging interacts with behavioural context to affect top-down cognitive influences on perception and fine control of finger movements during haptic sensing. The major overall hypothesis of this thesis is that the age-related decrease in haptic sensing performance could be due not only to bottom-up peripheral changes at the fingertip such as reduced sensory and motor innervation, but also to top-down changes at the central cortical level.

CHAPTER II. RESEARCH PAPERS

List of Published Research Papers

DOI 10.1007/s00221-008-1679-z

RESEARCH ARTICLE

Task-specific increase in corticomotor excitability during tactile discrimination

Sabah Master · François Tremblay

Received: 20 August 2008 / Accepted: 4 December 2008 / Published online: 23 December 2008

Abstract Task-dependant changes in corticomotor excitability have been described mainly in the context of grasp-oriented actions, neglecting the sensory aspects of hand function. Here, we contrasted task-dependant facilitation in small hand muscles [i.e., first dorsal interosseous (FDI) and abductor digiti minimi (ADM)] in the context of finger movements involving either discrimination or non discrimination (ND) of tactile features. Healthy young individuals ($n = 16$) were trained to produce rhythmic to and fro movements at the sound of metronome ticks (0.8 Hz frequency, 5 s total duration) with either the index or the little finger of the right hand. In the tactile discrimination (TD) condition, participants were asked to attend to the location of two different 2-D tactile shapes disposed on the explored surface, whereas in the ND condition, the finger was moved over a blank surface. In both conditions, a transcranial magnetic stimulation (TMS) pulse was delivered at a specific time point in the course of the finger movement. Corticomotor excitability was assessed by monitoring changes in the amplitude and latency of motor evoked potentials (MEPs) in the FDI and ADM. Changes in the duration of the silent period were also assessed. The analysis revealed a significant large effect of task conditions ($P < 0.001$) on MEP amplitude, owing to the increase in MEP size observed during the TD, as compared to the ND condition. No interaction between "Task" and "Muscle" was detected, however, indicating that MEPs in the two muscles were equally affected by the task conditions. No significant changes were detected for variations in MEP latency or in the SP duration. An additional control experiment performed in a subset of the participants ($n = 9$) showed that MEP facilitation was substantially reduced when attention to sensations arising from finger contact with the shapes was diverted away by completion of a concurrent cognitive task (counting backward by three). These findings provide further insights into the factors influencing task-dependant changes in corticomotor excitability during hand actions. Our results highlight the importance of behavioral context and attention, in particular, in leading to further enhancement in corticomotor excitability when the finger is actively engaged in TD.

Keywords Motor behavior · Tactile discrimination · Transcranial magnetic stimulation

---

[redacted]

Introduction

Voluntary contraction is known to lead to facilitation of motor evoked potentials (MEP's) elicited by transcranial magnetic stimulation (TMS). This facilitation is particularly prominent in intrinsic hand muscles, where even minimal contraction can lead to a substantial increase in MEP amplitude and reduction in onset latency (Mills and Kimiskidis 1996). At very low-level contractions, the facilitation is thought to reflect mainly an increase in intracortical excitability with further contribution of spinal mechanisms as the level of contraction increases above 30% of the maximum voluntary contraction (MVC) (Abbruzzese and Trompetto 2002).Other factors, besides the level of contraction, are also known to influence MEP facilitation. The nature of the task in particular has drawn much attention, prompted by observations from recordings in monkeys showing task-dependant variations in motor cortical discharge for different types of grip (Buys et al. 1986). Consistent with these observations, MEP facilitation elicited in small hand muscles was shown to vary depending on whether participants performed either isolated finger movements or fine precision grip, as opposed to power grip (Datta et al. 1989; Schieppati et al. 1996; Huesler et al. 1998; Hasegaw et al. 2001). Further insights into task-dependent modulation suggested that the degree of voluntary control required by the task was a major factor in leading to MEP facilitation during task execution (Datta et al. 1989; Flament et al. 1993). More recent TMS and neuroimaging studies in humans have confirmed that task complexity is indeed a critical factor in modulating activity in the corticospinal system, with more demanding tasks leading to greater activation and higher facilitation than less demanding tasks (Carey et al. 2006; Ni et al. 2006a; Bonnard et al. 2007).

One caveat surrounding reports on task-dependent facilitation is that most studies focused on task paradigms emphasizing the motor aspects of hand function (e.g., types of handgrips), neglecting its other important role as a sensory organ. Such distinction may seem trivial at first sight but it becomes more critical when one realizes that tactile sensing with the finger represents the archetypical precision demanding task, engaging a large cortical network with core activation in frontal motor areas (motor and premotor cortices), somatosensory areas and associative regions of the posterior parietal cortex and prefrontal cortex (Bodegård et al. 2001; Miquee et al. 2008). We could only find one TMS report addressing this issue. Hess et al. (1999) looked at variations in MEP amplitude and silent period (SP) in intrinsic hand muscles when TMS was delivered at random intervals while participants actively explored an object in their hand. The results showed a selective increase in the SP duration during tactile exploration with no changes in MEP amplitude or latency. While the absence of change in MEP's may seem surprising, the lack of proper control of the timing of TMS delivery during exploration may explain this lack of effect. In addition, since no details about the object explored were provided, one cannot determine the nature of the exploratory movements used. Indeed, both geometric (size, shape) and material properties (e.g., texture, temperature) are essential in dictating strategies used when haptically exploring objects (Lederman and Klatzky 1993).

In the present report, we attempted to address some of these limitations. We measured variations in corticomotor excitability in small hand muscles in the context of two tasks, which both involved precision movements of the finger but varied in terms of the behavioral demands. One task involved moving the finger in sync with a metronome, while the other task added a sensory discrimination component. Our primary goal was to determine whether equivalent movement conditions would lead to specific enhancement in corticomotor excitability when the finger is engaged in tactile discrimination (TD). A secondary aim was to contrast excitability changes measured in the first dorsal interosseus and the abductor digiti minimi (ADM) muscles when their corresponding finger (i.e., index finger and little finger) was engaged in the task conditions.

Materials and methods

The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received honorarium for his or her participation.

Participants

Sixteen healthy young adults (8 female, 8 male; mean age ± SD, 21.2 ± 1.9 years) were recruited among the student population in the Ottawa area. The majority of subjects were right-handed (14/16) based on self-report. Prior to the experimental session, all participants completed a medical questionnaire to ensure that there were no contraindications to TMS and no antecedents of conditions likely to affect their performance in the tests.

EMG recording and TMS

Electromyographic (EMG) activity was recorded using small auto-adhesive surface electrodes (10 mm diameter, Ag–AgCl) placed over the first dorsal interosseous (FDI) and ADM muscles of the right hand. EMG signals were amplified (100 µV/div) and filtered (bandwidth, 10 Hz–1 kHz) with a polygraph amplifier (RMP-6004, Nihon-Kohden Corp.). Signals were digitized at 2 kHz sampling rate using custom software on a PC running under Microsoft® Windows® XP equipped with a digital/analogue acquisition card (BNC-2090, National Instrument Corp.).

Transcranial magnetic stimulation was administered with participants comfortably seated in a recording chair.

Magnetic stimulation was delivered with a Magstim 200 (Magstim Co. Dyfed, UK) connected to a figure-eight coil (70 mm loop diameter). To determine the optimal site to evoke MEP's in the contralateral hand muscles, participants were fitted with a Lycra swimming cap with a grid traced onto it. A U-shaped neck cushion was used to restrain head movements. With the coil held ~45° in the mid-sagittal plane, the approximate location of the hand motor area on the left hemisphere was explored in 1 cm steps until reliable MEP's could be evoked in the target muscles (FDI and ADM). This site was then marked with a red dot to ensure consistent coil positioning. Cortical maps for intrinsic hand muscles are large and to some extent overlapping (Abbruzzese and Trompetto 2002), and thus we were able to maximally activate both the FDI and the ADM simultaneously by stimulating the same hotspot. After determination of this hotspot, the coil was held in place manually by one of the experimenters. The experimenter frequently reassessed the coil position to ensure that it remained over the optimal stimulation site throughout the experiment. Following this procedure, the relaxed motor threshold was determined using the method advocated by Mills and Nithi (1997). Starting from supra-threshold intensity, the stimulator's output was gradually decreased in 1% steps until no MEP could be evoked for 10 consecutive stimuli. This TMS intensity corresponded to the lower threshold value. From this point, the intensity was gradually increased until MEP's of at least 50 μV peak-to-peak amplitude could be evoked by ten consecutive stimuli. This latter intensity was recorded as the upper threshold value. The relaxed motor threshold was defined for each participant as the median intensity between the upper and lower threshold values. The TMS intensity was then fixed at 1.1 × threshold for the remainder of the experiment.

Recording of EMG during maximal voluntary contraction (MVC)

Maximal EMG values were derived from each muscle (FDI and ADM) to provide an index with which to compare the level of EMG produced in the context of the tactile exploration task. Testing for the MVC was always performed at the beginning of the testing session. For the FDI, participants were asked to pinch their right index finger and thumb together as hard as they could for the duration of a tone, which lasted 3,000 ms. The procedure was then repeated two times to get three MVC recordings. The same procedure was applied for the ADM except that participants were asked to push their little finger against the resistance provided by one of the experimenters. Maximal EMG values were obtained by rectifying and averaging the EMG signals produced during the last 2,000 ms epoch of the MVC for each muscle.

Recording of MEP's during finger movements

Recordings of MEP variations during finger movements were performed with participants comfortably seated in the recording chair with the forearm resting on the armrest. Prior to testing participants were trained to produce rhythmic finger to and fro movements at a speed of 0.8 Hz for 5 s with either the index or the little finger of the right hand. In training, participants were asked to pace their movement to the sound of computer-generated metronome ticks. Two task conditions were tested: (1) TD and (2) no discrimination (ND). In the TD condition, participants were blindfolded and then asked to discriminate between two half-circle stickers (3.2 mm radius, 16 mm apart) pasted on a block, by moving their finger in sync with the ticks. As shown in Fig. 1, the half-circles formed two different 2-D shapes depending on whether the straight edge was rotated to face upwards (Boat) or downwards (Hat). At the end of each trial, participants were asked to report the location (either to their right or to their left) of one of the specified shapes, i.e., the "Hat" or the "Boat". The position of the two shapes either to the right or the left varied from trial to trial according to a predetermined random sequence. The number of correct responses was recorded in each block of trials. In the ND condition, participants simply moved their finger in sync with the ticks on a blank block.

After familiarization with the procedures, formal testing began. Corticomotor excitability was assessed separately for each muscle under the two task conditions, TD and ND. In both conditions, a pre-recorded digitized audio-video sequence of the metronome ticks was used to set the timing of TMS pulse delivery based on the time frame using custom software. For both the TD and ND tasks, TMS was set to trigger at 3.75 s corresponding to the third tick in the sequence, when the target muscle was contracting concentrically to move the finger into abduction (see Fig. 1b). Sixteen trials were performed under each task condition for each muscle, the order of testing with the FDI or ADM being counterbalanced across participants. Each trial consisted of 1,000 ms epochs to allow for the quantification of MEP parameters and the background EMG level associated with the finger movements.

Control experiment for the effect of attention to finger sensation

To further examine the causal relationship between task parameters and MEP facilitation, a control condition was subsequently added to the protocol. This additional control experiment involved a subset of nine participants (3 males, 6 females) and was performed within 6 months after the initial session. This control experiment was designed to determine the effect of finger

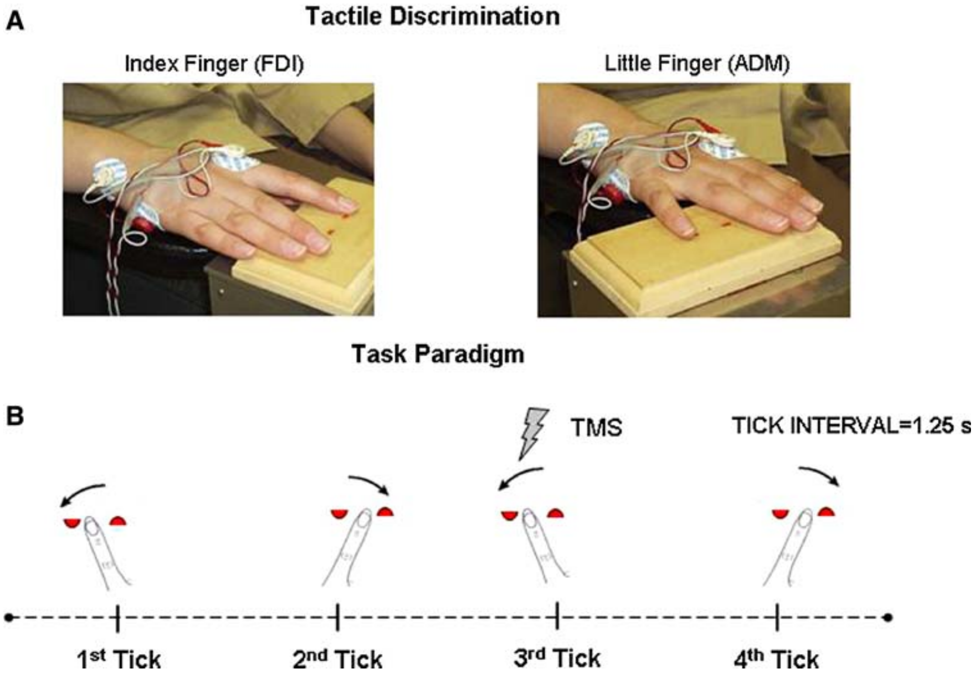

Fig. 1 **a** Experimental set-up showing the position of the finger (index finger and little finger) at the time of TMS pulse delivery during performance of the tactile discrimination (*TD*) task along with the location of the recording surface electrodes. **b** Schematic illustration of the task paradigm used to assess MEP facilitation. In the both the TD and non discrimination (*ND*) tasks, participants were trained to produce rhythmic finger to and fro movements in sync with the sound of a metronome at a frequency of 0.8 Hz for 5 s. In the TD condition, the finger moved over a surface containing two 2-D shapes (half circle stickers forming either a "Boat" or a "Hat", 3.2 mm radius, 16 mm apart) and participants were asked to report the location of one of the specified shapes at the end of the trial (only index finger shown here). The ND task was identical in performance to the TD task except that the finger moved over a blank surface. In each trial, the TMS pulse was set to trigger at a time corresponding to the third tick (3.75 s) in the trial when the tested finger was moving towards abduction

movements on MEP amplitude when attention was diverted away from tactile sensations arising from contact with the shapes. Thus, for this diverted attention (DA) task, the movement conditions were identical to those used before for the TD task, but this time, participants had to perform a concurrent cognitive task (counting backward by three) in their head as they moved their finger over the surface with the shapes. Before testing, participants were explicitly told to focus on the counting task disregarding the sensation arising from finger contact. To emphasize the counting task, participants were asked to report which number they were specifically at when the trial ended and each trial started from a pseudorandom number from 50 to 150. For this additional session, testing was restricted to the index finger (FDI muscle). The EMG recordings and TMS procedure (i.e., determination of the hotspot and motor threshold) were carefully repeated to reproduce the stimulation conditions. In fact, the stimulation intensity (1.1 × threshold) used to assess excitability changes at this second session was highly comparable to that used in the initial testing session (37 ± 7 vs. 36 ± 7%; respectively, paired *t*-test, $t_8 = 1.1$, $P = 0.30$); attesting to the reliability of the motor threshold estimations.

Analysis of MEP data and background EMG

Motor evoked potential amplitude (peak-to-peak) and latency were measured off-line for each trial and then averaged to derive mean individual values for each task condition. MEP traces were also analysed off-line to determine the duration of the SP, which was calculated as the time interval from the onset of the MEP to the first sign of EMG activity return. Finally, background EMG activity associated with each task condition was analysed to derive quantitative EMG values. For this analysis, the EMG activity recorded in the 500 ms time window preceding the TMS pulse, was rectified and then averaged to get average EMG values in μV. This average background EMG value was then expressed as a percentage of the maximal EMG produced during the MVC (see above) to provide an index of voluntary activation in each task condition.

Statistical methods

Motor evoked potential amplitudes were not normally distributed and so individual mean values were transformed into natural logarithm, as suggested by Nielsen (1996). Following this transformation, MEP amplitudes were normally distributed (Shapiro-Wilk $P > 0.05$). Latency and SP measurements were normally distributed and required no transformation. Repeated measures analysis of variance (ANOVA) was used to determine the impact of task conditions (TD, ND) and "Muscle" (FDI, ADM) on each set of variables measured, i.e., MEP log-amplitude, MEP latency, EMG level and SP duration. The significance level was set at $P < 0.01$ using the Bonferroni correction to adjust for multiple comparisons. An additional repeated measures ANOVA was performed on the data from the subset of participants who performed the DA task to determine the impact of task conditions (DA, TD, ND) on MEP log-amplitude. For this test Wilks' lambda was used to control for the small number of participants and the higher level of variability within the subset. Post-hoc tests were performed using the Bonferroni procedure to compare the tasks to each other. All tests were performed using SPSS software version 15.0 for Windows® (Chicago, IL, USA). Figures were prepared using GraphPad Prism version 5.00 for Windows (GraphPad Software, San Diego, CA, USA, http://www.graphpad.com).

Results

Task performance and background EMG: TD versus ND

In general, participants experienced no major difficulties in performing the TD task using either finger, although accuracy for locating the "Hat" or "Boat" was better with the index finger as compared to the little finger (mean correct 94 ± 8%, mean 73 ± 20%). EMG levels associated with performance of the two tasks corresponded, on average, to ~30 and 10% of the MVC, respectively, in the FDI (mean TD 32.7%, ND 32.1%) and ADM (mean TD 12.4%, ND 8.2%). A typical example of EMG activity recorded in the two muscles in both task conditions is shown in Fig. 2. It can be seen that the pattern of EMG activity as well the level were similar in the two task conditions. The ANOVA confirmed that task condition had no effect on background EMG levels ($F_{1,15} = 0.99$, $P = 0.34$). However, a "Muscle" effect was detected owing to the difference in level observed between the FDI and ADM ($F_{1,15} = 11.8$, $P = 0.004$).

Task-specific MEP facilitation: TD versus ND

The majority of participants (12/16) exhibited greater MEP facilitation under the TD, as compared to, the ND condition and this, both in the FDI and ADM. However, MEP's were generally of higher amplitude in the FDI irrespective of task conditions. A typical example of the differential effect of task conditions on MEP amplitude recorded in the FDI and ADM is shown in Fig. 3a along with the corresponding mean values computed from all the participants (Fig. 3b). The difference in MEP amplitude between the TD and ND conditions was confirmed by the ANOVA, which revealed

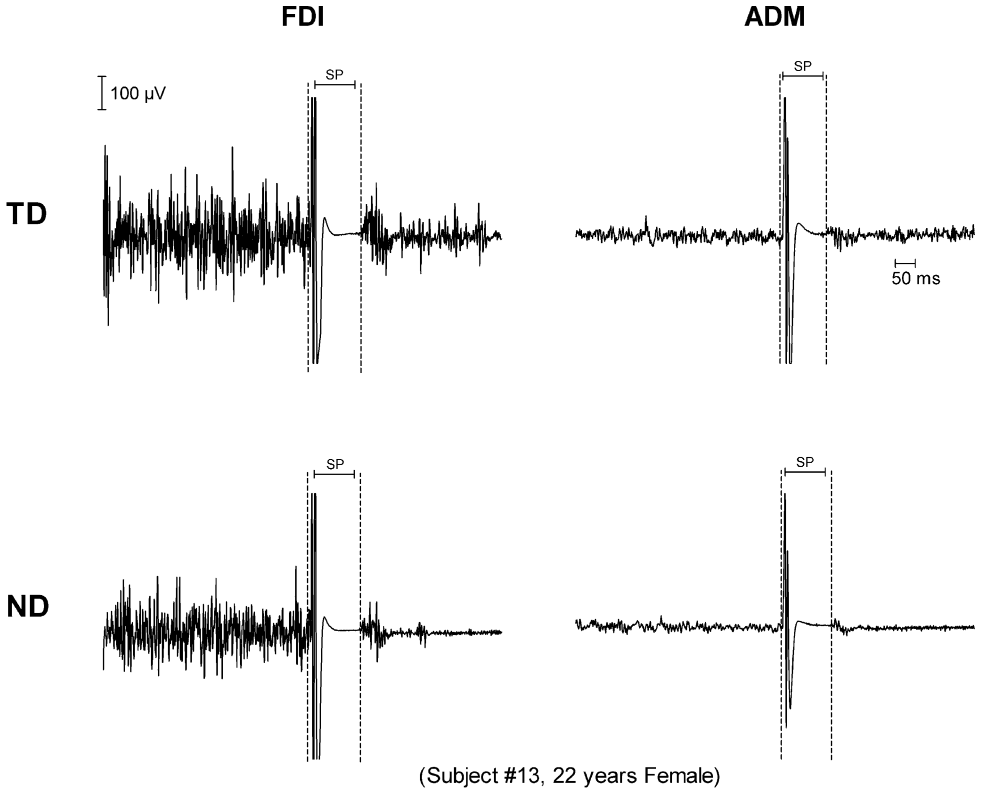

Fig. 2 A typical example of electromyographic (EMG) activity elicited during performance of the two finger movement tasks (discrimination *TD*, non discrimination *ND*). Note the similarity between the two tasks (TD vs ND) in terms of EMG patterns produced. In all participants, background EMG levels measured in the task conditions never exceeded 35% of the MVC. Note also that the duration of the silent period (*SP*) did not differ noticeably between the TD and ND task conditions for the two muscles

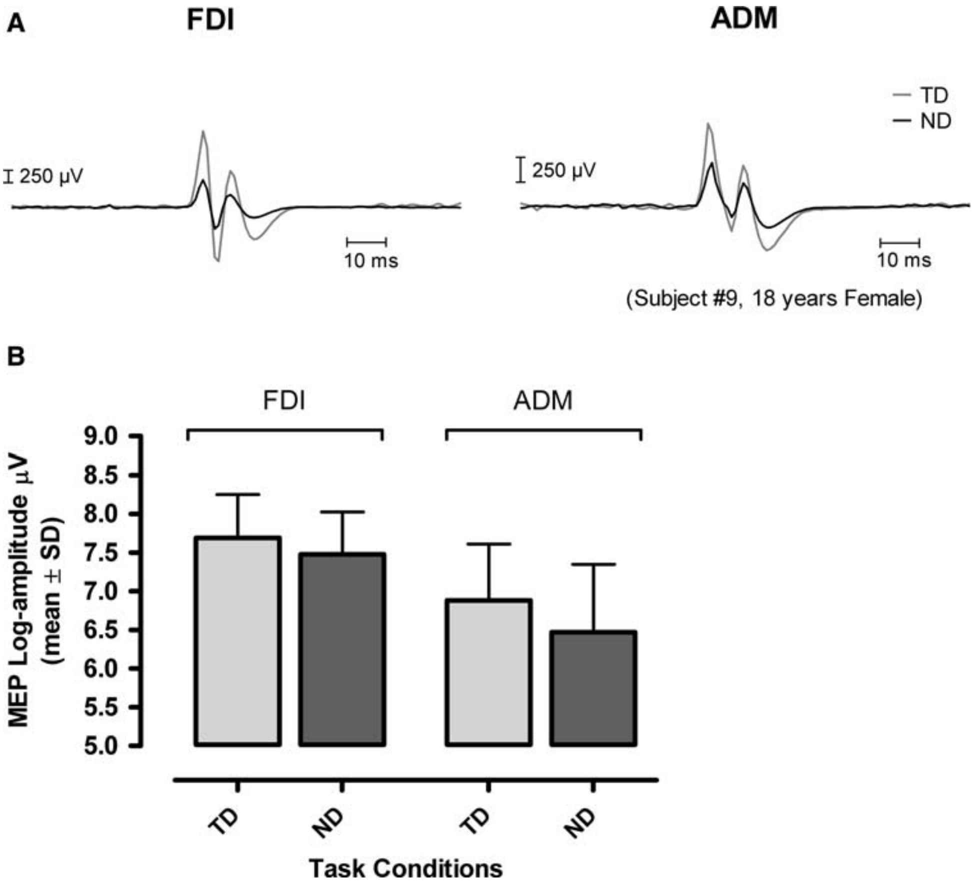

Fig. 3 **a** Example of task-specific facilitation recorded in the *FDI* and *ADM* in a typical participant. Note the difference in the amplitude of MEPs in the two muscles between the discrimination (*TD*) and non discrimination (*ND*) conditions. Each trace is an average of 16 responses. **b** Comparison of the mean MEP log-amplitude in two task conditions (TD and ND). Each bar represents the mean of individual values computed for the FDI and ADM under each task condition for all participants ($n = 16$). Note that the main effect of task condition was significant ($P < 0.001$) for the overall variations in MEP log-amplitude

a large effect of "Task"on MEP log-amplitude ($F_{1,15} = 21.0$, $P < 0.001$). While the task effect tended to be larger in the ADM than in the FDI (Fig. 3b), no "Task × Muscle" interaction was detected ($F_{1,15} = 0.1$, $P = 0.76$); indicating that the two muscles were equally affected by the task conditions. A main effect for "Muscle" was detected, however, owing to the difference between the FDI and ADM in terms of MEP size ($F_{1,15} = 28.5$, $P < 0.001$). Latency measurements were unaffected by task conditions in both the FDI (TD 19.2 ± 2.2 ms, ND 19.4 ± 1.3 ms) and the ADM (TD 18.5. ± 2 ms, ND 19 ± 2.0 ms). Accordingly, no main effect of "Task" or "Muscle" was detected in the ANOVA ($F_{1,15} < 2.5$, $P > 0.1$). Only minor differences were observed in SP durations between task conditions (FDI, TD 89 ± 37 ms, ND 90 ± 43 ms, ADM, TD 104 ± 35 ms, ND 94 ± 34 ms) and neither the effect of "Task" or "Muscle" was significant ($F_{1,15} < 3$, $P > 0.1$).

Control experiment for attention to finger sensation

In the subset of participants ($n = 9$) tested under the DA condition, that is when their attention was diverted away from sensations arising from the finger, comparisons with the TD and ND tasks revealed major differences between tasks. As shown in Fig. 4, both at the individual (Fig. 4a) and group level (Fig. 4b), attending to finger sensations elicited during movements to discriminate the shapes (TD) tended to produce the greatest level of MEP facilitation when compared to either the ND or DA conditions. Still, comparison between the latter two conditions showed that simply attending to finger sensations during movement produced larger MEPs than when attention was diverted away from the finger (DA condition). The ANOVA confirmed the significant effect of "Task" conditions on MEP amplitude ($F_{2,7} = 6.44$, $P < 0.03$). Further post-hoc comparisons revealed that MEP amplitude for both the TD and ND conditions was significantly greater than that for the DA condition (Bonferroni, $P = 0.03$), although the difference between the two was not (i.e., TD vs. ND $P > 0.5$). The latter absence of difference reflected the increased variability owing to the small number of participants in this subset.

Discussion

In the present report, we investigated task-dependant changes in corticomotor excitability during individuated finger movements performed with or without a sensory discrimination component. There were three main findings. First, actively moving the finger over a surface was associated

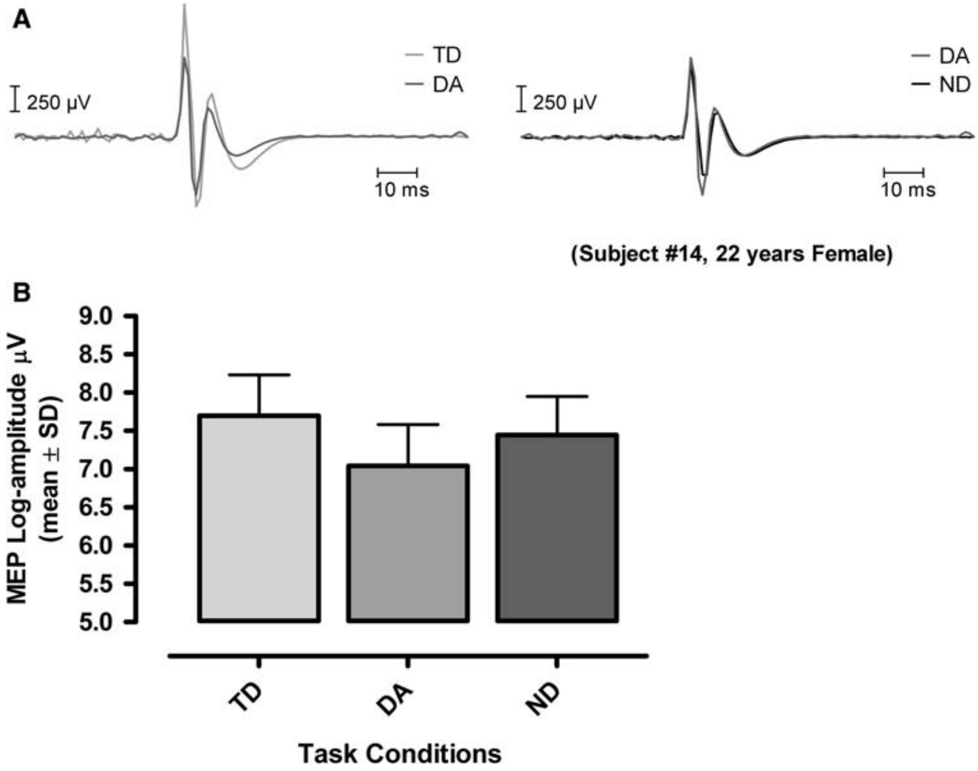

Fig. 4 Individual example (**a**) and group data (**b**) obtained from the subset of participants ($n = 9$) tested in the additional control condition. In this condition, the finger movements (only index finger tested) were identical to those performed under the TD conditions with the difference that attention diverted away (DA) from sensation arising from finger contact with the shapes by asking participants to perform a concurrent cognitive task (counting backward by 3). Figure legends and abbreviations as in Fig. 3. Note the presence of extra facilitation under the TD condition as compared to ND and DA conditions in A. For this small subset of participants, the difference in amplitude between the TD and ND condition was not significant. ($P < 0.05$)

with significantly larger MEP amplitude when participants were engaged in tactile sensing as opposed to simple movement execution; leaving onset latency and SP duration largely unchanged. Second, amplitude facilitation was present in both the FDI and the ADM when the corresponding finger acted as the sensory probe. Finally, as revealed by an additional control experiment, attending to sensations arising from the finger proved to be the critical factor in leading to extra MEP facilitation in the context of these experiments. In the following discussion, we will address first the significance of these results with regards to task-dependent effects in small hand muscles. Then, we will address the possible origin of the extra facilitation observed under the TD condition, especially with regard to the critical role of attention as a modulating factor of motor cortical responsiveness.

Influence of task conditions on MEP facilitation

As stated earlier, both recent TMS and neuroimaging reports have emphasized the importance of task demands in modulating motor activation during hand movements (Carey et al. 2006; Ni et al. 2006b; Bonnard et al. 2007). In this study, we specifically designed the task demands so that the motor control component would be equivalent in the two conditions. In fact, participants produced very similar patterns of contraction and equivalent levels of background EMG activity when tested under the two task conditions. In this regard, it is worth noting that in small hand muscles, MEP facilitation starts to plateau when contraction levels exceed 20% of the MVC, as shown by Wu et al. (2002). In our task conditions, the level of background EMG produced in the FDI and ADM corresponded to ~30 and ~10% of the MVC, respectively. This difference in background activation (see Fig. 2) could account for the tendency of MEP facilitation to be greater in the ADM than in FDI. The same report by Wu et al. (2002) also showed that higher levels of contraction (i.e., >80% MVC) were needed to reduce latency and that variations in contraction levels had little effect on SP duration. This may explain why we found no significant changes in either the MEP latency or the SP duration with our task conditions. Thus, the relatively low level of effort required to move the finger under each task condition likely provided a common base of facilitation upon which other influences could act, leading to further enhancement in excitability when the behavioral requirements of the task changed.

The present observations that MEP amplitude increased in hand muscles under the TD condition with no changes in SP may seem at odds with those of Hess et al. (1999), but any comparison with this study is difficult given the limitations raised earlier about the lack of proper controls over TMS delivery and task conditions. In addition, these authors elicited MEP's using a non-focal circular coil, which may have also contributed to the discrepancies between their results and ours. Although we did notice a trend for the SP to be prolonged under the TD condition in the ADM, it appears unlikely that changes in the SP are of major significance in the context of tactile exploration given the low level of voluntary drive generally involved (Wu et al. 2002). In the same vein, the facilitation reported here in the ADM during TD also seems at odds with the recent results of Ni et al. (2006b). These authors compared task-dependant facilitation during a force-matching precision task under dynamic and static conditions in the ADM and FDI, and reported significant differences only in the FDI. The authors attributed this difference to the greater functional role and the higher selectivity of control of the index finger, as compared to, the little finger. In the present study, we could not find such a difference. In fact, MEP facilitation tended to be even greater in the ADM than in the FDI under the TD condition. Differences between the task paradigms could explain this discrepancy since we looked at the influence of dynamic contractions in the context of TD. Like Ni et al. (2006b), however, we found a difference in performance between the two fingers, participants making more errors when scanning with the little finger, but this difference did not translate into reduced facilitation. The lower accuracy could be related to the fact that tactile spatial acuity is lower (~45% less) in the little finger as compared to the others (Sathian and Zangaladze 1996); a difference that is partly attributable to the reduced skin area at the tip. Still, the performance was well above chance (73% correct), indicating that participants were able to discriminate using the little finger. In terms of control selectivity, Hager-Ross and Schieber (2000) showed that the little finger was third after the thumb and index finger in the degree of individuation, but they also emphasized the large inter-subject variability; some individuals showing high selectivity even for little finger movements. In line with this observation, we did also notice some variability in the ability of our participants to perform individuated movements with the little finger, some finding it much harder compared with the index finger while others had no difficulty at all. It is thus possible that both the lower accuracy and the trend observed for higher MEP facilitation in the ADM reflected the greater degree of voluntary control and attention required to move and sense with that finger as compared to the index finger. Whatever the differences between the two fingers in terms of tactile acuity and control selectivity, our findings suggest that corticospinal projections to both the ADM and FDI are susceptible to facilitatory influences when their corresponding finger is engaged in active TD. In fact, our observations of similar levels of facilitation in the ADM and FDI would be in line with current concepts about the divergent nature of the neural control of hand movements, individuated finger movements being associated with activity distributed across multiple neurons and widespread activation in the entire motor cortex (Schieber and Santello 2004).

Origin of MEP amplitude facilitation with TD

We have already alluded to the fact that the observed difference between tasks in terms of amplitude facilitation was most likely due to the difference in behavioral context. In one condition, participants had to pace their finger movements with the metronome, whereas in the other condition they had, in addition, to discriminate between two tactile shapes. Thus, while the two conditions had a similar motor component, the TD task added an extra attentional component, which was likely a key factor in leading to further enhancement in MEP amplitude. The importance of this factor in leading to MEP facilitation was further confirmed by the addition of the control DA condition, which showed unequivocally that attending to finger sensations was indeed critical in leading to MEP facilitation. These attention-related effects were likely exerted predominantly at the cortical level, since attention to action appears to have little or even a depressive effect on spinal excitability (Honore et al. 1983; Oishi et al. 1994). At the level of the motor cortex, attention to somatic stimuli has been shown to have strong modulatory influences on cortical responsiveness to TMS. For instance, Rosenkranz and Rothwell (2004) reported that attending to long-lasting vibro-tactile trains applied to small hand muscles shaped their subsequent response to the same stimuli, such that MEP's in the non vibrated muscles that were normally depressed were enhanced when subjects attended to the stimulated hand. These effects were accompanied by parallel changes in the level of intra-cortical inhibition controlling the excitability of the vibrated and non-vibrated muscles. Recently, Thomson et al. (2008) confirmed that short-interval intra-cortical inhibition (SICI) could be reduced up to 1,000 ms after finger movements when spatial attention was directed toward the hand being stimulated as compared to when the attention was directed toward the non-stimulated hand. Thus, local changes in intra-cortical excitability, driven by attention to incoming tactile inputs generated as the finger explored the surface, might have been important in leading to enhanced MEP facilitation when participants were engaged in TD.

