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RESEARCH ARTICLE

The impact of light fingertip touch on haptic cortical processing during a standing balance task

David A. E. Bolton · William E. McIlroy · W. Richard Staines

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Abstract Availability of fingertip touch onto a stable surface reduces body sway for subjects standing with eyes closed. This is largely associated with sensory feedback from the fingertip when mechanical load is limited. Here, it is possible that the central nervous system facilitates cortical sensory processing to augment feedback to control upright stance. To test this, we compared cortical sensory excitability between tasks with and without light finger touch while standing. Subjects stood in tandem on a force plate with eyes closed while lightly touching a stable surface with the index finger. This was, in two different studies, compared to: (1) no haptic contact or (2) light touch on an object not referenced to balance. Throughout testing, the median nerve was stimulated and electroencephalography was used to measure somatosensory evoked potentials (SEPs). As expected, availability of stable light touch reduced medial–lateral COP sway. Peak amplitudes for SEP components revealed reduced P100 (48%), but increased P50 (31%), N140 (80%), and P200 (20%) during stable touch versus no touch. The modulation of P50 and N140 was no longer present when comparing stable to control (touch), which suggested that attending to touch on either surface, regardless of stability reference, accounted for these changes. Conversely, P200 was increased (19%) when touching the stable surface. Our data show SEP modulation during a standing balance task related to hand contact. Facilitation of P200 in particular may indicate task-specific regulation of the cortical representation of fingertip afferent input when it is relevant to providing stable cues for static balance control.

Keywords Balance · Haptic · EEG · SEP · Somatosensation · EMG

Introduction

Sensory feedback is necessary to control postural stability, and this feedback is primarily derived from visual, vestibular, and somatosensory cues (Day and Cole 2002; Day et al. 2002; Mergner et al. 2003, 2006). Any of these sensory modalities can provide signals relevant to control stability, making the sensory regulation of posture quite robust. However, as sources of feedback are progressively removed, markers of reduced stability can be observed. For example, subjects standing with their eyes closed demonstrate greater sway compared to when their eyes are open (Jeka and Lackner 1994). Similarly, ischemic block of the lower limb during quiet stance results in greater sway and therefore demonstrates the contribution of somatosensation to postural control (Mauritz and Dietz 1980). Although many sensory sources can be exploited to control stability, somatosensory cues, especially those from the support base (typically the feet), provide a particularly quick and important

D. A. E. Bolton (✉) · W. E. McIlroy · W. Richard Staines
Department of Kinesiology, University of Waterloo,
200 University Avenue W, Waterloo, ON N2L 3G1, Canada
e-mail: dbolton@uwaterloo.ca

D. A. E. Bolton · W. E. McIlroy · W. Richard Staines
Heart and Stroke Foundation Centre for Stroke Recovery,
Toronto, ON, Canada

W. E. McIlroy
Sunnybrook Health Sciences Centre Research Institute,
Toronto, ON, Canada

W. E. McIlroy
Department of Medicine (Neurology),
University of Toronto, Toronto, ON, Canada

route for this control (Stapley et al. 2002; Thompson et al. 2010; Ting and Macpherson 2004; Inglis et al. 1994).

Haptic cues, even from a body part not offering mechanical support, can significantly reduce postural sway. This effect has been shown with light contact at several body regions including the shoulder, leg, or finger (Jeka and Lackner 1994; Rogers et al. 2001; Krishnamoorthy et al. 2002). In fact, the increase in postural sway noted when subjects are deprived of vision is fully attenuated by light finger touch applied to a stable surface (Jeka and Lackner 1994). Given that the applied finger force in the aforementioned studies is very low (i.e. <1 Newton), it has been proposed that this effect is due to increased availability of relevant sensory feedback (Jeka 1997). In fact, when ischemic blockade of the arm is applied during this paradigm, the ability to attenuate sway is lost (Kouzaki and Masani 2008). Moreover, modeling studies on the amount of supportive force required to control postural sway further confirm that loads less than 1 Newton could not account for the observed reduction in sway (Holden et al. 1994). Importantly, even holding an unstable contact point (i.e., cane) that touches a surface which offers stable cues will lead to reduced sway (Albertsen et al. 2010). Overall, there is strong evidence indicating that access to increased haptic feedback from a surface that provides sway-relevant information leads to reduction in postural sway.

While many studies have confirmed the basic finding that sway decreases in the presence of light touch, the focus to date has been on external measures such as forces at the fingertips and feet, muscle activity, and video analysis of body motion (Jeka and Lackner 1994, 1995; Jeka 1997; Kouzaki and Masani 2008; Holden et al. 1994; Lackner et al. 2001). Conversely, the neural processes underlying this effect have not been addressed.

Many studies in somatosensory processing have indicated that these inputs are not static sources of information flowing into the central nervous system (CNS), but rather they are modulated by factors such as active or passive movement (Brooke et al. 1997; Nakata et al. 2003), attention (Staines et al. 2000; Nunez and Malmierca 2007), and environmental context (Prochazka 1989). Furthermore, it has been demonstrated that somatosensory information can be modulated based upon task relevance (Staines et al. 2000; Eimer and Forster 2003b; Iguchi et al. 2005). For example, Staines et al. (Staines et al. 2000) noted that when specific sensation from the lower limbs was relevant to performing a task, somatosensory evoked potentials (SEPs) originating from the sural or tibial nerves became selectively liberated from movement-related attenuation. Moreover, when touch sensation from the hands is necessary for task performance (e.g., detecting vibrotactile targets on the digits), cortical processing is often enhanced specifically for this sensory channel (Eimer and Forster 2003b; Iguchi et al. 2005; Giabbiconi et al. 2007). Many studies have now highlighted the potential role of the cortex in postural control (Slobounov et al. 2008; Mochizuki et al. 2010; Jacobs and Horak 2007). This demand for cortical involvement tends to increase with the postural challenge but is evident even during unperturbed standing with eyes closed, which results in heightened activity in the prefrontal cortex (Ouchi et al. 1999), an area intimately linked with controlling attention (Fuster 2008). Given the evidence for an attention demand in postural control (Woollacott and Shumway-Cook 2002), it would follow that any sensory input that conveys meaningful information regarding a stable earth reference might be facilitated.

Haptic signals from the hand pass into the spinal cord, ascending through the dorsal columns eventually projecting to the brainstem, cerebellum, and the cerebral cortex (via the thalamus). Electrical stimulation to the median nerve offers a probe into this pathway, and electroencephalography (EEG) is commonly used to measure neural processing of this signal as it passes throughout the brain. Following electrical stimulation, there are several stereotypical potentials with consistent latencies and spatial distributions across the scalp, reflecting various stages of processing. Sensory input from the hand enters the cerebral cortex via the primary somatosensory cortex (S1), then secondary somatosensory cortex (S2), and ultimately spreads to higher cortical association areas including pre-motor frontal regions (Mauguiere et al. 1997a). Consequently, the earliest potentials in the SEP waveform are mainly localized over S1 on the hemisphere contralateral to stimulation (e.g., N20, P27, and P50) and later potentials such as the N140 and P200 are typically larger in amplitude and more broadly distributed, thus reflecting a variety of neural generators (Hamalainen et al. 1990; Allison et al. 1991a, b). Whereas the earlier components represent somatosensory processing more directly, the later SEP stages often reflect more endogenous and abstract levels of influence (Chapman and Meftah 2005; Adler et al. 2009).

Several studies have demonstrated modulation of one or more SEP components based on attention (Nakata et al. 2003; Desmedt and Robertson 1977; Michie et al. 1987). Components as early as the P50 have been shown to be enhanced when that spatial location is attended (Michie et al. 1987; Schubert et al. 2008), suggesting that S1 can be primed to become more responsive to the incoming signal. Such a conclusion is highly consistent with previous imaging work, which demonstrated enhanced activity in S1 during attention-demanding tasks (Staines et al. 2002). Moreover, later components such as the P100, N140, or P200 have also been shown to be clearly modulated in relation to attention (Nakata et al. 2003; Eimer and Forster 2003a, b; Desmedt and Robertson 1977; Michie et al. 1987). The N140 for example has been suggested to play a role in comparing a tactile signal held in working memory against the current sensory experience when that stimulus is task-relevant (Desmedt and Tomberg 1989, 1994). Although it is presently unclear what role each component plays in processing a sensory signal, a picture is beginning to emerge whereby relevance of the signal leads to changes in how this signal is processed by the cortex. Moreover, many sites along the processing chain often show some degree of facilitation when dealing with this attended/task-relevant input (Nakata et al. 2003; Adler et al. 2009; Desmedt and Robertson 1977; Michie et al. 1987; Eimer and Forster 2003a, b).

The main purpose of our study was to investigate cortical processing of haptic information from the hand during conditions where the hand is either providing relevant feedback to stabilize balance compared to when the finger is not touching a surface or when the finger must maintain light touch on an object that is not referenced to stability and therefore has no relevance to the control of sway. To address this, we measured changes in SEP modulation associated with light hand contact onto a stable surface versus two control conditions: (a) control (no touch) and (b) control (touch). Presumably, when additional quality information on a stable earth reference is available to the CNS, sensory transmission from this source will be up-regulated. Therefore, we hypothesized that during a standing balance test, light hand touch on a stable surface would result in improved postural sway as well as a facilitated cortical representation of sensory inputs from that hand compared to both no touch and light touch on an object not referenced to standing balance. We further hypothesized that this facilitation would be specific to the hand in contact with the stable surface rather than a generalized influence of stability.

Methods

Subjects

Twenty healthy volunteer subjects (age range 19–37) participated in the study after providing informed written consent. Ten subjects per group participated in two separate experiments as outlined below. Two participants were excluded due to excessive signal noise (one subject from each group). No subjects reported any history of neurological or musculoskeletal deficits. All experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

Stimulation procedures

Somatosensory evoked potentials (SEPs) were evoked by electrical stimulation of the right median nerve in experiment 1, and both the right and left median nerves in experiment 2. A square wave pulse of 1 ms (GRASS S88 stimulator with SIU5 stimulus isolation unit, West Warwick, RI) was delivered over the median nerve via surface electrodes. The intensity of stimulation was set at 1.2× the threshold to elicit a minimally visible thumb twitch. Stimuli were randomly delivered approximately once every 5–8 s per hand during trials, resulting in 4–6 stimuli delivered per trial.

Recording procedures

All force plate data were acquired and analyzed using a custom-made program (LabVIEW 8.5, National Instruments, Austin, TX). Force plate data were also digitized at 1,000 Hz and stored on computer for subsequent analysis.

Electroencephalographic (EEG) data were amplified (20,000×), filtered online (bandpass DC-200 Hz), and digitized at 1,000 Hz (SynAmps2, Neuroscan, Charlotte, NC). For experiment 1, EEG activity was recorded from 14 electrode sites (FP1, FP2, F3, FZ, F4, C3, CZ, C4, CP3, CPZ, CP4, P3, PZ, and P4) in accordance with the international 10–20 system for electrode placement and referenced to linked mastoids. For experiment 2, EEG activity was recorded from a full 32-channel electrode cap. The impedance of all EEG channels was <5 kΩ. Electromyography (EMG) data were amplified (1,000×), filtered online (bandpass DC-200 Hz), and digitized at 1,000 Hz (SynAmps2, Neuroscan, Charlotte, NC). EMG activity was recorded from the right and left peroneal muscles in experiment 2.

Protocol

Each subject stood in tandem on a force plate with the left foot directly in front of the right. Once the correct foot position was determined, adhesive tape was used as a landmark for consistent foot placement throughout testing. A touch platform was positioned directly beside the subject and set to ensure the arm could hang in a neutral position and provide only minimal finger contact force. The contact surface for the finger consisted of a patch of one-sided adhesive grip tape attached to a flat plexiglass platform. This platform was mounted over a load cell to monitor forces exerted by the right finger throughout testing. The platform and load cell were secured onto a tripod to allow height adjustment for each subject. All subjects were briefly trained in the force range they were allowed to use when touching the platform (<1 Newton) and provided with verbal feedback during testing to ensure they did not exceed this amount. Subjects were allowed to briefly practice standing in tandem holding their eyes closed.

In experiment 1, subjects were instructed to either (a) lightly contact the stable touch platform with their right index finger, referred to as the stable touch condition or

(b) to keep their arms free by their side, referred to as the control (no touch) condition. In the control (no touch) trials, the platform was temporarily removed to avoid any contact. For both conditions, once subjects were set and looking straight ahead, they were instructed to close their eyes. At this stage, data collection and median nerve stimuli were initiated for a period of 30 s. Following each trial, subjects were instructed to open their eyes and were provided the opportunity for a brief rest. Each subject completed both stable touch and control (no touch) conditions in random order for no more than 16 trials per condition (10 trials on average).

In experiment 2, a different group of subjects performed the light touch onto a stable surface and the control of light touch onto an object not referenced to upright stability. They were instructed to either (a) lightly contact the stable touch platform with their right index finger as before or (b) to maintain light touch on a contact point fixed to the right wrist, referred to as the control (touch) condition. This contact consisted of a small foam-tipped wire (113.5 g solder wire, 1.2 mm dia.), which was secured to the right wrist and positioned approximately 2 cm away from the neutral-hanging index finger. Subjects were instructed to maintain light contact with their right index finger throughout the entire trial for both conditions. Note that for the latter condition (b), the touch surface was not passively contacting the neutral-hanging finger, but rather subjects were required to actively position their finger onto the contact surface over the entire trial. This task was selected to ensure a comparison to the light touch on a stable surface that controlled for the active task requirement of maintaining finger position and receiving haptic inputs. As a result this, task was referred to as control (touch) and was compared to stable touch condition.