For the most part, the attention effects were likely mediated by activity in the parieto-frontal network involved in TD. In this regard, the dorsolateral prefrontal cortex and the premotor regions might have been particularly important since both have been shown to be highly active when the finger is engaged in fine spatial discrimination (Stoesz et al. 2003; Harada et al. 2004) and both are densely interconnected with the motor cortex (Dum and Strick 2002). In addition, attending to action during execution appears to enhance effective connectivity between the two areas (Rowe et al. 2002). Thus, when the participants were engaged in the attention-demanding tactile task, the enhanced coupling between activity of the dorsal prefrontal cortex and premotor cortex may have provided an additional source of top down excitatory influences on the motor cortex that contributed to enhance its responsiveness to TMS. The fact that attentional processes could alter MEP facilitation in small hand muscles through premotor-to-motor connections was confirmed recently by Conte et al. (2007). Similar mechanisms could account for the difference observed between the ND and DA conditions in the subset of participants tested in the control experiment, since in the ND condition participants likely attended to finger movements even if they were moving over a smooth surface.

One last potential influence that may have contributed to enhance motor excitability in the task conditions could have been the nature of the peripheral feedback in itself. While the re-afferent signal generated as the finger moved during the task was likely similar in the two conditions, the contact with the 2-D shapes in the TD task provided an external source of afferent information. Recordings from mechanoreceptive afferents in the primate hand have shown that slowly and rapidly adapting type I (SAI, RAI) afferents are particularly responsive to minute surface irregularities and asperities, as compared to smooth surfaces (Johnson et al. 2000; Yoshioka et al. 2001). Thus, an increased discharge of the SAI and RAI tactile afferents can be inferred when the fingertip contacted the raised patterns during the TD task. This task-specific increase in tactile afferent discharge might have led to a transient increase in excitability at the spinal or cortical level, as shown recently by Shibuya and Ohki (2004). However, this suggestion needs to be tempered by the observations that contact with the 2-D shapes in the control DA condition failed to produce extra MEP facilitation. This leads back to the notions discussed above about the critical role of attention in modulating cortical responsiveness to incoming sensory inputs and the importance of the behavioral context for the coupling between sensation and action.

In conclusion, the present findings provide further insights into the factors influencing corticomotor excitability during hand actions. Our results highlight the importance of tactile attention and behavioral context in leading to further enhancements in corticomotor excitability when the finger is actively engaged in TD. Our findings also reveal a functional equivalence between the mechanisms controlling the excitability of the corticospinal projections destined to the ADM and FDI muscles, when it comes to facilitation exerted in the context of tactile exploration. Further studies are needed to pinpoint the neural mechanisms underlying the reported extra facilitation with TD, especially with regards to the role of changes in intra-cortical inhibition.

Acknowledgments The authors wish to thank all participants for their time and patience during testing. Special thanks to Patricia Oliver, Francisca Avila-Ramirez and Liam Dessureault-Crawly for their help with data collection. Part of this work served as a partial fulfillment for a research practicum in experimental psychology by Sabah Master. François Tremblay is supported by NSERC (Canada).

References

Abbruzzese G, Trompetto C (2002) Clinical and research methods for evaluating cortical excitability. J Clin Neurophysiol 19:307–321

Bodegård A, Geyer S, Grefkes C, Zilles K, Roland PE (2001) Hierarchical processing of tactile shape in the human brain. Neuron 31:317–328

Bonnard M, Gallea C, De Graaf JB, Pailhous J (2007) Corticospinal control of the thumb-index grip depends on precision of force control: a transcranial magnetic stimulation and functional magnetic resonance imagery study in humans. Eur J Neurosci 25:872–880

Buys EJ, Lemon RN, Mantel GW, Muir RB (1986) Selective facilitation of different hand muscles by single corticospinal neurones in the conscious monkey. J Physiol 381:529–549

Carey JR, Greer KR, Grunewald TK, Steele JL, Wiemiller JW, Bhatt E, Nagpal A, Lungu O, Auerbach EJ (2006) Primary motor area activation during precision-demanding versus simple finger movement. Neurorehabil Neural Repair 20:361–370

Conte A, Gilio F, Iezzi E, Frasca V, Inghilleri M, Berardelli A (2007) Attention influences the excitability of cortical motor areas in healthy humans. Exp Brain Res 182:109–117

Datta AK, Harrison LM, Stephens JA (1989) Task-dependent changes in the size of response to magnetic brain stimulation in human first dorsal interosseous muscle. J Physiol 418:13–23

Dum RP, Strick PL (2002) Motor areas in the frontal lobe of the primate. Physiol Behav 77:677–682

Flament D, Goldsmith P, Buckley CJ, Lemon RN (1993) Task dependence of responses in first dorsal interosseous muscle to magnetic brain stimulation in man. J Physiol 464:361–378

Hager-Ross C, Schieber MH (2000) Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies. J Neurosci 20:8542–8550

Harada T, Saito DN, Kashikura K-I, Sato T, Yonekura Y, Honda M, Sadato N (2004) asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study. J Neurosci 24:7524–7530

Hasegaw Y, Kasai T, Kinoshita H, Yahagi S (2001) Modulation of a motor evoked response to transcranial magnetic stimulation by the activity level of the first dorsal interosseous muscle in humans when grasping a stationary object with different grip widths. Neurosci Lett 299:1–4

Hess A, Kunesch E, Classen J, Hoeppner J, Stefan K, Benecke R (1999) Task-dependent modulation of inhibitory actions within the primary motor cortex. Exp Brain Res 124:321–330

Honore J, Demaire C, Coquery JM (1983) Effects of spatially oriented attention on the facilitation of the H reflex by a cutaneous stimulus. EEG Clin Neurophysiol 55:156–161

Huesler EJ, Hepp-Reymond MC, Dietz V (1998) Task dependence of muscle synchronization in human hand muscles. Neuroreport 9:2167–2170

Johnson KO, Yoshioka T, Vega-Bermudez F (2000) Tactile functions of mechanoreceptive afferents innervating the hand. J Clin Neurophysiol 17:539–558

Lederman SJ, Klatzky RL (1993) Extracting object properties through haptic exploration. Acta Psychol (Amst) 84:29–40

Mills KR, Kimiskidis V (1996) Cortical and spinal mechanisms of facilitation to brain stimulation. Muscle Nerve 19:953–958

Mills KR, Nithi KA (1997) Corticomotor threshold to magnetic stimulation: normal values and repeatability. Muscle Nerve 20:570–576

Miquee A, Xerri C, Rainville C, Anton JL, Nazarian B, Roth M, Zennou-Azogui Y (2008) Neuronal substrates of haptic shape encoding and matching: a functional magnetic resonance imaging study. Neuroscience 152:29–39

Ni Z, Liang N, Takahashi M, Yamashita T, Yahagi S, Tanaka Y, Tsuji T, Kasai T (2006a) Motor strategies and excitability changes of human hand motor area are dependent on different voluntary drives. Eur J Neurosci 23:3399–3406

Ni Z, Takahashi M, Yamashita T, Liang N, Tanaka Y, Tsuji T, Yahagi S, Kasai T (2006b) Functional demanded excitability changes of human hand motor area. Exp Brain Res 170:141–148

Nielsen JF (1996) Logarithmic distribution of amplitudes of compound muscle action potentials evoked by transcranial magnetic stimulation. J Clin Neurophysiol 13:423–434

Oishi K, Kimura M, Yasukawa M, Yoneda T, Maeshima T (1994) Amplitude reduction of H-reflex during mental movement simulation in elite athletes. Behav Brain Res 62:55–61

Rosenkranz K, Rothwell JC (2004) The effect of sensory input and attention on the sensorimotor organization of the hand area of the human motor cortex. J Physiol (Lond) 561:307–320

Rowe J, Friston K, Frackowiak R, Passingham R (2002) Attention to action: specific modulation of corticocortical interactions in humans. Neuroimage 17:988–998

Sathian K, Zangaladze A (1996) Tactile spatial acuity at the human fingertip and lip: bilateral symmetry and interdigit variability. Neurology 46:1464–1466

Schieber MH, Santello M (2004) Hand function: peripheral and central constraints on performance. J Appl Physiol 96:2293–2300

Schieppati M, Trompetto C, Abbruzzese G (1996) Selective facilitation of responses to cortical stimulation of proximal and distal arm muscles by precision tasks in man. J Physiol (Lond) 491:551–562

Shibuya S, Ohki Y (2004) Cutaneous inputs can activate the ipsilateral primary motor cortex during bimanual sensory-driven movements in humans. J Neurophysiol 92:3200–3209

Stoesz MR, Zhang M, Weisser VD, Prather SC, Mao H, Sathian K (2003) Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks. Int J Psychophysiol 50:41–49

Thomson RHS, Garry MI, Summers JJ (2008) Attentional influences on short-interval intracortical inhibition. Clin Neurophysiol 119:52–62

Wu L, Goto Y, Taniwaki T, Kinukawa N, Tobimatsu S (2002) Different patterns of excitation and inhibition of the small hand and forearm muscles from magnetic brain stimulation in humans. Clin Neurophysiol 113:1286–1294

Yoshioka T, Gibb B, Dorsch AK, Hsiao SS, Johnson KO (2001) Neural coding mechanisms underlying perceived roughness of finely textured surfaces. J Neurosci 21:6905–6916

Master and Tremblay *BMC Neuroscience* 2010, **11**:149
http://www.biomedcentral.com/1471-2202/11/149

BMC
Neuroscience

RESEARCH ARTICLE **Open Access**

Differential modulation of corticospinal excitability during haptic sensing of 2-D patterns vs. textures

Sabah Master[1,3], François Tremblay[1,2,3*]

Abstract

Background: Recently, we showed a selective enhancement in corticospinal excitability when participants actively discriminated raised 2-D symbols with the index finger. This extra-facilitation likely reflected activation in the premotor and dorsal prefrontal cortices modulating motor cortical activity during attention to haptic sensing. However, this parieto-frontal network appears to be finely modulated depending upon whether haptic sensing is directed towards material or geometric properties. To examine this issue, we contrasted changes in corticospinal excitability when young adults (n = 18) were engaged in either a roughness discrimination on two gratings with different spatial periods, or a 2-D pattern discrimination of the relative offset in the alignment of a row of small circles in the upward or downward direction.

Results: A significant effect of task conditions was detected on motor evoked potential amplitudes, reflecting the observation that corticospinal facilitation was, on average, ~18% greater in the pattern discrimination than in the roughness discrimination.

Conclusions: This differential modulation of corticospinal excitability during haptic sensing of 2-D patterns vs. roughness is consistent with the existence of preferred activation of a visuo-haptic cortical dorsal stream network including frontal motor areas during spatial vs. intensive processing of surface properties in the haptic system.

Background

Haptic sensing involves bringing the hand in contact with objects and surfaces to determine their properties. In the case of surfaces, the presence of repeated raised elements characterizes textures, of which roughness is a major perceptual attribute. Recognition of 2-D patterns is another perceptual attribute provided by surfaces. Geometric properties such as the relative orientation of 2-D patterns are processed differently in the somatosensory system from material properties such as roughness and hardness. Neurons in Brodmann's area 1 have been shown to respond preferentially to surface features including roughness and texture [1,2], whereas neurons in Brodmann's area 2 are sensitive to differences in shape primitives, such as edges and curvature [2,3]. In primates, removal of areas 1 and 2 impairs performance on texture and shape discrimination tasks, repectively [2].

At the neural level, material properties are intensively coded, meaning that they can be distinguished based only on the amplitude of neural output at the cortical level [1,4-11]. In contrast, behavioural evidence has shown that geometric properties are likely spatially coded and must be mapped to a specific location within a particular frame of reference [12]. The haptic modality encodes geometric surface properties relatively inefficiently compared to material properties such as roughness [12]. This inefficiency can be attributed to several factors. Firstly, physical limitations of mechanoreceptor number and density lead to difficulties in the integration of limited inputs, as from a single 2-D raised element on a planar surface [12]. Secondly, the exploratory strategy for identifying a 2-D pattern is contour following, which entails a high working memory load [12-14]. Finally, spatial coding requires intensive coding to be completed first so that each 2-D raised element can first

---

[redacted]

be detected, before it is located within the frame of reference, making it more computationally demanding than intensive coding alone [12].

Behavioural evidence has shown clear differences in the efficiency with which the haptic system processes intensively and spatially coded properties, observers showing faster responses with roughness discrimination than for identification of the relative orientation of 2-D raised elements, a key element involved in pattern discrimination [12]. Recent neuroimaging studies have contrasted the areas activated during texture and shape discrimination, revealing that different brain regions are preferentially activated during the haptic processing of material and geometric properties [15-19]. For instance, in participants making judgements about surface texture, more activation was seen in ventral and posterior regions including the parietal operculum and posterior insula along with activation in ventrally located extrastriate visual areas (e.g., lingual gyrus) [15,16]. Such activation pattern for haptic texture seems to reflect the preferential recruitment of a ventral stream specializing in object *perception* and semantic object representations [15,16]. In contrast, shape discrimination elicited preferential activation in frontal motor regions (e.g., premotor cortex) and in dorsal parietal areas commonly associated with reaching and grasping behaviours (e.g., intra-parietal sulcus, IPS; superior parietal gyrus, SPG); indicating a tendency for the recruitment of a dorsal stream for *action* when geometric properties about touched objects are processed [15-19]. Attending to geometric properties of objects either in the tactile or visual modality also leads to robust activation in the region of the lateral occipital complex (LOC), an area which seems critical for object recognition [15-19]. It is important to stress that the reported selectivity of activation for either texture (directed ventrally) or shape (directed dorsally) is more relative than absolute; the two forms of haptic processing relying to a large extent on an overlapping cortical network [15,16].

In recent investigations, we used transcranial magnetic stimulation (TMS) to examine task-dependant modulation in corticospinal excitability when participants were engaged in haptic sensing [20-23]. These investigations revealed that activation of a haptic network for discrimination of 2-D raised symbols resulted in enhanced excitability of the motor cortex, compared to performance of the same movement without the sensing component, or when attention was distracted away from the task [21]. This attention-related modulation of corticospinal facilitation during haptic sensing suggested that the observed effects were due to top-down mechanisms, including activation of a haptic sensing network involving somatosensory, multisensory, and motor areas [24]. However, this previous work investigated only modulation in the context of haptic sensing of the geometric properties of a surface, i.e. discrimination of the relative orientation of 2-D symbols. Given the reported differences in terms of complexity of neural processing and distribution of cortical activation between texture and shape discrimination by touch, we sought to determine in the present report whether such differences would lead to an increase in corticospinal excitability when participants are engaged in task conditions involving spatial coding (i.e. sensing the orientation of a 2-D pattern) versus intensive coding (i.e., sensing differences in degree of roughness) of surface features.

Results

Task performance

In general, participants exhibited very reliable discrimination performance in the two tasks, although they tended to be better at discriminating patterns as compared to surface roughness (84.4 ± 11.4% vs. 93.9 ± 6.4%, respectively). While task conditions had a significant effect on performance levels ($F_{1,16} = 13.21$, $p = 0.002$), this actually reflected only a minor difference in terms of the number of errors ($n_{incorrect}/16$ trials) between the two tasks (i.e., pattern, $n_{incorrect} = 1.0 \pm 1.0$ trials, roughness, $n_{incorrect} = 2.5 \pm 1.8$ trials). Gender had no effect ($F_{1,16} = 0.72$, $p = 0.41$) on performance levels. In terms of muscle activation, execution of the stroking action in the two tasks elicited a very similar pattern of activity in the FDI msucle, characterized by a sustained increase in activity as the index finger moved over either the pattern or grating presented (Figure 1B and 1C). As shown in Figure 1C, the average level of activation elicited in the period preceding the TMS pulse corresponded to ~ 25% of the MVC in the two task conditions (mean, 23.81% vs. 22.55%, pattern and roughness, respectively). Paired comparison revealed no difference in the normalized level of EMG activity between the two tasks in the 500 ms period preceding the TMS pulse (paired t-test, $t_{17} = -0.09$, $p = 0.93$).

Task-specific corticospinal facilitation

The majority of the participants (11/18) exhibited larger MEP responses in the pattern, as opposed to, the roughness discrimination task. An individual example of such differential MEP modulation in the two task conditions is shown in Figure 2A. The relative effect of task conditions on MEP amplitude can also be appreciated in Figure 2B, where the individual MEP values measured under the two tasks have been plotted against each other. The differential effect of task conditions on MEP amplitude was confirmed by the ANOVA ($F_{1,16} = 5.60$, $p = 0.03$) owing to the larger MEP responses seen for the pattern task (18% increase, on average). Gender had no influence on MEP amplitude ($F_{1,16} = 0.28$, $p = 0.60$)

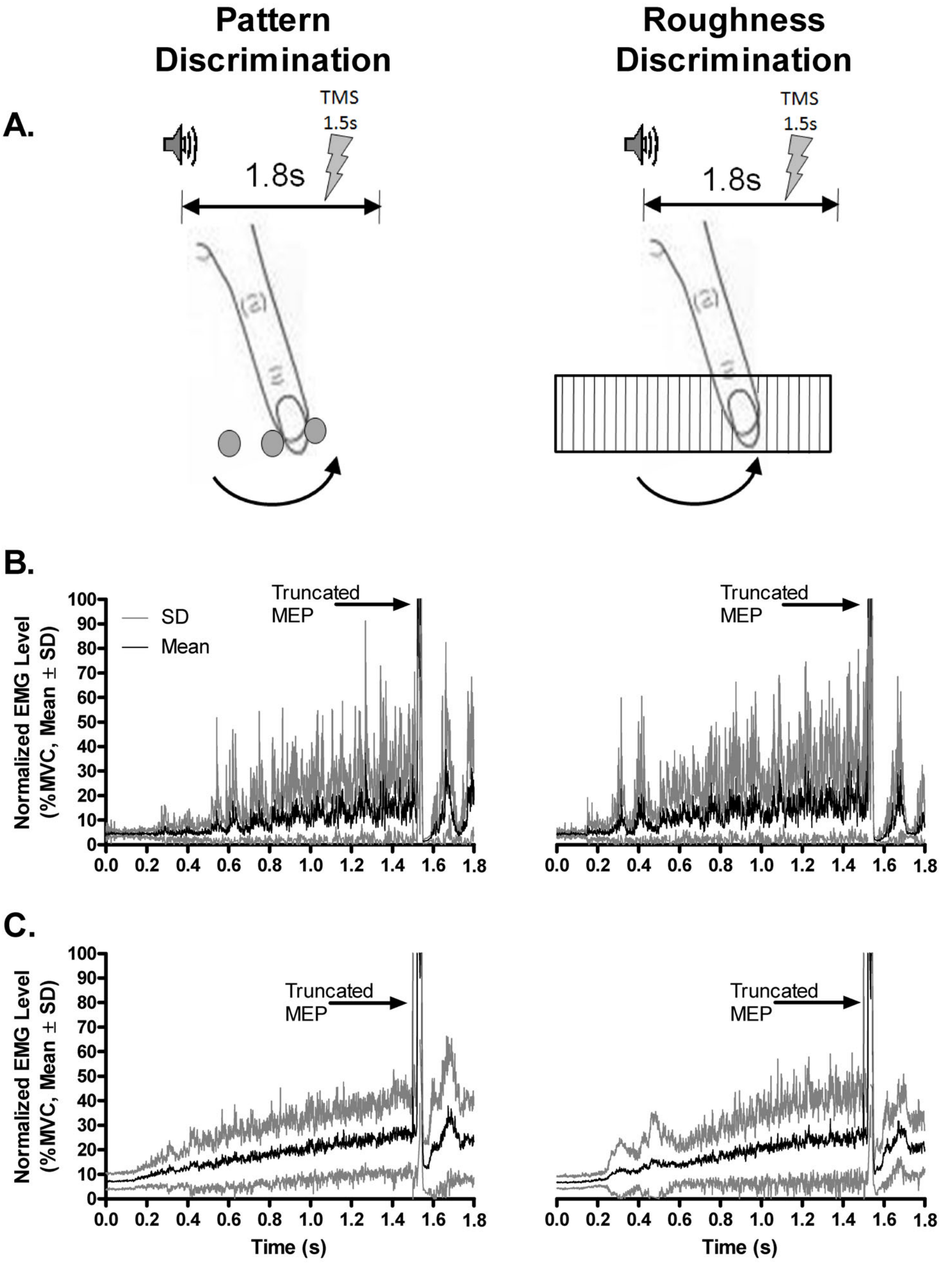

Figure 1 Task paradigm used to assess corticospinal excitability. A. In both discrimination tasks, participants were trained to produce a single stroking index finger movement in sync with the sound of a tone lasting for 1.8 s. In the pattern task, the finger moved over three circular stickers placed in a row, with the last circle off-set either upwards or downwards relative to the first two (3.2 mm radius, 10 mm centre-to-centre). Participants were asked to report whether the last circle was up or down. The roughness task required a judgement about the relative roughness of two grating surfaces, whose spacing between elements differed by 25%. Participants used the same stroking action to determine whether the surface presented was either the rougher (1 mm grating) or smoother (0.75 mm grating) of the two. In each trial, the TMS pulse was set to trigger 1.5s after the tone, corresponding to the time point when the finger was moving towards full abduction. B. Individual example of typical muscle activation patterns elicited in the FDI during execution of the index finger stroking action in the two tasks (right-handed male, aged 23 years). The traces represent the mean with associated SD of the rectified electromyographic (EMG) activity normalized as a percentage of the participant's maximal rectified average EMG value for all 16 trials under each task condition. C. Similar representation as in B showing the overall task-related pattern of EMG activation in all subjects (n = 18). The trace represents the mean (± SD) of all participants' normalized rectified average EMG activity level. Note the close similarity in the pattern of muscular activation between the two tasks. The amplitude of MEP's is truncated in both B and C because the scale has been adjusted to show the level of background EMG activity.

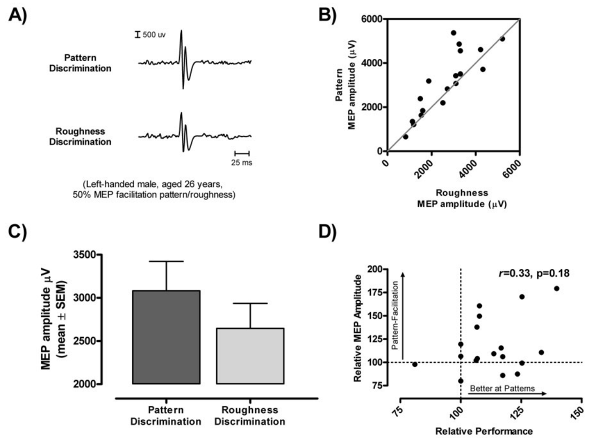

Figure 2 MEP amplitudes during 2-D pattern vs. roughness discrimination. A. Examples of task-related differential modulation in MEP amplitude under the two task conditions (left-handed male, aged 26 years, 50% MEP facilitation pattern/roughness). Each trace is an average of 16 responses. B. Scatter plot showing the relative distribution of MEP amplitudes in the two tasks for all participants. Note the tendency for MEP responses to be larger in the pattern discrimination task. C. Comparison of mean MEP amplitudes in the two task conditions (pattern and roughness discrimination). Each bar represents the mean of individual values computed under each task condition for all participants (n = 18). Note that the main effect of task condition was significant for the overall variations in MEP amplitude ($p < 0.05$). D. Scatter plot showing the distribution of individual MEP amplitude task ratios (% $MEP_{pattern}/MEP_{roughnes}$) against corresponding performance task ratios. Note that the two variables are not significantly related to one another.

and showed no interactions with task conditions ($F_{1,16}$ = 0.13, p = 0.73). Variations in MEP latency (19.3 ± 1.8 vs. 19.1 ± 1.6 ms, pattern and roughness, respectively) and in the silent period (SP) duration (99 ± 37 vs. 94 ± 38 ms, pattern and roughness, respectively) were not influenced by task conditions (latency, $F_{1,16}$ = 0.44, p = 0.51; silent period, $F_{1,16}$ = 2.10, p = 0.17).

Influence of task performance

The observation that participants tended to perform better at discriminating relative orientation, as compared to roughness, prompted a secondary analysis to determine if this increased performance was associated with the greater MEP facilitation during pattern discrimination. For this analysis, task ratios for MEP amplitude and performance ($n_{correct}/16$) were computed as a percent of pattern over roughness (e.g., % $MEP_{pattern}/MEP_{roughness}$) for each participant, so that 100% would correspond to equivalence between the two tasks. We then used Pearson's *r* moment correlation to test for the presence of an association between MEP amplitude and performance task ratios. As shown in Figure 2D, this analysis failed to detect any significant association (*r* = 0.33, p = 0.18) between task-related MEP facilitation and performance.

Discussion

In the present study, we examined task dependant corticomotor facilitation while participants were engaged in two different types of surface discrimination using active index finger movements, i.e. detection of 2-D spatial orientation and roughness discrimination. Our results reveal that for most participants pattern discrimination increases task-related MEP facilitation in the FDI, relative to roughness discrimination. In the following discussion, we will address the possible factors that may have contributed to this observed differential modulation of tactile-related motor facilitation by first considering task demands and bottom-up activity from peripheral afferents, and then top-down effects at the level of central processing.

Task demands

As in our previous study showing tactile-related MEP facilitation, the movement conditions and level of background EMG were highly consistent between tasks, reflecting the fact that participants were able to reproduce the movement pattern at the prescribed speed from trial to trial. Thus the observed differences in motor cortical excitability could not have been due to the use of different motor exploration strategies during pattern and roughness discrimination. Given that participants used identical controlled timed lateral scanning movements for both tasks, differences in proprioceptive and kinematic factors could not have accounted for the observed enhancement in motor facilitation during the pattern discrimination, relative to the roughness discrimination [9,10]. The two tasks were also relatively easy to perform (accuracy > 80%), although participants did perform better on the pattern discrimination than on the roughness discrimination. However, as stressed earlier, this difference in performance represented only a minor difference in number of errors, given the limited number of trials tested in each task (n = 16). In this regard, this difference in performance can be considered as trivial. In line with this, secondary analysis failed to reveal any association between performance and MEP facilitation (Figure 2D).

Contribution of bottom-up activity from peripheral afferents

The major difference between the two task conditions in terms of afferent input was the nature of the cutaneous feedback. The Merkel discs and associated slowly adapting type I (SAI) afferent system would have been most important in providing the coding information for the type of roughness discrimination used in the present study (spacing between raised elements > 0.2 mm), although the rapidly adapting type I (RAI) afferent system may also have contributed [11,25,26]. At the level of S1, inputs from SAI afferents are processed by cortical neurons that fire at higher rates for coarser textures, and the output of these neurons is thought to give rise to the percept of roughness [8,11,12,25,27]. Indeed, roughness has been shown to be coded intensively at the cortical level by neurons recorded in macaque monkey areas S1 and the secondary somatosensory cortex (S2), with a majority of these graded-response cells showing increased firing in response to rougher textured surfaces with larger groove widths [1,4-11]. Further, this activity has been shown to be minimally influenced by the difficulty of the texture discrimination (the percent difference in the spacing of raised elements), with such effects being minor relative to the observed changes in somatosensory cortical firing rate correlated with roughness [9,10].

Psychophysical data on response times and accuracy also suggest that roughness is coded intensively in the somatosensory cortex, while geometric properties such as relative orientation and position are likely resolved by comparing spatially distributed deformation patterns [12]. This has been shown to be a less efficient process due to the nesting of intensive coding within this computation, and the requirement for a spatial reference frame [12]. However, due to the intensive nature of the roughness code, both textures would likely have elicited more neural activity in S1 and S2, roughness-selective cells firing at higher frequencies relative to the spatially selective firing pattern indicative of the spatial location of a stimulus during pattern discrimination. For the pattern discrimination used in the present study, there would also have been less activity at the level of inputs from SAI afferents, since these afferents would have responded only to the edges in the pattern, which contained far fewer edges than the regularly ridged textures. The roughness discrimination, on the other hand, would have elicited much SA1 afferent activity given the spacing between the raised elements of the gratings used in the present study. RAI and PC afferent activity would also have been much lower during the pattern discrimination, due to the very low frequency of vibrations generated at the fingertip in response to the 2-D contours relative to those generated by the movement of the fingertip across the two textures [11,26-28]. The roughness discrimination thus also likely resulted in more peripheral afferent tactile activity than the geometric pattern discrimination. Whereas the relative roughness of a texture could in theory be extracted centrally as early as area 3b in S1, shape discrimination would likely require further processing in area 1 where speed of finger movement could be integrated with spatially distinct firing patterns to gain an overall representation of the pattern being scanned [29]. However, further processing in S2 or area 2 would likely not have been necessary for the simple 2-D pattern discrimination used in the present study [29]. The roughness discrimination would therefore have resulted in more somatosensory cortical activity overall, although this processing would have been simpler and more efficient than that required for the pattern discrimination.

It is possible that the intensity and diversity of peripheral afferent inputs, and the resulting activity in S1 and S2, could have determined motor cortical excitability during active tactile discrimination. The dense anatomical and functional connectivity between these regions and the primary motor cortex (M1) provides support for the presence of such bottom-up effects [30,31], and leads to the prediction of increased motor facilitation during the exploration of the densely packed raised elements composing the two textures as compared to during exploration of the relatively sparse elements (three circles) composing the two patterns. Indeed, task-specific increases in cutaneous afferent discharge have been shown to transiently increase both spinal and motor cortical excitability [32]. However, in the present study, only a small minority of individuals (3/18) showed evidence of greater MEP facilitation during active stroking of textured surfaces as compared to patterns. Therefore, simple bottom-up mechanisms associated with the degree and quality of tactile afferent feedback reaching M1 cannot account for the observed enhancement in task-related motor facilitation during the pattern discrimination.

Contribution of top-down central factors

The present findings seem compatible with a top-down central origin for the observed difference in motor facilitation. This explanation is in line with our previous findings on the importance of attention to discrimination for tactile-related MEP facilitation. In this regard, the possibility that lower attention levels could have contributed to the decreased MEP facilitation associated with the roughness task seems highly unlikely for the reasons given above concerning the trivial nature of the observed differences in performance between tasks and the absence of any relationship between performance and MEP amplitude. Instead of difference in attention level, the explanation may lie with neuroimaging observations of a relative increase in the activation of a dorsal processing stream for *action* during the haptic processing of geometric properties such as 2-D patterns, as compared to during processing of material properties such as textures [15,21,25,33]. However, it is important to note that both of these types of stimuli would activate both somatosensory processing streams, but to varying degrees [15]. For example, texture is also important for determining how tightly to grasp an object, providing information regarding the amount of friction between the skin and the surface [11]. Nevertheless, texture may be less important in providing information related to grasping and manipulating objects compared to object shape or 2-D patterns, which provide inputs that help to determine how the fingers and hand are shaped [15].

Neuroimaging evidence also indicates that primary visual and dorsal extra-striate multisensory areas, such as the LOC, are also selectively activated during haptic shape recognition and imagery, compared to texture discrimination and imagery [15-19]. Haptic texture discrimination and imagery, on the other hand, preferentially activate the ventrally located medial occipital complex (MOC) and the inferior extra-striate regions [16,19]. These activations reflected both bottom-up somatosensory inputs and top-down modulation from the posterior parietal cortex [15,24]. Furthermore, during haptic shape discrimination in particular, a selective network was revealed involving bottom-up inputs from the S1 to the IPS and LOC, and top-down modulation from these regions to S1 [34]. Comparing shape to texture processing in the visual modality also revealed similar patterns of differential brain activation during these two types tasks [35]. Indeed, recent evidence suggests that both visual and haptic peripheral inputs lead to the activation of the same central networks for texture and shape processing [36,37]. Thus, segregation between the processing of texture and shape in the haptic and visual modalities may reflect common ventral and dorsal visuo-haptic networks specializing in the processing of texture and shape, respectively [15].

On the other hand, it has also been argued that spatial properties and shape are not processed by the dorsal parietal areas thought to make up the somatosensory dorsal stream for action (*where/how*) at all, and that evidence for shape processing in parts of the IPS may indicate that some parts of this region may contribute to the ventral, and others to the dorsal, somatosensory processing streams [29]. However, it is important to note that this explanation is based on studies using familiar shapes and objects that would likely preferentially activate ventral areas given their emotional significance and ability to trigger past memories. In the present study, we were interested only in motor cortical excitability during haptic identification of simple 2-D patterns, without much contribution of these other emotional and long-term memory factors. Although shape and texture could both be used as inputs to both dorsal and ventral stream networks [38], the present findings indicate that pattern discrimination may increase activation of motor areas to a greater degree relative to roughness discrimination. However, it is important to note that the haptic system is generally more tuned to 3D object perception than to 2-D pattern discrimination, such that the ability to recognize real objects is much better than recognition of raised line drawings [13,39,40]. This can be explained in part by the fact that a broader range of exploratory procedures is available for 3D objects, which changes the quality and quantity of information obtainable during 3D haptic sensing. Thus a stronger dorsal involvement may be expected when observers discriminate 3D objects as compared to simple 2D lined patterns, and this comparison would be an interesting avenue for future study.

These findings might also be interpreted in the context of the requirement for increased mental resources for the pattern discrimination due to the less efficient nature of spatial processing in the cortex, relative to the intensive processing presumably used during the roughness discrimination [12,41]. It is possible that the type of spatial haptic processing required by the pattern discrimination could have primed the motor cortex for action more than the intensive type of processing likely used for the roughness discrimination [15]. Both the relative functional importance of the type of afferent input (for example for motor activities such as shaping the fingers for grasping) and the complexity associated with processing the stimuli at the cortical level likely contributed to the observed corticomotor facilitation during pattern discrimination.

Conclusions

This work builds on our previous findings of enhanced motor cortical excitability during active tactile discrimination of 2-D symbols versus finger movements alone [21], highlighting the importance of the specific haptic sensing demands with regards to the type of stimuli (pattern discrimination vs. roughness discrimination) for corticomotor facilitation. Together with this previous work, the present findings may help in developing functionally relevant tactile discrimination tasks for the re-education of hand function, tasks which would recruit frontal, parietal and occipital multisensory brain regions preferentially to facilitate finger movements. Indeed, the evidence presented here merits further investigation, in particular with regards to how task difficulty could interact with these task-type effects on M1 [15].

Methods

The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received an honorarium for his or her participation.

Participants

Twenty healthy young adults (10 males, 10 females, mean age ± SD, 22 ± 2.3 years) from the Ottawa area were included in the study. The majority of subjects were right-handed (16/20) according to the Edinburgh Handedness Questionnaire. Prior to the experimental session, all participants completed a medical questionnaire to ensure that there were no contra-indications to TMS and no antecedents of conditions likely to affect their performance in the tests. In addition, all participants were screened for the presence of undiagnosed peripheral neuropathies using a graduated Rydel-Seiffer tuning fork, which has been shown to be a valid and reliable instrument for assessing sensory nerve function in the extremities [42,43].

Training in tactile discrimination tasks

Participants were trained to perform two tactile discrimination tasks involving active movement of the right index finger over a surface. The training first focused on the production of consistent stroking actions with the index finger from right to left in sync with a tone lasting 1.8 s. Then participants were trained in the two discrimination tasks, which consisted of two-alternatives forced choice tasks. As illustrated in Figure 1, in one condition, the task consisted of discriminating between two patterns formed by three circular stickers (3.2 mm radius, 10 mm centre-to-centre) disposed on a small wooden block (13 cm × 8.5 cm). Participants were required to actively stroke the pattern in sync with the tone and to report the orientation of the last circle as being either in the upward or downward direction relative to the two other preceding circles. In the second task, participants performed a similar stroking action with the index finger but this time the task consisted of making a judgement about the relative roughness of gratings. Specifically, participants were required to discriminate between two fine grating surfaces (2 cm X 9 cm), each pasted on a wooden block. One grating was perceived as rougher than the other one, owing to a 25% increase in spatial period (1 mm vs. 0.75 mm, 0.2 mm constant ridge width). As for the pattern task, participants actively stroked the grating in sync with the tone to determine whether the surface was either the smoother (0.75 mm grating) or rougher (1 mm grating) of the two. In both tasks, participants received appropriate training prior to testing to achieve stable levels of performance and reliable discrimination (i.e., ≥75% correct). During both training and testing, participants were asked to verbally report their judgement about either the pattern or the roughness presented, immediately at the end of the trial, and were rapidly prompted to respond if no report had been made after the trial completion.