Analysis

SEPs were extracted by averaging epochs time-locked to the onset of median nerve stimulation with an epoch length of -100 to 500 ms. SEP traces were visually inspected to exclude trials containing artifacts from further analysis (i.e., eye blinks, high-frequency noise from clenching the jaws). The total number of individual SEP samples that remained following artifact rejection was approximately 40–60 per touch condition for each subject.

Peak amplitudes for several SEP components were determined from individual subject averaged data. This was done separately for each touch condition and at each electrode used in the analysis. A clearly defined peak was necessary for inclusion. The N20, P27, and N30 components were analyzed first using the original bandpass filtering of DC–200 Hz. Analysis on all subsequent components was performed with data bandpass filtered at 1–30 Hz. These later components of interest were as follows: P50, N70, P100, N140, and P200. Comparisons for the N20, P27, P50, N70, and P100 were limited to the CP3 electrode, while N30, N140, and P200 comparisons were limited to CZ where the respective components were maximal. We hypothesized that one or more EEG components would be facilitated during the stable touch condition compared to the control (no touch) and the control (touch) conditions. Paired t-tests were used to compare peak amplitudes for touch versus no-touch conditions in experiment 1. For experiment 2, the same paired t-test comparisons were performed between the stable touch and control (touch) conditions for stimuli delivered to the right hand. In experiment 2, a separate analysis was also performed to compare the right- and left-hand median nerve stimuli. This analysis was focused on the issue of general stability effects between hands; thus, our comparison was restricted to between-hand SEP comparison only when the right hand was touching a stable surface (i.e., stable touch with the right hand vs. the left no-touch hand). Moreover, the analysis was limited to the endogenous N140 and P200 components at the CZ electrode. Our hypotheses for experiment 2 were that the same SEP components facilitated in experiment 1 would again show facilitation. Moreover, we predicted that the facilitation of the endogenous N140 and P200 at CZ would be specific to the right hand (i.e., stable touching finger).

From the force plate, we extracted center of pressure sway amplitude in the frontal plane (CoPx). Specifically, the root mean square (RMS) was calculated over the entire testing interval to compare touch conditions. Paired t tests were used to test the hypotheses by comparing the RMS CoPx sway between the touch conditions within experiment 1 and 2 separately. We hypothesized that the stable touch condition would result in reduced sway compared with the no-touch condition in experiment 1. We further hypothesized that that stable touch would result in improved stability reflected by reduced COP sway compared with control (touch) in experiment 2. For experiment 2, average muscle activity was measured over each trial and compared between the stable and unstable touch conditions. We hypothesized that average muscle activity for both peroneal muscles would decrease during stable touch compared with unstable touch. Significance level was taken as $P < 0.05$ for all comparisons.

Results

Experiment 1

CoPx sway and fingertip force

The RMS for CoPx sway was significantly reduced when subjects touched a stable surface ($t_8 = 5.61$, $P = 0.01$) compared to control (no touch) (Fig. 1). On average, sway was

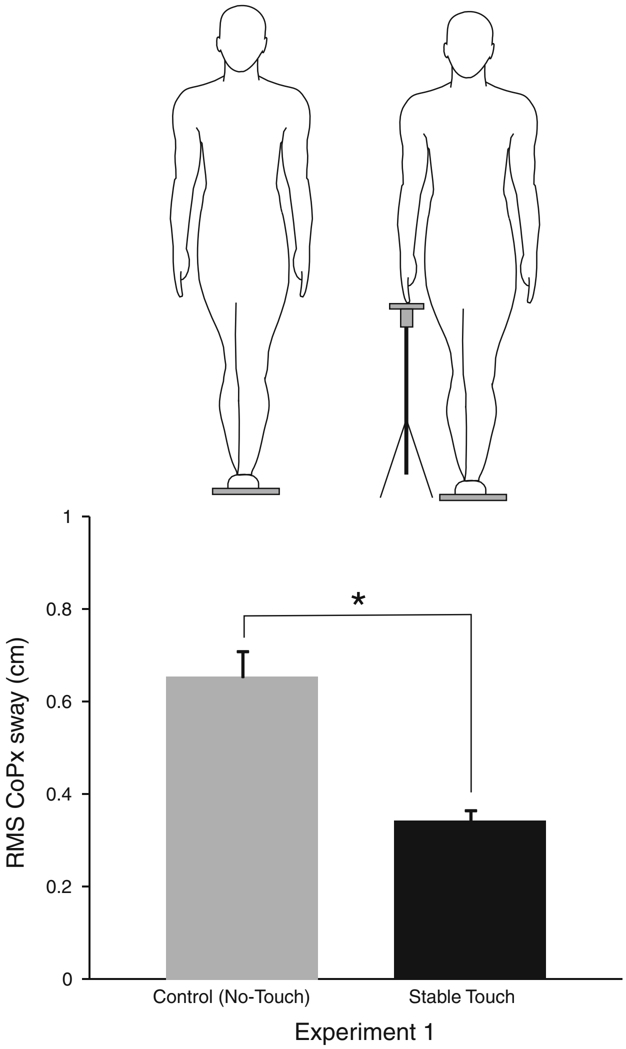

Fig. 1 *Above* Subject depicted in tandem stance on a force plate, while touching the touch apparatus with their *right finger*. For the control (no touch) condition, the apparatus was removed. *Below* RMS CoPx sway amplitude averaged for all subjects measured in cm. *Light grey bars* represent control (no touch) and *black bars* represent stable touch. * significance at $P < 0.05$

reduced by 48% across subjects when touching a stable surface versus the no-touch condition. Average vertical loading force at the fingertip was 0.53 (±0.07) N during the stable touch trials.

SEPs

The average latency and peak amplitude for all components are displayed in Table 1. Peak latencies were similar between the touch and control (no touch) conditions; however, significant differences were noted in the peak amplitude of several components, particularly in the later stages as depicted in Fig. 2. The N20 and P27 were the earliest components to be consistently detected across subjects, reaching a maximum at CP3. The peak amplitudes for these components were not significantly modified by the touch condition: N20 ($t_8 = 0.07$, $P = 0.94$) and P27 ($t_8 = 0.01$, $P = 0.98$). Similar to the N20 and P27, the N30 was relatively small but consistently detected in all subjects. The N30 was present across several frontal electrode sites; however, it was maximal at CZ. This component was not significantly modified by touch condition ($t_8 = 0.46$, $P = 0.64$).