EMG recording and TMS

The recording techniques and TMS procedure have been reported previously (see [21]). Briefly, EMG activity was recorded using small auto-adhesive surface electrodes (10 mm diameter, Ag-AgCl) placed over the FDI of the right hand. EMG signals were amplified (100-500 μV/div), filtered (bandwidth, 16 Hz to 1 kHz), and digitized at 1 kHz (RMP-6004, Nihon-Kohden Corp.; BNC-2090, National Instrument Corp.). Magnetic stimulation was delivered with a Magstim 200 (Magstim Co. Dyfed, UK) connected to a figure-eight coil (70 mm loop diameter). To determine the optimal site to evoke MEPs in the contralateral hand muscles, the approximate location of the hand motor area on the left hemisphere was explored in 1 cm steps until reliable MEPs could be evoked in the target muscle (FDI). Following this procedure, the relaxed motor threshold was determined using the method advocated by Mills and Nithi [44]. Starting from supra-threshold intensity, the stimulator's output was gradually decreased in 1% steps until no MEP could be evoked for 10 consecutive stimuli. This TMS intensity corresponded to the lower threshold value.

From this point, the intensity was gradually increased until MEP's of at least 50 μV peak-to-peak amplitude could be evoked by ten consecutive stimuli. This latter intensity was recorded as the upper threshold value. The relaxed motor threshold was defined for each participant as the median intensity between the upper and lower threshold values. The TMS intensity was then fixed at 1.1 X threshold for the remainder of the experiment.

Recording of EMG during maximal voluntary contraction (MVC)

The procedure for EMG recording during the MVC is described in Master and Tremblay [21]. Briefly, maximal EMG values were measured for the FDI muscle at the beginning of the testing session. Participants were asked to push their index finger as hard as they could against the resistance provided by one of the experimenters for the duration of a tone lasting 3000 ms. The procedure was then repeated to get three MVC recordings.

Recording of MEP's during haptic sensing

Corticospinal excitability was tested under the two task conditions (pattern and roughness discrimination) with participants comfortably seated in a recording chair and blindfolded. The order of testing with the two tasks alternated between participants to control for potential confounders due to variations in attention level, motivation and fatigue [21,23]. In each task condition, trials were presented in a random order (n = 16) with the two alternatives for each task (ie., pattern discrimination: up/down;

roughness discrimination: rough/smooth) being equally probable. For both tasks (Figure 1), TMS was set to trigger towards the end of the stroking finger movement at 1.5s in the course of the 1.8 s trial. Sixteen trials of 1800 ms epochs were recorded under each task condition.

Rationale for task design and selection of tactile stimuli

Tactile stimuli were specifically chosen to control for the degree of difficulty between tasks so that task performance would allow sufficient time to investigate task-specific facilitation in response to TMS. For the pattern discrimination, the three circular stickers were spaced to span a natural index finger adduction movement during tactile exploration of surface features. Pilot testing indicated that movement duration of ~2 s was consistent with such a natural finger exploration. The spacing and offset of the last of the three circles for the pattern discrimination was determined by further pilot testing, asking participants if they were still sensing and making their decision regarding the displacement of the last circle upwards or downwards when TMS was delivered towards the end of the stroking movement. Similarly, the two textures for the roughness discrimination were selected on the basis of previous experiments indicating that discrimination of smooth gratings (≤ 1 mm spatial period, ridge-to-ridge distance) is more difficult than coarser gratings (1-3 mm, spatial period) [9]. The two grating surfaces therefore consisted of relatively smooth gratings whose spatial period differed by 25% (i.e., 0.75 vs. 1 mm). As shown by Sinclair & Burton [9], such a difference in spatial period between gratings is relatively hard to detect by observers when allowed only one single stroke per trial. Pilot testing confirmed that participants were still sensing the texture (as judged by verbal reports) when TMS was delivered towards the end of the movement. Thus, the 1.5 s delay chosen for the time of TMS delivery provided an optimal time point to examine MEP facilitation, as participants were actively engaged in haptic sensing for surface features (either spatial orientation or roughness).

Analysis of MEP data and EMG traces

Although a total of 20 participants were initally included in the analysis, careful re-examination of individual recordings revealed technical errors in the settings (trial duration was not properly adjusted) that invalidated the data for two participants (one male, one female). Therefore the MEP and EMG analysis was performed on the remaining 18 participants (9 males, 9 females, 4 left handed). The details for the procedure for analysis of MEP data are given in Master & Tremblay [21]. Briefly, MEP amplitude (peak to peak), latency, and EMG traces were measured off-line and averaged to derive mean individual values. For the MVC, the EMG signals produced during the last 2000 ms epoch were rectified and averaged to get a maximal rectified average EMG value. For the background EMG activity during test trials, the signal in the 500 ms window preceding the TMS pulse was rectified on a trial-by-trial basis for each participant, and these rectified values were then averaged and expressed as a percentage of each particiant's maximal rectified average EMG value (see Figure 1B and 1C). Finally, the SP was estimated as the interval from MEP onset to the first sign of EMG return.

Statistical methods

A paired-samples t-test was performed on EMG levels (expressed as a percent of each participant's MVC) recorded during the two tasks, pattern discrimination and roughness discrimination. MEP amplitudes were normally distributed (Shapiro-Wilk $P > 0.05$) and did not need to be transformed. Four repeated measures ANOVAs were used to determine the impact of task condition (pattern/roughness discrimination) and gender on each dependent variable: 1) discrimination performance,2) MEP amplitude, 3) MEP latency, and 4) SP duration. The significance level was set at $P < 0.05$ for all tests. All tests were performed using SPSS software version 17.0 for Windows® (Chicago, IL, USA). Figures were prepared using GraphPad Prism version 5.02 for Windows (GraphPad Software, San Diego California USA, http://www.graphpad.com).

Acknowledgements

The authors wish to thank all participants for their time and patience during testing. Special thanks to Sonia Hussain for her help with data collection and analysis. This work will serve as a partial fulfilment for a doctoral thesis in experimental psychology by Sabah Master. This project was made possible in part by support from the Élisabeth Bruyère Research Institute.

Author details

[redacted]

Authors' contributions

SM participated in the design of the study, carried out the behavioral testing, performed the statistical analysis and drafted the manuscript. FT conceived of the study, and participated in its design and coordination and drafted the manuscript. Both authors read and approved the manuscript and its revisions.

Received: 19 August 2010 Accepted: 25 November 2010
Published: 25 November 2010

References

1. Hsiao S, Johnson KO, Twombly IA: **Roughness coding in the somatosensory system.** *Acta Psychol* 1993, **84(1)**:53-67.
2. Randolph M, Semmes J: **Behavioral consequences of selective subtotal ablations in the postcentral gyrus of Macaca mulatta.** *Brain Res* 1974, **70(1)**:55-70.
3. Iwamura Y, Tanaka M: **Postcentral neurons in hand region of area 2: their possible role in the form discrimination of tactile objects.** *Brain Research* 1978, **150(3)**:662-666.

4. Darian-Smith I, Sugitani M, Heywood J, Karita K, Goodwin A: Touching Textured Surfaces: Cells in Somatosensory Cortex Respond Both to Finger Movement and to Surface Features. *Science* 1982, **218(4575)**:906-909.
5. Pruett JR Jr, Sinclair RJ, Burton H: Response Patterns in Second Somatosensory Cortex (SII) of Awake Monkeys to Passively Applied Tactile Gratings. *J Neurophysiol* 2000, **84(2)**:780-797.
6. Pruett JR Jr, Sinclair RJ, Burton H: Neural Correlates for Roughness Choice in Monkey Second Somatosensory Cortex (SII). *J Neurophysiol* 2001, **86(4)**:2069-2080.
7. Jiang W, Tremblay F, Chapman CE: Neuronal encoding of texture changes in the primary and the secondary somatosensory cortical areas of monkeys during passive texture discrimination. *J Neurophysiol* 1997, **77(3)**:1656-1662.
8. Chapman CE, Tremblay F, Jiang W, Belingard L, Meftah E-M: Central neural mechanisms contributing to the perception of tactile roughness. *Behav Brain Res* 2002, **135(1-2)**:225-233.
9. Sinclair RJ, Burton H: Neuronal activity in the primary somatosensory cortex in monkeys (Macaca mulatta) during active touch of textured surface gratings: responses to groove width, applied force, and velocity of motion. *J Neurophysiol* 1991, **66(1)**:153-169.
10. Sinclair RJ, Burton H: Neuronal activity in the second somatosensory cortex of monkeys (Macaca mulatta) during active touch of gratings. *J Neurophysiol* 1993, **70(1)**:331-350.
11. Diamond ME: Texture sensation through the fingertips and the whiskers. *Curr Opin Neurobiol* 2010, **20(3)**:319-327.
12. Lederman SJ, Klatzky RL: Relative Availability of Surface and Object Properties during Early Haptic Processing. *J Exp Psychol Hum Percept Perform* 1997, **23(6)**:1680-1707.
13. Magee LE, Kennedy JM: Exploring pictures tactually. *Nature* 1980, **283(5744)**:287-288.
14. Lederman SJ, Klatzky RL: Extracting object properties through haptic exploration. *Acta Psychol (Amst)* 1993, **84(1)**:29-40.
15. Stilla R, Sathian K: Selective visuo-haptic processing of shape and texture. *Hum Brain Mapp* 2008, **29(10)**:1123-1138.
16. Newman SD, Klatzky RL, Lederman SJ, Just MA: Imagining material versus geometric properties of objects: an fMRI study. *Cognitive Brain Research* 2005, **23(2-3)**:235-246.
17. Amedi A, Jacobson G, Hendler T, Malach R, Zohary E: Convergence of Visual and Tactile Shape Processing in the Human Lateral Occipital Complex. *Cerebral Cortex* 2002, **12(11)**:1202-1212.
18. Amedi A, Malach R, Hendler T, Peled S, Zohary E: Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience* 2001, **4(3)**:324.
19. Deibert EMD, Kraut MMDP, Kremen SBA, Hart JJMD: Neural pathways in tactile object recognition. *Neurology* 1999, **52(7)**:1413-1417.
20. Oliver P, Tremblay F: Selective increase in corticospinal excitability in the context of tactile exploration. *Somatosens Mot Res* 2009, **26(2)**:64-73.
21. Master S, Tremblay F: Task-specific increase in corticomotor excitability during tactile discrimination. *Exp Brain Res* 2009, **194(2)**:163-172.
22. Master S, Tremblay F: Selective increase in motor excitability with intraactive (self) versus interactive touch. *NeuroReport* 2010, **21(3)**:206-209.
23. Master S, Tremblay F: Tactile-dependant corticomotor facilitation is influenced by discrimination performance in seniors. *Behav Brain Funct* 2010, **6(1)**:16.
24. Deshpande G, Hu X, Stilla R, Sathian K: Effective connectivity during haptic perception: A study using Granger causality analysis of functional magnetic resonance imaging data. *NeuroImage* 2008, **40(4)**:1807-1814.
25. Hollins M: Somesthetic Senses. *Annu Rev Psychol* 2010, **61(1)**:243-271.
26. Hollins M, Bensmaia SJ: The coding of roughness. *Can J Exp Psychol* 2007, **61(3)**:184-195.
27. Johnson KO, Yoshioka T, Vega-Bermudez F: Tactile functions of mechanoreceptive afferents innervating the hand. *J Clin Neurophysiol* 2000, **17(6)**:539-558.
28. Goodwin AW, Wheat HE: Sensory signals in neural populations underlying tactile perception and manipulation. *Annu Rev Neurosci* 2004, **27**:53-77.
29. Hsiao S: Central mechanisms of tactile shape perception. *Curr Opin Neurobiol* 2008, **18(4)**:418-424.
30. Matelli M, Camarda R, Glickstein M, Rizzolatti G: Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J Comp Neurol* 1986, **251(3)**:281-298.
31. Friedman DP, Murray EA, O'Neill JB, Mishkin M: Cortical connections of the somatosensory fields of the lateral sulcus of macaques: evidence for a corticolimbic pathway for touch. *J Comp Neurol* 1986, **252(3)**:323-347.
32. Shibuya S, Ohki Y: Cutaneous inputs can activate the ipsilateral primary motor cortex during bimanual sensory-driven movements in humans. *J Neurophysiol* 2004, 00937.02003.
33. Li Hegner Y, Lee Y, Grodd W, Braun C: Comparing tactile pattern and vibrotactile frequency discrimination: a human FMRI study. *J Neurophysiol* 2010, **103(6)**:3115-3122.
34. Peltier S, Stilla R, Mariola E, LaConte S, Hu X, Sathian K: Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. *Neuropsychologia* 2007, **45(3)**:476-483.
35. Cavina-Pratesi C, Kentridge RW, Heywood CA, Milner AD: Separate Processing of Texture and Form in the Ventral Stream: Evidence from fMRI and Visual Agnosia. *Cereb Cortex* 2010, **20(2)**:433-446.
36. Whitaker TA, Simões-Franklin C, Newell FN: Vision and touch: Independent or integrated systems for the perception of texture? *Brain Res* 2008, **1242**:59-72.
37. Tal N, Amedi A: Multisensory visual-tactile object related network in humans: insights gained using a novel crossmodal adaptation approach. *Exp Brain Res* 2009, **198(2)**:165-182.
38. Dijkerman HC, de Haan EHF: Somatosensory processes subserving perception and action. *Behav Brain Sci* 2007, **30(2)**:189-201.
39. Loomis JM, Klatzky RL, Lederman SJ: Similarity of tactual and visual picture recognition with limited field of view. *Perception* 1991, **20(2)**:167-177.
40. Klatzky RL, Lederman SJ, Metzger VA: Identifying objects by touch: An "expert system". *Perception & Psychophysics* 1985, **37(4)**:299-302.
41. Lederman SJ, Klatzky RL: Haptic perception: A tutorial. *Atten Percept Psychophys* 2009, **71(7)**:1439-1459.
42. Kastenbauer T, Sauseng S, Brath H, Abrahamian H, Irsigler K: The value of the Rydel-Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer. *Diabet Med* 2004, **21(6)**:563-567.
43. Pestronk A, Florence J, Levine T, Al-Lozi MT, Lopate G, Miller T, Ramneantu I, Waheed W, Stambuk M: Sensory exam with a quantitative tuning fork: rapid, sensitive and predictive of SNAP amplitude. *Neurology* 2004, **62(3)**:461-464.
44. Mills KR, Nithi KA: Corticomotor threshold to magnetic stimulation: normal values and repeatability. *Muscle Nerve* 1997, **20(5)**:570-576.

doi:10.1186/1471-2202-11-149
Cite this article as: Master and Tremblay: Differential modulation of corticospinal excitability during haptic sensing of 2-D patterns vs. textures. *BMC Neuroscience* 2010 **11**:149.

Master and Tremblay *Behavioral and Brain Functions* 2010, **6**:16
http://www.behavioralandbrainfunctions.com/content/6/1/16

BEHAVIORAL AND BRAIN FUNCTIONS

RESEARCH **Open Access**

Tactile-dependant corticomotor facilitation is influenced by discrimination performance in seniors

Sabah Master[1], François Tremblay[2*]

Abstract

Background: Active contraction leads to facilitation of motor responses evoked by transcranial magnetic stimulation (TMS). In small hand muscles, motor facilitation is known to be also influenced by the nature of the task. Recently, we showed that corticomotor facilitation was selectively enhanced when young participants actively discriminated tactile symbols with the tip of their index or little finger. This tactile-dependant motor facilitation reflected, for the large part, attentional influences associated with performing tactile discrimination, since execution of a concomitant distraction task abolished facilitation. In the present report, we extend these observations to examine the influence of age on the ability to produce extra motor facilitation when the hand is used for sensory exploration.

Methods: Corticomotor excitability was tested in 16 healthy seniors (58-83 years) while they actively moved their right index finger over a surface under two task conditions. In the tactile discrimination (TD) condition, participants attended to the spatial location of two tactile symbols on the explored surface, while in the non discrimination (ND) condition, participants simply moved their finger over a blank surface. Changes in amplitude, in latency and in the silent period (SP) duration were measured from recordings of motor evoked potentials (MEP) in the right first dorsal interosseous muscle in response to TMS of the left motor cortex.

Results: Healthy seniors exhibited widely varying levels of performance with the TD task, older age being associated with lower accuracy and vice-versa. Large inter-individual variations were also observed in terms of tactile-specific corticomotor facilitation. Regrouping seniors into higher (n = 6) and lower performance groups (n = 10) revealed a significant task by performance interaction. This latter interaction reflected differences between higher and lower performance groups; tactile-related facilitation being observed mainly in the former group. Latency measurements and SP durations were not affected by task conditions.

Conclusions: The present findings provide further insights into the factors influencing task-dependant changes in corticomotor excitability in the context of aging. Our results, in particular, highlight the importance of adjusting task demands and controlling for attention when attempting to elicit task-specific motor facilitation in older persons engaged in fine manual actions. Such information could be critical in the future for planning interventions to re-educate or maintain hand function in the presence of neurological impairments.

Background

In everyday life, we often rely on our sense of touch when it comes to appreciating object and surface properties, as when searching for keys inside the pocket. Such a task typically engages the finger in fine exploratory movements to detect specific tactile features, which can then lead to fast object recognition [1]. While trivial in appearance, tactile discrimination (TD) tasks have been shown to engage a large cortical network involving primary and secondary motor and sensory areas, as well as, associative regions of the frontal and parietal lobes [2-5]. Recently [6], we investigated task-dependant changes in corticomotor excitability with transcranial magnetic stimulation (TMS) when young adults actively moved their index or little finger over a surface. Our results showed a large selective enhancement in

---

[redacted]

corticomotor excitability when participants discriminated between surface features, as opposed to simply moving the finger over a blank surface. Further to this, we showed that such tactile-dependant extra facilitation was largely abolished when participants performed a concurrent distraction task. This suggested that task influences, linked with the increased attentional demands associated with tactile sensing, were primarily responsible for the observed extra facilitation.

In the present report, we attempted to extend those observations on tactile-dependant increase in corticomotor excitability to healthy seniors to investigate whether age-related alterations in sensorimotor capacities and cognitive functions would affect the ability to produce motor facilitation in the context of active finger movements. Previous reports in this regard have produced mixed results. For instance, D'Esposito et al. [7] examined task-dependant changes in motor cortical activation using functional magnetic resonance imaging (fMRI) and reported an age-related decrease both in the number of subjects showing detectable activation and in the volume of activation during performance of a button press task. This suggested a decline with age in the ability to activate the motor cortex during simple finger movement execution. The fact that older subjects also displayed higher levels of background noise might have affected the results, however. The issue of age-related differences in motor activation was further examined by McConnell et al. [8] who combined TMS with fMRI to measure motor cortical activity induced either by volitional movement or by direct stimulation using TMS. Their results revealed no differences in haemodynamic responses with age for both voluntary-induced and TMS-induced finger movements, indicating a preserved capacity to drive the corticomotor system in normal aging. Similar results were reported by Sale and Semmler [9] who examined right-left differences in corticomotor excitability in young and old adults. Their results showed that older adults had preserved MEP responses in the right hand, although MEP amplitude tended to be reduced in the left hand. No such bilateral difference was found in young adults. Interestingly, they observed that performance of a complex hand action (using gardening shears, as opposed to a simple action) produced large MEP facilitation in the right hand of old adults, whereas no such facilitation could be elicited in the left hand. The authors attributed this asymmetry in the older group to a lifetime preferential use of the dominant hand in executing fine motor tasks.

Using a different task paradigm, Leonard and Tremblay [10] showed recently that older adults were capable of producing corticomotor facilitation in their dominant hand in the context of overt and covert action execution, i.e. during observation, imagination and imitation of a complex hand action (scissoring action). This preserved capacity for motor facilitation in older adults was however less specific than that seen in young adults in terms of muscle selectivity; older adults showing facilitation in both the task and non-task relevant muscles. This loss in selectivity was thought to reflect compensatory mechanisms in older adults whereby performance of simple motor actions often leads to extra activation in areas that are not normally recruited in younger subjects, such as the pre-supplementary motor area, predorsal premotor area, rostral cingulate, and prefrontal cortex [11-14]. For Heuninckx et al. [11], such a wide activation extending to associative areas of the cortex reflected the need for older adults to exert greater cognitive control over on-going actions to maintain performance at the desired level [see also [15]]. This penetration of cognition into motor control with age raises the issue of resource allocation when task demands are increased, given the expected decline in selective attention and working memory with aging [16,17]. With limited resources, older participants might be particularly challenged when hand movements require fine control such as when the finger is used to explore tactile features for recognition. As stated earlier, in the present report, we attempted to address this issue using TMS to measure task-dependant corticomotor facilitation elicited in a demanding task paradigm wherein participants had to actively move their index finger at a prescribed speed over a surface with or without constraints for tactile sensing at the fingertip.

Methods

The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received an honorarium for his or her participation.

The methods and procedures have been detailed previously in our report [see [6]] in young adults, where we used the same experimental paradigm as in the present experiment. Briefly, corticomotor facilitation was tested in a group of healthy seniors (8 female, 8 male; mean age: 68.0 years, range: 58-83 years, 15 right-handers) using a Magstim 200 stimulator (Magstim Co. Dyfed, UK) connected to a figure-eight coil (70 mm loop diameter). Before testing participants were screened for contra-indications to TMS and for the presence of sensory neuropathies using a graduated Rydel-Seiffer tuning fork [18,19]. Corticomotor excitability was determined by monitoring changes in the amplitude and latency of motor evoked potentials recorded in the first dorsal interosseous (FDI) using surface electrodes (10 mm diameter, Ag-AgCl). We intended initially, as in our previous study in young adults, to include observations on *adductor digiti minimi*, but this turned out to be impossible because most participants could not perform the task properly with the little finger. Electromyographic (EMG) signals were amplified and filtered (5 Hz to 5 kHz) using a polygraph amplifier (RMP-6004, Nihon-Kohden Corp.) and stored on computer (digitized @ 1 kHz, BNC-2090, National Instrument Corp.) for off-line analyses.

Testing of task-related corticomotor facilitation was performed with participants blindfolded and seated in a recording chair. Prior to testing, participants underwent a period of familiarization with the task conditions. During that period, they were trained to produce rhythmic index finger to and fro movements in sync with metronome ticks at 0.8 Hz for 5 s. Then, participants were introduced to the two task conditions: 1) no discrimination (ND) and 2) tactile discrimination (TD). In the ND condition, participants simply moved their finger in sync with the ticks on a blank wooden block. In the TD condition, participants were required as they moved their finger to attend to the position of two tactile symbols (hat and boat) formed by two half-circle stickers (3.2 mm radius, 16 mm apart) pasted on a wooden block (see Figure 1). Participants had to report the location (right or left) of one of the tactile symbols in each trial within a block of 16 trials. Once familiarized with the task conditions, corticomotor excitability was tested in each participant under the two task conditions (TD and ND), the order of testing in the two being counterbalanced across participants. Corticomotor excitability was tested during each task by delivering a TMS pulse at 110% of the relaxed motor threshold at 3.75 s in the course of the task execution. This timing was selected based on our previous report in young adults and corresponded to the 3rd tick in the sequence of cyclic movements when the FDI was actively moving the index finger into abduction (see Figure 1). Sixteen trials of 1000 ms epochs were recorded under each task condition. MEP amplitude, latency, and EMG traces were measured off-line and averaged to derive mean individual values. The EMG activity in the 500 ms preceding the TMS pulse was rectified, averaged and expressed as a percentage of the maximum voluntary contraction. Finally, the silent period (SP) was estimated as the interval from MEP onset to the first sign of EMG return.

A paired-samples t-test was performed on background EMG levels (% MVC) recorded during the two tasks, TD and ND. As suggested by Nielsen [20] and Schmidt et al. [21], MEP amplitudes were log-transformed to get a normal distribution (Shapiro-Wilk $P > 0.1$). Repeated measures analyses of variance (ANOVAs) were then performed on the dependent variables of MEP log-amplitude, MEP latency, and SP duration with task condition (TD, ND) as the repeated factor and discrimination performance as the between-subjects factor. The latter factor was entered into the ANOVA as a dichotomized variable (high vs. low) after examining the distribution of individual performance values with respect to age (see Results). The level of significance was set at $P < 0.05$. All tests were performed using SPSS software version 17.0 for Windows™ (Chicago, IL, USA). Figures were prepared using GraphPad Prism version 5.02 for Windows (GraphPad Software, San Diego California USA, http://www.graphpad.com). All values are reported as mean ± 1 SD.

Results

Task performance

Participants exhibited various levels of performance in discriminating between the two symbols while performing the TD task (i.e., from perfection down to chance level; mean correct 65 ± 13%). Further inspection of individual performance data indicated that the older seniors generally experienced greater difficulty in performing the task than younger seniors. This inverse association is clearly apparent in Figure 2A, where corresponding individual performance data have been plotted with respect to age. Pearson's correlation confirmed that the two factors were indeed inversely related. On the basis of this relationship and given the difficult nature of the TD task, participants were regrouped into two subsets, i.e. those with a relatively high performance (≥ 69% correct, mean 77 ± 12%) and those with a relatively low performance (< 63% correct, mean 58 ± 7%). As evident in Figure 2B, the two subsets also reflected the age difference, the lower performance group being, on average, seven years older (71 ± 8 yrs) than the higher performance group (64 ± 4 yrs; $t_{14} = 1.99$, $p = 0.03$).

While the TD task proved to be challenging perceptually for seniors, the performance of the task at the motor level was not different from that seen when executing the ND task. A typical example of EMG activity recorded in both task conditions is shown in Figure 3A. In terms of background muscle activation, the two tasks elicited relatively low levels of EMG activity in the FDI (mean TD, 11.8%; ND, 14.8% of the MVC). As in our previous study using the TD paradigm in young adults [6], no difference in EMG levels was found between the two tasks ($t_{15} = -1.09$, $p = 0.29$).

Task-specific facilitation

As observed for the discrimination performance, senior participants also exhibited a great deal of variability in terms of modulation of MEP amplitude in response to changes in task conditions (mean relative increase, 21 ± 39%). In spite of this variability, a significant main

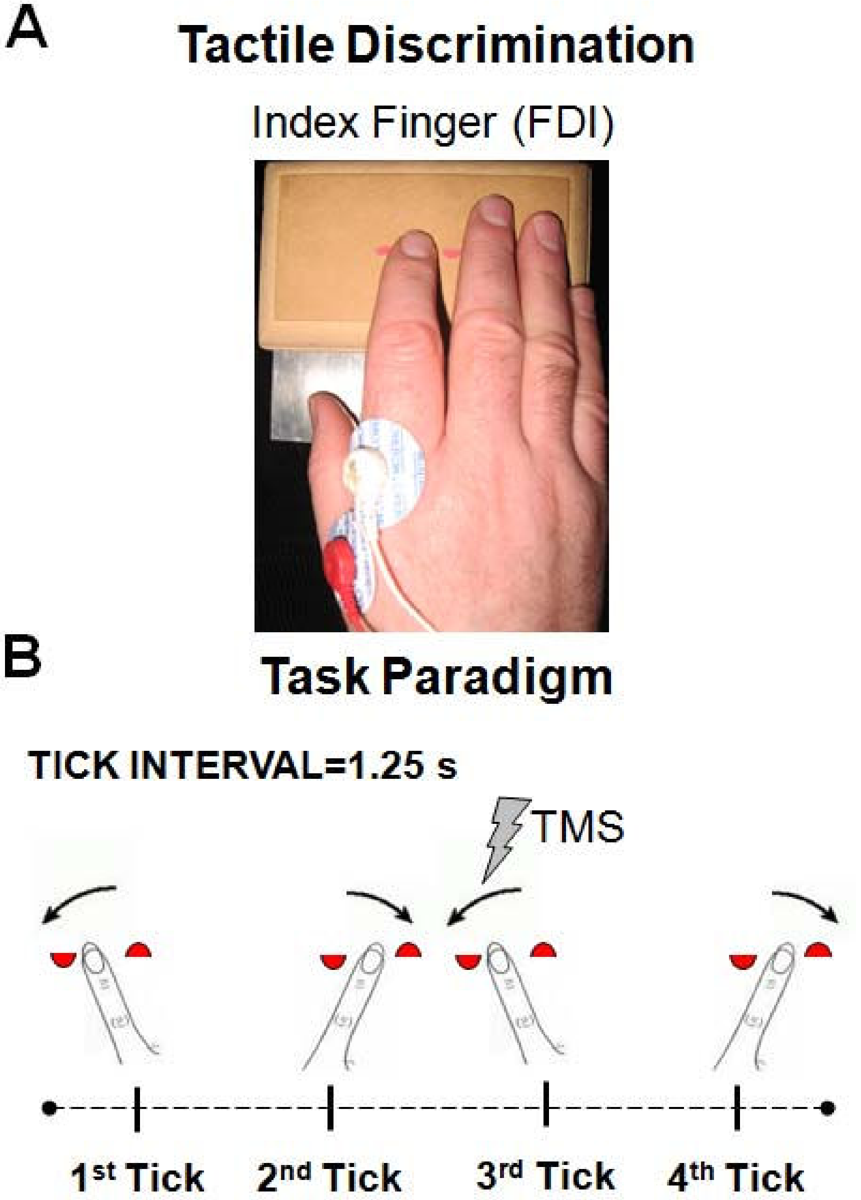

Figure 1 Experimental set-up and schematic illustration of the TD paradigm. A. Experimental set-up showing the position of the index finger just before TMS pulse delivery during performance of the tactile discrimination (TD) task and the location of the recording surface electrodes. B. Schematic illustration of the task paradigm used to assess motor evoked potential (MEP) facilitation. In both the TD and non discrimination (ND) tasks, participants were trained to produce rhythmic finger to and fro movements in sync with the sound of a metronome at a frequency of 0.8 Hz for 5 s. In the TD condition, the finger moved over a surface containing two tactile symbols (half circle stickers forming either a "Boat" or a "Hat", 3.2 mm radius, 16 mm apart) and participants were asked to report the location of one of the specified symbols at the end of the trial. The ND task was identical in performance to the TD task except that the finger moved over a blank surface. In each trial, the TMS pulse was set to trigger at a time corresponding to the 3rd tick (3.75 s) in the trial when the index finger was moving towards abduction.

effect of task conditions on MEP amplitude was detected in the ANOVA ($F_{1,14}$ = 5.35, p = 0.04). The ANOVA also revealed a significant task × performance interaction ($F_{1,13}$ = 5.82, p = 0.03), which indicated that performance levels (high vs. low) did influence observed task-related variations in MEP amplitude. In fact, this interaction accounted for 26% of the overall variance in MEP amplitude. Typical examples of MEP modulation seen under the two task conditions are illustrated in Figure 3B, where the contrast between high and low performance is easily apparent. The influence of discrimination performance on MEP amplitude can also be appreciated in Figure 4, which compares the mean tactile-related change in MEP amplitude (TD/ND) in the two

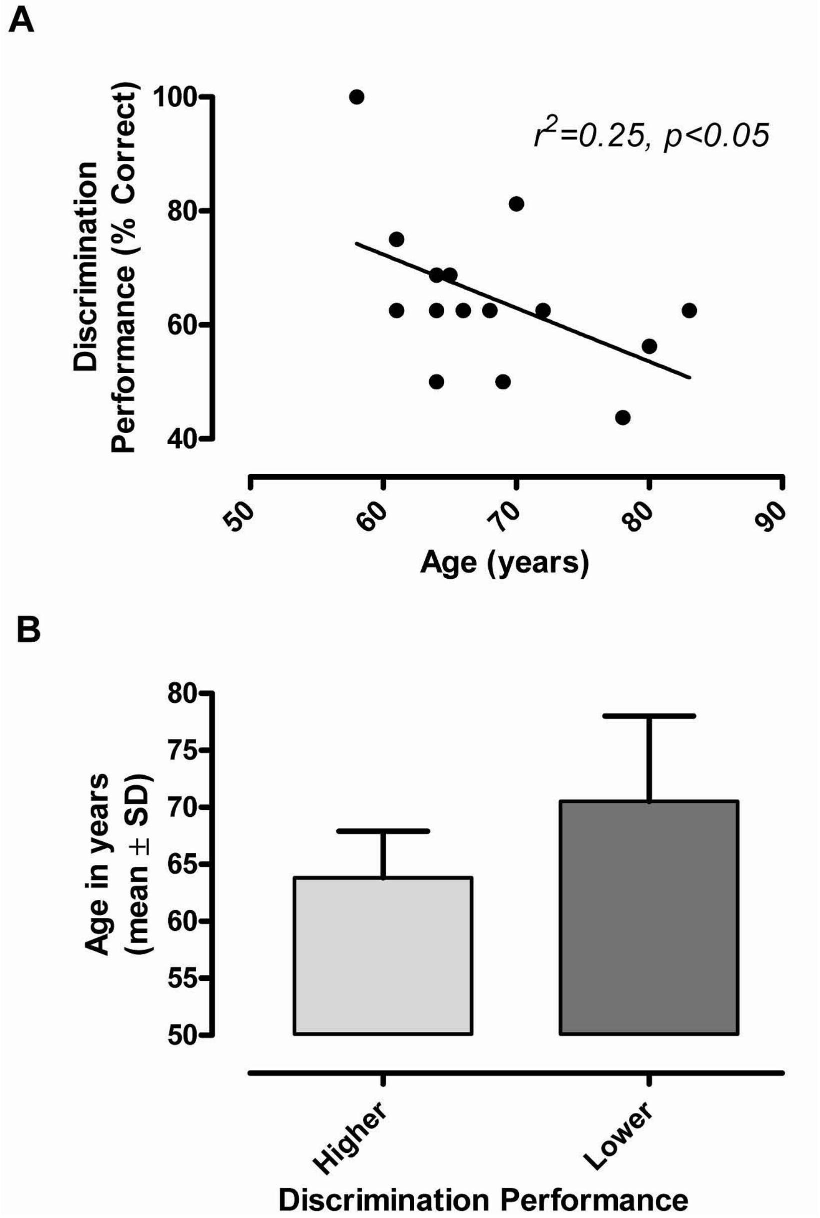

Figure 2 Age and task performance. A. Scatterplot showing the inverse association between performance in the TD task and age (r value represents Pearson's correlation coefficient). B. Comparison of the mean age of participants after allocation to either a higher performance (≥ 69% correct, n = 6) or a lower performance group (<63% correct, n = 10). Note that individuals with higher discrimination performance were significantly younger (64 ± 4.1 yrs) than those (71 ± 7.5) with lower performance (t_{14} = 1.99, p = 0.03).

performance groups. Latency (TD, 20.2 ± 2.2 ms; ND, 20.1 ± 1.6 ms) and SP durations (TD, 70 ± 29 ms, ND, 77 ± 30 ms) did not differ between task conditions, and no interaction was found with discrimination performance ($F_{1,14} < 1$, $p > 0.1$).

Discussion

In the present report, we extend our previous observations on task-specific motor facilitation in young adults [6] to healthy seniors. In this respect, our results reveal important differences between our former observations in young adults and the way seniors responded to increasing task demands in the context of this experiment. First, seniors tended to show much larger variability in terms of their ability to cope with increasing task demands, i.e. from simple auditory paced rhythmic finger movements to rhythmic finger movement combined with tactile sensing. Second, age greatly influenced task

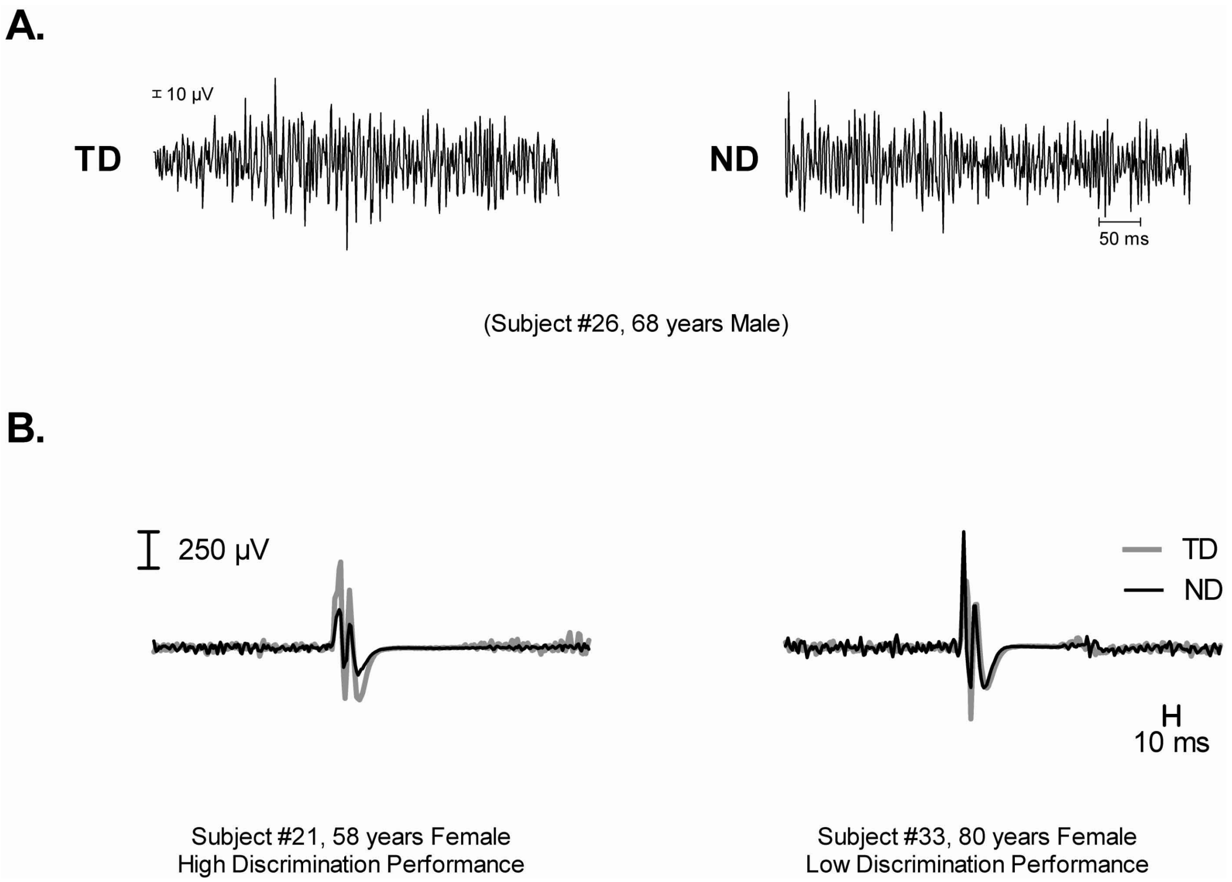

Figure 3 Electromyographic (EMG) activity and MEP traces. A. typical example of electromyographic (EMG) activity elicited in the FDI muscle during performance of the two finger movement tasks (discrimination, TD; non discrimination, ND). Note the similarity between the two tasks (TD vs. ND) in terms of EMG patterns produced. B. Examples of task-specific facilitation recorded in the FDI in two individuals, one having high (100%) and another having low (56%) discrimination performance. Note the task-related increase in MEP amplitude in the TD condition in the younger senior with high discrimination performance, and the similarity in MEP amplitudes between the TD and ND conditions in the older senior with low discrimination performance.

performance, which in turn, affected levels of MEP facilitation.

The issue of greater variability in behavioural and neurophysiological responses with advancing age is a common theme in aging studies. In the present study, participants in the older age group tended to exhibit lower performance with accompanying low or absent MEP facilitation under the TD condition, when compared to younger seniors. In our previous work on tactile sensation and aging, we observed a similar pattern of results with more variable performance and greater decline in tactile acuity being observed for individuals over 75 years [22,23]. Such variability was also observed in a TMS study by Peinemann et al. [24] looking at levels of intra-cortical inhibition (ICI) and intra-cortical facilitation (ICF) elicited in older adults in response to paired pulse stimulation. They noticed, much like in the present study, a differential pattern of modulation in a subgroup of older participants aged >60 years, where the expected increase in ICF was actually replaced by a decline. An increase in MEP amplitude variability with age was also reported by Pitcher et al [25], when examining variations in MEP size with increasing TMS intensities (i.e., stimulus-response curve). Interestingly, they found that the age-related difference in stimulus-response profiles, reflecting the strength of corticospinal projections, was evident only in older female subjects but not in male subjects; again illustrating the inherent variability associated with aging. Thus, it is not uncommon in aging studies to find subsets of participants exhibiting different patterns of responses, as we found in the present study.

Before addressing the issue as to why certain participants showed task-specific facilitation, while others did not, it is important to ascertain that motor over-activity was not a factor in limiting the ability to produce

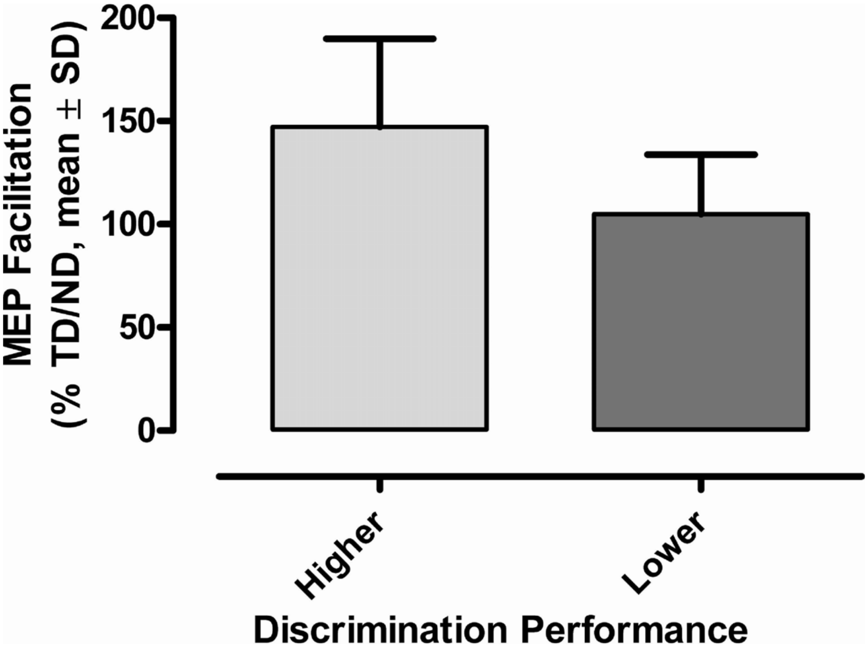

Figure 4 Tactile-related MEP increase and performance level. Mean tactile-related changes in MEP amplitude are shown for the two subsets of participants, i.e. higher (n = 6) and lower (n = 10) performance groups. Each bar represents the average of individual changes in MEP amplitude measured under the TD task using the ND task as a baseline (i.e., %TD/ND).

corticomotor facilitation. This question is critical since seniors tend to show compensatory activity and higher activation levels in both motor and non motor areas of the cortex even when executing simple finger movements [11-14,26,27]. This possibility is unlikely, however, given that no participants actually showed signs of MEP saturation under the TD task condition. In fact, MEP's were actually reduced in amplitude in all but two of the participants who failed to show extra facilitation with tactile sensing. The fact that the finger movements in the two tasks were associated with relatively low levels of background EMG activity likely contributed to limit the level of motor activation, associated with the finger movements. In fact, our observations of task-related MEP facilitation with tactile sensing in seniors fit with the recent findings of Van Impe et al. [28] who measured cortical activation during a hand-foot coordination task in older adults. Their results showed that, although age was associated with activation of a larger brain network, this activation reflected increased attentional deployment to enhance somatosensory processing and integration rather than increased motor cortical activity. Thus, other factors, besides motor over-activity, likely contributed to the variations observed in MEP amplitude under the two task conditions in our group of seniors.

We have already mentioned that performance in the tactile task largely influenced MEP facilitation in our group of seniors. In fact, the present results show that the degree of task-specific facilitation was linked with the actual perceptual performance of seniors in discriminating the tactile symbols; a higher performance being associated with large MEP facilitation, while a lower performance was not. In many respects, the present results are reminiscent of our previous findings in young adults, where high performance (mean, 84% correct) was associated with substantial tactile-related MEP facilitation (mean relative increase, 45%), while the same facilitation was abolished when attention was diverted away from the tactile inputs by performance of a concurrent cognitive task. Together, these observations strongly suggest that the observed task-related corticomotor facilitation seen during tactile sensing is central in origin, reflecting enhanced excitability mediated by top-down attentional mechanisms acting on the motor cortex to facilitate task performance. This idea is further supported by recent findings showing a participation of anterior motor cortical area 4 in complex somatosensory processing [29], highlighting the importance of finely tuned central motor control during the execution of tactile exploratory tasks.

In light of these observations, the inverse association between age and task performance can be explained, in the case of older seniors, by a difficulty in attending to the tactile stimuli as the finger moved over the surface. The converse can be said for younger seniors, where effective coping with task demands likely allowed them to selectively attend to the tactile symbols as the index finger moved, resulting in higher discrimination performance and MEP facilitation during tactile sensing. However, it is still possible that a greater degree of peripheral decline in tactile sensibility in older seniors might have affected their ability to sense the tactile spatial features when touching the stimuli. Two arguments mitigate this possibility, however. First, all participants were screened for the presence of sensory deficits at the outset of the study using validated vibratory thresholds as an index of tactile sensation. Second, the spatial dimensions of the tactile symbols (3.2 mm radius, 0.18 mm relief) were in the range of easily detectable spatial stimuli, even for individuals advanced in age [23]. In fact, the great majority of participants experienced no difficulties in discriminating between the two tactile symbols in the familiarization period before formal testing. It seems more likely, as we suggested above, that ineffective coping mechanisms in the context of multiple task demands was responsible for the poor performance in older seniors. Such an explanation would be consistent with observations suggesting that deficits in top-down modulation mechanisms are critical in leading to cognitive decline in normal aging; older adults being particularly impaired in their ability to selectively suppress task-irrelevant information [30]. As recently shown by Gazzeley et al [31], such an inability seems to result from excessive attention towards distracting stimuli early in the sensory encoding process, resulting in lower processing speed and decreased performance (i.e., longer response time and lower accuracy). In the context of our TD task, the sound of metronome ticks in the background could have drawn too much attention on the part of certain older seniors to the detriment of the tactile information arising from contact with the symbols; leading to low discrimination performance and inefficient task-related corticomotor facilitation.

The deficit in top-down modulation with age is thought to correspond to changes in the frontal and parietal lobes and the resulting decreased connectivity of the anterior-to-posterior network, in particular the frontal associative areas and the motor cortex [32,33]. In support of this argument, Rowe [27] showed recently that cortical connectivity between the contralateral premotor and prefrontal cortices was impaired during an externally paced randomized button-pressing task in seniors. Indeed, the anterior-to-posterior network would have been important for the TD task, given that it is involved in haptic sensing [34-36] and attention to action [37]. A recent review of the literature on somatosensory-motor interactions by Bressler [38] supports the idea that attentional mechanisms are part of the large-scale, synchronized cortical network controlling motor activity, and can mediate the critical relationship between the somatosensory and motor cortices.

Limitations

The present results are based on a relatively small sample of healthy seniors, which might not be representative of the elderly population in general. In addition, the degree of difficulty associated with the TD task proved to be very challenging for some seniors. It would be important for future studies investigating task-related motor facilitation in older adults to control for the degree of task difficulty, providing some adjustments when necessary, to account for the increased variability generally observed in this population in terms of perceptual performance.

Conclusions

In conclusion, the present findings provide further insights into the factors influencing tactile-dependant changes in corticomotor excitability, in the context of aging. Our results, in particular, highlight the importance of adjusting task demands and modulating attentional influences at the individual level to elicit proper task-specific facilitation when older persons are engaged in fine motor actions. Such information could be critical in the future for planning interventions to re-educate hand function in the presence of neurological impairments.

Acknowledgements
The authors wish to thank all participants for their time and patience during testing. Special thanks to Francisca Avila-Ramirez and Catherine Lebel for their help with data collection. Part of this work served as a partial fulfillment for a research practicum in experimental psychology by Sabah Master. François Tremblay is supported by NSERC (Canada).

Author details
[redacted]

Authors' contributions
SM participated in the design of the study, carried out the behavioral testing, performed the statistical analysis and drafted the manuscript. FT conceived of the study, and participated in its design and coordination and drafted the manuscript. Both authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

Received: 4 January 2010
Accepted: 5 March 2010 Published: 5 March 2010

References

1. Jones LA: **The assessment of hand function: a critical review of techniques.** *J Hand Surg Am* 1989, **14a**:221-228.
2. Deibert E, Kraut M, Kremen S, Hart J Jr: **Neural pathways in tactile object recognition.** *Neurology* 1999, **52**:1413-1417.
3. Bodegård A, Geyer S, Grefkes C, Zilles K, Roland PE: **Hierarchical Processing of Tactile Shape in the Human Brain.** *Neuron* 2001, **31**:317-328.

4. Stoeckel MC, Weder B, Binkofski F, Buccino G, Shah NJ, Seitz RJ: **A fronto-parietal circuit for tactile object discrimination: an event-related fMRI study.** *Neuroimage* 2003, **19**:1103-1114.
5. Miquee A, Xerri C, Rainville C, Anton JL, Nazarian B, Roth M, Zennou-Azogui Y: **Neuronal substrates of haptic shape encoding and matching: a functional magnetic resonance imaging study.** *Neuroscience* 2008, **152**:29-39.
6. Master S, Tremblay F: **Task-specific increase in corticomotor excitability during tactile discrimination.** *Exp Brain Res* 2009, **194**:163-172.
7. D'Esposito M, Zarahn E, Aguirre GK, Rypma B: **The effect of normal aging on the coupling of neural activity to the bold hemodynamic response.** *Neuroimage* 1999, **10**:6-14.
8. McConnell KA, Bohning DE, Nahas Z, Shastri A, Teneback C, Lorberbaum JP, Lomarev MP, Vincent DJ, George MS: **BOLD fMRI response to direct stimulation (transcranial magnetic stimulation) of the motor cortex shows no decline with age.** *J Neural Transm* 2003, **110**:495-507.
9. Sale MV, Semmler JG: **Age-related differences in corticospinal control during functional isometric contractions in left and right hands.** *J Appl Physiol* 2005, **99**:1483-1493.
10. Leonard G, Tremblay F: **Corticomotor facilitation associated with observation, imagery and imitation of hand actions: a comparative study in young and old adults.** *Exp Brain Res* 2007, **177**:167-175.
11. Heuninckx S, Wenderoth N, Debaere F, Peeters R, Swinnen SP: **Neural basis of aging: the penetration of cognition into action control.** *J Neurosci* 2005, **25**:6787-6796.
12. Hutchinson S, Kobayashi M, Horkan CM, Pascual-Leone A, Alexander MP, Schlaug G: **Age-related differences in movement representation.** *Neuroimage* 2002, **17**:1720-1728.
13. Ward NS: **Compensatory mechanisms in the aging motor system.** *Ageing Res Rev* 2006, **5**:239-254.
14. Mattay VS, Fera F, Tessitore A, Hariri AR, Das S, Callicott JH, Weinberger DR: **Neurophysiological correlates of age-related changes in human motor function.** *Neurology* 2002, **58**:630-635.
15. De Serres SJ, Fang NZ: **The accuracy of perception of a pinch grip force in older adults.** *Can J Physiol Pharmacol* 2004, **82**:693-701.
16. Scialfa CT: **The role of sensory factors in cognitive aging research.** *Can J Exp Psychol* 2002, **56**:153-163.
17. Iachini T, Poderico C, Ruggiero G, Iavarone A: **Age differences in mental scanning of locomotor maps.** *Disabil Rehabil* 2005, **27**:741-752.
18. Kastenbauer T, Sauseng S, Brath H, Abrahamian H, Irsigler K: **The value of the Rydel-Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer.** *Diabet Med* 2004, **21**:563-567.
19. Pestronk A, Florence J, Levine T, Al-Lozi MT, Lopate G, Miller T, Ramneantu I, Waheed W, Stambuk M: **Sensory exam with a quantitative tuning fork: rapid, sensitive and predictive of SNAP amplitude.** *Neurology* 2004, **62**:461-464.
20. Nielsen JF: **Logarithmic distribution of amplitudes of compound muscle action potentials evoked by transcranial magnetic stimulation.** *J Clin Neurophysiol* 1996, **13**:423-434.
21. Schmidt S, Cichy RM, Kraft A, Brocke J, Irlbacher K, Brandt SA: **An initial transient-state and reliable measures of corticospinal excitability in TMS studies.** *Clin Neurophysiol* 2009, **120**:987-993.
22. Tremblay F, Backman A, Cuenco A, Vant K, Wassef MA: **Assessment of spatial acuity at the fingertip with grating (JVP) domes: validity for use in an elderly population.** *Somatosens Mot Res* 2000, **17**:61-66.
23. Tremblay F, Wong K, Sanderson R, Cote L: **Tactile spatial acuity in elderly persons: assessment with grating domes and relationship with manual dexterity.** *Somatosens Mot Res* 2003, **20**:127-132.
24. Peinemann A, Lehner C, Conrad B, Siebner HR: **Age-related decrease in paired-pulse intracortical inhibition in the human primary motor cortex.** *Neurosci Lett* 2001, **313**:33-36.
25. Pitcher JB, Ogston KM, Miles TS: **Age and sex differences in human motor cortex input-output characteristics.** *J Physiol* 2003, **546**:605-613.
26. Talelli P, Ewas A, Waddingham W, Rothwell JC, Ward NS: **Neural correlates of age-related changes in cortical neurophysiology.** *Neuroimage* 2008, **40**:1772-1781.
27. Rowe JB, Siebner H, Filipovic SR, Cordivari C, Gerschlager W, Rothwell J, Frackowiak R: **Aging is associated with contrasting changes in local and distant cortical connectivity in the human motor system.** *Neuroimage* 2006, **32**:747-760.
28. Van Impe A, Coxon JP, Goble DJ, Wenderoth N, Swinnen SP: **Ipsilateral coordination at preferred rate: Effects of age, body side and task complexity.** *Neuroimage* 2009, **47**:1854-1862.
29. Terumitsu M, Ikeda K, Kwee IL, Nakada T: **Participation of primary motor cortex area 4a in complex sensory processing: 3.0-T fMRI study.** *Neuroreport* 2009, **20**:679-683.
30. Gazzaley A, D'Esposito M: **Top-down modulation and normal aging.** *Ann N Y Acad Sci* 2007, **1097**:67-83.
31. Gazzaley A, Clapp W, Kelley J, McEvoy K, Knight RT, D'Esposito M: **Age-related top-down suppression deficit in the early stages of cortical visual memory processing.** *Proc Natl Acad Sci USA* 2008, **105**:13122-13126.
32. Langley LK, Fuentes LJ, Vivas AB, Bagne AG: **Differential age effects on attention-based inhibition: Inhibitory tagging and inhibition of return.** *Psychol Aging* 2005, **20**:356-360.
33. Poliakoff E, Ashworth S, Lowe C, Spence C: **Vision and touch in ageing: Crossmodal selective attention and visuotactile spatial interactions.** *Neuropsychologia* 2006, **44**:507-517.
34. Stoesz MR, Zhang M, Weisser VD, Prather SC, Mao H, Sathian K: **Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks.** *Int J Psychophysiol* 2003, **50**:41-49.
35. Harada T, Saito DN, Kashikura K, Sato T, Yonekura Y, Honda M, Sadato N: **Asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study.** *J Neurosci* 2004, **24**:7524-7530.
36. Dum RP, Strick PL: **Motor areas in the frontal lobe of the primate.** *Physiol Behav* 2002, **77**:677-682.
37. Rowe J, Friston K, Frackowiak R, Passingham R: **Attention to action: specific modulation of corticocortical interactions in humans.** *Neuroimage* 2002, **17**:988-998.
38. Bressler SL: **The sensory component of tonic motor control.** *Clin Neurophysiol* 2009, **120**:1035-1036.

doi:10.1186/1744-9081-6-16
Cite this article as: Master and Tremblay: **Tactile-dependant corticomotor facilitation is influenced by discrimination performance in seniors.** *Behavioral and Brain Functions* 2010 **6**:16.

Master and Tremblay *BMC Neuroscience* 2012, **13**:27
http://www.biomedcentral.com/1471-2202/13/27

BMC Neuroscience

RESEARCH ARTICLE **Open Access**

Task-related enhancement in corticomotor excitability during haptic sensing with the contra- or ipsilateral hand in young and senior adults

Sabah Master[1,3†] and François Tremblay[1,2,3*†]

Abstract

Background: Haptic sensing with the fingers represents a unique class of manipulative actions, engaging motor, somatosensory and associative areas of the cortex while requiring only minimal forces and relatively simple movement patterns. Using transcranial magnetic stimulation (TMS), we investigated task-related changes in motor evoked potential (MEP) amplitude associated with unimanual haptic sensing in two related experiments. In Experiment I, we contrasted changes in the excitability of the hemisphere controlling the task hand in young and old adults under two trial conditions, i.e. when participants either touched a fine grating (*smooth trials*) or touched a coarse grating to detect its groove orientation (*grating trials*). In Experiment II, the same contrast between tasks was performed but with TMS applied over the hemisphere controlling the resting hand, while also addressing hemispheric (right vs. left) and age differences.

Results: In Experiment I, a main effect of *trial type* on MEP amplitude was detected ($p = 0.001$), MEPs in the task hand being ~50% larger during grating than smooth trials. No interaction with age was detected. Similar results were found for Experiment II, *trial type* having a large effect on MEP amplitude in the resting hand ($p < 0.001$) owing to selective increase in MEP size (~2.6 times greater) for grating trials. No interactions with age or side (right vs. left) were detected.

Conclusions: Collectively, these results indicate that adding a haptic component to a simple unilateral finger action can elicit robust corticomotor facilitation not only in the working hemisphere but also in the opposite hemisphere. The fact that this facilitation seems well preserved with age, when task difficulty is adjusted, has some potential clinical implications.

Background

Interhemispheric interactions associated with performance of unimanual actions have been the object of much study in recent years. For instance, functional neuroimaging studies have provided evidence that both task complexity and advancing age are critical factors in leading to extra cortical activation in sensori-motor areas ipsilateral to the task hand when participants executed actions with one hand [e.g., [1,2]]. Further evidence for the involvement of ipsilateral motor cortex during unilateral hand actions has come from transcranial magnetic stimulation (TMS) studies in young adults. However, TMS reports in this regard have produced mixed results with evidence of both facilitation and suppression in the ipsilateral "resting hemisphere" while the opposite hemisphere was engaged during unilateral performance of the contralateral hand [e.g., [3-7]. Whether the "resting" hemisphere is facilitated or inhibited appears to depend on factors such as the nature of the unimanual task, particularly the task demands (e.g. low-force phasic vs. high force tonic pinch, congruence between real and imagined movements of the "resting" and task hands), which are known to affect interactions between hemispheres at the sensori-motor level. In view of these findings in young adults, there is a need to better characterize how task demands influence corticomotor facilitation in both the

---

[redacted]

active and resting hemisphere during unimanual actions, especially in the context of human aging.

In a recent series of experiments, we have investigated with TMS the neurophysiological correlates of motor cortical activation associated with unimanual performance using various forms of haptic sensing tasks [8-11]. Haptic sensing with the fingers represents a unique class of manipulative actions, engaging motor, somatosensory and associative areas of the cortex while requiring only minimal forces and relatively simple movement patterns [12,13]. For instance, pattern recognition at the fingertip typically leads to unilateral small amplitude movements to extract spatial information from contour exploration [14]. While such task requires only minimal effort at the motor execution level, pattern recognition is nevertheless cognitively demanding for contour exploration is a slow serial process relying on tactile working memory to integrate spatial information to allow for recognition [14].

Such a class of actions thus provide a unique window to investigate the influence of task demands on motor facilitation associated with unimanual actions. Indeed, our observations showed that robust corticomotor facilitation could be elicited in hemisphere controlling the task hand when participants sensed pattern with the index finger. The fact that this haptic-related enhancement could be abolished by disengaging tactile attention [9] during finger movements pointed to a centrally mediated top-down effect rather than a simple bottom-up afferent mediated increase in corticospinal excitability. Indeed, attending to tactile inputs in the context of haptic sensing engages several cortical regions in the parietal and frontal lobes, including premotor areas [15,16], and the recruitment of this cortical network was likely critical in leading to enhanced corticomotor excitability in the working hemisphere. Such facilitation could be important in finely modulating the corticospinal drive to allow for optimal detection of tactile features as the finger moves. Similar experiments performed in older adults showed that haptic-related enhancement in excitability was still present but depended upon the individual's capacity to perform fine discrimination at the fingertip [17].

In the present report, we extend our previous observations on haptic-related corticomotor facilitation in two series of related experiments destined to further characterize the influence of task demands associated with pattern recognition in young and older adults. In Experiment I, we asked whether haptic-related enhancement in motor excitability in the working hemisphere would be similar between young and older adults, when task difficulty is adjusted to accommodate for age-related changes in tactile perception. In Experiment II, we asked the same question but with regard to the "resting hemisphere", that is whether engaging one hemisphere and one hand in haptic sensing would influence the excitability of the opposite hemisphere and the resting hand to the same extent in young and older adults. We also asked if such crossed modulation would be different depending on whether the right or left hemisphere is engaged in haptic sensing.

Results

Experiment I. Corticospinal excitability in the working hemisphere

Task performance

In terms of muscle activation, grating and smooth trials elicited a very similar pattern of activity in the FDI muscle, characterized by a sustained increase in activity as the index finger pressed down against the dome. This pattern of EMG activity was similar for both young and senior adults when normalized as a percent of the individual's maximum voluntary contraction (MVC), as shown in Figure 1A and 1B. The average level of activation corresponded to ~10% of the MVC in the two blocks of trials (smooth, 10.0%; grating, 11.7%). Paired comparison revealed no significant difference between the two blocks of trials on mean rectified EMG activity in the 500 ms period preceding the TMS pulse (paired t-test, $t_{30} = 2.0$, $p > 0.05$).

Task-specific corticospinal facilitation

In general, participants in both age groups exhibited very reliable discrimination in the grating trials with accuracy > 90%, on average. While young participants made slightly more errors (mean, 1.2 ± 0.4) than their senior counterparts (0.3 ± 0.1), the difference was not statistically significant (Mann-Whitney test, $p = 0.19$). As shown in Figure 2, younger and senior participants showed facilitation of MEP amplitudes during the grating discrimination trials. The main effect of trial type on MEP amplitude was highly significant ($F_{1,30} = 12.72$, $p = 0.001$, partial eta squared = 0.30). Age had a main effect on MEP amplitude ($F_{1,30} = 7.57$, $p = 0.01$, partial eta squared = 0.20) because seniors generally exhibited smaller MEP sizes than their younger counterparts, irrespective of trial type. No interaction was detected, however, between age and trial type ($F_{1,30} = 0.06$, $p = 0.81$), as the two age groups exhibited comparable levels of MEP enhancement in the grating trials (young adults, 46 ± 13%; senior adults, 56 ± 29%). Variations in MEP latency (20.6 ± 0.4 vs. 20.6 ± 0.3 ms, grating and smooth, respectively) and SP duration (101 ± 7.6 vs. 93 ± 6.2 ms, grating and smooth, respectively) were not influenced by trial type (latency, $F_{1,30} = 0.06$, $p = 0.81$; silent period, $F_{1,30} = 1.76$, $p = 0.20$), age (latency, $F_{1,30} = 0.86$, $p = 0.36$; silent period, $F_{1,30} = 3.91$, $p = 0.057$), or interactions between trial type and age ($F < 2$, $p > 0.2$).

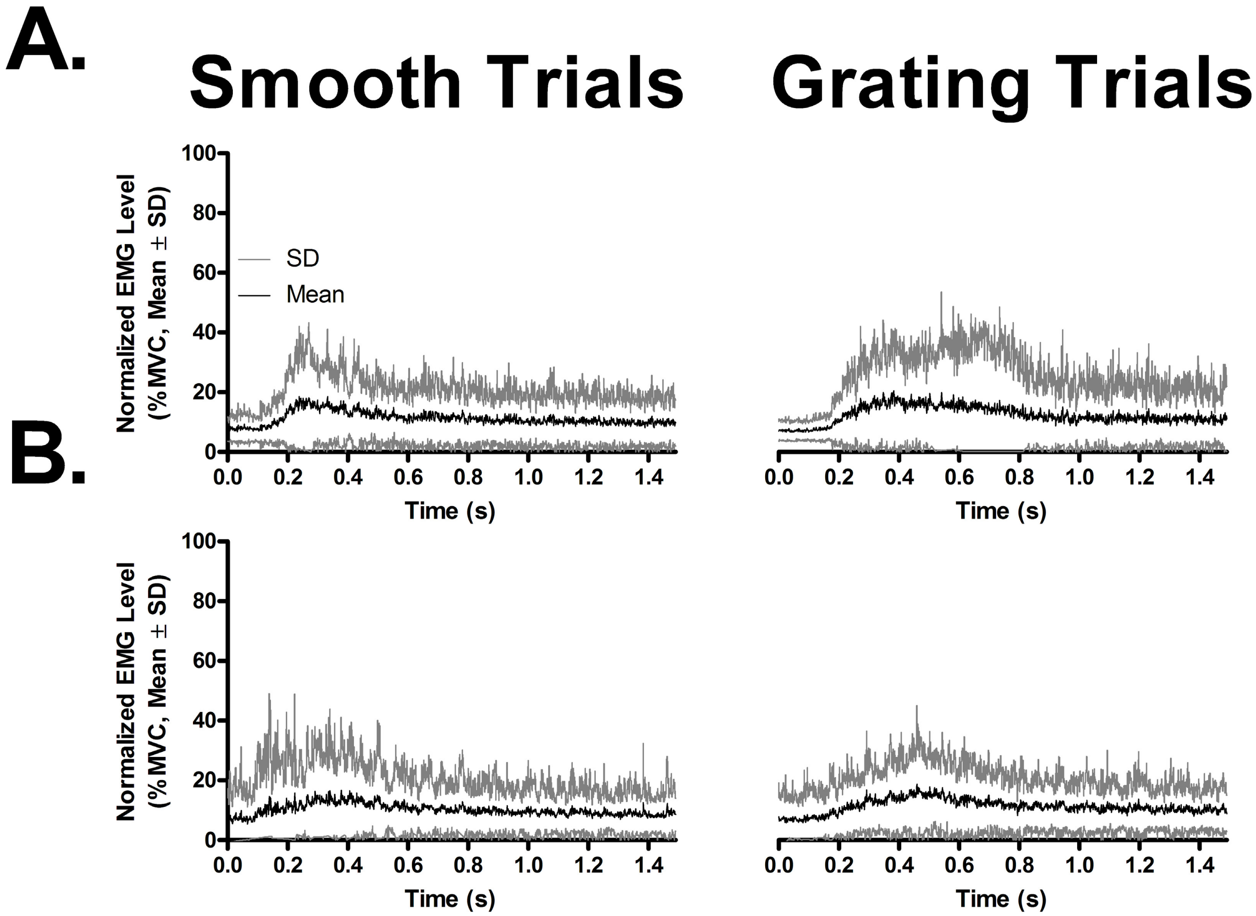

Figure 1 EMG activity during grating and smooth trials in young and older adults. Muscle activation pattern elicited in the right FDI in Experiment I during task execution in young (A) and older (B) adults. The traces represent the overall mean (± SD) of all participants' rectified electromyographic (EMG) activity level in each age group (n = 16) recorded prior to application of TMS pulse over the left primary motor cortex, normalized as a percentage of each participant's MVC, for all grating (n = 12) and smooth (n = 12) trials. Note the close similarity in the pattern of muscular activation between the two types of trials, and in both age groups.

Experiment II. Corticospinal excitability in the resting hemisphere

Task performance

Observations with regard to background EMG level elicited in the task hand were similar to Experiment I, with no significant difference in average levels being detected between smooth and grating trials for both the right hand (smooth, 10.6%, grating, 12.0%, $t_{31} = 1.5$, $p = 0.13$) and the left hand (smooth, 10.8%, grating, 11.7%, $t_{31} = 1.3$, $p = 0.19$). In the resting hand, mean EMG activity in the resting hand was equivalent to background noise (i.e., ~2% of MVC) for all trials for both the right and left sides in young (2.1%) and older (2.0%) adults.

Task-specific corticospinal facilitation

As in Experiment I, participants of both age groups exhibited very reliable and comparable discrimination performance (i.e., > 90%, on average) in the grating trials (overall mean error rate, young, 0.9 ± 0.2; seniors, 0.3 ± 0.1; Mann-Whitney test, $p = 0.30$). As shown in Figure 3, younger and senior participants showed large MEP facilitation in the resting hand when the other hand was discriminating the grating orientation ($F_{1,30} = 16.98$, $p < 0.001$, partial eta squared = 0.36). MEPs in the resting hand were, on average, 2.6 times larger during grating discrimination trials than either during smooth trials or at baseline (Bonferroni's $p \leq 0.001$). In fact, MEPs elicited during smooth trials were equivalent in size to those measured at baseline in the resting state (Bonferronni's $p = 1.0$). As for Experiment I, there was a main effect of age on MEP amplitude in the resting hand ($F_{1,30} = 19.18$, $p < 0.001$ partial eta squared = 0.39), owing to the age-related difference in MEP size. There was no interaction between trial type and age in the resting hand ($F_{1,30} = 0.37$, $p = 0.55$), seniors showing as much grating facilitation on average (right hand, 183 ±

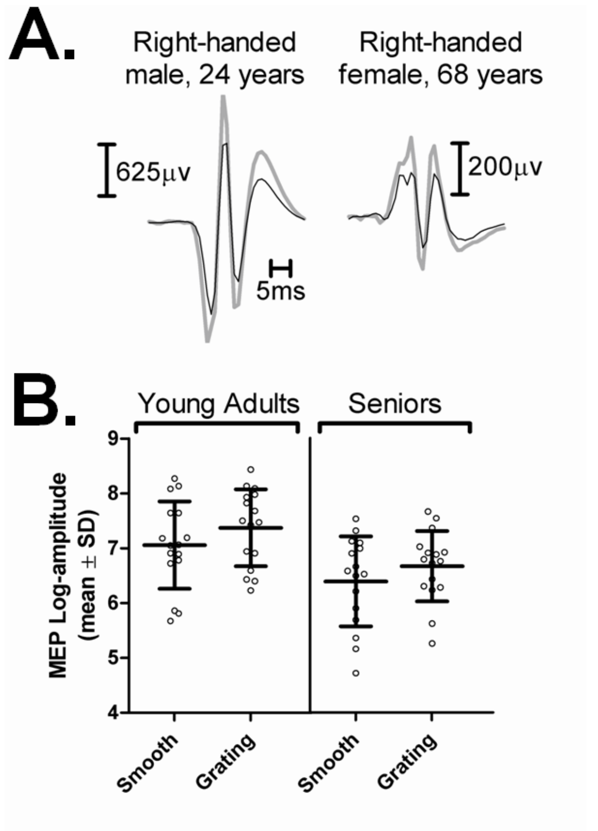

Figure 2 MEP amplitudes during the smooth vs. grating trials in Experiment I. A. Examples of task-related differential modulation in MEP amplitude under the two trial types in a typical young (right-handed male, aged 23 years) and a typical older (right-handed female, aged 68 years) participant. Each trace is an average of 12 responses. B. Comparison of mean MEP log-amplitudes in the two trial types (grating/smooth). Each bar represents the mean of individual values computed under each trial type for all young adult (N = 16) and senior participants (N = 16). Note that extra facilitation was observed during the grating trials compared to the smooth trials, and the main effect of trial type was significant for the overall variations in MEP log-amplitude ($F_{1,30}$ = 12.72, p = 0.001, partial eta squared = 0.30).

30%; left hand, 288 ± 77%) as young adults (right hand, 202 ± 25%; left hand, 362 ± 166%). Hemispheric side ($F_{1,30}$ = 0.74, p = 0.40) had no influence on MEP amplitude and showed no interactions with trial type or age ($F < 1$, $p > 0.3$). Variations in MEP latency were not influenced by trial type ($F_{1,29}$ = 0.01, p = 0.95), age ($F_{1,29}$ = 2.46, p = 0.13), hand ($F_{1,29}$ = 1.06, p = 0.31), or interactions between any of these factors ($F_{1,29} < 4$, $p > 0.05$).

Discussion

In the present study, we examined variations in corticomotor excitability associated with unimanual pattern recognition at the fingertip in young and older adults. In Experiment I, we showed that haptic enhancement in corticomotor excitability in the working hemisphere was similar in magnitude in young and older adults, when task difficulty was adjusted for age difference. In Experiment II, we showed that haptic enhancement in corticomotor excitability could also be reliably detected in the "resting" hemisphere opposite to the working hemisphere and that this cross-modulation was similar in magnitude between the two age groups and regardless of which hemisphere (i.e., right or left) was engaged in haptic sensing. We will first address the significance of the haptic enhancement observed in Experiment I in the context of aging. Then, we will examine issues pertaining to bilateral corticomotor facilitation as assessed by TMS, in the context of aging with an emphasis on the importance of task demands, in line with the haptic enhancement observed in Experiment II in the "resting" hemisphere.