The P50 and N70 were only evident at central and parietal sites, contralateral to the median nerve stimulus. There was a significant increase of 31% in P50 peak amplitude at CP3 ($t_8 = 2.40$, $P = 0.03$) during the touch condition as shown in Fig. 3a. The N70 revealed no difference between touch conditions ($t_7 = 1.30$, $P = 0.23$). Figure 3 displays the effect of touch on peak amplitudes for several SEP components at CP3. The P100 was broadly distributed throughout the scalp; however, it was most prominent at central and parietal sites, contralateral to the median nerve stimulation, and was significantly decreased by 48% during touch at CP3 ($t_7 = 3.16$, $P = 0.01$).

The longer-latency components of N140 and P200 were consistently present at all measured electrode sites, and both showed significant facilitation with touch. Figure 3b demonstrates the impact of touch on the N140 and P200 at CZ where these components were largest. Here, both the N140 and P200 showed significant increases of 80 and 20%, respectively, during the touch condition (N140: $t_8 = 3.18$, $P = 0.01$; P200: $t_8 = 3.13$, $P = 0.01$).

Experiment 2

CoPx sway, fingertip force and EMG activity

The RMS for CoPx sway was significantly reduced when subjects touched a stable surface ($t_8 = 2.16$, $P = 0.002$) compared to the control (touch) condition (Fig. 4a). On average, sway was reduced by 45% across subjects when touching a stable surface versus control (touch). Additionally, average EMG activity was significantly higher for the control (touch) condition versus stable touch with both the right ($t_8 = 2.48$, $P = 0.02$) and left peroneal muscles ($t_8 = 4.79$, $P = 0.0007$) shown in Fig. 4b. Average vertical loading force at the fingertip was 0.59 (±0.06) N during the stable touch trials. Note that we did not have a measure of the vertical loading during the control (touch) condition.

SEPs

Median nerve stimulation of the light touch (right) hand

The average latency and peak amplitude for all components in experiment 2 are displayed in Table 2. As in experiment 1, peak latencies were similar between the touch conditions but there were significant differences in peak amplitude between touch conditions for several later components. The

Table 1 Average latency (ms) and peak amplitude (µV) for all measured SEP components in both the stable touch and control (no touch) conditions from experiment 1

SEP component	Electrode	Average latency in ms (SE)		Peak amplitude in µV (SE)	
		Control (no touch)	Stable touch	Control (no touch)	Stable touch
N20	CP3	18.6 (0.7)	18.8 (0.7)	−2.36 (0.90)	−2.45 (0.94)
P27	CP3	28.0 (1.2)	27.4 (0.6)	3.27 (0.68)	3.27 (0.99)
N30	CZ	34.4 (1.2)	33.3 (1.6)	−2.71 (0.89)	−2.32 (0.55)
P50	CP3	48.4 (2.7)	45.3 (1.3)	4.16 (0.78)	5.43 (0.51)*
N70	CP3	72.4 (3.6)	71.9 (4.0)	−2.94 (1.77)	−1.88 (1.16)
P100	CP3	101 (2.5)	99.6 (3.7)	5.50 (1.53)	2.85 (1.31)*
N140	CZ	130.2 (3.7)	126.4 (4.7)	−6.95 (1.92)	−12.49 (2.07)*
P200	CZ	196.4 (8.9)	195.4 (7.4)	23.78 (3.98)	28.60 (4.68)*

These values originate from the electrode site where the peak amplitude reaches a maximum (provided in the electrode column). Standard errors are in brackets. * Significant difference between touch and control (no touch) ($P < 0.05$)

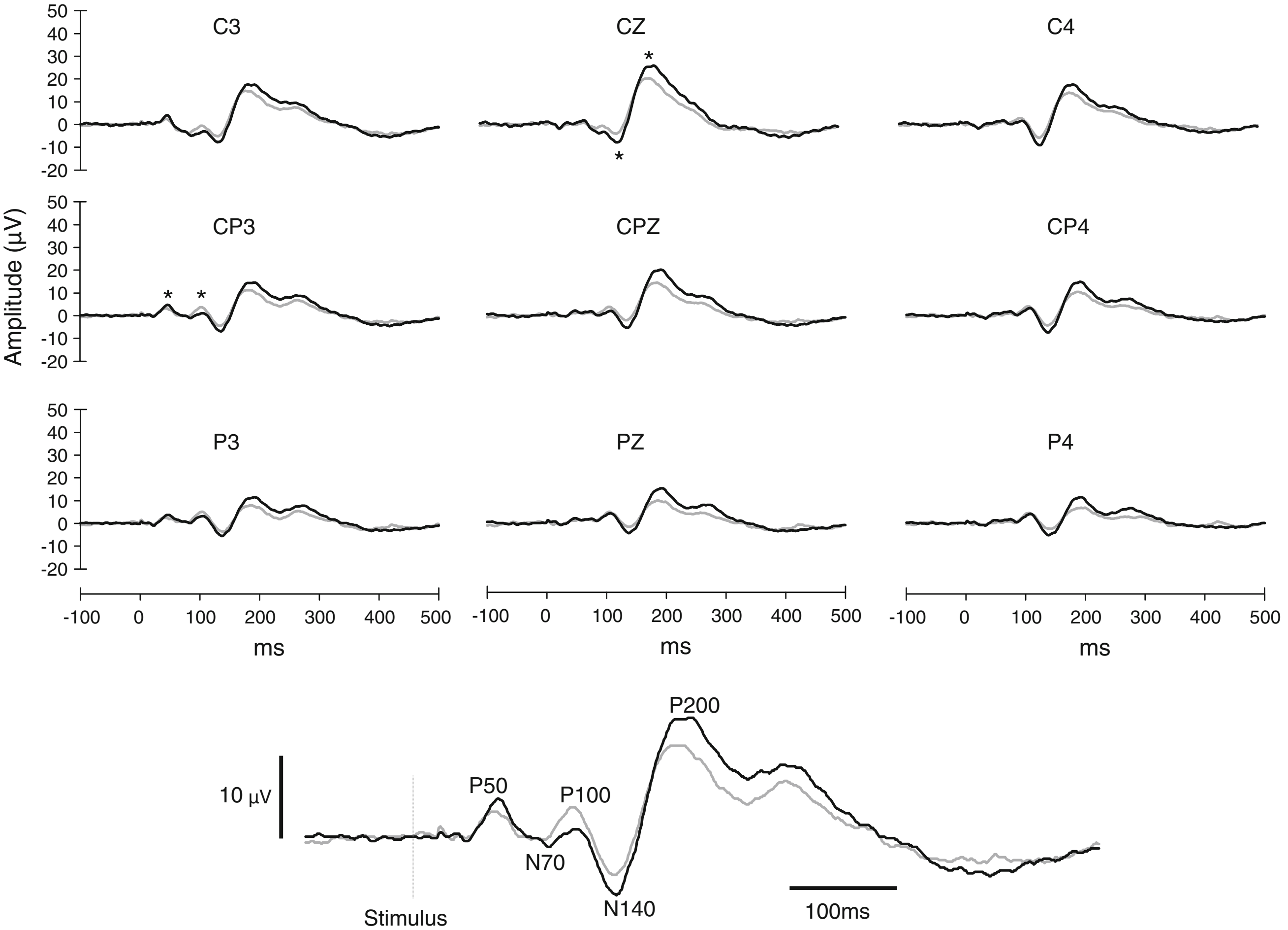

Fig. 2 Group-averaged SEP data are displayed using 9 electrode sites. The control (no touch) condition is represented with *light grey lines*, and the stable touch condition uses *black lines*. * Significant difference between touch conditions at $P < 0.05$. CP3 from this group data is expanded and shown below to highlight the major SEP components of interest