Experiment I. Corticospinal excitability in the working hemisphere

In our previous investigation into task-related corticomotor facilitation [17], we found that MEP enhancement with haptic sensing was highly variable in seniors, a variability that linked with the participant's ability to reliably perform haptic discriminations when the task consisted of identifying raised patterns by active stroking of the index finger at a prescribed speed. In this previous study, the inherent difficulty associated with pattern recognition was further complicated by the fact that participants had to externally pace their stroking movement to an auditory tone; hence the possibility of interference with the primary tactile task. In the present study, we show that haptic-related enhancement in corticomotor excitability can be easily elicited in healthy seniors when task demands associated with haptic sensing are reduced both at the kinematics level (i.e., from stroking to simple pressing action) and at the perceptual level (i.e., from patterns to simple grating dimensions). In fact, senior exhibited as much task-related facilitation as young adults when performing grating orientation discriminations. Simplifying task demands in the context of inherently difficult pattern recognition tasks was likely critical in allowing seniors to allocate attentional resources towards tactile inputs coming from the fingertip during grating trials. This observation in seniors, along with the fact that the MEP enhancement was specific for grating trials, reinforces our previous suggestion [9,17] that the likely source of this corticomotor facilitation resides in the activation of the parieto-frontal network subserving tactile attention and tactile processing during haptic sensing. These observations, altogether, indicate that controlling for task difficulty and demand represents a crucial issue when working with older adults in interventions destined to improve fine dexterity.

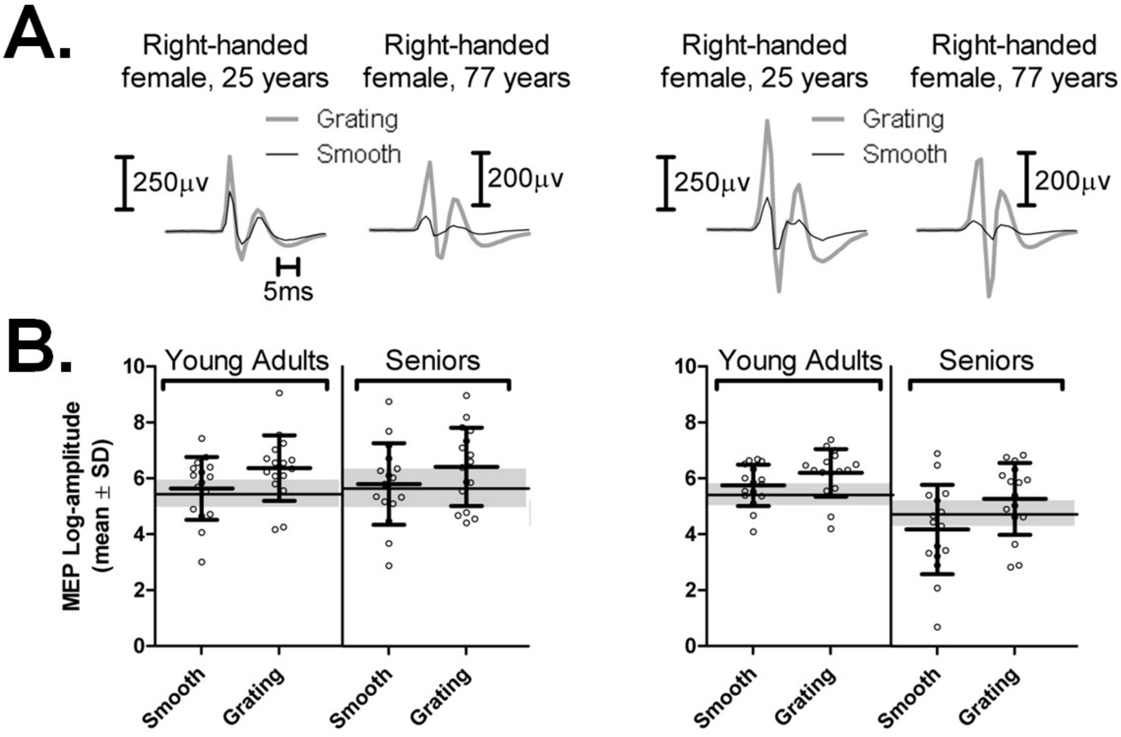

Figure 3 MEP amplitudes during the smooth vs. grating trials in Experiment II. A. Examples of task-related differential modulation in MEP amplitude under the two trial types in the left and right resting hands in typical young (right-handed female, aged 25 years) and older (right-handed female, aged 77 years) participants. Each trace is an average of 12 responses. B. Comparison of mean MEP log-amplitudes in the resting hand when the task hand was performing the two trial types (grating/smooth). The gray area represents the mean and standard error of the baseline resting MEP log-amplitudes in the young adult and senior age groups. Each bar represents the mean of individual values computed for the resting hand when the task hand performed each trial type (grating/smooth) for all young adult (N = 16) and senior participants (N = 16). Note the main effect of trial type in the task hand was significant for the overall variations in MEP log-amplitude in the resting hand ($F_{1,30}$ = 16.98, $p < 0.001$, partial eta squared = 0.36), reflecting enhanced MEP amplitudes in the resting hand when the other hand was doing the grating trials vs. the smooth trials (Bonferroni's p = 0.001) or resting baseline values (Bonferroni's $p < 0.001$), which were not different from one another (Bonferroni's p = 1.0).

Experiment II. Corticospinal excitability in the resting hemisphere

As stressed before, increases in ipsilateral sensorimotor activity have been observed at different levels in the motor system (i.e. peripheral and central) during a variety of unimanual tasks [18-20]. In the present study, we observed that engaging one hemisphere and one hand in haptic sensing was associated with enhanced excitability of the opposite hemisphere associated with the resting hand. In addition, this enhancement was comparable in magnitude between young and old participants, regardless of which hemisphere was engaged in the task. In this regard, our observations are consistent with many TMS reports in young adults, wherein enhanced corticomotor excitability on the "resting" hemisphere has been described when the other was engaged in various unimanual tasks [4,19,21-25]. The present findings may also be interpreted in light of neuroimaging data showing increases in the activity of the ipsilateral sensorimotor cortex during various unimanual tasks, particularly more complex tasks [1,26]. This raises the question as to why smooth trials, which produced similar pattern of background EMG as that seen with grating trials in the task hand, failed to elicit any detectable changes in MEP amplitude in the resting hand; even when compared to baseline values in the resting state. One possible reason for this may reside in the nature of the finger movement, which required only minimal effort on the part of the participant and was simple and highly predictable from trial to trial. In line with this, Tinazzi and Zanette [4] observed a gradual decrease in corticomotor facilitation in the resting hand when the task performed with the opposite hand became more automatic after sequential training. Evidently, grating trials were not susceptible to such training effects with repetitions, because participants were required to deploy tactile attention and use cognitive resources at each trial to discriminate the grating orientation.

Concerning the neural mechanism for the observed haptic enhancement in the "resting" hemisphere, as indicated before, the selectivity of the effect for grating trials points to the parietal-frontal network recruited during tactile attention associated with haptic sensing [15,16] as the primary source of facilitatory influences. In principle, such central facilitation could be exerted at two sites, i.e. either indirectly through the active hemisphere or directly through the "resting" hemisphere. With regard to the first possibility, one possible source is descending ipsilateral facilitation coming from the activated motor cortex through uncrossed corticospinal projections reaching spinal motoneurons. Such a possibility is very unlikely, however, given that ipsilateral corticospinal projections destined to distal hand muscles are rare in primates [27], and were shown recently to have only very weak effects in modulating ipsilateral motoneuronal activity during hand movements [28]. Another related source is irradiation of facilitatory influences or a release from inhibition from the activated primary motor cortex to the homologous cortex through transcallosal projections. Such a possibility is also unlikely, however, for three major reasons. First, most TMS studies looking at interhemispheric influences between motor cortices have emphasized the inhibitory nature of these interactions [see [29] for review] such that conditioning stimuli applied to one hemisphere lead to suppression of MEPs elicited from the opposite hemisphere over a wide range of inter-stimulus intervals. Interhemispheric facilitation can also be elicited but the phenomena has been described as less reliable and remains highly susceptible to variations in experimental paradigm [e.g., [30]. Second, the fact that no mirror activity was detected in the resting FDI homologous to the one engaged in haptic sensing, and that smooth trials elicited no sign of MEP facilitation, argue against the notion of a simple spread of excitation from one motor cortex to the other as the primary source for the observed corticomotor facilitation. Finally, both anatomical tracer work in non-human primates [31] and tractography analyses of diffusion tensor imaging in humans [32] converge to show that primary motor and somatosensory cortices have relatively scant callosal connections when compared to secondary motor or somatosensory areas. This leaves the "resting" hemisphere ipsilateral to the task hand as the most probable site of origin for the observed MEP facilitation in the resting hand. In this respect, a likely source of ipsilateral facilitation during trials with grating discrimination is the recruitment of secondary motor areas, such as the pre-SMA, SMA proper and ventral premotor cortex; which all have been shown to be activated to some degree in tasks involving haptic sensing with the finger [15,16]. As stressed earlier, these secondary motor areas have dense callosal connections and are also densely interconnected with M1 intra-cortically [31,33]. In addition, both SMA and premotor neurons are known to exhibit pre-movement activity during ipsilateral unimanual movement, which contrasts to MI neurons where such premovement activity is seldom found [34,35]. Therefore, bilateral recruitment of secondary motor areas associated with cognitive demand and tactile attention in the context of unilateral haptic sensing seems the most likely source of facilitation to raise motor excitability in the "resting" hemisphere. Yet, one can ask as to why a large increase in corticomotor excitability in the resting hemisphere was not accompanied by overt motor overflow in the resting hand. In this respect, it is possible that interhemispheric inhibitory influences from the active hemisphere to the "resting" hemisphere likely balanced out the facilitation mediated by the secondary motor areas recruited during haptic sensing, reducing it to a sub-threshold level so as to prevent overt mirror movements of the non task hand [36]. To summarize, although we cannot totally rule out the possibility that irradiation from the active hemisphere contributed to the observed ispsilateral MEP enhancement, both anatomical and physiological evidence point to the "resting" hemisphere as the most likely site for the facilitation in link with the recruitment of secondary motor areas in the context of haptic processing.

In line with a previous TMS study comparing right-left differences in the excitability of corticomotor projections to the resting hand when the other hand performed simple movements of varying intensities [37], no difference was found between the two hemispheres with regard to task-related enhancement in corticomotor excitability. However, ipsilateral cortical activity during unimanual performance has often been reported to be more pronounced in the left hemisphere and more important for left hand task performance, particularly for complex tasks [e.g., [1,38]. The present observation that haptic-related corticomotor facilitation in the resting hemisphere was unaffected by hand could be related to the nature of our task, as we have argued before. The fact that our finger task consisted of a simple action requiring minimal effort at the muscular level could have contributed to accentuate differences arising from central influences at the motor cortical level between smooth and grating trials; leading to similar facilitation irrespective of the hand performing the task. Similar to observation between hemispheres, no differences was also observed between young and old participants in the level of MEP facilitation elicited in the “resting” hemisphere when the opposite one was engaged in haptic sensing. This is somewhat in contrast to previous neuroimaging and behavioural studies reporting age-dependant increase in bilateral sensorimotor activation and in peripheral muscle activity during simple unimanual tasks [20,39-41]. Seniors also exhibited less interhemispheric motor inhibition than young adults during performance of unimanual tasks, suggesting that attending to a task may affect inhibitory modulation of ipsilateral motor cortical activity with aging [42]. However, in the present study, the possibility of motor overflow affecting the status of the “resting” hand was greatly reduced by asking participants to refrain from contracting their muscles in the relaxed state and by constant monitoring of EMG level. Such active strategy has been shown to be highly effective in suppressing mirror movements in the non-task hand when complex movements were performed with the other hand in both young and old adults [43]. Thus, any age-dependant increases in motor overflow might have been mitigated by our active control over spreading muscle activity in the resting hand as senior and young participants performed the finger task. Another factor that might have contributed to attenuate age differences is the fact that we controlled for the level of task difficulty. In general, older adults tend to exhibit more widespread cortical activation than younger subjects when motor task demands are increased in terms of complexity [e.g., [2,20,39-41,44]. On this basis, one could have predicted greater haptic-related motor facilitation in the older group owing to the recruitment of a more extensive bilateral frontal and parietal network associated with discrimination of the grating orientation; but this was not the case. As suggested before, such compensatory over-recruitment might have been largely cancelled out in this study by the combined effect of using a simple finger action task and adjusting the level of perceptual difficulty for age for the haptic component. Overall, these observations with regard to the effect of age would be compatible with the compensation-related utilization of neural circuits hypothesis (CRUNCH) theory [45]. This theory suggests that aging results in a loss of hemispheric specialization only in situations in which performance deterioration is evident, to increase compensatory recruitment of available cognitive resources and help improve task performance in seniors [45]. Indeed, poorer unimanual motor task performance in seniors was associated with greater recruitment of ipsilateral M1, decreased callosal size, and integrity, indicating a shift towards excitation in the balance of excitatory and inhibitory interhemispheric interactions [36,39,46]. In the present study, given the careful design of task demands and stimuli to facilitate good performance in seniors in the haptic sensing trials, there would be no reason to expect a compensatory over-recruitment of ipsilateral or contralateral motor areas.

Conclusions

Finger movements performed in the context of haptic sensing produced a task-specific facilitation in the corticospinal projections destined to intrinsic hand muscles in both senior and young adults, when task demands are adjusted for age. This task-specific facilitation is not only detectable in the working hemisphere controlling the task hand but also in the opposite hemisphere associated with the resting hand. Such results highlight the importance of cognitive factors and task demands in modulating corticospinal output during performance of unimanual actions. These results might have implications in the design of rehabilitative interventions in aging populations. For instance, one could conceive interventions in stroke patients, where haptic sensing is incorporated into hand retraining to facilitate corticospinal drive to the paretic hand. Along the same line, interventions could be directed also at the less affected hand using more demanding haptic sensing tasks to elicited bilateral corticomotor facilitation aiming at promoting recovery of the affected hand. Future work is required to test various haptic sensing tasks in the context of rehabilitation in stroke patients.

Methods

The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received an honorarium for his or her participation.

Participants

Sixteen healthy young adults (9 males, 7 females, mean age ± SD, 22 ± 2.5 years) and 16 healthy seniors (8 males, 8 females, mean age ± SD: 68 ± 5.1 yrs) from the Ottawa area were included in the study. The majority of subjects were right-handed (young, 13/16; older, 16/16) according to the Edinburgh Handedness Questionnaire. Prior to the experimental session, all participants completed a medical questionnaire to ensure that there were no contra-indications to TMS and no antecedents of conditions likely to affect their performance in the tests. In addition, all participants were screened for the presence of undiagnosed peripheral neuropathies using a graduated Rydel-Seiffer tuning fork, which has been shown to be a valid and reliable instrument for assessing sensory nerve function in the extremities [47,48]. None showed signs of peripheral neuropathy.

Prior to testing participants were also tested to determine spatial acuity theshold at the tip of the right index finger using the JVP domes (Stoelting Co., Wood Dale, IL, USA). The methods and stimuli have been described in detail elsewhere [49]. Briefly, participants were presented successive blocks of trials (n = 30) starting with a wide grating dome (e.g, 3.5 mm-width) and progressing to finer gratings until performance fell to chance level. Each trial consisted of presenting the grating dome in one of two orthogonal orientations according to a predetermined pseudo-random sequence. Subjects reported the perceived orientation of the grating (i.e., either along or across the fingertip) according to a two-alternative forced-choice paradigm. The tactile spatial acuity threshold was determined by calculating the grating width corresponding to 75% correct discrimination, using a linear interpolation technique [50]. This assessment confirmed that our sample participants, young (mean ± SEM, 1.24 ± 0.1 mm) and senior (1.89 ± 0.2 mm), exhibited spatial acuity thresholds within the range reported previously for similar groups of healthy subjects [49,51,52].

General procedure for EMG recording and TMS

The recording techniques and TMS procedure have been reported previously [see [9]]. Briefly, EMG activity was recorded using small auto-adhesive surface electrodes (10 mm diameter, Ag-AgCl) placed over the FDI of the right and left hands. EMG signals were amplified (100-500 μV/div), filtered (bandwidth, 16 Hz to 1 kHz), and digitized at 2 kHz (RMP-6004, Nihon-Kohden Corp.; BNC-2090, National Instrument Corp.).

Magnetic stimulation was delivered with a Magstim 200 (Magstim Co. Dyfed, UK) connected to a figure-eight coil (70 mm loop diameter). To determine the optimal site to evoke MEPs in the contralateral hand muscles, the approximate location of the hand motor area on the left hemisphere was explored in 1 cm steps until reliable MEPs could be evoked in the target muscle (FDI). Following this procedure, the relaxed motor threshold was determined using the method advocated by Mills and Nithi [53]. Starting from supra-threshold intensity, the stimulator's output was gradually decreased in 1% steps until no MEP could be evoked for 10 consecutive stimuli. This TMS intensity corresponded to the lower threshold value. From this point, the intensity was gradually increased until MEP's of at least 50 μV peak-to-peak amplitude could be evoked by ten consecutive stimuli. This latter intensity was recorded as the upper threshold value. The relaxed motor threshold (RMT) was defined for each participant as the median intensity between the upper and lower threshold values. Mean RMTs were lower in the right hand, and in young adults (right hand, 35 ± 8.4; left hand, 38 ± 9.2) compared to seniors (right hand, 45 ± 9.7; left hand, 51 ± 8.8; F). The TMS intensity was then fixed at 110% of motor threshold for the remainder of the experiment.

As in our previous studies [9], prior to formal testing, all participants underwent two series of baseline measurements. First, baseline MEP values were derived for each hemisphere (right and left) by delivering TMS with participants instructed to relax. For each side, 12-15 MEPs were recorded at rest with an interstimulus interval of ~ 5 s. Second, estimates of maximal EMG activity for the FDI were derived for each hand by recording muscle activity produced during maximal voluntary contractions (MVC). This was performed by asking participants to abduct (open) their fingers as hard as they could for the duration of a tone lasting 3000 ms against the resistance provided by one of the experimenters (SM) using both hands to hold all four fingers together. The procedure was repeated three times for each with 5 s rest between contractions.

Experiment I. Corticospinal excitability in the working hemisphere

In Experiment I, we measured varations in corticomotor excitability in the hemisphere controlling the task hand under two set of conditions which both required participants to gently touch a grating dome (JVP domes, see above) with the distal pad of the index finger. One dome consisted of a fine grating with 0.5 mm groove width, which was designated as the "smooth" dome. This dome was used in *smooth trials*, where participants were simply asked to gently press against the dome without any other requirements. In the second set of trials (*grating trials*), participants performed the same unilateral touching action but this time they were required to report the perceived orientation of the grooves in the presented dome. In grating trials, two different grating dimensions were used for young and senior participants to ensure stimuli would be 150% above mean spatial acuity thresholds in both groups, and thus easily perceptible. The 1.5 mm dome was used in young subjects, whereas the 3.0 mm dome was used in seniors. These grating dimensions were selected on the basis of our estimates of the participants' spatial acuity prior to testing. The orientation of the 1.5 and 3.0 mm grating domes were both reported to be easily detectable by the participants of each age group, though they still required attention. The tasks were always performed with the right index finger and TMS was applied over the left motor cortex to evoke contralateral MEPs in the task hand (see Figure 4A). Participants were first trained to perform smooth trials with the 0.5 mm dome. The task consisted of gently pressing against the dome by flexing the index finger in sync with a tone lasting

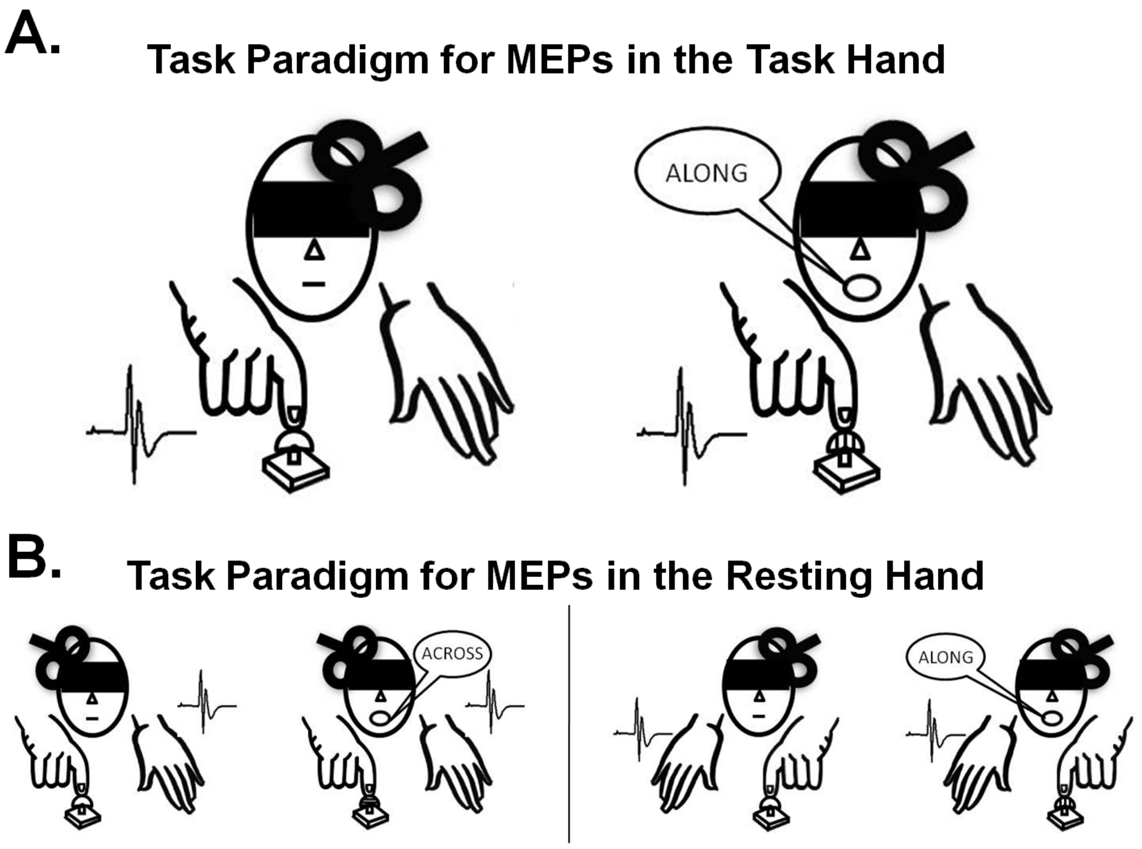

Figure 4 Task paradigm used to assess corticospinal excitability. A. *Experiment I*. In both grating and smooth trials, participants were trained to produce a single gentle downwards right index finger movement in sync with the sound of a tone lasting for 1.8 s. During the smooth trials, the finger moved downwards to touch a relatively smooth grating dome (0.5 mm spatial period) with no discrimination requirement. During the grating trials, participants touched a coarse grating dome (1.5 or 3 mm spatial period) and reported whether the grooves ran *along* or *across* the fingertip. In each trial, the TMS pulse was set to trigger over the left motor cortex 1.5 s after the tone, corresponding to the time point in the trial when the finger was touching the dome and the participant was actively discriminating during the grating trials. Contralateral MEPs were recorded in the task hand. B. *Experiment II*. The task conditions were identical to Experiment I except that both the right and left hands were tested in Experiment II, and contralateral MEPs were always recorded in the resting hand instead of the task hand.

1.8 s. Then, participants were trained to perform grating discrimination trials with either the 1.5 (young) or 3.0 mm (senior) dome. The conditions were identical to the smooth trials except that participants were required to attend to the perceived orientation of the grooves as they pressed against the dome. The grating orientation was presented as either *along* or *across* the long axis of the distal finger pad (see, Figure 4A). Immediately at the end of the trials, participants were required to report their responses verbally and were rapidly prompted to respond if no report had been made after the trial completion. Discrimination performance was recorded as the number of correct responses. Participants received appropriate training prior to testing to ensure that contact force and movement characteristics were similar under the two sets of conditions (i.e., smooth trials and grating trials). In both age groups, this training to perform the finger movement in time with the tone and to complete the grating discrimination and report their response only at the end of the trial required 3-5 practice trials (or less than a minute) to complete. The experimenters ensured that participants did not move their finger more during the grating trials than the smooth trials.

Corticospinal excitability was tested with participants comfortably seated in a recording chair and blindfolded. Trials with the smooth and grating domes were presented in two separated blocks of 12 consecutive trials in an order that alternated between participants to control for potential confounders due to variations in attention level, motivation and fatigue [9,17]. In the grating trials, the two orthogonal orientations (across and along) were presented in a pre-determined pseudo-random order with equal probability. In all trials (Figure 4a), TMS was set to trigger towards the end of the task @ 1.5 s in the course of the 1.8 s trial. Pilot testing confirmed that participants were still sensing the grating orientation (as judged by verbal reports) when TMS was delivered at the 1.5 s delay. This delay thus provided an optimal time point to examine task-related MEP facilitation, as participants were actively engaged in sensing for grating orientation. Twelve trials of 1800 ms epochs were recorded under each task condition.

Experiment II. Corticospinal excitability in the resting hemisphere

In Experiment II, the same task paradigm as in Experiment I was repeated in the same group of participants but this time TMS was applied on the motor cortex of the hemisphere controlling the resting hand (Figure 4B). This experiment allowed for investigation of interhemispheric modulation, as one hemisphere was actively engaged in unimanual performance (i.e., smooth or grating trials) while the opposite hemisphere and opposite hand were at rest. TMS was performed on each resting hemisphere with half the participants being stimulated first on the left (task hand: left) and then on the right (task hand: right), while the other half were tested in the reverse order (i.e., right hemisphere first).

Analysis of MEP data and background EMG

The details for the procedure for analysis of MEP data and background EMG are given in Master & Tremblay [9]. Briefly, MEP amplitude, latency, silent period (SP), background EMG were measured off-line and averaged to derive mean individual values. For the MVC, EMG signals produced during the last 2000 ms epoch of the MVC were rectified and averaged. This mean rectified maximal EMG value was then used to quantify and compare background EMG level (% MVC) produced during the finger task in Experiment I and II. For this analysis, background EMG levels produced during smooth and grating trials were rectified and averaged using a 500 ms time window preceding the TMS pulse (see Figure 1). Finally, the SP duration was estimated as the interval from MEP onset to the first sign of EMG return.

Statistical Analysis

MEP amplitudes were not normally distributed (Shapiro-Wilk $p < 0.05$) and so individual mean values were transformed using the natural logarithm, as suggested by Nielsen [54]. Following this transformation, MEP amplitudes were normally distributed (Shapiro-Wilk $p > 0.1$). In both Experiment I and II, repeated measures ANOVAs were used to examine the effect of within- and between-subjects factors on each dependent variable. In Experiment I (task hand), the impact of trial type (grating/smooth) and age group (young adults vs. seniors) on the following dependant variables was examined: 1) MEP log-amplitude, 2) MEP latency, and 3) SP duration. In Experiment II (resting hand), baseline was entered into the ANOVA along with smooth and grating trials as repeated factors to contrast variations in MEP amplitude across the three types of trials recorded with the target hand at rest (baseline, smooth, grating). In addition,"hand” was also entered as a repeated factor to examine laterality effects (right vs. left). Age group was the between-subjects factor. The dependent variables were MEP log-amplitude and MEP latency. In both experiments, paired-sample t-tests were used to test for differences on background EMG levels produced between grating and smooth trials. Paired-sample t-tests were also used to test for differences between MEPs recorded in the subset of seniors at 10% of pinch grip and MEPs recorded in these participants during the grating and smooth trials in Experiment I. Performance in the grating task was compared between age groups using the Mann-Whithney U test for performance values were strongly skewed to the left (skewness < -1.0) owing to the low level of task difficulty. All tests were performed using SPSS software version 17.0 for Windows® (Chicago, IL, USA). Figures were prepared using GraphPad Prism version 5.02 for Windows (GraphPad Software, San Diego California USA, http://www.graphpad.com). All values are reported as mean ± SEM.

Acknowledgements
The authors wish to thank all participants for their time and patience during testing. Special thanks to Sonia Hussain for her help with data collection and analysis. This work will serve as a partial fulfilment for a doctoral thesis in experimental psychology by Sabah Master. Sabah Master is supported by FRSQ (Canada). Part of this work was made possible through support from a discovery grant from NSERC (Canada) and the Research Development Funds, Faculty of Health Sciences, University of Ottawa.

Author details
[redacted]

Authors’ contributions
SM participated in the design of the study, carried out the behavioral testing, performed the statistical analysis and drafted the manuscript. FT conceived of the study, and participated in its design and coordination and drafted the manuscript. Both authors read and approved the manuscript and its revisions.

Received: 9 November 2011 Accepted: 14 March 2012
Published: 14 March 2012

References

1. Verstynen T, Diedrichsen J, Albert N, Aparicio P, Ivry RB: **Ipsilateral Motor Cortex Activity During Unimanual Hand Movements Relates to Task Complexity.** *J Neurophysiol* 2005, **93(3)**:1209-1222.
2. Hutchinson S, Kobayashi M, Horkan CM, Pascual-Leone A, Alexander MP, Schlaug G: **Age-related differences in movement representation.** *Neuroimage* 2002, **17(4)**:1720-1728.
3. Stedman A, Davey NJ, Ellaway PH: **Facilitation of human first dorsal interosseous muscle responses to transcranial magnetic stimulation during voluntary contraction of the contralateral homonymous muscle.** *Muscle Nerve* 1998, **21(8)**:1033-1039.
4. Tinazzi M, Zanette G: **Modulation of ipsilateral motor cortex in man during unimanual finger movements of different complexities.** *Neurosci Lett* 1998, **244(3)**:121-124.
5. Hess CW, Mills KR, Murray NMF: **Magnetic stimulation of the human brain: Facilitation of motor responses by voluntary contraction of ipsilateral and contralateral muscles with additional observations on an amputee.** *Neurosci Lett* 1986, **71(2)**:235-240.
6. Liepert J, Dettmers C, Terborg C, Weiller C: **Inhibition of ipsilateral motor cortex during phasic generation of low force.** *Clin Neurophysiol* 2001, **112(1)**:114-121.
7. Liang N, Funase K, Narita T, Takahashi M, Matsukawa K, Kasai T: **Effects of unilateral voluntary movement on motor imagery of the contralateral limb.** *Clin Neurophysiol* 2011, **122(3)**:550-557.
8. Oliver P, Tremblay F: **Selective increase in corticospinal excitability in the context of tactile exploration.** *Somatosens Mot Res* 2009, **26(2)**:64-73.
9. Master S, Tremblay F: **Task-specific increase in corticomotor excitability during tactile discrimination.** *Exp Brain Res* 2009, **194(2)**:163-172.
10. Master S, Tremblay F: **Selective increase in motor excitability with intraactive (self) versus interactive touch.** *Neuroreport* 2010, **21(3)**:206-209.
11. Master S, Tremblay F: **Differential modulation of corticospinal excitability during haptic sensing of 2-D patterns vs. textures.** *BMC Neurosc* 2010, **11(1)**:149.
12. Bodegard A, Geyer S, Grefkes C, Zilles K, Roland PE: **Hierarchical processing of tactile shape in the human brain.** *Neuron* 2001, **31(2)**:317-328.
13. Miquee A, Xerri C, Rainville C, Anton JL, Nazarian B, Roth M, Zennou-Azogui Y: **Neuronal substrates of haptic shape encoding and matching: a functional magnetic resonance imaging study.** *Neurosc* 2008, **152(1)**:29-39.
14. Lederman SJ, Klatzky RL: **Relative availability of surface and object properties during early haptic processing.** *J Exp Psychol [Hum Percept]* 1997, **23(6)**:1680-1707.
15. Stoesz MR, Zhang M, Weisser VD, Prather SC, Mao H, Sathian K: **Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks.** *Int J Psychophysiol* 2003, **50(1-2)**:41-49.
16. Harada T, Saito DN, Kashikura K, Sato T, Yonekura Y, Honda M, Sadato N: **Asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study.** *J Neurosci* 2004, **24(34)**:7524-7530.
17. Master S, Tremblay F: **Tactile-dependant corticomotor facilitation is influenced by discrimination performance in seniors.** *Behav Brain Funct* 2010, **6(1)**:16.
18. Gordon AM, Lee JH, Flament D, Ugurbil K, Ebner TJ: **Functional magnetic resonance imaging of motor, sensory, and posterior parietal cortical areas during performance of sequential typing movements.** *Exp Brain Res* 1998, **121(2)**:153-166.
19. Uematsu A, Obata H, Endoh T, Kitamura T, Hortobágyi T, Nakazawa K, Suzuki S: **Asymmetrical modulation of corticospinal excitability in the contracting and resting contralateral wrist flexors during unilateral shortening, lengthening and isometric contractions.** *Exp Brain Res* 2010, **206(1)**:59-69.
20. Koerte I, Eftimov L, Laubender RP, Esslinger O, Schroeder AS, Ertl-Wagner B, Wahllaender-Danek UTE, Heinen F, Danek A: **Mirror movements in healthy humans across the lifespan: effects of development and ageing.** *Dev Med Child Neurol* 2010, **52(12)**:1106-1112.
21. Verstynen T, Ivry RB: **Network dynamics mediating ipsilateral motor cortex activity during unimanual actions.** *J Cogn Neurosci* 2011, **0(0)**:1-13.
22. Muellbacher W, Facchini S, Boroojerdi B, Hallett M: **Changes in motor cortex excitability during ipsilateral hand muscle activation in humans.** *Clin Neurophysiol* 2000, **111(2)**:344-349.
23. Perez MA, Cohen LG: **Mechanisms underlying functional changes in the primary motor cortex ipsilateral to an active hand.** *J Neurosci* 2008, **28(22)**:5631-5640.
24. Perez MA, Cohen LG: **Scaling of motor cortical excitability during unimanual force generation.** *Cortex* 2009, **45(9)**:1065-1071.
25. Hortobagyi T, Taylor JL, Petersen NT, Russell G, Gandevia SC: **Changes in segmental and motor cortical output with contralateral muscle contractions and altered sensory inputs in humans.** *J Neurophysiol* 2003, **90(4)**:2451-2459.
26. Shibasaki H, Sadato N, Lyshkow H, Yonekura Y, Honda M, Nagamine T, Suwazono S, Magata Y, Ikeda A, Miyazaki M, *et al*: **Both primary motor cortex and supplementary motor area play an important role in complex finger movement.** *Brain* 1993, **116(6)**:1387-1398.
27. Yoshino-Saito K, Nishimura Y, Oishi T, Isa T: **Quantitative inter-segmental and inter-laminar comparison of corticospinal projections from the forelimb area of the primary motor cortex of macaque monkeys.** *Neurosc* 2010, **171(4)**:1164-1179.
28. Soteropoulos DS, Edgley SA, Baker SN: **Lack of Evidence for Direct Corticospinal Contributions to Control of the Ipsilateral Forelimb in Monkey.** *J Neurosc* 2011, **31(31)**:11208-11219.
29. Reis J, Swayne OB, Vandermeeren Y, Camus M, Dimyan MA, Harris-Love M, Perez MA, Ragert P, Rothwell JC, Cohen LG: **Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control.** *J Physiol* 2008, **586(2)**:325-351.
30. Voineskos AN, Farzan F, Barr MS, Lobaugh NJ, Mulsant BH, Chen R, Fitzgerald PB, Daskalakis ZJ: **the Role of the corpus callosum in transcranial magnetic stimulation induced interhemispheric signal propagation.** *Biol Psychiatry* 2010, **68(9)**:825-831.
31. Rouiller EM, Babalian A, Kazennikov O, Moret V, Yu XH, Wiesendanger M: **Transcallosal connections of the distal forelimb representations of the primary and supplementary motor cortical areas in macaque monkeys.** *Exp Brain Res* 1994, **102(2)**:227-243.
32. Fling BW, Kwak Y, Peltier SJ, Seidler RD: **Differential relationships between transcallosal structural and functional connectivity in young and older adults.** *Neurobiol Aging* , doi: 10.1016/j.neurobiolaging.2011.11.018.
33. Dum RP, Strick PL: **Frontal lobe inputs to the digit representations of the motor areas on the lateral surface of the hemisphere.** *J Neurosci* 2005, **25(6)**:1375-1386.
34. Tanji J, Okano K, Sato KC: **Neuronal activity in cortical motor areas related to ipsilateral, contralateral, and bilateral digit movements of the monkey.** *J Neurophysiol* 1988, **60(1)**:325-343.
35. Brinkman C, Porter R: **Supplementary motor area in the monkey: activity of neurons during performance of a learned motor task.** *J Neurophysiol* 1979, **42(3)**:681-709.
36. Fling BW, Peltier S, Bo J, Welsh RC, Seidler RD: **Age differences in interhemispheric interactions: callosal structure, physiological function, and behavior.** *Front Neurosci* 2011, **5**:38.
37. Stinear C, Walker K, Byblow W: **Symmetric facilitation between motor cortices during contraction of ipsilateral hand muscles.** *Exp Brain Res* 2001, **139(1)**:101-105.
38. Chen R, Gerloff C, Hallett M, Cohen LG: **Involvement of the ipsilateral motor cortex in finger movements of different complexities.** *Ann Neurol* 1997, **41(2)**:247-254.
39. Langan J, Peltier S, Bo J, Fling BW, Welsh RC, Seidler RD: **Functional implications of age differences in motor system connectivity.** *Front Syst Neurosci* 2010, **4**:17.
40. Mattay VS, Fera F, Tessitore A, Hariri AR, Das S, Callicott JH, Weinberger DR: **Neurophysiological correlates of age-related changes in human motor function.** *Neurology* 2002, **58(4)**:630-635.
41. Sailer A, Dichgans J, Gerloff C: **The influence of normal aging on the cortical processing of a simple motor task.** *Neurology* 2000, **55(7)**:979-985.
42. Talelli P, Waddingham W, Ewas A, Rothwell J, Ward N: **The effect of age on task-related modulation of interhemispheric balance.** *Exp Brain Res* 2008, **186(1)**:59-66.
43. Addamo PK, Farrow M, Bradshaw JL, Moss S, Karistianis NG: **The effect of attending to motor overflow on its voluntary inhibition in young and older adults.** *Brain Cogn* 2010, **74(3)**:358-364.
44. Ward NS, Frackowiak RSJ: **Age-related changes in the neural correlates of motor performance.** *Brain* 2003, **126(4)**:873-888.
45. Cabeza R: **Cognitive neuroscience of aging: Contributions of functional neuroimaging.** *Scand J Psychol* 2001, **42(3)**:277-286.