peak amplitudes for the N20 and P27 components were not significantly modified by the touch condition: N20 ($t_8 = 0.75$, $P = 0.24$) and P27 ($t_8 = 0.58$, $P = 0.29$) both at CP3. The N30 was maximal across central and frontal electrode sites; however, this component was not significantly modified by touch condition (CZ: $t_7 = 0.72$, $P = 0.25$).

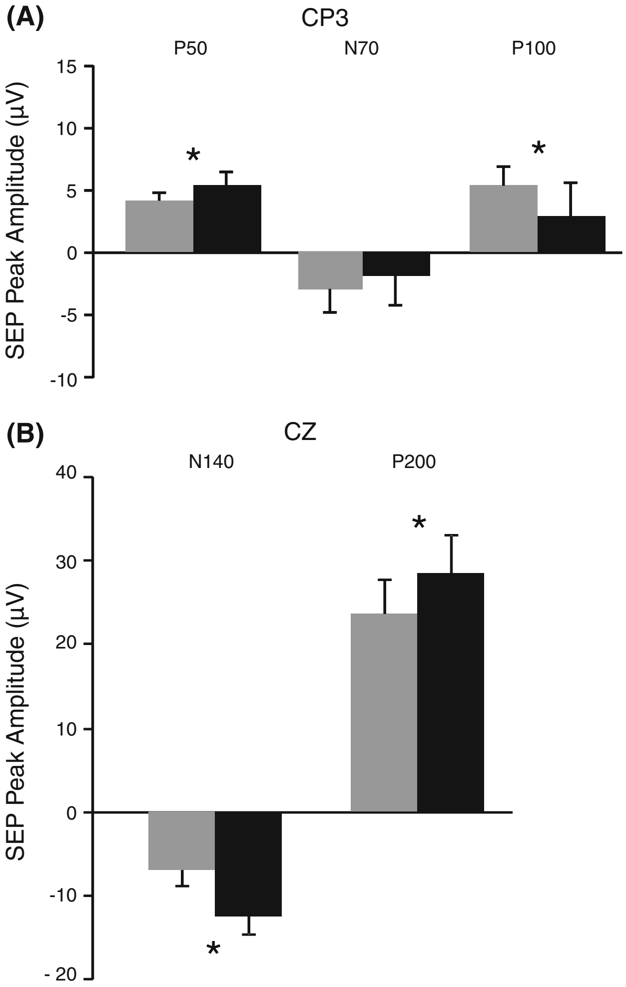

Fig. 3 Group-averaged peak amplitudes for those SEP components detected at **a** CP3 and **b** CZ are depicted in separate bar graphs. All values are in microvolts (µV). *Light grey bars* represent control (no touch), and *black bars* represent stable touch. * Significance at $P < 0.05$

The P50, N70, and P100 were prominent at CP3. The P50 and N70 revealed no significant peak amplitude differences between conditions (P50: $t_8 = 0.78$, $P = 0.23$ and N70: $t_8 = 0.77$, $P = 0.23$). The P100 revealed a significant decrease of 26% during stable touch ($t_7 = 2.55$, $P = 0.02$). Figure 5 displays the effect of stable versus unstable touch on SEP components at CP3 highlighting the scalp topography for P50 and P100. Figure 6 demonstrates the impact of stable versus unstable touch on the N140 and P200 at the CZ electrode. Here, the N140 revealed no significant differences between touch conditions ($t_8 = 1.57$, $P = 0.08$) while the P200 showed a significant increase of 19% during stable touch compared to control (touch) ($t_8 = 3.59$, $P = 0.004$). As a follow-up to the significant increase in P200, a Pearson's product–moment correlation coefficient was computed to test if whether the increase in P200 amplitude (stable touch minus control touch) was positively correlated with the reduction in sway. Our results failed to show any significant correlation between the two variables ($r = 0.16$, $n = 9$, $P = 0.34$).

SEP modulation of the light touch (right) hand versus the no-touch (left) hand The comparison between the right and left hands, during stable touch with the right hand, was focused on the endogenous N140 and P200 components. These comparisons were performed to test for the specificity of the task-related increases on these later SEP components. Figure 7 displays stable touch SEPs for electrode CZ when comparing between stimulation of the left hand (not in contact with a surface) and the right hand (touching the stable surface). The N140 and P200 were both significantly greater for the right hand as compared with the left hand stimulation at CZ (N140: $t_8 = 6.49$, $P = 0.00009$; P200: $t_8 = 2.07$, $P = 0.04$).

Discussion

As expected from previous work, light fingertip contact on a stable support surface resulted in reduced postural sway when subjects stood in tandem with their eyes closed. Importantly, sensory cortical transmission from the hand was modulated during this standing task related to whether or not that fingertip was contacting a stable surface. In the first experiment, median nerve stimulation of the touch hand resulted in the facilitation of the P50, N140, and P200 compared to when the hand was not contacting a surface. To further address whether sensory information was facilitated from the hand based upon the provision of a stable earth reference, we compared two conditions of light touch in a second experiment. Here, subjects maintained light finger touch onto either an externally fixed support surface or a surface attached to their wrist so that any haptic information provided no relevant information regarding stability control. When subjects applied consistent light touch onto either surface, P50 and N140 modulation was no longer present, suggesting that attention to light touch itself could account for some of the previously observed changes in sensory processing. Conversely, the P200 was facilitated for stable touch over control (touch), which may reflect task-specific regulation of afferent information from the hand when it provides relevant cues for the control of postural sway. Comparison between the hand directly engaged in touching a stable surface and the opposite free hand revealed that modulation was specific to the contact hand.