46. Fling BW, Chapekis M, Reuter-Lorenz PA, Anguera J, Bo J, Langan J, Welsh RC, Seidler RD: **Age differences in callosal contributions to cognitive processes.** *Neuropsychologia* 2011, **49(9)**:2564-2569.
47. Kastenbauer T, Sauseng S, Brath H, Abrahamian H, Irsigler K: **The value of the Rydel-Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer.** *Diabet Med* 2004, **21(6)**:563-567.
48. Pestronk A, Florence J, Levine T, Al-Lozi MT, Lopate G, Miller T, Ramneantu I, Waheed W, Stambuk M: **Sensory exam with a quantitative tuning fork: rapid, sensitive and predictive of SNAP amplitude.** *Neurology* 2004, **62(3)**:461-464.
49. Tremblay F, Backman A, Cuenco A, Vant K, Wassef MA: **Assessment of spatial acuity at the fingertip with grating (JVP) domes: validity for use in an elderly population.** *Somatosens Mot Res* 2000, **17(1)**:61-66.
50. Van Boven RW, Johnson KO: **The limit of tactile spatial resolution in humans: grating orientation discrimination at the lip, tongue, and finger.** *Neurology* 1994, **44(12)**:2361-2366.
51. Sathian K, Zangaladze A: **Tactile spatial acuity at the human fingertip and lip: bilateral symmetry and interdigit variability.** *Neurology* 1996, **46(5)**:1464-1466.
52. Tremblay F, Wong K, Sanderson R, Coté L: **Tactile spatial acuity in elderly persons: assessment with grating domes and relationship with manual dexterity.** *Somatosens Mot Res* 2003, **20(2)**:127-132.
53. Mills KR, Nithi KA: **Corticomotor threshold to magnetic stimulation: normal values and repeatability.** *Muscle Nerve* 1997, **20(5)**:570-576.
54. Nielsen JF: **Logarithmic distribution of amplitudes of compound muscle action potentials evoked by transcranial magnetic stimulation.** *J Clin Neurophysiol* 1996, **13(5)**:423-434.

doi:10.1186/1471-2202-13-27
Cite this article as: Master and Tremblay: **Task-related enhancement in corticomotor excitability during haptic sensing with the contra- or ipsilateral hand in young and senior adults.** *BMC Neuroscience* 2012 **13**:27.

Contact Force Profiles Differ by Age During Tactile Letter Recognition with the Fingertip

Sabah Master[1,3] and Francois Tremblay[2,3*]

University of Ottawa, School of Psychology[1] and Rehabilitation Sciences[2] and Elisabeth Bruyere Research Institute[3]

ABSTRACT

Contact force profiles deployed at the finger tip in the context of tactile letter recognition were compared in young and older adults. Older adults showed lower normal force and increased letter-to-letter variability in normal force as compared to young adults. This likely contributed to longer contact times and lower performance accuracy in older adults, suggesting a central contribution to the decline with age in tactile letter recognition.

KEYWORDS: experimentation, human factors, performance.

1 INTRODUCTION

One behavioural measure of the cortical control of manual dexterity is the biomechanical variable of force output. Control of grip force has been robustly shown to decrease with increasing age, and in particular older adults consistently show more variability in maintaining force output with visual feedback during precision grips involving both static and dynamic contractions of hand muscles [e.g., 1, 2]. This is likely a major contributor to the observed decreases in manual dexterity with aging. In line with these behavioural observations, neurophysiological investigations have also revealed that aging is also associated with decreased task-specific facilitation of corticospinal excitability during precision hand actions [e.g., 3].

This work on control of force output during precision hand actions has focussed on different types of grips. Tactile exploration at the fingertip is another aspect of hand function involving fine precision motor control. Contact force profiles have not, however, been characterized in the context of this task. The ability to resolve complex spatial patterns such as embossed letters declines in parallel with fine motor control over precision force output in aging [e.g., 4, 5]. The reduced ability for spatial discrimination in older adults has been largely attributed to reduction in cutaneous receptor populations in the glabrous skin [e.g., 6, 7]. However, other alterations at the central level could also play a role as pattern recognition often fails in older adults in spite of a preserved spatial acuity [8]. Similarly, age related differences in force control are likely due to alterations in both peripheral mechanisms such as motor unit firing rate variability [e.g., 9, 10], and central processes such as sensorimotor processing [e.g., 1].

Thus in the present report, we sought to determine whether the observed decline in tactile pattern recognition at the fingertip with aging was associated with changes at the motor cortical level in the active control exerted by individuals over both the normal and tangential contact forces deployed at the fingertip. Contact force strategies used by young and older adult observers were compared when tactile exploration was performed over a force plate. As in our previous study [8], we used the letter recognition task developed by Johnson and colleagues [11, 12] to characterize pattern recognition performance. Although our primary focus was to examine age differences, we also looked at “hand” as a potential co-factor influencing contact force profiles and recognition performance.

2 MATERIALS AND METHODS

The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received an honorarium for his or her participation.

2.1 Participants

Nineteen community-dwelling, literate and healthy individuals were recruited from the Ottawa area. The two groups of participants consisted of 10 young adults (24 ± 2 years, 5 males), and 9 seniors (70 ± 6 years, 5 males). Handedness was assessed using the Edinburgh questionnaire and only 1/19 participants was classified as a (weak) left-hander. Prior to the experimental session, senior participants were specifically screened for undiagnosed sensory neuropathy using a Rydel–Seiffer tuning fork to estimate vibration extinction thresholds. Such vibration thresholds have been shown to be valid and reliable markers of peripheral nerve function in the extremities [13, 14]. The tuning fork was applied to the dorsal aspect of the distal joint of the dominant index finger [14, 15]. All seniors’ threshold values were found to be within the limits of previously published norms for their age [15].

2.2 Letter Recognition Task

The tactile stimuli consisted of 6 embossed capital letters (A, D, F, G, S, and X; sans serif, Stewardson font) with 1-mm relief, 6-mm height and 0.5-mm stroke width (Figure 1). The letters were produced via a photo-etching process using flexible nylon plates exposed to UV-rays . The 6 letter stimuli were selected on the basis of our previous observations on letter recognition in young and older adults [detailed in 4]. The rationale for this selection was to ensure that recognition performance would be optimal across the two groups of participants by limiting the number of possible responses (from 26 down to 6). Limiting the number of stimuli was necessary to improve consistency of performance in older adults. Each testing session began with a period of familiarization, wherein participants were invited to inspect each of the 6 letters visually and tactually. They were asked to attend to specific details of each letter (e.g., horizontal bars in “F”). Then participants completed practice trials, receiving verbal feedback on performance. Note that learning effects due to repeated exposure to tactile letter stimuli are expected to be minimal (~4% improvement in accuracy), as shown previously by Vega-Bermudez et al (1991). Once the individual was comfortable with the task, testing began. For testing, participants were seated comfortably on a chair in a quiet, dim room so that blindfolding was not required to obscure the participants’ vision of the letters (the letters were not visible in the dim room). In each trial, one of

IEEE Haptics Symposium 2012
4-7 March, Vancouver, BC, Canada
978-1-4673-0809-0/12/$31.00 ©2012 IEEE

the 6 letters was presented in a predetermined random sequence. Participants rested their hand on an armrest with the index positioned near the top of the force plate. Each trial began when the experimenter placed the letter to be scanned on the force plate, and activated acquisition of force data using a custom software (Stimo). The start of data acquisition was signaled by a short auditory tone, and participants were instructed to start scanning the letter with their finger once they heard the tone signaling them to start scanning. Participants were instructed to scan the letter with contour following using the tip of either the right or the left index finger and to report its identity as quickly as possible by speaking it aloud (e.g., "D"). The experimenter recorded the participant's response on the response sheet. Participants were instructed to lift their finger as soon as they knew the answer, and were encouraged to respond as quickly and as accurately as possible, although no time constraint was imposed. No feedback was provided on performance during the test trials. For testing, each of the 6 letters was presented one time to each hand, for a total of 6 trials/ hand. The order of testing with each hand was counterbalanced in each age group so that half of the males and half of the females started testing with the right hand, while the other half started with the left hand.

2.3 Acquisition and Analysis of Contact Forces

Contact forces in the horizontal and normal planes (Fx, Fy, Fz) were recorded for the duration of the scanning (sampling 200 Hz) using an instrumented tactile force plate (range 0.01-5 N, 0.001 N resolution). From contact force recordings, three measures were derived: mean contact time derived by analysis of individual trials, mean normal force (FN) obtained from averaging Fz values, and mean resultant tangential force (1):

$$F\tan = \sqrt{Fy^2 + Fx^2} \qquad (1)$$

Contact time was measured as the window of time when contact forces were detected on the force plate. The experimenter ensured that the participant only contacted the force plate with the index finger, that no other part of the hand was resting on the force plate during testing, and that participants did lift their finger at the same time as they reported their answer orally. The recognition performance was determined for each participant by computing for each hand the mean accuracy in terms of percentage correct and the mean contact time. The presence of possible outliers, which can be an issue especially for contact time measurements, was verified with the Grubb's test (available at http://www.graphpad.com/quickcalcs/grubbs2.cfm). No outlier was detected at an alpha of 0.05 in the two age groups for both accuracy and contact time data. Contact times were entered into a two-way repeated measures ANOVA with age group (young-adults/seniors) as the between-subjects factor, and hand (left/right) as the within subjects measure. Force data were entered into a three-way repeated measures ANOVA with age group (young-adults/seniors) as the between-subjects factor, and hand (left/right) and force (normal/tangential) as the within subjects measures. The letter-to-letter standard deviation of force was entered into a three-way repeated measures ANOVA with age group (young-adults/seniors) as the between-subjects factor, and hand (left/right) and force (normal/tangential) as the within subjects measures.

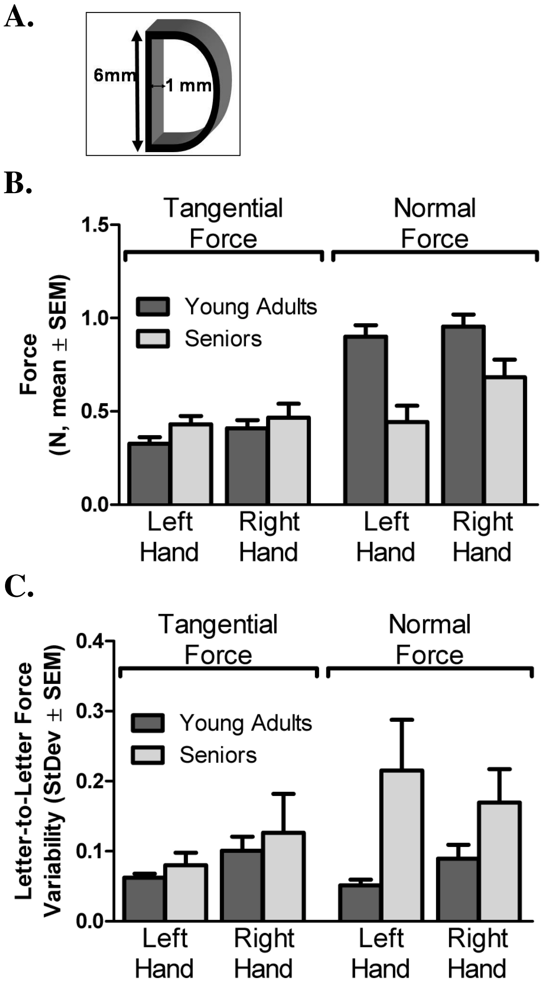

Figure 1. A. Diagram showing the dimensions of the letters used during the experiment (letter D). B. Mean normal and tangential forces deployed. C. Mean letter-to-letter variability (standard deviation) of forces deployed by young adults and seniors for letter recognition.

3 RESULTS

3.1 Task Performance: Accuracy and Contact Time

Young adult participants exhibited good accuracy (95 ± 7%) in recognizing the letters by touch, which suggests that tactile recognition was effective in the majority of cases. Seniors, however, were largely outperformed by young adults (69 ± 24%). As for recognition accuracy, the largest differences in contact times were also found between age groups, while differences attributable to hand were negligible. In fact, no main effect or interactions were detected for the factor "hand" ($F_{1,17}$=1.78, p=0.20). There was a large effect of "age" ($F_{1,17}$=88.98, p<0.0001, partial eta^2=84%, observed power=100%) on contact times, seniors responding ~3x slower than young adults (mean, 14 ± 5s vs. 4 ± 0.8s). It can be seen that, while seniors tended to display larger inter-subject variability, they also tended to show much longer contact times in comparison to young adults.

3.2 Deployment of Contact Forces at the Fingertip

Multivariate tests revealed main effects of force ($F_{1,17}$=57.56; Wilks'Lambda p<0.0001, partial eta^2=77%, observed power=100%) and age group ($F_{1,17}$=6.4; p=0.02, partial eta^2=27%, observed power=66%) on the amplitude of contact force deployed at the index fingertip during the sensing and recognition of raised letters by touch. This effect could be explained by the significant interaction between the factors "force" and "age" group ($F_{1,17}$=47.83; Wilks'Lambda p<0.0001, partial eta^2=74%, observed power=100%). Younger adults deployed greater levels of normal force at the fingertip during letter recognition than did their older counterparts (Figure 2C). No significant main effect or interactions with hand (p>0.2) were detected. Older adults also showed a greater standard deviation of contact force deployed between each of the six letters than younger adults, an effect that was particularly pronounced for the normal force ($F_{1,17}$=6.18; p=0.02; Figure 2D). A secondary analysis was performed to test if longer contact times were associated with lower normal forces and increased variability of normal forces and tangential forces. Spearman's two-tailed correlations revealed that lower normal forces were strongly and significantly associated with longer response times (rho^2= -0.49, p<0.0001), while force variability (normal or tangential) was not (p>0.2).

4 DISCUSSION AND CONCLUSIONS

The present study provides strong evidence that seniors deploy a more variable, lower level of normal contact force during the recognition of raised letters by touch at the fingertip than young adults. Conversely, the level of tangential force applied and its variability was comparable between the two age groups. Secondary analysis revealed that smaller perpendicular forces were associated with slower letter detection while higher forces were associated with faster detection. Reduced normal forces in old age in the presence of equal tangential forces (across young and old) means that the fingertip force vector directions were different between young and old (i.e., directed further away from normal for old adults). This would have led to less deformation at the finger pulp and less efficient interaction with tactile receptors in older adults. This type of difference in force output may underlie age-related deficits in the ability to efficiently apply the specific exploratory pattern spontaneously used by observers identify raised letters by touch: contour exploration [16]. This difference in effectiveness of exploration strategy could explain why seniors took ~ 3x longer to identify letters and exhibited much slower contact times than their younger counterparts. Indeed, intrinsic hand muscles show disproportionate weakening with age [17]. Further, older adults have been observed to show increased variability of force output [18, 19]. This variability, in combination with a decreased afferent sensitivity, may explain their compensatory tendency to use higher perpendicular forces for precision grips to increase the safety margin to prevent slipping [18, 19]. However, the range of force used during prehensile action and the mode of control is qualitatively different than in haptic sensing, where movement and fingertip forces are tuned to allow sensory acquisition as opposed to just automatic adjustments to ensure grip stability. In the present study, older adults may compensate for increased variability of perpendicular force output by applying lower normal forces in order to maintain a smooth contour exploration pattern (without too much friction resulting in stopping and starting of the finger movement over the letter due to too much normal force and not enough tangential force) at the cost of decreased fingertip pulp deformation and tactile receptor activation. Indeed, even in tactile exploration studies, young adult observers tend to used consistent force patterns within a limited range [20].

The present findings suggest that differences between the two age groups at the level of central processing, in particular, motor control, may explain the finding of longer contact times in seniors. This difference in exploration strategy may also have contributed to lower recognition accuracy. Indeed, control over the direction of force output has been observed to hamper performance on fine precision tasks involving the fingers in stroke patients as well [21]. These observations of particular declines with aging in the cortical control of precision hand movements are in line the idea that such tasks are highly demanding in terms of recruitment of voluntary motor areas. This has been demonstrated by findings of enhanced corticospinal excitability using TMS during precision grip versus power grip tasks [e.g., 22]. Along the same lines, fine dynamic precision force control has been shown to result in increased activation of the primary motor cortex even when very low forces are generated, whereas static power grips requiring high levels of force output activate this voluntary motor control area far less [2, 23]. Anatomical findings that the level of organization of spinal white matter in the lateral CS tract decreased with aging in a manner correlated with decreases in grip force control also support this idea [24]. Further, cortical sensorimotor areas and frontal regions in humans lose both white matter and gray matter between the ages of 20 and 50 [25]. Complementary evidence from neuroimaging of healthy young and old rhesus macaques also showed an age-related loss in the prefrontal areas and around the superior temporal sulcus [26]. These changes in brain structure likely contribute to both the decreases in manual dexterity, and cutaneous sensation, observed in healthy aging [4, 27-30].

The present results suggest that perhaps age-related declines in performance on complex tactile recognition tasks may be associated with changes in central motor control over forces deployed at the fingertip during tactile exploration. Additionally, recognition of 2-D patterns through contour exploration is taxing in terms of working memory. Parts of the age-related difference in response times could be ascribed to decline in tactile attention and tactile working memory with age. Indeed, a reduced ability to attend to tactile features may hamper sensorimotor control of force production during tactile exploration that normally optimizes the gathering of information regarding surface features by touch [16, 31-33]. As evidenced by neuroimaging studies, tactile pattern recognition at the fingertip relies on an extensive cortical network involving primary and secondary motor and sensory areas, as well as associative regions of the frontal and parietal lobes [34-36]. These observations suggest that one factor that could be responsible for the difference between age groups is attentional demand. Older adults have been suggested to have attentional deficits in comparison to younger adults in perceptual motor tasks [37]. Indeed, the current findings are consistent with findings demonstrating that older adults have decrements in sensory attention processing [38]. Thus, the present findings support the ideas that both age-related deficits in force control and complex tactile processing are not exclusively due to peripheral changes in musculature or afferent innervation, but may also be mediated by central processes such as attention to the sensorimotor guidance and control of fine finger movements.

5 ACKNOWLEDGEMENTS

The authors wish to thank all participants for their time and patience during testing. Special thanks to Patricia Oliver, Francesca Avila and Caitlin Merritt for their help with data analysis. This work will serve as a partial fulfillment for a doctoral thesis in experimental psychology by Sabah Master.

Sabah Master is supported by FRSQ (Quebec) and François Tremblay is supported by NSERC (Canada).

REFERENCES

[1] J. Sosnoff and K. Newell. "Information processing limitations with aging in the visual scaling of isometric force," *Experimental Brain Research,* 170:423-432, 2006.

[2] C. Voelcker-Rehage and J. L. Alberts. "Age-related changes in grasping force modulation," *Experimental Brain Research,* 166:61-70, 2005.

[3] G. Leonard and F. Tremblay. "Corticomotor facilitation associated with observation, imagery and imitation of hand actions: A comparative study in young and old adults," *Experimental Brain Research,* 177:167-175, 2007.

[4] H. Manning and F. Tremblay. "Age differences in tactile pattern recognition at the fingertip," *Somatosens Mot Res,* 23:147-55, 2006.

[5] E. A. Christou and L. G. Carlton. "Old adults exhibit greater motor output variability than young adults only during rapid discrete isometric contractions," *J Gerontol A Biol Sci Med Sci,* 56:B524-32, 2001.

[6] J. C. Stevens and M. Q. Patterson. "Dimensions of spatial acuity in the touch sense: changes over the life span," *Somatosens Mot Res,* 12:29-47, 1995.

[7] F. Tremblay, et al. "Assessment of spatial acuity at the fingertip with grating (JVP) domes: validity for use in an elderly population," *Somatosens Mot Res,* 17:61-6, 2000.

[8] S. Master, et al. "Characterization of human tactile pattern recognition performance at different ages," *Somatosens Mot Res,* 27:60-7, 2010.

[9] K. W. Kornatz, et al. "Practice reduces motor unit discharge variability in a hand muscle and improves manual dexterity in old adults," *J Appl Physiol,* 98:2072-2080, 2005.

[10] A. M. Taylor, et al. "Multiple features of motor-unit activity influence force fluctuations during isometric contractions," *J Neurophysiol,* 90:1350-61, 2003.

[11] F. Vega-Bermudez and K. O. Johnson. "Spatial acuity after digit amputation," *Brain,* 125:1256-64, 2002.

[12] F. Vega-Bermudez, et al. "Human tactile pattern recognition: Active versus passive touch, velocity effect and patterns of confusion," *Journal of Neurophysiology,* 65:531-546, 1991.

[13] T. Kastenbauer, et al. "The value of the Rydel-Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer," *Diabet Med,* 21:563-7, 2004.

[14] A. Pestronk, et al. "Sensory exam with a quantitative tuning fork: rapid, sensitive and predictive of SNAP amplitude," *Neurology,* 62:461-4, 2004.

[15] I. S. J. Martina, et al. "Measuring vibration threshold with a graduated tuning fork in normal aging and in patients with polyneuropathy," *J Neurol Neurosurg Psychiatry,* 65:743-747, 1998.

[16] S. J. Lederman and R. L. Klatzky. "Extracting object properties through haptic exploration," *Acta Psychol (Amst),* 84:29-40, 1993.

[17] M. Shinohara, et al. "Age effects on force produced by intrinsic and extrinsic hand muscles and finger interaction during MVC tasks," *Journal of Applied Physiology,* 95:1361-1369, 2003.

[18] K. J. Cole , et al. "Mechanisms for Age-Related Changes of Fingertip Forces during Precision Gripping and Lifting in Adults," *The Journal of Neuroscience,* 19:3238-3247, 1999.

[19] K. J. Cole. "Grasp Force Control in Older Adults," *Journal of Motor Behavior,* 23:251-258, 1991.

[20] A. Smith, et al. "Deployment of fingertip forces in tactile exploration," *Experimental Brain Research,* 147:209-218, 2002.

[21] N. Seo, et al. "Altered digit force direction during pinch grip following stroke," *Experimental Brain Research,* 202:891-901, 2010.

[22] M. Bonnard, et al. "Corticospinal control of the thumb-index grip depends on precision of force control: a transcranial magnetic stimulation and functional magnetic resonance imagery study in humans," *European Journal of Neuroscience,* 25:872-880, 2007.

[23] B. Keisker, et al. "Differential representation of dynamic and static power grip force in the sensorimotor network," *European Journal of Neuroscience,* 31:1483-1491, 2010.

[24] P. G. Lindberg, et al. "White Matter Organization in Cervical Spinal Cord Relates Differently to Age and Control of Grip Force in Healthy Subjects," *Journal of Neuroscience,* 30:4102-4109, 2010.

[25] P. Pieperhoff, et al. "Deformation Field Morphometry Reveals Age-Related Structural Differences between the Brains of Adults up to 51 Years," *J. Neurosci.,* 28:828-842, 2008.

[26] G. E. Alexander, et al. "Age-related regional network of magnetic resonance imaging gray matter in the rhesus macaque," *Journal of Neuroscience,* 28:2710-2718, 2008.

[27] V. S. Mattay, et al. "Neurophysiological correlates of age-related changes in human motor function," *Neurology,* 58:630-635, 2002.

[28] S. Heuninckx, et al. "Systems Neuroplasticity in the Aging Brain: Recruiting Additional Neural Resources for Successful Motor Performance in Elderly Persons," *J. Neurosci.,* 28:91-99, 2008.

[29] R. M. Enoka, et al. "Mechanisms that contribute to differences in motor performance between young and old adults," *Journal of Electromyography and Kinesiology,* 13:1-12, 2003.

[30] S. W. Shaffer and A. L. Harrison. "Aging of the somatosensory system: A translational perspective," *Physical Therapy,* 87:193-207, 2007.

[31] S. Master and F. Tremblay. "Task-specific increase in corticomotor excitability during tactile discrimination," *Exp Brain Res,* 194:163-72, 2009.

[32] S. Master and F. Tremblay. "Tactile-dependant corticomotor facilitation is influenced by discrimination performance in seniors," *Behav Brain Funct,* 6:16, 2010.

[33] S. J. Lederman and R. L. Klatzky. "Haptic perception: A tutorial," *Atten Percept Psychophys,* 71:1439-1459, 2009.

[34] R. Stilla, et al. "Posteromedial Parietal Cortical Activity and Inputs Predict Tactile Spatial Acuity," *J. Neurosci.,* 27:11091-11102, 2007.

[35] H. Burton, et al. "Reading embossed capital letters: an fMRI study in blind and sighted individuals," *Hum Brain Mapp,* 27:325-39, 2006.

[36] R. W. Van Boven, et al. "Tactile form and location processing in the human brain," *Proc Natl Acad Sci U S A,* 102:12601-5, 2005.

[37] C. Pesce, et al. "Effects of aging on visual attentional focusing," *Gerontology,* 51:266-76, 2005.

[38] C. T. Scialfa. "The role of sensory factors in cognitive aging research," *Canadian Journal of Experimental Psychology,* 56:153-163, 2002.

Somatosensory and Motor Research, June 2010; 27(2): 60–67

informa
healthcare

ORIGINAL ARTICLE

Characterization of human tactile pattern recognition performance at different ages

SABAH MASTER[1,2], MÉLISSA LARUE[3], & FRANÇOIS TREMBLAY[1,2,3]

[redacted]

(Received 24 January 2010; accepted 11 April 2010)

Abstract

This study examined tactile pattern recognition performance in human observers ($N = 44$) in the context of a letter recognition task at the fingertip. Participants were recruited from three different age groups (youth, $n = 17$; young adults, $n = 14$; seniors, $n = 13$) to examine age-related differences in performance. The influence of gender (males vs females) and hand (right vs left) was also examined. Performance was characterized in terms of both response accuracy and associated response times (RTs). Patterns of confusion between letters were also examined. Results showed that age was the most important factor in determining the capacity of our participants to perform fast and accurate pattern recognition. In this respect, younger participants (i.e., youth and young adults) clearly outperformed seniors by showing not only better accuracy and less confusion but also 2–3 times faster RT. By comparison, the combined influence of ‘‘hand’’ and ‘‘gender’’ on recognition performance was only marginal. These results indicate that the ability to perform complex tactile pattern recognition is already well established in youth 10–14 years of age with only minor refinements occurring later in early adulthood. With advancing age, such ability becomes far less efficient, as judged by the drastic increase in RT observed in seniors, in spite of a relatively good accuracy. This suggests that alterations not only at the peripheral receptor level but also at the central processing level might play an important role in limiting the ability of seniors to perform fast and efficient pattern recognition at the fingertip.

Keywords: *Tactile discrimination, pattern recognition, age, youth*

Introduction

Humans are particularly skilled at discriminating patterns and recognizing tactile forms at the fingertip, where dense populations of mechanoreceptors afford great spatial resolution. For example, young adults can easily resolve simple spatial details, such as gaps or grooves, in the 1-mm range (Johnson and Phillips 1981; Van Boven and Johnson 1994). The discrimination of more complex tactile patterns, such as those formed by Braille characters or embossed Roman letters, is however more challenging for the common observer (Klatzky et al. 1987; Lederman and Klatzky 1997). Such spatial discriminations rely on slow contour explorations to extract specific features of the touched pattern to allow for successful identification (Lederman and Klatzky 1993). This process is inherently slow and prone to errors because any interference at the level of peripheral encoding, in the transmission of the spatial image, or in the processing of that image at the central level may lead to a failure in recognition (Loomis 1981, 1990). Yet, psychophysical studies of tactile pattern recognition show that adult observers are particularly good at identifying complex forms through active exploration with the fingertip (Loomis 1990; Vega-Bermudez et al. 1991). Such observations indicate that at maturity the human tactile perceptual system is highly effective in processing spatial information arising from the exploration of two-dimensional patterns. Still, many questions remain as to how the ability to perform fine spatial discrimination develops in

---

[redacted]

ISSN 0899–0220 print/ISSN 1369–1651 online © 2010 Informa Healthcare Ltd.
DOI: 10.3109/08990220.2010.485959

humans and how it is affected by the natural aging process. Previous investigations in this regard have produced a fairly wide range of observations using a variety of spatial stimuli from the simple (e.g., edges or gaps) to the more complex (e.g., character recognition). From these investigations, it appears that the ability to resolve simple spatial attributes, such as gaps or edges, is largely achieved in children by 6–8 years of age (Stevens and Patterson 1995; Stevens and Choo 1996). Discrimination of more complex forms, such as orientation of grooves in a grating, however, is achieved only later and reaches adult status only after 10 years of age (Bleyenheuft et al. 2006). At the other end of the spectrum, the deleterious effect of aging on tactile spatial acuity at the fingertip has been well documented. In persons over 60 years of age, even detection of simple gap stimuli will sometimes require a two- to threefold increase in spacing when compared to young adults (Stevens and Choo 1996; Goldreich and Kanics 2003, 2006; Tremblay et al. 2005). Likewise, the ability to resolve complex spatial patterns, such as embossed letters, is also greatly reduced in healthy aging, as we reported previously (Tremblay et al. 2003; Manning and Tremblay 2006). The reduced ability for spatial discrimination in older adults has been largely attributed to peripheral factors and linked to histological evidence of age-related reductions in the number of mechanoreceptors in the glabrous skin (Bruce 1980; Stevens and Patterson 1995; Tremblay et al. 2000). Although reduced tactile innervation certainly contributes to poor spatial discrimination performance in aging, other alterations at the central level could also play a role, as pattern recognition often fails in older adults in spite of a preserved spatial acuity (Manning and Tremblay 2006). Indeed, as evidenced by neuroimaging studies, tactile pattern recognition at the fingertip relies on an extensive cortical network involving primary and secondary motor and sensory areas, as well as associative regions of the frontal and parietal lobes (Van Boven et al. 2005; Burton et al. 2006; Stilla et al. 2007).

Still, most of the observations on human tactile pattern recognition have been derived from simple performance indicators, such as response accuracy, neglecting other important aspects of the performance, like time for recognition. Incorporating additional performance indicators, besides accuracy, could provide further insights as to the capacity of human observers to perform efficient pattern recognition. In the present report, we sought to better characterize the ability of human observers to perform complex tactile pattern recognition at the fingertip by looking at several performance indicators (accuracy, response time, and patterns of errors) in three groups of participants recruited from different age groups, that is, youth, young adults, and seniors. As in our previous study, we used the letter recognition task developed by Johnson and colleagues (Vega-Bermudez et al. 1991; Vega-Bermudez and Johnson 2002) to characterize pattern recognition performance. Although our primary focus was to examine age differences, we also looked at "hand" and "gender" as potential co-factors influencing recognition performance. While the evidence for strong asymmetries between hands or between genders is rather weak in the tactile modality (Voyer 1996; Hiscock et al. 1999), more recent work (Goldreich and Kanics 2003, 2006) suggests that gender might be a factor to account for, especially where fine spatial discrimination at the fingertip is concerned. The present results have been presented in abstract form (Master et al. 2009).

Material and methods

Participants

Forty-four community-dwelling, literate, and healthy individuals (22 females, 22 males) were recruited from the Ottawa area. The three groups of participants consisted of 17 youth (mean ± SD, 12 ± 1 year, 7 males), 14 young adults (23 ± 2 years, 7 males), and 13 seniors (62 ± 4 years, 8 males). Handedness was assessed using the Edinburgh questionnaire and only 4/44 participants were classified as strong left-handers. Prior to the experimental session, participants completed a questionnaire to ensure that there were no medical conditions likely to affect their performance in the test. Senior participants were also specifically screened for undiagnosed sensory neuropathy using a Rydel–Seiffer tuning fork to estimate vibration extinction thresholds. Such vibration thresholds have been shown to be valid and reliable markers of peripheral nerve function in the extremities (Kastenbauer et al. 2004; Pestronk et al. 2004). The tuning fork was applied to the dorsal aspect of the distal interphalangeal joint of the dominant index finger (Martina et al. 1998; Pestronk et al. 2004). All seniors' threshold values were found to be within the limits of previously published norms for their age (Martina et al. 1998). In addition, tactile spatial acuity thresholds could be obtained from 7/13 seniors[1] using the JVP domes^{TM} and the grating orientation discrimination task (see Manning and Tremblay 2006 for details). In this subgroup of seniors, spatial acuity was relatively well preserved with threshold values ranging from 2.1 to 1.0 mm and a mean threshold of 1.4 ± 0.4 mm. The Institutional Review Ethics Board approved the study procedure in accordance with the principles of the Declaration of Helsinki and informed consent

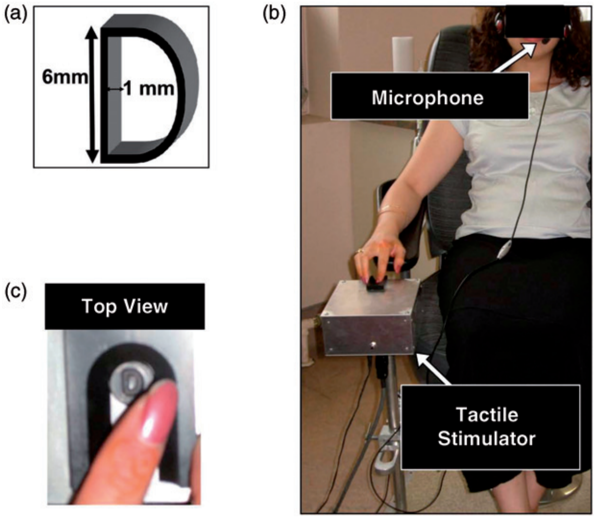

Figure 1. Experimental set-up used to assess tactile pattern recognition. (A) Diagram showing the dimensions of the letters used during the experiment (letter D). (B) Top view of the tactile stimulator, showing the aperture where each letter was presented to the fingertip. (C) Experimental set-up showing a participant performing the letter recognition task.

was obtained before the experimental session. All assessments were performed in a controlled laboratory environment. Each participant received an honorarium for his or her participation.

Letter stimuli

The tactile stimuli consisted of ten embossed capital letters (D, E, G, K, L, P, S, T, V, and Z; sans serif, Stewardson font) with 1-mm relief, 6-mm height, and 0.5-mm stroke width (Figure 1A). The letters were produced via a photo-etching process using flexible nylon plates exposed to UV-rays (detailed in Manning and Tremblay 2006). The ten letter stimuli were selected on the basis of our previous observations on letter recognition in young and older adults (Manning and Tremblay 2006). The rationale for this selection was to ensure that recognition performance would be optimal across the three groups of participants by limiting the number of possible responses (from 26 down to 10) and using only letters with high legibility (>85% accuracy) and low confusion rates. For testing, a tactile stimulator (Figure 1B, C) was built to automate the letter presentation and control the sequence of events. The tactile stimulator consisted of a metal enclosure (10 cm^3) concealing a series of 28 individual pegs (1-cm diameter), which could be rotated using a stepped motor. Each letter was glued on top of a peg and rotation of the stepped motor positioned the letter for presentation to the finger via a small circular aperture made at the top of the metal enclosure (Figure 1B). Once in position, the letter was raised into the aperture using a spring-lever system. Depressing the letter with minimal contact force (threshold 0.1 N) triggered data acquisition.

Letter recognition task

For testing, participants were seated comfortably on a chair in a dim, quiet room, wearing a headset with a small microphone (Figure 1C). The tactile stimulator was affixed to the chair on the side being tested. Each testing session began with a period of familiarization, wherein participants were invited to inspect each of the ten letters visually and tactually. They were asked to attend to specific details of each letter (e.g., horizontal bars in "E"). Then participants completed practice trials, receiving verbal feedback on performance. Once the individual was comfortable with the task, testing began. In each trial, one of the ten letters was presented in a predetermined random sequence. Participants rested their hand over the tactile stimulator with the index positioned near the aperture at the top. Each trial began when the tactile stimulator was activated to move the selected letter into position. Once in position the letter rose into the aperture and an auditory cue was emitted into the headphones, signalling the participant to start scanning. Participants were instructed to scan the letter with the tip of their index and to report its identity as quickly as possible by speaking it aloud in the microphone (e.g., "D"). By default the computer registered the letter just presented as the response. When errors were made, the experimenter entered the participant's response manually into the database. The computer also automatically recorded the response time (RT) as the time (in ms) from initial contact with the letter to the verbal response recorded by the microphone (11-kHz recording sampling rate, sensitivity level adjusted for each participant). Participants were encouraged to respond as quickly and as accurately as possible and, although no time constraint was imposed, trials were automatically aborted if no response had been made after 60 s. This occurred in <5% of the trials and was observed only in seniors. Aborted trials were simply repeated at the end of the testing block. No feedback was provided on performance during the test trials. Each of the ten letters was presented 3 times to each hand, for a total of 30 trials/hand. The order of testing with each hand was counterbalanced in each age group so that half of the males and half of the females started testing with the right hand, while the other half started with the left hand. Note that learning effects due to repeated exposure to tactile letter stimuli are expected to be minimal (~4% improvement in accuracy), as shown previously by Vega-Bermudez et al. (1991).

Table I. Performance accuracy in tactile letter recognition (mean % correct ± SD).

	Female			Male			
	Left hand	Right hand	Mean	Left hand	Right hand	Mean	Overall
Age group[a]							
Youth ($n = 17$)	94.0 ± 12.6	88.0 ± 14.8	91.0 ± 13.7	97.1 ± 7.6	90.0 ± 11.5	93.6 ± 10.1	92.1 ± 12.3
Young adults ($n = 14$)	98.6 ± 3.8	94.3 ± 7.9	96.4 ± 6.3	84.3 ± 16.2	87.1 ± 13.8	85.7 ± 14.5	91.1 ± 12.3
Seniors ($n = 13$)	78.0 ± 14.8	76.0 ± 13.4	77.0 ± 13.4	83.8 ± 11.9	77.5 ± 17.5	80.6 ± 14.8	79.2 ± 14.1
Overall	91.8 ± 13.3	87.3 ± 13.9	89.5 ± 13.6	88.2 ± 13.3	84.5 ± 15.0	86.4 ± 14.2	

[a] Significant main effect ($F_{2,38} = 8.03$, $p = 0.001$).

Statistical analysis

The recognition performance was determined for each participant by computing for each hand the mean accuracy in terms of percentage correct and the mean RT. The presence of possible outliers, which can be an issue especially for RT measurements, was verified with the Grubb's test (available at http://www.graphpad.com/quickcalcs/grubbs2.cfm). No outlier was detected at an alpha of 0.05 in the three age groups for both accuracy and RT data. Each participant's performance was also scrutinized to derive patterns of confusion by determining the number of times each letter stimulus elicited a given response (e.g., how often "G" was called "S" and vice versa). Performance data (accuracy and RT) were entered into three-way repeated measures ANOVAs with age group (youth/young adults/seniors) and gender as between-subjects factors, and hand (left/right) as the within-subjects measure. Upon detection of a significant main effect, *post hoc* comparisons were performed using the Bonferroni procedure. The significance level was set at $p < 0.05$ for all tests. All tests were performed using SPSS software version 17.0 for Windows® (Chicago, IL, USA). Figures were prepared using GraphPad Prism version 5.02 for Windows (GraphPad Software, San Diego, CA, USA, www.graphpad.com).

Results

Recognition accuracy

The mean accuracy computed from each hand with participants sorted by gender is shown in Table I. From inspection of Table I, it can be seen that, in general, participants exhibited good accuracy in recognizing the letters by touch, which suggests that tactile recognition was effective in the majority of cases. Closer inspection of Table I also reveals that differences between hands or between genders were only marginal, when compared to differences attributable to age. In fact, in spite of their relatively good accuracy, seniors were largely outperformed by youth and young adults. This age difference was confirmed by the ANOVA, with age accounting for almost one-third of the total variance in recognition accuracy ($F_{2,38} = 8.03$, $p = 0.001$). In contrast, no significant main effects or interactions were found for the "hand" ($F_{1,38} = 2.1$, $p = 0.15$) or "gender" ($F_{1,38} = 0.26$, $p = 0.61$) co-factors. *Post hoc* Bonferroni comparisons confirmed that the differences observed between the two younger groups (youth and young adults) and the seniors were highly significant (youth, $p = 0.002$; young adults, $p = 0.008$).

Response time

Table II shows the mean RTs measured from the right and left hands of male and female participants of each age group. As for recognition accuracy, the largest differences were found between age groups, while differences attributable to hand and gender were comparatively smaller in size. In fact, no main effect or interactions were detected for the factor "hand" ($F_{1,38} = 1.2$, $p = 0.28$), while "gender" did approach significance ($F_{1,38} = 3.78$, $p = 0.06$). The latter effect reflected the fact that women tended to produce faster RTs than men. The large effect of "age" ($F_{2,38} = 14.7$, $p < 0.001$) on RTs can be further appreciated in Figure 2, which shows the distribution of individual responses in the three age groups, with the data collapsed across hands. It can be seen that, while seniors tended to display larger inter-subject variability, they also tended to show much longer RTs in comparison to either youth or young adults. These differences between groups were highly significant (youth and young adults vs seniors, $p < 0.001$, Bonferroni post-test comparisons).

Confusion patterns

The observed age difference in terms of accuracy and RT was also reflected in the analysis of confusion patterns. As shown in Table III, with the exception of male participants in the younger groups, only seniors exhibited consistent confusion patterns (i.e., pairs of letters confused in >20% of trials).

Table II. Response times for tactile letter recognition (mean ± SD in seconds).

	Female			Male			
	Left hand	Right hand	Mean	Left hand	Right hand	Mean	Overall
Age group[a]							
Youth ($n = 17$)	5.0 ± 1.0	6.3 ± 2.2	5.6 ± 1.8	6.1 ± 3.0	5.7 ± 1.8	5.9 ± 2.4	5.8 ± 2.0
Young adults ($n = 14$)	2.2 ± 1.1	2.6 ± 1.6	2.4 ± 1.3	5.0 ± 2.9	5.7 ± 2.5	5.4 ± 2.6	3.9 ± 2.5
Seniors ($n = 13$)	12.1 ± 12.4	10.0 ± 6.8	11.1 ± 9.5	15.0 ± 8.3	18.6 ± 9.5	16.8 ± 8.8	14.6 ± 9.3
Overall	5.7 ± 6.6	6.0 ± 4.4	5.8 ± 5.6	9.0 ± 7.1	10.4 ± 8.6	9.7 ± 7.8	

[a] Significant main effect ($F_{2,38} = 14.7$, $p < 0.001$).

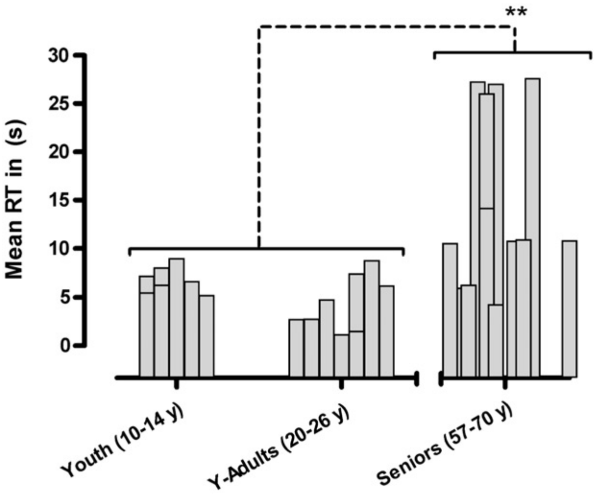

Figure 2. Distribution of individual response times (RTs) measured in the three age groups for the tactile letter recognition task. RT data have been collapsed across the two hands to improve clarity. Note the large increase in RTs in the group of seniors ($n = 13$) relative to either youth ($n = 17$) or young adults ($n = 14$). The differences between groups were highly significant ($^{**}p < 0.001$, Bonferoni post-test comparisons).

Table III. Pairs of letters frequently confused by participants.

Confusion pairs[a]	Youth	Young adults	Seniors	
	Male	Male	Female	Male
E ⇆ K	–	14 ⇆ 7	–	–
E ⇆ S	–	14 ⇆ 14	–	–
K ⇆ G	–	–	–	31 ⇆ 0
K ⇆ P	–	–	10 ⇆ 20	–
K ⇆ Z	0 ⇆ 21	–	20 ⇆ 10	–
S ⇆ Z	–	–	20 ⇆ 10	9 ⇆ 13

[a] Each entry represents pairs of letters that were mistaken for each other more often than would be expected by chance (i.e., letter pairs with confusion rates > 20%). Each value represents the percentage of trials in which one letter in the confusion pair was mistaken for the other, and vice versa. For instance, in seniors, "S" was mistaken for "Z" in 20% of the trials, whereas "Z" was mistaken for "S" in 10% of the trials.

Interestingly, the confusion pairs in the younger groups were restricted to letters sharing isomorphic features like "K" and "Z", whereas confusions in seniors involved both isomorphic and non-isomorphic letters (e.g., K and P). In fact, the analysis revealed that letters containing curvilinear elements were mistaken just as frequently as letters containing internal horizontal elements (e.g., G, see Table III).

Correlations between accuracy and response time in seniors

As reported above, the performance of seniors tended to be more variable than in the other groups, participants showing various levels of accuracy associated with large variations in RTs. To further examine this issue, a Pearson's correlation was performed to look for a possible association between recognition accuracy and RT in seniors. The association between spatial acuity and recognition performance data was also examined with Pearson's correlation. For these analyses, observations from the two hands were collapsed to derive a mean value for each participant. The first correlation revealed that accuracy levels were largely independent of RTs ($r = -0.1$, $p = 0.77$, $n = 13$), so that slow RTs were not necessarily associated with a lower accuracy, the converse being also true. Similarly, in the seven seniors whose spatial acuity was determined (see "Methods"), accuracy and RT did not significantly correlate with resolution thresholds ($r < 0.20$, $p > 0.65$).

Discussion

In the present study, we sought to better characterize the ability of human observers to recognize complex tactile patterns, such as raised Roman letters, at the fingertip. We measured not only recognition accuracy but also the time to recognition, and assessed patterns of confusion. While our primary focus was to look for differences with age, we also examined how the performance would vary between the two hands and between men and women. Our results showed that age was by far the most important factor in determining the capacity of our participants to perform efficient pattern recognition. By comparison, no laterality effect with regard to right vs left differences in performance was found. Similarly, only marginal differences were found between men and women. In the following paragraphs, we will discuss the significance of each of these factors for human pattern recognition performance.

Age differences

Unsurprisingly, amongst the three factors examined in the present study, only age proved to be a determinant influencing tactile pattern recognition. In characterizing the performance of seniors, we found that not only did they make more mistakes in identifying the letters, but they also exhibited much slower responses than their younger counterparts. Relatively speaking, this difference in RTs largely outweighed the differences observed in recognition accuracy. In fact, senior participants, while being slow to respond, still managed to perform with a relatively good level of accuracy (see Table I). Yet, the time to reach recognition was delayed by as much as 20 s in some senior participants. Which factors could have contributed to produce such delays in tactile recognition? One obvious source of slowing could be linked with the sensing aspect of the task, seniors being less capable of extracting information from tactile exploration owing to the expected decline in manual dexterity and tactile sensibility with age (Stevens and Patterson 1995; Stevens and Choo 1996; Tremblay et al. 2000, 2003). While we cannot totally exclude this possibility, we would like to argue that such factors probably played only a minor role in delaying RTs in seniors. First, it would seem rather counter-intuitive to think that a group of carefully screened seniors with a mean age of 62 years would exhibit such a deficit in sensibility that their ability to extract information from active touch would be almost completely obliterated (hence, the prolonged RTs). The fact that our group of seniors was relatively young, showed normal sensitivity to vibration and, for about half of them, also showed good spatial acuity at the fingertip, makes such an interpretation highly unlikely. Second, the patterns of confusion exhibited by seniors did not fit with the asymmetries one would predict on the basis of faulty peripheral encoding. Pattern recognition is known to rely primarily on the spatial encoding properties exhibited by slowly adapting type I afferents (SAI) supplying the distal finger pad (Johnson 2001). While SAI afferents have been shown to convey a faithful spatial image of touched patterns (Phillips et al. 1988), certain spatial details, such as horizontal elements (e.g., bars in the letter E) tend to be less accurately represented in the neural discharge (Vega-Bermudez et al. 1991). These properties explain why certain pairs of letters tend to be confused more than others and why certain confusion asymmetries arise (e.g., B is often mistaken for D, but not the reverse). Following this line of reasoning, in the context of our task one would have predicted more confusion between pairs like "D and G" or "E and K". However, such asymmetries were observed only in younger participants, seniors exhibiting variable and unexpected patterns, like confusing "K and G" (see Table III). At this point, it is worth emphasizing that the letter stimuli used in the present study consisted of highly legible characters whose dimensions (6-mm high) largely exceeded the limit of spatial resolution in human observers, even for aged participants. The size issue is critical given that cutaneous spatial resolution becomes less critical in limiting effective recognition as the size of the patterns increases to become more legible, as suggested by Loomis (1990). Accordingly, for patterns of highly legible dimensions, such as the letters used here, central factors become far more important than peripheral factors for effective recognition. Interestingly, this is actually what we observed in our subset of seniors tested for spatial acuity, where resolution thresholds were only poorly related to recognition performance (i.e., accuracy and RT). Thus, all the preceding observations concur to suggest that the limiting factor in affecting the performance of seniors was not in sensing the pattern per se, but in processing tactile information centrally to attain perceptual recognition. In this regard, our interpretation would be in line with that of Legge et al. (2008), who also recently invoked central factors in trying to explain why blind individuals retained good tactile spatial acuity, even at advancing age. These authors dismissed peripheral factors on the basis of observations showing that physical changes affecting the fingertip with age (e.g., skin's pliability, reduced blood flow, wear and tear) could not account for differences in spatial acuity in older persons (Stevens et al. 2003; Vega-Bermudez and Johnson 2004). The same arguments can be applied here for the observed increase in RTs in seniors.

Which central factors then might have contributed to prolong RTs in seniors? As stated before, discrimination of 2-D patterns is an inherently difficult process that occurs over time and space, taxing attentional resources and loading working memory (Lederman and Klatzky 1997). In the face of such task demands, it is easy to see why older persons could be particularly challenged cognitively. We propose that the exceedingly prolonged RTs exhibited by some seniors could actually reflect a delayed central processing time due to slower integration of incoming spatiotemporal information as the pattern was explored tactually. Such an interpretation would be consistent with recent advances in the field of cognitive aging showing that with age, the early stages of sensory processing are often affected by the tendency of older adults to display excessive attention towards irrelevant stimuli, neglecting more critical relevant stimuli (Valeriani et al. 2003; Gazzaley et al. 2005; Gazzaley and D'Esposito 2007). One can easily conceive that during letter scanning excessive attention towards some spatial details such as the curve in the letter "P", could have affected the capacity of some seniors to produce fast responses, and in some other cases, to mistaken identity and incorrect responses. In the same vein, the unexpected confusion patterns displayed by certain seniors could have reflected a failure of perceptual integration mechanisms, leading subjects to simply try their "best guess" as to the letter's identity.

With regards to the groups of young participants, the results showed that, on average, youth and young adults had comparable performance both in terms of accuracy and in terms of RTs. These results are in agreement with the observations of Bleyenheuft et al. (2006) on children's ability after age 10 to perform simple discriminations of spatial orientation. The present observations now extend these youth's capacities to the resolution of complex spatial patterns, like raised letters. Still, youth tended to display slightly longer RTs than young adults, which may indicate that bottom-up and top-down processes involved in tactile recognition might not be fully optimal until one reaches early adulthood.

Gender and hand differences

In the present study, we found that pattern recognition at the fingertip was little affected by the hand used for exploration or by the sex of the participants. As stated earlier, the absence of a strong "hand" effect could be predicted on the basis of previous observations demonstrating equivalence between the two hands in terms of spatial discrimination capacity (Sathian and Zangaladze 1998; Vega-Bermudez and Johnson 2002). The present observations thus provide further evidence against the existence of any strong right–left asymmetry in the tactile domain. With regards to gender effects, although we could not find significant main effects or interactions we did notice a trend towards a difference between males and females for variations in RTs. This trend reflected the tendency of females, particularly in the young adult group and in the senior group, to respond faster than their male counterparts. While marginally significant, the observation that young and elderly women tended to be faster at pattern recognition than men is in line with recent evidence suggesting a better spatial discrimination in females (Goldreich and Kanics 2003, 2006). However, as suggested very recently by Peters et al. (2009), the finer spatial acuity exhibited by women may simply reflect differences in finger size, as individuals with smaller fingers tend to exhibit higher spatial acuity than individuals with large fingers, irrespective of gender. On this account, one would have predicted better recognition performance in youth than in the other two groups, but this was not the case. Such an observation provides further support for our earlier suggestion about the relative importance of central factors over peripheral factors in explaining the observed age differences in pattern recognition performance at the fingertip.

In conclusion, the present study shows that the ability to perceive complex tactile patterns at the fingertip is already well established in youth 10–14 years of age. With maturation, this ability only refines to become optimal in young adulthood, presumably reflecting a more efficient central processing of tactile spatial information. With advancing age, tactile pattern recognition becomes less efficient with lower accuracy and substantial increases in RT. While this decline could be interpreted as an alteration in peripheral sensing ability with age, we would like to suggest that in healthy seniors with preserved hand sensibility, central factors and perceptual integration might actually play a greater role in limiting the ability of older persons to perform fast and efficient pattern recognition by touch.

Acknowledgements

The authors wish to thank all participants for their time and patience during testing. Thanks to Roxanne Oetelaar, Sophie Richer, and Caroline Rivard for their help with data collection. Part of this project was conducted in the context of a CIHR summer studentship by Melissa Larue.

Declaration of interest: This work was supported by a grant from the Natural Sciences & Engineering Research Council of Canada to François Tremblay. The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

Note

1. Testing for spatial acuity could be performed only in a subset of senior participants due to time constraints and participants' availability.

References

Bleyenheuft Y, Cols C, Arnould C, Thonnard J-L. 2006. Age-related changes in tactile spatial resolution from 6 to 16 years old. Somatosens Mot Res 23:83–87.

Bruce MF. 1980. The relation of tactile thresholds to histology in the fingers of elderly people. J Neurol Neurosurg Psychiatry 43:730–734.

Burton H, McLaren DG, Sinclair RJ. 2006. Reading embossed capital letters: An fMRI study in blind and sighted individuals. Hum Brain Mapp 27:325–339.

Gazzaley A, Cooney JW, Rissman J, D'Esposito M. 2005. Top-down suppression deficit underlies working memory impairment in normal aging. Nat Neurosci 8:1298–1300.

Gazzaley A, D'Esposito M. 2007. Top-down modulation and normal aging. Ann NY Acad Sci 1097:67–83.

Goldreich D, Kanics IM. 2003. Tactile acuity is enhanced in blindness. J Neurosci 23:3439–3445.

Goldreich D, Kanics IM. 2006. Performance of blind and sighted humans on a tactile grating detection task. Percept Psychophys 68:1363–1371.

Hiscock M, Inch R, Hawryluk J, Lyon PJ, Perachio N. 1999. Is there a sex difference in human laterality? III. An exhaustive survey of tactile laterality studies from six neuropsychology journals. J Clin Exp Neuropsychol 21:17–28.

Johnson KO, Phillips JR. 1981. Tactile spatial resolution. I. Two-point discrimination, gap detection, grating resolution, and letter recognition. J Neurophysiol 46:1177–1192.

Johnson KO. 2001. The roles and functions of cutaneous mechanoreceptors. Curr Opin Neurobiol 11:455–461.

Kastenbauer T, Sauseng S, Brath H, Abrahamian H, Irsigler K. 2004. The value of the Rydel–Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer. Diabet Med 21:563–567.

Klatzky RL, Lederman SJ, Reed C. 1987. There's more to touch than meets the eye: Relative salience of object dimension for touch with and without vision. J Exp Psychol 116:356–369.

Lederman SJ, Klatzky RL. 1993. Extracting object properties through haptic exploration. Acta Psychol (Amst) 84:29–40.

Lederman SJ, Klatzky RL. 1997. Relative availability of surface and object properties during early haptic processing. J Exp Psychol Hum Percept Perform 23:1680–1707.

Legge GE, Madison C, Vaughn BN, Cheong AMY, Miller JC. 2008. Retention of high tactile acuity throughout the life span in blindness. Percept Psychophys 70:1471–1488.

Loomis JM. 1981. On the tangibility of letters and Braille. Percept Psychophys 29:37–46.

Loomis JM. 1990. A model of character recognition and legibility. J Exp Psychol 16:106–120.

Manning H, Tremblay F. 2006. Age differences in tactile pattern recognition at the fingertip. Somatosens Mot Res 23:147–155.

Martina ISJ, van Koningsveld R, Schmitz PIM, van der Meche FGA, van Doorn PA. 1998. Measuring vibration threshold with a graduated tuning fork in normal aging and in patients with polyneuropathy. J Neurol Neurosurg Psychiatry 65:743–747.

Master S, Larue M, Tremblay F. Haptic perception is modified by age, gender and laterality Soc for Neurosci: Neuroscience Meeting Planner, Chicago, IL, 2009: Program No. 78.10.

Pestronk A, Florence J, Levine T, Al-Lozi MT, Lopate G, Miller T, Ramneantu I, Waheed W, Stambuk M. 2004. Sensory exam with a quantitative tuning fork: Rapid, sensitive and predictive of SNAP amplitude. Neurology 62:461–464.

Peters RM, Hackeman E, Goldreich D. 2009. Diminutive digits discern delicate details: Fingertip size and the sex difference in tactile spatial acuity. J Neurosci 29:15756–15761.

Phillips JR, Johnson KO, Hsiao SS. 1988. Spatial pattern representation and transformation in monkey somatosensory cortex. Proc Natl Acad Sci USA 85:1317–1321.

Sathian K, Zangaladze A. 1998. Perceptual learning in tactile hyperacuity: Complete intermanual transfer but limited retention. Exp Brain Res 118:131–134.

Stevens JC, Patterson MQ. 1995. Dimensions of spatial acuity in the touch sense: Changes over the life span. Somatosens Mot Res 12:29–47.

Stevens JC, Choo KK. 1996. Spatial acuity of the body surface over the life span. Somatosens Mot Res 13:153–166.

Stevens JC, Alvarez-Reeves M, Dipietro L, Mack GW, Green BG. 2003. Decline of tactile acuity in aging: A study of body site, blood flow, and lifetime habits of smoking and physical activity. Somatosens Mot Res 20:271–279.

Stilla R, Deshpande G, LaConte S, Hu X, Sathian K. 2007. Posteromedial parietal cortical activity and inputs predict tactile spatial acuity. J Neurosci 27:11091–11102.

Tremblay F, Cuenco A, Backman A, Vant K, Wassef M-A. 2000. Assessment of spatial acuity at the fingertip with grating (JVP) domes: Validity for use in an eldery population. Somatosens Mot Res 17:61–66.

Tremblay F, Wong K, Sanderson R, Cote L. 2003. Tactile spatial acuity in elderly persons: Assessment with grating domes and relationship with manual dexterity. Somatosens Mot Res 20:127–132.

Tremblay F, Mireault AC, Dessureault L, Manning H, Sveistrup H. 2005. Postural stabilization from fingertip contact. II. Relationships between age, tactile sensibility and magnitude of contact forces. Exp Brain Res 164:155–164.

Valeriani M, Ranghi F, Giaquinto S. 2003. The effects of aging on selective attention to touch: A reduced inhibitory control in elderly subjects? Int J Psychophysiol 9:75–87.

Van Boven RW, Johnson KO. 1994. The limit of tactile spatial resolution in humans: Grating orientation discrimination at the lip, tongue, and finger. Neurology 44:2361–2366.

Van Boven RW, Ingeholm JE, Beauchamp MS, Bikle PC, Ungerleider LG. 2005. Tactile form and location processing in the human brain. Proc Natl Acad Sci USA 102:12601–12605.

Vega-Bermudez F, Johnson KO, Hsaio SS. 1991. Human tactile pattern recognition: Active versus passive touch, velocity effect and patterns of confusion. J Neurophysiol 65:531–546.

Vega-Bermudez F, Johnson KO. 2002. Spatial acuity after digit amputation. Brain 125:1256–1264.

Vega-Bermudez F, Johnson KO. 2004. Fingertip skin conformance accounts, in part, for differences in tactile spatial acuity in young subjects, but not for the decline in spatial acuity with aging. Percept Psychophys 66:60–67.

Voyer D. 1996. On the magnitude of laterality effects and sex differences in functional lateralities. Laterality 1:51–83.

CHAPTER III. GENERAL DISCUSSION AND CONCLUSION

The works presented in this thesis are the first to highlight the importance of haptic attention for corticomotor facilitation. These works provide strong evidence supporting the role of central factors in contributing to aging effects on motor and perceptual aspects of haptic sensing abilities. In particular, the present observations indicate that with age there is a change in contact force deployment and patterns of confusion, in addition to a substantial reduction in response times during haptic letter recognition. However, it is shown that older adults retain a capacity to elicit haptic-related corticomotor facilitation when attentional demand and stimuli are adjusted for age. Thus, limits with age on fast and efficient haptic pattern recognition may not be due exclusively to peripheral changes in afferent innervation or musculature, but rather mediated by central processes such as attention to sensorimotor guidance of fine finger movements.

A central origin for age differences suggests such declines may be amenable to interventions enhancing neuro-plasticity such as age-tailored haptic sensing tasks. Specifically, Experiments III-VI reveal that task difficulty with regards to attentional demand is a critical consideration when designing interventions destined to improve hand function in older adults with neurological impairments. The results of Experiment IV in particular provide a physiological basis for rehabilitation specialists to develop better task-related intervention strategies recruiting bilateral frontal, parietal and occipital multisensory brain regions preferentially to facilitate finger movements. For instance, simple haptic sensing may incorporated into hand retraining for stroke to facilitate corticospinal drive to the paretic hand. Alternatively, more demanding haptic sensing tasks could be prescribed for the less affected hand to elicit bilateral corticomotor facilitation, promoting recovery of the affected hand. Indeed, task performance in rehabilitation can affect excitability and plasticity even more than drugs while having only mild, temporary side-effects if any [31]. The use of complementary inter-disciplinary techniques adds strength to the conclusions drawn and richness to the research landscape to which this thesis contributes.

In addition to the strengths described above, there are also several limitations of the present works. Firstly, the results of Experiments III-VI are based on a relatively small sample of self-selected healthy, active and social seniors, those who would be interested, able and motivated to come to the lab for testing, which might not be representative of the elderly population in general. Additionally, participants were further screened for intact peripheral sensation at the fingertips with the vibration detection test (all Experiments I-VI), safety for application of TMS (Experiments I-IV) and health of the hands (Experiments V-VI) once at the lab (see APPENDIX A. TESTS FOR VIBRATION DETECTION AND TACTILE ACUITY and APPENDIX B. HEALTH QUESTIONNAIRES). Lastly, the vast majority of all participants in Experiments I-VI were right-handed, and effects of handedness were not investigated. Thus the observed variability may be an underestimate of the true variability in young adults and in healthy aging, and future work should address these issues. Indeed, recent findings have shown that corticomotor facilitation during haptic sensing is modulated differently in right and left-handers, with left-handers showing less reliable haptic-related corticomotor facilitation than right-handers, in both the preferred and less preferred hand [159].

Further, it is important to note that the somatosensory system is generally more tuned to 3D object perception than to 2-D pattern discriminations of the type used in Experiments I-IV [160-162]. Enhanced corticospinal excitability may thus be expected when observers discriminate 3D objects vs. 2D lined patterns, and this comparison would be an interesting and functionally relevant avenue for future study. Further studies are also needed to pinpoint the neural mechanisms underlying the extra facilitation with haptic sensing reported in Experiments I-IV, especially with regards to the role of changes in intra-cortical inhibition. Further to the clinical application of the present findings, the effectiveness of various haptic sensing tasks must be tested in the rehabilitative setting.

Another interesting avenue for future studies is the investigation of multisensory interactions, i.e. to examine how the combination of visual or auditory inputs with haptic touch could enhance perceptual performance. There is evidence that such combinations can lead to enhanced tactile acuity [163, 164]. This could be particularly interesting in the context of aging. We are currently investigating multisensory interactions to see if combining visual, auditory and touch inputs could lead to further enhancement in corticomotor facilitation and also improved discrimination performance in seniors [167].

In conclusion, the present work provides a unique contribution to the field of human haptic touch in showing that adding a haptic sensing component to a simple, minimally demanding finger movement can reliably elicit large enhancements in corticospinal excitability in the sensing hand and in the "resting" hand. Further, this haptic-related corticomotor facilitation can be elicited to the same extent in older adults when attentional demand and stimuli are adjusted for age. Finally, the present findings provide strong support for a central, top-down origin for age-related declines in motor and perceptual aspects of haptic sensing abilities. Taken together, this work highlights the importance of using task-related rehabilitation strategies to enhance neuro-plasticity at the central level in older adults, and argues against the idea that deficits in haptic sensing with age are primarily a result of irreversible sensory and motor nerve damage at the periphery.

REFERENCES

1. Hallett, M., *Transcranial magnetic stimulation and the human brain.* Nature, 2000. **406**(6792): p. 147.
2. Watson, A.H., *What can studying musicians tell us about motor control of the hand?* J Anat, 2006. **208**(4): p. 527-42.
3. Lederman, S.J. and R.L. Klatzky, *Haptic perception: A tutorial.* Atten Percept Psychophys, 2009. **71**(7): p. 1439-1459.
4. Booth, D.A. and R.P.J. Freeman, *Discriminative feature integration by individuals.* Acta Psychologica, 1993. **84**(1): p. 1-16.
5. Burton, H. and R.J. Sinclair, *Attending to and remembering tactile stimuli: a review of brain imaging data and single-neuron responses.* J Clin Neurophysiol, 2000. **17**(6): p. 575-91.
6. Rothwell, J.C., *Overview of neurophysiology of movement control.* Clinical Neurology and Neurosurgery, 2012. **114**(5): p. 432-435.
7. Lacroix, S., et al., *Bilateral corticospinal projections arise from each motor cortex in the macaque monkey: A quantitative study.* The Journal of Comparative Neurology, 2004. **473**(2): p. 147-161.
8. Donoghue, J.P. and J.N. Sanes (2001) *Motor system organization*. Encyclopedia of Life Sciences, DOI: 10.1038/npg.els.0000185.
9. Weiler, N., et al., *Top-down laminar organization of the excitatory network in motor cortex.* Nature Neuroscience, 2008. **11**(3): p. 360-366.

10. Anderson, C.T., et al., *Sublayer-specific microcircuits of corticospinal and corticostriatal neurons in motor cortex.* Nat Neurosci, 2010. **13**(6): p. 739-744.

11. McFarland, N.R. and S.N. Haber, *Thalamic Relay Nuclei of the Basal Ganglia Form Both Reciprocal and Nonreciprocal Cortical Connections, Linking Multiple Frontal Cortical Areas.* J. Neurosci., 2002. **22**(18): p. 8117-8132.

12. Schleicher, A., et al., *Cortical Orofacial Motor Representation in Old World Monkeys, Great Apes, and Humans.* Brain, Behavior & Evolution, 2004. **63**(2): p. 61-81.

13. Berkowitz, A. (2005) *Motor output from the brain and spinal cord*. Encyclopedia of Life Sciences, DOI: 10.1038/npg.els.0004079.

14. Lemon, R.N., *Descending Pathways in Motor Control.* Annual Review of Neuroscience, 2008. **31**(1): p. 195-218.

15. Johansson, R.S. and J.R. Flanagan, *Coding and use of tactile signals from the fingertips in object manipulation tasks.* Nat Rev Neurosci, 2009. **10**(5): p. 345-359.

16. Lederman, S.J. and R.L. Klatzky, *Extracting object properties through haptic exploration.* Acta Psychol (Amst), 1993. **84**(1): p. 29-40.

17. Van Soens, I. and L.M. Van Ham, *Assessment of motor pathways by magnetic stimulation in human and veterinary medicine.* Veterinary Journal, 2011. **187**(2): p. 174-181.

18. Groppa, S., et al., *A practical guide to diagnostic transcranial magnetic stimulation: Report of an IFCN committee.* Clinical Neurophysiology, 2012. **123**(5): p. 858-882.

19. Abbruzzese, G. and C. Trompetto, *Clinical and research methods for evaluating cortical excitability.* Journal of Clinical Neurophysiology, 2002. **19**(4): p. 307-321.

20. Cowey, A., *The Ferrier Lecture 2004 what can transcranial magnetic stimulation tell us about how the brain works?* Philos Trans R Soc Lond B Biol Sci, 2005. **360**(1458): p. 1185-205.

21. George, M.S., S.H. Lisanby, and H.A. Sackeim, *Transcranial magnetic stimulation: Applications in neuropsychiatry.* Archives of General Psychiatry, 1999. **56**(4): p. 300-311.

22. Silva, S., P.J. Basser, and P.C. Miranda, *Elucidating the mechanisms and loci of neuronal excitation by transcranial magnetic stimulation using a finite element model of a cortical sulcus.* Clinical Neurophysiology, 2008. **119**(10): p. 2405-2413.

23. Thielscher, A. and T. Kammer, *Electric field properties of two commercial figure-8 coils in TMS: calculation of focality and efficiency.* Clinical Neurophysiology, 2004. **115**(7): p. 1697-1708.

24. Chen, M. and D.J. Mogul, *Using Increased Structural Detail of the Cortex to Improve the Accuracy of Modeling the Effects of Transcranial Magnetic Stimulation on Neocortical Activation.* Biomedical Engineering, IEEE Transactions on, 2010. **57**(5): p. 1216-1226.

25. Hallett, M., *Transcranial Magnetic Stimulation: A Primer.* Neuron, 2007. **55**(2): p. 187-199.

26. Chen, R., *Studies of human motor physiology with transcranial magnetic stimulation.* Muscle Nerve Suppl, 2000. **9**: p. S26-32.

27. Balslev, D., et al., *Inter-individual variability in optimal current direction for transcranial magnetic stimulation of the motor cortex.* Journal of Neuroscience Methods, 2007. **162**(1-2): p. 309-313.

28. Brasil-Neto, J.P., et al., *Optimal Focal Transcranial Magnetic Activation of the Human Motor Cortex: Effects of Coil Orientation, Shape of the Induced Current Pulse, and Stimulus Intensity.* Journal of Clinical Neurophysiology, 1992. **9**(1): p. 132-136.