In experiment 1, the P50, N140, and P200 were facilitated with touch versus no touch. It is noteworthy that the parietal P50 observed on the hemisphere contralateral to stimulation was greater when participants lightly touched the stable surface with their fingertip. This component has been demonstrated to arise from the primary somatosensory

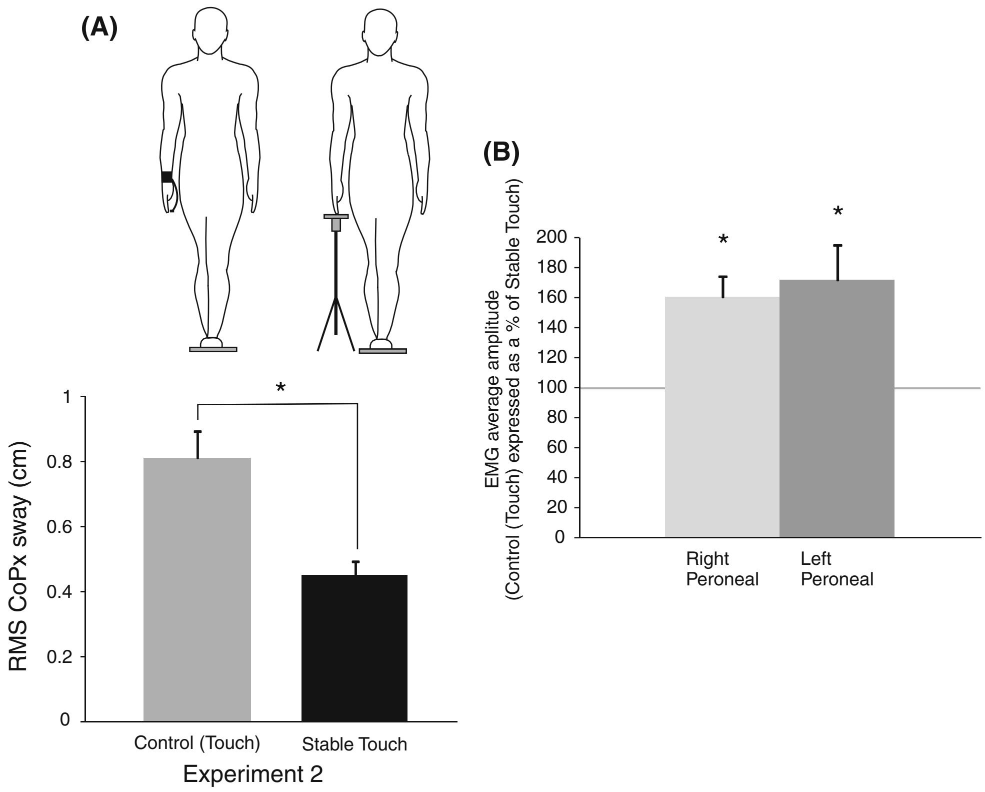

Fig. 4 **a** *Above* Subject depicted in tandem stance on a force plate, while touching the stable touch apparatus with their *right finger*. For the control (touch) condition, subjects maintained light finger contact with a foam-tipped wire attached to the right wrist. *Below* RMS CoPx sway amplitude averaged for all subjects measured in cm. *Light grey bars* represent control (touch) and *black bars* represent stable touch. **b** EMG average amplitude for the right and left peroneal muscles during trials showing control (touch) as a percentage of stable touch average amplitude for each muscle. *Significance at $P < 0.05$

Table 2 Average latency (ms) and peak amplitude (μV) for all measured SEP components during stable touch and control (touch) conditions from experiment 2

Right hand stimulation					
SEP component	Electrode	Average latency in ms (SE)		Peak amplitude in μV (SE)	
		Stable touch	Control (touch)	Stable touch	Control (touch)
N20	CP3	21.9 (0.7)	22.0 (0.5)	−3.3 (1.1)	−2.4 (0.8)
P27	CP3	28.9 (0.9)	27.6 (0.8)	2.2 (1.4)	3.1 (1.2)
N30	CZ	33.3 (0.6)	33.1 (0.8)	−5.8 (0.8)	−7.2 (1.0)
P50	CP3	53.3 (1.8)	50.0 (1.3)	6.1 (0.8)	5.5 (1.2)
N70	CP3	75.4 (3.1)	73.0 (2.4)	−1.4 (1.4)	−2.1 (1.3)
P100	CP3	100.4 (3.9)	104.0 (2.9)	5.1 (1.8)	6.9 (1.9)*
N140	CZ	130.4 (2.9)	130.1 (3.8)	−20.6 (3.6)	−18.5 (3.5)
P200	CZ	198.9 (4.5)	194.8 (4.0)	31.6 (5.1)	27.0 (4.6)*

These values originate from the electrode site where the peak amplitude reaches a maximum (provided in the electrode column). Standard errors are in brackets. * Significant difference between stable touch and control (touch) ($P < 0.05$)

cortex (S1) (Hamalainen et al. 1990; Allison et al. 1989). Given that S1 is the initial processing point for somatosensory input at the cortical level, this indicates that signal transmission is modulated for fingertip afferents at the earliest stage of cortical processing for this task. The elevation of S1 activity in experimental conditions where tactile cues are relevant to an ongoing task has previously been demonstrated using both functional magnetic resonance imaging (Staines et al. 2002) and EEG (Giabbiconi et al. 2007). Importantly, such functional modulation of S1 has been

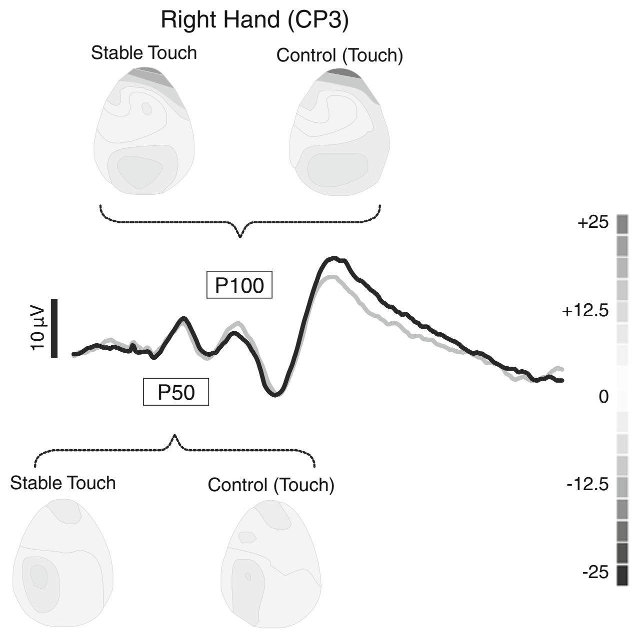

Fig. 5 Group-averaged SEP data from experiment 2 is displayed for CP3. Control (touch) is represented with *light grey lines*, and stable touch uses *black lines*. Scalp topography for the P50 and P100 peaks are displayed for both conditions over each component