29. Di Lazzaro, V., et al., *The physiological basis of transcranial motor cortex stimulation in conscious humans.* Clinical Neurophysiology, 2004. **115**(2): p. 255-266.

30. Di Lazzaro, V., et al., *Effects of voluntary contraction on descending volleys evoked by transcranial stimulation in conscious humans.* J Physiol, 1998. **508**(Pt 2): p. 625-33.

31. Siebner, H.R. and J.C. Rothwell, *Transcranial magnetic stimulation: New insights into representational cortical plasticity.* Experimental Brain Research, 2003. **148**(1): p. 1-16.

32. Chen, R., et al., *The clinical diagnostic utility of transcranial magnetic stimulation: Report of an IFCN committee.* Clinical Neurophysiology, 2008. **119**(3): p. 504-532.

33. Reis, J., et al., *Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control.* J Physiol, 2008. **586**(2): p. 325-51.

34. Rossini, P.M., et al., *Clinical neurophysiology of aging brain: From normal aging to neurodegeneration.* Progress in Neurobiology, 2007. **83**(6): p. 375-400.

35. Ziemann, U., *TMS and drugs.* Clinical Neurophysiology, 2004. **115**(8): p. 1717-1729.

36. Chen, R., et al., *Time course of corticospinal excitability in reaction time and self-paced movements.* Annals of Neurology, 1998. **44**(3): p. 317-325.

37. Mills, K.R. and K.A. Nithi, *Corticomotor threshold to magnetic stimulation: Normal values and repeatability.* Muscle & Nerve, 1997. **20**(5): p. 570-576.

38. Mills, K.R. and V. Kimiskidis, *Cortical and spinal mechanisms of facilitation to brain stimulation.* Muscle Nerve, 1996. **19**(8): p. 953-8.

39. Baker, S.N., E. Olivier, and R.N. Lemon, *Task-related variation in corticospinal output evoked by transcranial magnetic stimulation in the macaque monkey.* J Physiol, 1995. **488**(Pt 3): p. 795-801.

40. Muir, R.B. and R.N. Lemon, *Corticospinal neurons with a special role in precision grip.* Brain Research, 1983. **261**(2): p. 312-316.

41. Reilly, K.T. and C. Mercier, *Cortical topography of human first dorsal interroseus during individuated and nonindividuated grip tasks.* Human Brain Mapping, 2008. **29**(5): p. 594-602.

42. Ni, Z., et al., *Functional demanded excitability changes of human hand motor area.* Experimental Brain Research, 2006. **170**(2): p. 141-148.

43. Ferreri, F., et al., *Human brain cortical correlates of short-latency afferent inhibition: a combined EEG-TMS study.* J Neurophysiol, 2012. **108**(1): p. 314-23.

44. Golaszewski, S.M., et al., *Modulation of motor cortex excitability by different levels of whole-hand afferent electrical stimulation.* Clinical Neurophysiology, 2012. **123**(1): p. 193-199.

45. Rosenkranz, K. and J.C. Rothwell, *The effect of sensory input and attention on the sensorimotor organization of the hand area of the human motor cortex.* Journal of Physiology, 2004. **561**(1): p. 307-320.

46. Mizuguchi, N., et al., *Influence of somatosensory input on corticospinal excitability during motor imagery.* Neurosci Lett, 2012. **514**(1): p. 127-30.

47. Hess, A., et al., *Task-dependent modulation of inhibitory actions within the primary motor cortex.* Exp Brain Res, 1999. **124**(3): p. 321-330.

48. Oliver, P. and F. Tremblay, *Selective increase in corticospinal excitability in the context of tactile exploration.* Somatosens Mot Res, 2009. **26**(2): p. 64-73.

49. Fujiyama, H., et al., *Age-related differences in corticospinal excitability and inhibition during coordination of upper and lower limbs.* Neurobiology of Aging, 2012. **33**(7): p. 1484.e1-1484.e14.

50. Fujiyama, H., et al., *Age-related differences in corticomotor excitability and inhibitory processes during a visuomotor RT task.* J Cogn Neurosci, 2012. **24**(5): p. 1253-63.

51. Cirillo, J., G. Todd, and J.G. Semmler, *Corticomotor excitability and plasticity following complex visuomotor training in young and old adults.* European Journal of Neuroscience, 2011. **34**(11): p. 1847-1856.

52. Leonard, G. and F. Tremblay, *Corticomotor facilitation associated with observation, imagery and imitation of hand actions: A comparative study in young and old adults.* Experimental Brain Research, 2007. **177**(2): p. 167-175.

53. Semmler, J.G., et al., *Diminished task-related plasticity of common inputs to hand muscle motor neurons in older adults.* Aust Soc Med Res, 2003. **42**: p. 38.

54. Eisen, A., et al., *Age-dependent decline in motor evoked potential (MEP) amplitude: With a comment on changes in Parkinson's disease.* Electroencephalography and Clinical Neurophysiology - Electromyography and Motor Control, 1991. **81**(3): p. 209-215.

55. Pitcher, J.B., K.M. Ogston, and T.S. Miles, *Age and sex differences in human motor cortex input-output characteristics.* J Physiol, 2003. **546**(Pt 2): p. 605-13.

56. Oliviero, A., et al., *Effects of aging on motor cortex excitability.* Neuroscience Research, 2006. **55**(1): p. 74-77.

57. Rossini, P.M., M.T. Desiato, and M.D. Caramia, *Age-related changes of motor evoked potentials in healthy humans: non- invasive evaluation of central and peripheral motor tracts excitability and conductivity.* Brain Res, 1992. **593**(1): p. 14-9.

58. Sala, S., et al., *Microstructural changes and atrophy in brain white matter tracts with aging.* Neurobiology of Aging, 2012. **33**(3): p. 488-498.e2.

59. Voineskos, A.N., et al., *Age-related decline in white matter tract integrity and cognitive performance: a DTI tractography and structural equation modeling study.* Neurobiol Aging, 2012. **33**(1): p. 21-34.

60. Hasan, K.M., et al., *Quantification of the spatiotemporal microstructural organization of the human brain association, projection and commissural pathways across the lifespan using diffusion tensor tractography.* Brain Structure and Function, 2010. **214**(4): p. 361-373.

61. Lindberg, P.G., A. Feydy, and M.A. Maier, *White Matter Organization in Cervical Spinal Cord Relates Differently to Age and Control of Grip Force in Healthy Subjects.* Journal of Neuroscience, 2010. **30**(11): p. 4102-4109.

62. Pieperhoff, P., et al., *Deformation Field Morphometry Reveals Age-Related Structural Differences between the Brains of Adults up to 51 Years.* J. Neurosci., 2008. **28**(4): p. 828-842.

63. Alexander, G.E., et al., *Age-related regional network of magnetic resonance imaging gray matter in the rhesus macaque.* Journal of Neuroscience, 2008. **28**(11): p. 2710-2718.

64. Aanerud, J., et al., *Brain energy metabolism and blood flow differences in healthy aging.* Journal of Cerebral Blood Flow and Metabolism, 2012. **32**(7): p. 1177-1187.

65. Andrews-Hanna, J.R., et al., *Disruption of Large-Scale Brain Systems in Advanced Aging.* Neuron, 2007. **56**: p. 924-935.

66. Diermayr, G., T.L. McIsaac, and A.M. Gordon, *Finger force coordination underlying object manipulation in the elderly - A mini-review.* Gerontology, 2011. **57**(3): p. 217-227.

67. Mattay, V.S., et al., *Neurophysiological correlates of age-related changes in human motor function.* Neurology, 2002. **58**(4): p. 630-635.

68. Heuninckx, S., N. Wenderoth, and S.P. Swinnen, *Systems Neuroplasticity in the Aging Brain: Recruiting Additional Neural Resources for Successful Motor Performance in Elderly Persons.* J. Neurosci., 2008. **28**(1): p. 91-99.

69. Enoka, R.M., et al., *Mechanisms that contribute to differences in motor performance between young and old adults.* Journal of Electromyography and Kinesiology, 2003. **13**(1): p. 1-12.

70. Manning, H. and F. Tremblay, *Age differences in tactile pattern recognition at the fingertip.* Somatosensory and Motor Research, 2006. **23**(3-4): p. 147-155.

71. Shaffer, S.W. and A.L. Harrison, *Aging of the somatosensory system: A translational perspective.* Physical Therapy, 2007. **87**(2): p. 193-207.

72. Sailer, A., J. Dichgans, and C. Gerloff, *The influence of normal aging on the cortical processing of a simple motor task.* Neurology, 2000. **55**(7): p. 979-985.

73. Cirillo, J., N. Rogasch, and J. Semmler, *Hemispheric differences in use-dependent corticomotor plasticity in young and old adults.* Experimental Brain Research, 2010. **205**(1): p. 57-68.

74. Bugnariu, N. and J. Fung, *Aging and selective sensorimotor strategies in the regulation of upright balance.* Journal of NeuroEngineering and Rehabilitation, 2007. **4**.

75. Amirjani, N., et al., *Normative values and the effects of age, gender, and handedness on the Moberg Pick-Up Test.* Muscle and Nerve, 2007. **35**(6): p. 788-792.

76. Jones, L.A. and S.J. Lederman, *Human Hand Function*. 2006: Oxford University Press.

77. Davis, S.W., et al., *Que PASA? The Posterior-Anterior Shift in Aging.* Cereb. Cortex, 2008. **18**(5): p. 1201-1209.

78. Eyler, L.T., et al., *A review of functional brain imaging correlates of successful cognitive aging.* Biological Psychiatry, 2011. **70**(2): p. 115-122.

79. Dumas, J.A. and P.A. Newhouse, *The cholinergic hypothesis of cognitive aging revisited again: Cholinergic functional compensation.* Pharmacology Biochemistry and Behavior, 2011. **99**(2): p. 254-261.

80. Grady, C., *The cognitive neuroscience of ageing.* Nature Reviews Neuroscience, 2012. **13**(7): p. 491-505.

81. Freyer, F., et al., *Repetitive tactile stimulation changes resting-state functional connectivity-implications for treatment of sensorimotor decline.* Front Hum Neurosci, 2012. **6**: p. 144.

82. Kalisch, T., M. Tegenthoff, and H.R. Dinse, *Repetitive electric stimulation elicits enduring improvement of sensorimotor performance in seniors.* Neural Plast, 2010. **2010**: p. 690531.

83. Kalisch, T., M. Tegenthoff, and H.R. Dinse, *Improvement of sensorimotor functions in old age by passive sensory stimulation.* Clinical Interventions in Aging, 2008. **3**(4): p. 673-690.

84. Klatzky, R.L. and S.J. Lederman, *Haptic object perception: spatial dimensionality and relation to vision.* Philosophical Transactions of the Royal Society B: Biological Sciences, 2011. **366**(1581): p. 3097-3105.

85. Turvey, M.T. and C. Carello, *Obtaining information by dynamic (effortful) touching.* Philosophical Transactions of the Royal Society B: Biological Sciences, 2011. **366**(1581): p. 3123-3132.

86. Schmelz, M., *Neuronal sensitivity of the skin.* European journal of dermatology : EJD, 2011. **21 Suppl 2**: p. 43-47.

87. Galie, J. and L. Jones, *Thermal cues and the perception of force.* Experimental Brain Research, 2010. **200**(1): p. 81-90.

88. Ho, H.-N. and L.A. Jones, *Contribution of thermal cues to material discrimination and localization.* Perception & Psychophysics, 2006. **68**(1): p. 118-128.

89. Tiest, W.M.B. and A.M.L. Kappers, *Thermosensory reversal effect quantified.* Acta Psychologica, 2008. **127**(1): p. 46-50.

90. Tiest, W.M.B. and A.M.L. Kappers, *Tactile perception of thermal diffusivity.* Attention, Perception, & Psychophysics, 2009. **71**(3): p. 481-489.

91. McGlone, F. and D. Reilly, *The cutaneous sensory system.* Neuroscience and Biobehavioral Reviews, 2010. **34**(2): p. 148-59.

92. Macefield, V., *Physiological characteristics of low-threshold mechanoreceptors in joints, muscle and skin in human subjects.* Clinical and Experimental Pharmacology and Physiology, 2005. **32**(1-2): p. 135-144.

93. Johnson, K.O., *The roles and functions of cutaneous mechanoreceptors.* Current Opinion in Neurobiology, 2001. **11**(4): p. 455-461.

94. Johnson, K.O., T. Yoshioka, and F. Vega-Bermudez, *Tactile functions of mechanoreceptive afferents innervating the hand.* J Clin Neurophysiol, 2000. **17**(6): p. 539-58.

95. Goodwin, A.W. and H.E. Wheat, *Sensory signals in neural populations underlying tactile perception and manipulation.* Annu Rev Neurosci, 2004. **27**: p. 53-77.

96. Goodwin, A.W. (2005) *Somatosensory Systems*. Encyclopedia of Life Sciences, DOI: 10.1038/npg.els.0004082.

97. Gardner, E. (2010) *Touch*. Encyclopedia of Life Sciences, DOI: 10.1002/9780470015902.a0000219.pub2.

98. Pei, Y.C., et al., *Shape invariant coding of motion direction in somatosensory cortex.* PLoS biology, 2010. **8**(2).

99. Pei, Y.C., et al., *Convergence of submodality-specific input onto neurons in primary somatosensory cortex.* Journal of Neurophysiology, 2009. **102**(3): p. 1843-1853.

100. Thomson, A.M. and C. Lamy, *Functional maps of neocortical local circuitry.* Frontiers in Neuroscience, 2007. **1**: p. 23.

101. Thomson, A.M., *Neocortical Layer 6, a review.* Frontiers in Neuroanatomy, 2010. **4**.

102. Sato, T., et al., *Distributions of sensory spots in the hand and two-point discrimination thresholds in the hand, face and mouth in dental students.* Journal of Physiology-Paris, 1999. **93**(3): p. 245-250.

103. Minato, A., et al., *Preferred chewing side-dependent two-point discrimination and cortical activation pattern of tactile tongue sensation.* Behavioural Brain Research, 2009. **203**(1): p. 118-126.

104. Sathian, K. and A. Zangaladze, *Tactile spatial acuity at the human fingertip and lip: Bilateral symmetry and interdigit variability.* Neurology, 1996. **46**(5): p. 1464-1466.

105. Rath, E.M. and G.K. Essick, *Perioral somesthetic sensibility: Do the skin of the lower face and the midface exhibit comparable sensitivity?* Journal of Oral and Maxillofacial Surgery, 1990. **48**(11): p. 1181-1190.

106. Tamura, Y., et al., *Oral structure representation in human somatosensory cortex.* NeuroImage, 2008. **43**(1): p. 128-135.

107. Trulsson, M. and R.S. Johansson, *Orofacial mechanoreceptors in humans: encoding characteristics and responses during natural orofacial behaviors.* Behavioural Brain Research, 2002. **135**(1-2): p. 27-33.

108. Chen, L.M., R.M. Friedman, and A.W. Roe, *Optical Imaging of SI Topography in Anesthetized and Awake Squirrel Monkeys.* J. Neurosci., 2005. **25**(33): p. 7648-7659.

109. Krubitzer, L., et al., *Organization of Area 3a in Macaque Monkeys: Contributions to the Cortical Phenotype.* Journal of Comparative Neurology, 2004. **471**(1): p. 97-111.

110. Iwamura, Y., *Hierarchical somatosensory processing.* Current Opinion in Neurobiology, 1998. **8**(4): p. 522-528.

111. Iwamura, Y., et al., *Rostrocaudal gradients in the neuronal receptive field complexity in the finger region of the alert monkey's postcentral gyrus.* Experimental Brain Research, 1993. **92**(3): p. 360-368.

112. Friedman, R.M., L.M. Chen, and A.W. Roe, *Modality maps within primate somatosensory cortex.* Proceedings of the National Academy of Sciences of the United States of America, 2004. **101**(34): p. 12724-12729.

113. Hsiao, S., *Central mechanisms of tactile shape perception.* Curr Opin Neurobiol, 2008. **18**(4): p. 418-424.

114. Hsiao, S., J. Lane, and P. Fitzgerald, *Representation of orientation in the somatosensory system.* Behavioural Brain Research, 2002. **135**(1-2): p. 93-103.

115. Sripati, A.P., et al., *Spatiotemporal receptive fields of peripheral afferents and cortical area 3b and 1 neurons in the primate somatosensory system.* J Neurosci, 2006. **26**(7): p. 2101-14.

116. Nolte, J., *The Human Brain. An Introduction to Its Functional Anatomy*. 6 ed. 2009, Philadelphia: Mosby Elsevier. 736.

117. O' Conaire, E., A. Rushton, and C. Wright, *The assessment of vibration sense in the musculoskeletal examination: Moving towards a valid and reliable quantitative approach to vibration testing in clinical practice.* Manual Therapy, 2011. **16**(3): p. 296-300.

118. Pestronk, A., et al., *Sensory exam with a quantitative tuning fork: rapid, sensitive and predictive of SNAP amplitude.* Neurology, 2004. **62**(3): p. 461-4.

119. Kastenbauer, T., et al., *The value of the Rydel-Seiffer tuning fork as a predictor of diabetic polyneuropathy compared with a neurothesiometer.* Diabet Med, 2004. **21**(6): p. 563-7.

120. Van Boven, R.W. and K.O. Johnson, *The limit of tactile spatial resolution in humans: Grating orientation discrimination at the lip, tongue, and finger.* Neurology, 1994. **44**(12): p. 2361-2366.

121. Kalisch, T., et al., *Cognitive and tactile factors affecting human haptic performance in later life.* PLoS One, 2012. **7**(1).

122. Reuter, E.M., et al., *Touch perception throughout working life: effects of age and expertise.* Exp Brain Res, 2012. **216**(2): p. 287-97.

123. Lenz, M., et al., *Increased excitability of somatosensory cortex in aged humans is associated with impaired tactile acuity.* J Neurosci, 2012. **32**(5): p. 1811-6.

124. Humes, L.E., et al., *The effects of age on sensory thresholds and temporal gap detection in hearing, vision, and touch.* Attention, Perception, and Psychophysics, 2009. **71**(4): p. 860-871.

125. Tremblay, F., et al., *Assessment of spatial acuity at the fingertip with grating (JVP) domes: Validity for use in an eldery population.* Somatosensory & Motor Research, 2000. **17**(1): p. 61-66.

126. Tremblay, F., et al., *Tactile spatial acuity in elderly persons: assessment with grating domes and relationship with manual dexterity.* Somatosens Mot Res, 2003. **20**(2): p. 127-32.

127. Stevens, J.C. and M.Q. Patterson, *Dimensions of spatial acuity in the touch sense: changes over the life span.* Somatosens Mot Res, 1995. **12**(1): p. 29-47.

128. Stevens, J.C. and K.K. Choo, *Spatial acuity of the body surface over the life span.* Somatosens Mot Res, 1996. **13**(2): p. 153-66.

129. Stevens, J.C. and L.A. Cruz, *Spatial acuity of touch: ubiquitous decline with aging revealed by repeated threshold testing.* Somatosens Mot Res, 1996. **13**(1): p. 1-10.

130. Sosnoff, J. and K. Newell, *Information processing limitations with aging in the visual scaling of isometric force.* Experimental Brain Research, 2006. **170**(3): p. 423-432.

131. Sosnoff, J. and K. Newell, *The Generalization of Perceptual-Motor Intra-Individual Variability in Young and Old Adults.* The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 2006. **61**(5): p. P304-P310.

132. Voelcker-Rehage, C. and J.L. Alberts, *Age-related changes in grasping force modulation.* Experimental Brain Research, 2005. **166**(1): p. 61-70.

133. Keisker, B., et al., *Differential representation of dynamic and static power grip force in the sensorimotor network.* European Journal of Neuroscience, 2010. **31**(8): p. 1483-1491.

134. Salat, D.H., et al., *Thinning of the Cerebral Cortex in Aging.* Cereb. Cortex, 2004. **14**(7): p. 721-730.

135. Scialfa, C.T., *The role of sensory factors in cognitive aging research.* Canadian Journal of Experimental Psychology, 2002. **56**(3): p. 153-163.

136. Mahoney, J.R., et al., *The effect of multisensory cues on attention in aging.* Brain Res, 2012.

137. Iachini, T., et al., *Age differences in mental scanning of locomotor maps.* Disability and Rehabilitation, 2005. **27**(13): p. 741-752.

138. Bolton, D.A. and W.R. Staines, *Age-related loss in attention-based modulation of tactile stimuli at early stages of somatosensory processing.* Neuropsychologia, 2012. **50**(7): p. 1502-13.

139. Dolcos, F., H.J. Rice, and R. Cabeza, *Hemispheric asymmetry and aging: Right hemisphere decline or asymmetry reduction.* Neuroscience and Biobehavioral Reviews, 2002. **26**(7): p. 819-825.

140. Fabiani, M., *It was the best of times, it was the worst of times: A psychophysiologist's view of cognitive aging.* Psychophysiology, 2012. **49**(3): p. 283-304.

141. Cottone, C., et al., *Physiological Aging Impacts the Hemispheric Balances of Resting State Primary Somatosensory Activities.* Brain Topogr, 2012.

142. De Serres, S.J. and N.Z. Fang, *The accuracy of perception of a pinch grip force in older adults.* Canadian Journal of Physiology and Pharmacology, 2004. **82**(8-9): p. 693-701.

143. Brown, L.N. and R.S. Sainsbury, *Hemispheric equivalence and age-related differences in judgments of simultaneity to somatosensory stimuli.* Journal of Clinical and Experimental Neuropsychology, 2000. **22**(5): p. 587-598.

144. Sathian, K. and A. Zangaladze, *Perceptual learning in tactile hyperacuity: complete intermanual transfer but limited retention.* Exp Brain Res, 1998. **118**(1): p. 131-4.

145. Vega-Bermudez, F. and K.O. Johnson, *Spatial acuity after digit amputation.* Brain, 2002. **125**(Pt 6): p. 1256-64.

146. Boles, D.B. and S.M. Givens, *Laterality and sex differences in tactile detection and two-point thresholds modified by body surface area and body fat ratio.* Somatosensory and Motor Research, 2011. **28**(3-4): p. 102-109.

147. Tomlinson, S.P., et al., *Hemispheric specialisation in haptic processing.* Neuropsychologia, 2011. **49**(9): p. 2703-2710.

148. Borgo, F., C. Semenza, and P. Puntin, *Hemispheric differences in dichaptic scanning of verbal and spatial material by adult males and females.* Neuropsychologia, 2004. **42**(14): p. 1896-1901.

149. Harada, T., et al., *Asymmetrical Neural Substrates of Tactile Discrimination in Humans: A Functional Magnetic Resonance Imaging Study.* J. Neurosci., 2004. **24**(34): p. 7524-7530.

150. Stoesz, M.R., et al., *Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks.* International Journal of Psychophysiology, 2003. **50**(1-2): p. 41-49.

151. Van Boven, R.W., et al., *Tactile form and location processing in the human brain.* Proc Natl Acad Sci U S A, 2005. **102**(35): p. 12601-5.

152. Sadato, N., et al., *Gender Difference in Premotor Activity during Active Tactile Discrimination.* NeuroImage, 2000. **11**(5): p. 532-540.

153. Libouton, X., et al., *Tactile roughness discrimination threshold is unrelated to tactile spatial acuity.* Behavioural Brain Research, 2010. **208**(2): p. 473-478.

154. Goldreich, D. and I.M. Kanics, *Performance of blind and sighted humans on a tactile grating detection task.* Perception and Psychophysics, 2006. **68**(8): p. 1363-1371.

155. Peters, R.M., E. Hackeman, and D. Goldreich, *Diminutive Digits Discern Delicate Details: Fingertip Size and the Sex Difference in Tactile Spatial Acuity.* J Neurosci, 2009. **29**(50): p. 15756-15761.

156. Zuidhoek, S., A.M.L. Kappers, and A. Postma, *Haptic orientation perception: Sex differences and lateralization of functions.* Neuropsychologia, 2007. **45**(2): p. 332-341.

157. Vega-Bermudez, F. and K.O. Johnson, *Fingertip skin conformance accounts, in part, for differences in tactile spatial acuity in young subjects, but not for the decline in spatial acuity with aging.* Percept Psychophys, 2004. **66**(1): p. 60-7.

158. Woodward, K.L., *The relationship between skin compliance, age, gender and tactile discriminative treholds in humans.* Somatosensory and Motor Research, 1992. **10**: p. 63-67.

159. Cormier, J.-M. and F. Tremblay, *Asymmetry in corticomotor facilitation revealed in right-handers in the context of haptic discrimination.* Laterality: Asymmetries of Body, Brain and Cognition, 2012: p. 1-19.

160. Loomis, J.M., R.L. Klatzky, and S.J. Lederman, *Similarity of tactual and visual picture recognition with limited field of view.* Perception, 1991. **20**(2): p. 167-77.

161. Klatzky, R.L., S.J. Lederman, and V.A. Metzger, *Identifying objects by touch: An "expert system".* Perception & Psychophysics, 1985. **37**(4): p. 299-302.

162. Magee, L.E. and J.M. Kennedy, *Exploring pictures tactually.* Nature, 1980. **283**(5744): p. 287-288.

163. Ro, T., et al., *Sound enhances touch perception.* Experimental Brain Research, 2009. **195**(1): p. 135-143.

164. Serino, A., F. Pizzoferrato, and E. Làdavas, *Viewing a Face (Especially One's Own Face) Being Touched Enhances Tactile Perception on the Face.* Psychological Science, 2008. **19**(5): p. 434-438.

APPENDIX A. TESTS FOR VIBRATION DETECTION AND TACTILE ACUITY

PARTICIPANT # : ________ DATE OF TESTING: ____________________
EXAMINER :___________________ DATE OF BIRTH: ______________________
SEX F ☐ M ☐ AGE :_____________________________
HAND DOMINANCE : ☐Right ☐Left

- ☐ Welcome and explain the research project
- ☐ Read and sign the informed consent form
- ☐ Fill out health questionnaire for TMS application
- ☐ Fill out Questionnaire for Health Status (specific to the hand)
- ☐ Edinburgh Laterality Test
- ☐ Pay participant and sign receipt
- ☐ Test tactile sensitivity to vibration (Rydel-Seiffer Tuning Fork)

VIBRATION DETECTION
RYDEL-SEIFFER TUNING FORK (64 Hz)

SITE OF APPLICATION: a) dorsal surface of the distal interphalangial joint of the index

POSITION : the participant is seated comfortably, wrist in pronation, hand resting on a cushioned support and out of view for the testing session

PROCEDURE : allow the participant to practice with feedback (visual and verbal) on their performance. The protocol consists of touching the distal interphalangial joint of the index or the styloid process of the ulna of the dominant upper limb of the participant with the tuning fork placed perpendicularly in a random manner with maximal vibration. The **participant must then report when the vibration is no longer felt**. Do 3 trials for each region. Record the threshold indicated on the scale (0-8) and calculate the average of the 3 trials for each region.

VIBRATION DETECTION TESTING WITH THE TUNING FORK

Trial	INDEX R
1	/8
2	/8
3	/8
TOTAL/ AVERAGE	/8

Exclusion if the vibro-tactile thresholds for **seniors** is **< 6.0/8** and for **young adults** is **< 6.5/8**

INSTRUCTIONS FOR THE TACTILE ACUITY TEST

- I'm going to apply a small dome on your finger which consists of a grating with grooves. The grating will be applied for approx. 2 seconds with two specific orientations: ALONG or ACROSS (show on finger).
- After the application, I will ask you to report verbally which orientation was presented: ALONG or ACROSS
- I will then respond either : correct or incorrect
- It is also important that you remain attentive during the test. Try to focus your attention at the sensation coming from your fingertip.

INSTRUCTIONS POUR LE TEST D'ACUITÉ TACTILE

- Je vais appliquer sur votre doigt une petite sonde qui comporte des sillons formant un grillage. Je vais placer ce grillage pendant environ 2 sec. sur votre peau suivant 2 orientation : **le long du doigt et à travers le doigt**.
- Après je vais vous informez tout de suite « correcte » ou « incorrecte ». Essayez de votre mieux.
- Il est important que vous restez attentif tout au long du test. Concentrez votre attention sur les sensations en provenance de votre doigt.

SPATIAL ACUITY TESTING WITH JVP DOMES

PART #:______________________________________

SITE OF APPLICATION: At the center of the tip of index finger (presence of callus ☐)

POSITION: Participant comfortably seated. Wrist in supination, hand resting on a padded support, index immobilized with adhesive tape. EYES CLOSED OR HAND OUT OF SIGHT FOR THE TESTING SESSION.

PROCEDURE: Allow participant to practice with feedback (visual & verbal) on performance. Start testing with the 3 mm dome. Apply with slight pressure for ≈ 2 s, then ask participant to report the perceived orientation: **ACROSS (=) OR ALONG (||).** Continue until performance falls ***well below 75%*** **(e.g. 18/30, 60%).** Check **only successful** trials ☒**.**

GRATING ORIENTATION DISCRIMINATION

trial	*3 mm*		*2.5 mm*		**2 mm**		1.5 mm		1.25 mm		1 mm		0.75 mm	
1	||	☐	||	☐	=	☐	=	☐	=	☐	||	☐	||	☐
2	||	☐	||	☐	=	☐	||	☐	=	☐	||	☐	||	☐
3	=	☐	||	☐	||	☐	||	☐	||	☐	=	☐	||	☐
4	=	☐	=	☐	||	☐	=	☐	=	☐	||	☐	=	☐
5	=	☐	||	☐	||	☐	||	☐	||	☐	=	☐	||	☐
6	||	☐	||	☐	=	☐	=	☐	||	☐	=	☐	||	☐
7	=	☐	=	☐	=	☐	||	☐	=	☐	||	☐	=	☐
8	||	☐	||	☐	||	☐	=	☐	=	☐	=	☐	||	☐
9	||	☐	=	☐	||	☐	=	☐	||	☐	||	☐	=	☐
10	=	☐	=	☐	=	☐	||	☐	=	☐	=	☐	=	☐
11	||	☐	=	☐	||	☐	=	☐	||	☐	||	☐	=	☐
12	||	☐	||	☐	=	☐	||	☐	||	☐	||	☐	||	☐
13	=	☐	=	☐	||	☐	=	☐	=	☐	=	☐	=	☐
14	=	☐	=	☐	=	☐	||	☐	||	☐	=	☐	=	☐
15	||	☐	||	☐	||	☐	=	☐	||	☐	||	☐	||	☐
16	=	☐	||	☐	=	☐	||	☐	=	☐	=	☐	||	☐
17	||	☐	=	☐	||	☐	=	☐	||	☐	=	☐	=	☐
18	=	☐	||	☐	=	☐	||	☐	||	☐	||	☐	||	☐
19	||	☐	||	☐	||	☐	=	☐	=	☐	=	☐	||	☐
20	||	☐	=	☐	=	☐	=	☐	=	☐	||	☐	=	☐
21	=	☐	=	☐	||	☐	||	☐	||	☐	||	☐	=	☐
22	||	☐	||	☐	=	☐	=	☐	=	☐	||	☐	||	☐
23	=	☐	=	☐	||	☐	||	☐	||	☐	=	☐	=	☐
24	||	☐	||	☐	=	☐	=	☐	=	☐	||	☐	||	☐
25	||	☐	||	☐	=	☐	=	☐	||	☐	=	☐	||	☐
26	||	☐	||	☐	||	☐	||	☐	=	☐	||	☐	||	☐
27	=	☐	=	☐	=	☐	=	☐	||	☐	||	☐	=	☐
28	||	☐	||	☐	||	☐	||	☐	=	☐	=	☐	||	☐
29	=	☐	=	☐	||	☐	=	☐	||	☐	||	☐	=	☐
30	=	☐	||	☐	=	☐	||	☐	||	☐	=	☐	||	☐
	I30		*I30*		/30		/30		/30		/30		/30	

APPENDIX B. HEALTH QUESTIONNAIRES

uOttawa

L'Université canadienne
Canada's university

Faculté des sciences de la santé
École des sciences de la réadaptation

Faculty of Health Sciences
School of Rehabilitation Sciences

HEALTH QUESTIONNAIRE FOR TRANSCRANIAL MAGNETIC STIMULATION APPLICATIONS

IMPORTANT NOTICE

The present study involves the use of a magnetic stimulator to induce micro-current in the brain through a coil applied on the scalp. Although the technique is known to be safe and virtually painless, we need to screen our subjects to exclude those who might be at risk. This is why we ask you to fill this health questionnaire, as a potential participant.

Part. # ____

Have you consulted a physician recently (i.e., in the last 12 months)?
☐ Yes
☐ No
If No, when was your last visit? ____________________ months/years

Have you ever been diagnosed with any of the following conditions?
☐ Epilepsy
☐ Migraine
☐ Traumatic brain injury
☐ Depression
☐ Stroke or TIA (Transient Ischemic Attack)
☐ Heart Conditions (angina, hearth failure)
☐ Hypertension (high blood pressure)
☐ Sciatica or disc problems
☐ Arthritis
☐ Diabetes
☐ Any other conditions? (e.g., Parkinson's, MS, pain, numbness, etc.)
☐ Yes please specify:_____________________________________
☐ No,

Are you presently (in the last month) taking any prescribed medication? (e.g., antidepressants, cough or cold, insulin)
☐ Yes please specify:_______________
☐ No,
Do you have any metal implants in your body?
☐ Yes please specify where :___________________________
☐ No,

Do you a have a "pace-maker" for cardiac stimulation?
☐ Yes
☐ No,

Are you presently receiving any form of medical treatment?

☐ Yes please specify the reason:_____________________________
☐ No

For women, are you pregnant or do you think you might be?
☐ Yes
☐ No

Do you tend to faint or have strong reactions in response to unusual situations (e.g., seeing blood, being on the dentist's chair)?
☐ Yes, please specify in which context:____
☐ No

Do you consider yourself in good health?
☐ Yes
☐ No,

Do you have any other health condition of which we should be made aware?
☐ Yes, please specify:_______________
☐ No

I acknowledge that I have answered this questionnaire to the best of my knowledge and that my answers truly reflect my health status.

☐ Yes
☐ No

____
Date

QUESTIONNAIRE
ÉTAT DE SANTÉ/HEALTH STATUS

Code sujet: ______________________________ Année de naissance/Year of Brith:______________
Genre/ Gender : F ☐ M☐ Âge/ Age:_______

Directives/*Directions* :

Lire les questions suivantes et répondre en cochant la case appropriée. Noter que toutes ces informations seront gardées strictement confidentielles.
Please read the following questions and check the appropriate answer. Note that all information will be kept strictly confidential.

Votre médecin vous a-t-il déjà parlé que vous aviez une maladie chronique telle l'arthrite rhumatoïde, le diabète, la sclérose en plaques, le Parkinson) pouvant nuire grandement à votre capacité de faire de l'activité physique ou des tâches domestiques?	*OUI* ☐ *NON* ☐
Votre médecin vous a-t-il déjà parlé que vous aviez une maladie chronique du système nerveux affectant la sensation dans les membres tel un nerf coincé, un tunnel carpien. Si oui, veuillez spécifier la ou les régions atteintes :	*OUI* ☐ *NON* ☐
Est-ce que votre métier ou passe-temps actuel ou dans le passé nécessitait l'utilisation de vos mains lors de tâches répétitives (e.g., clacier ordinateur, tricot) ou l'utilisation continuelle d'outils mécaniques produisant des vibrations (marteau-piqueur, scie à chaîne) ? Si oui, *Quelle tâche ou outil?* *Pendant combien Heures/ jour:* *Nombre d'années*:	*OUI* ☐ *NON* ☐
Has your doctor ever said that you have a chronic condition (e.g., diabetes, arthritis, multiple sclerosis, paralysis, stroke, Parkinson) that could seriously interfere with your ability to perform physical activities or household tasks?	*YES* ☐ *NO* ☐
Has your doctor ever said that you have a chronic condition (e.g., neuropathy, carpal tunnel syndrome) that could interfere with your ability to feel sensation in the extremities? *If yes, please specify the regions affected:*	*YES* ☐ *NO* ☐
Does your previous or current occupation or leisure require you to use your hands by performing any repetitive movements (e.g., computer use, knitting) or to use power tools (drill, chainsaw)? *If yes,* *What type of task or tool?:* *How many hours/day?* *For how long:* *years*	*YES* ☐ *NO* ☐