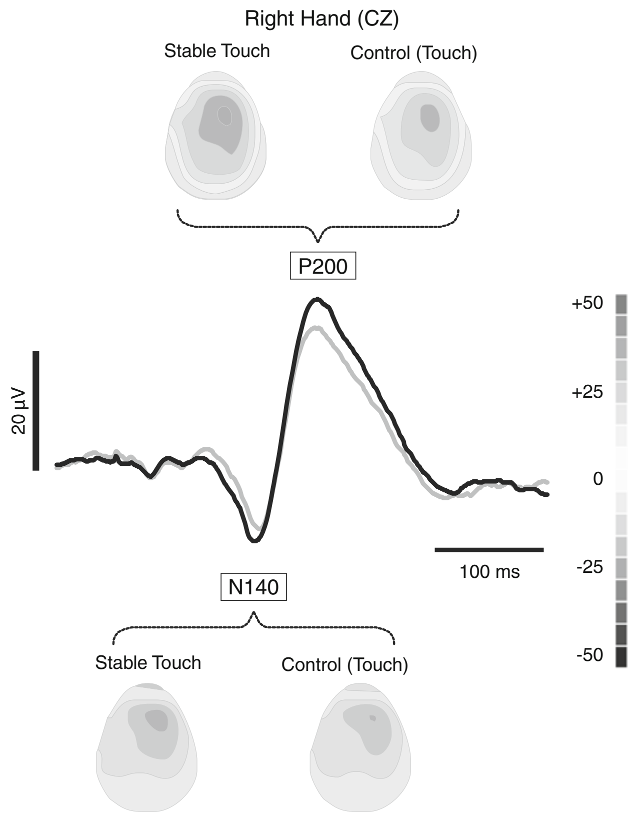

Fig. 6 Group-averaged SEP data from experiment 2 is displayed for CZ. Control (touch) is represented with *light grey lines*, and stable touch uses *black lines*. Scalp topography for the N140 and P200 peaks are displayed for both conditions over each component

shown to relate to improved performance in a tactile-related task (Braun et al. 2002). It should be noted that the N20 and P27, the earliest components measured in our study, are generated in area 3b and area 1, respectively, (Allison et al. 1991b) and neither revealed modulation between touch conditions. It is presently unclear why the S1-generated P50 would demonstrate task-related modulation and not these earlier components, although this may reflect the broad attribution of P50 to S1 versus some fraction of S1. Furthermore, reciprocal projections from S2 and posterior parietal cortex acting onto S1 may not come into effect until the P50 latency (Mauguiere et al. 1997a) and may account for this difference.

The N140 and P200 components were also facilitated for touch versus no touch and revealed a much more distributed impact on brain activity. These later components are commonly altered by psychological factors such as attention (Adler et al. 2009; Desmedt and Robertson 1977; Michie et al. 1987). Unlike the P50, they originate from multiple and distributed generators throughout the cortex (Mauguiere et al. 1997a; Hamalainen et al. 1990; Allison et al. 1992). Moreover, they tend to reflect higher-order stages of cognitive processing, thus making it more difficult to interpret their role in processing the sensory signal. Desmedt and colleagues noted a phase locking of contralateral prefrontal cortex (PFC) and parietal cortex in the gamma frequency band, approximately 130 ms following a mechanical stimulus to the finger when that finger was attended (Desmedt and Tomberg 1994). The authors interpreted this to reflect a function-based binding of these regions. Consequently, the N140 may represent a conveyance of tactile sensory experience from the touched object into perceptual awareness. Furthermore, during tactile discrimination tasks, tactile ERPs occurring in this latency range may provide a comparison mechanism for presently attended tactile signals against a template held in working memory (Desmedt et al. 1983). Although our experiment did not overtly tax attention, it is likely that the maintenance of upright stance involves a continual comparison of ongoing sensory input against a desired balance template represented at some level in the CNS. Moreover, with global facilitation of the later components, it is difficult to tease out how much of this may reflect a more complex sensorimotor transformation, which relays fingertip cues to motor actions in the legs and trunk, or even the arm itself.

A major outcome from the addition of experiment 2 is that modulation of the P50 and N140 was related to the maintenance of light finger touch regardless of whether the touch was relevant to stability control. While we predicted enhancement of a sensory channel that afforded sway-relevant cues, our results suggest that P50 and N140 facilitation

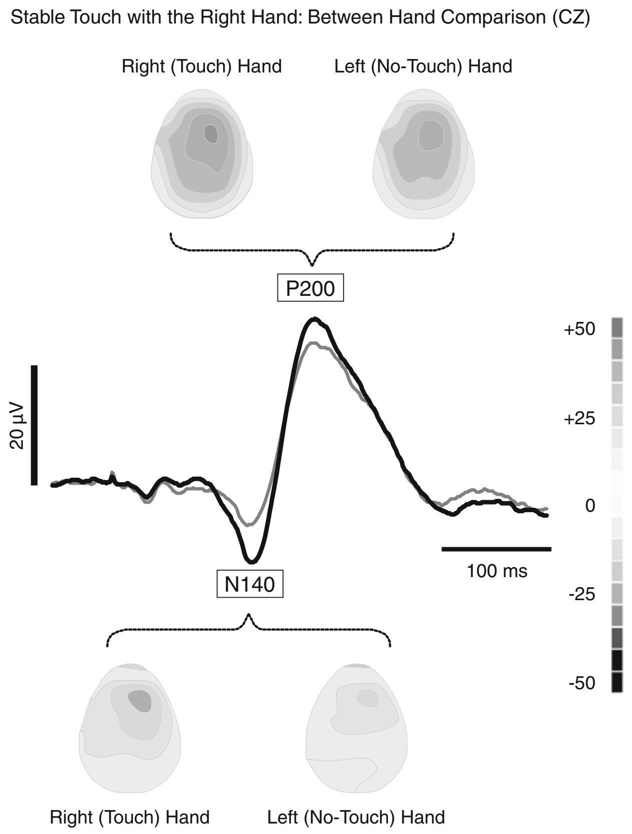

Fig. 7 Group-averaged SEP data from experiment 2 is displayed for CZ showing the comparison between the *right* and *left hand* during stable touch with the *right hand*. *Left hand* (no-touch hand) is represented with *grey lines* and *right hand* (stable touch hand) with *black lines*. Scalp topography for the N140 and P200 peaks are displayed for both hands over each component

noted in experiment 1 is likely a consequence of general attention to the finger when lightly touching a surface. Modulation of both the P50 (Schubert et al. 2008) and N140 (Desmedt and Robertson 1977; Michie et al. 1987; Garcia-Larrea et al. 1995) is consistent with previous work on selective spatial attention to the hand. The fact that maintaining light finger contact required attentional resources is in line with previous work where the stabilizing postural effects of light touch during a similar standing balance task were associated with impaired performance on an auditory reaction time test (Vuillerme et al. 2006). The authors interpreted this result to mean that the sustained application of light touch demanded greater attention. Our data would suggest that at least a portion of this attention allocation may be directed simply toward the task of maintaining the light touch contact.

An unexpected finding from our study was the suppression of P100 specific to touch on a stable surface. From our original hypothesis, we predicted an overall facilitation of cortical somatosensory processing when a particular sensory channel (i.e., the touching hand) afforded information on a stable earth reference. The proposed generator for P100 is the secondary somatosensory cortex (S2) (Mauguiere et al. 1997a; Hamalainen et al. 1990), which unlike S1 offers a less direct transfer of physical stimulus characteristics and relates more to abstract levels of somatosensory processing (Chapman and Meftah 2005; Romo et al. 2002). It is unclear why this component would be specifically reduced during the present balance task. One possibility is that there is an actual attention-related suppression of haptic input from the hand at this processing stage when the hand is contacting a stable surface. However, it is important to note that even during studies on overt attention to tactile targets, the modulation of ERP waveforms is complex. For example, several components such as the P100 and N140 will either increase or decrease depending on how difficult the task is (Adler et al. 2009) and whether attention is sustained or transient (Eimer and Forster 2003a). In this regard, Eimer and Forster (2003a) observed that when attention to the hand was sustained, modulation of tactile ERPs shifted toward S1-generated components with no effect on the P100; however, this effect reversed when attention was transiently shifted. Therefore, it is feasible that attention itself might not be acting to suppress the P100 but rather suppression may originate from a separate source. It has been demonstrated for example that both passive and active movements can modify early SEP components (Nakata et al. 2003; Staines et al. 1998), and this modulation is typically suppressive. The current study did not measure motion or muscle activity at the hand; therefore, we are unable to verify such differences. However, it is conceivable that P100 suppression during stable light touch emerges from a paucity of attention-related modulation, combined with some inhibitory influence related to hand use.

Combined results from experiments 1 and 2 demonstrated a facilitation of the P200 during stable touch compared to the no-touch and touch control conditions. Therefore, in contrast to the P50 and N140 modulation, which appears to be more related to maintaining light touch itself, the P200 was related exclusively to touch on a stable surface, and moreover, this effect was specific to the touch hand. To help elucidate why the P200 would be selectively enhanced during stable touch, it is prudent to recall the proposed cortical generators and function that this component represents. Following median nerve stimulation, there is serial progression of somatosensory input first through S1 contralateral to stimulation, ipsi- and contralateral S2, the contralateral intraparietal region, and eventually pre-motor frontal sources on both hemispheres (Mauguiere et al. 1997a). The latter components reflect accumulated activity from all these regions (including S1and S2) approximately 100–200 ms after stimulus onset, indicating that all areas remain active during the P200 time period (Mauguiere et al. 1997a). In selective spatial attention tasks, frontal generators contribute more heavily to these latter components (Mauguiere et al. 1997a, b). Similar to the N140, the P200 has been suggested to index a stimulus evaluation process, whereby sensory input is compared to a template maintained by working memory (Dowman 2004). Importantly, this requires not only prefrontal activity but a continued engagement of unimodal processing centers via top-down control (Pasternak and Greenlee 2005). Given that the current paradigm drives heightened attentional demand with light touch (Vuillerme et al. 2006), it is possible that the presently reported P200 may serve a similar role related to ongoing working memory. Additionally, because our task imposes unique postural demands without the aid of vision and with the extra task of maintaining light touch, other brain regions are likely engaged which may impact how tactile information is processed. Thus, an assortment of neural centers, particularly frontal regions associated with task complexity, may vary in sensory responsiveness to the touch hand in the present study.

Potentially, this increased P200 activity may reflect a different finger precision demand in the stable touch task. Riley and colleagues demonstrated how the demands of a suprapostural precision task could necessitate tighter regulation of postural sway by having subjects maintain light touch on a suspended curtain (Riley et al. 1999). Interestingly, simple finger contact with the curtain did not attenuate sway; however, when subjects were instructed to minimize curtain movement at the fingertip, sway was reduced. The authors claimed that the suprapostural demand for precise finger contact led to attenuated sway. In the present study, it is possible that whereas body sway would need to be reduced when regulating precise hand contact onto a fixed object, the postural precision to keep the hand on the wrist-fixed object may not be as demanding. Thus, if our results of heightened P200 activity did in fact reflect task differences in maintaining the finger on the stable object, this finger precision would likely need to recruit heightened postural precision as well. Our results would be unable to distinguish between up-regulating a sensory signal to specifically boost arm precision versus using this sensory information to attenuate sway more directly.

Alternatively, the P200 may be facilitated for this sensory channel related to postural relevance more directly. Several lines of evidence support this idea including the observation that when subjects hold an unstable object which is not fixed but still provides cues relevant for a stable earth reference, sway is reduced (Albertsen et al. 2010). In fact, when the touch finger of a subject is clipped in place, thus negating any need for active control to position the finger, sway lessens even more than during active touch (Krishnamoorthy et al. 2002). Similarly, when the application of light touch is passively applied to other body areas such as the shoulder or neck sway is also reduced (Krishnamoorthy et al. 2002). Thus, active control over positioning the hand at a fixed external location is not requisite for the reduction in postural sway. These points offer support for Jeka's proposal that the chief advantage afforded by light touch in this paradigm is access to additional stable reference information (Jeka 1997). Another key finding is that reweighting of various sensory channels is associated with regulation of sway, and this can occur automatically and in a manner unrelated to other suprapostural tasks. For example, when subjects are exposed to a perceptual tilting illusion via galvanic vestibular stimulation (GVS), the sway evoked by this illusion is much greater when the eyes are closed (Fitzpatrick et al. 1994) and again amplified in subjects lacking somatosensory feedback from the lower limbs (Day et al. 2002; Fitzpatrick et al. 1994). These findings suggest up-regulation of a sensory system (vestibular in this example) with a direct influence onto postural sway. Jeka and colleagues have demonstrated that this reweighting occurs automatically and dynamically when integrating inputs from a variety of sensory sources and in the context of how helpful or reliable these inputs are in controlling balance and avoiding falls (Oie et al. 2002; Jeka et al. 2008).

It is also important to recognize that forces at the fingertip have been shown to precede relevant leg muscle activity by about 150 ms, and this muscle activity precedes the sway response by another 150 ms (Jeka and Lackner 1995). Indeed, from both previous research (Jeka and Lackner 1995) and our present study, average EMG in the peroneal muscles was significantly lower during stable touch meaning that sway was actually attenuated using less leg muscle activity, which suggests heightened efficiency in postural control. Overall, it appears that fingertip forces offer anticipatory cues for sway-relevant responses in the leg muscles. While it is possible that this reduced sway is accomplished to serve precise hand placement, the fact that sway is equally reduced in conditions of passive touch would argue that sensory information from the finger in this context may be importantly linked to postural control itself.

In conclusion, the present study confirms that light fingertip touch while standing in tandem with eyes closed significantly attenuates postural sway. This outcome was associated with modulated cortical representation of fingertip sensation. Present results indicate that cortical transmission of sensation from the fingertip is facilitated when the fingertip is in contact with a stable surface, possibly affording a higher resolution of a stable earth reference to control posture.

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