Fast-adapting mechanoreceptors are important for force control in precision grip but not for sensorimotor memory

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Sensory feedback from cutaneous mechanoreceptors in the fingertips is critical in effective object manipulation (Johansson and Flanagan 2009). Tactile afferents enable appropriate scaling and synchronous coupling of grip (GF) and load (LF) forces to prevent excessive force or, conversely, object slippage during precision grip (Johansson and Westling 1984). However, control of GF and LF also relies on anticipatory force predictions based on prior experience, with sensorimotor memories utilized to anticipate force requirements involved in predictable object interactions (Flanagan et al. 2001). There are four classes of mechanosensitive afferents in the hand, fast-adapting (FA) and slowly adapting (SA) types I and II (Johansson and Flanagan 2009). Fast-adapting (FAI) and slowly adapting (SAI) type I mechanosensitive afferents are highly enriched in the fingertips (Johansson and Valbo 1979), while FAII and SAI are found at a uniform but lower density (Johansson and Flanagan 2009). Classically, FAI afferents are associated with perception of high-frequency, dynamic events while SAI afferents are sensitive to low-frequency skin deformation. FAI afferents detect transient events such as vibration, and SAI afferents respond to stretching and may function as proprioceptors (Johansson and Flanagan 2009). However, the relative contribution of sensory feedback via FAI and SAI mechanoreceptors to online force scaling and the buildup of a sensorimotor memory have remained incompletely understood.

Deficits in tactile feedback produce significant functional difficulties, demonstrated in patients with sensory neuropathies (Nowak and Hermsdörfer 2004) or in experimental reduction of tactile sensation in healthy volunteers by digital anesthesia (Augurelle et al. 2003; Johansson et al. 1992; Monzée et al. 2003; Nowak et al. 2001). While neuropathy and digital anesthesia underscore the importance of sensory feedback in force scaling and memory buildup, they lead to a noneselective degradation of sensory afferent outflow from the fingertip. In the present study, we studied the functional consequences following selective reduction of the sensitivity of mechanoreceptors, achieved via wearing two layers of latex gloves.

PSYCHOPHYSICAL tasks have been developed that may provide a selective readout of FAI and SAI mechanoreceptor function. Spatial acuity can be determined by the grating orientation task, which is encoded by the activity in SAI mechanoreceptors in primates (Johnson and Phillips 1981; Phillips and Johnson et al. 1981). By contrast, the detection of a small elevated dot on a smooth surface or bumplike stimulus as in braille is signaled by...
by FAI mechanoreceptors (LaMotte and Whitehouse 1986) and can be assessed by the “Bumps task” (Kennedy et al. 2011). Examination of FAI and SAI firing activity during precision grip via microneurography has provided correlative evidence that both FAI and SAI afferents are important in grip control but that FAI fibers are chiefly responsible for controlling GF scaling (Macefield et al. 1996). However, the potential contribution of FAI fibers to control of GF scaling has not been experimentally demonstrated. We examined the hypothesis that the potentially selective reduction of activity in one mechanoreceptor (FAI) pathway leads to an impairment of online force scaling but not sensorimotor memory.

**METHODS**

Twelve healthy volunteers were recruited [6 men and 6 women; age 32.7 ± 1.3 yr (mean ± SE)]. Ethics approval was obtained from the London City and East National Research Ethics Service Committee, and participants provided written informed consent. The Edinburgh Handedness Inventory (Oldfield 1971) established all participants as right-handed. Participants completed all tasks with and without the addition of two pairs of surgical latex gloves appropriate for their hand size (0.27 mm thick; Biogel Surgeons Gloves, Mölnlycke Health Care, Göteborg, Sweden). Multiple sizes were available to ensure appropriate fit. Two layers of gloves were chosen in order to ensure that tactile sensitivity was significantly reduced, as prior studies have identified elevations in sensory thresholds with multiple layers of latex gloves (Shih et al. 2001). The order of presentation was pseudorandomized, so that half of the participants completed the tasks without gloves to begin with while the other half started with gloves on first.

**Psychophysical and behavioral tasks.** All psychophysical tests were undertaken on the distal phalanx of the right index finger. For two tests the finger was stabilized with adhesive putty to prevent movement.

Assessment of tactile spatial acuity was undertaken via the grasping orientation task with plastic JVP domes (Stoelting) with groove widths varying from 0.35 to 12 mm and starting from the 0.5-mm spacing. The grooved dome was pressed steadily against the index finger for 3 s, and the participants reported the orientation of the grooves (either parallel or perpendicular to the finger) without vision in a two-alternative forced-choice paradigm of 10 stimulus presentations each in a pseudorandom sequence. The threshold corresponding to 75% correct discrimination was determined via linear interpolation as described previously (Van Boven and Johnson 1994).

Assessment of mechanical sensitivity was undertaken with calibrated monofilaments (Optihar 2, MARSTOCK nervtest, Schriesheim, Germany) as in Rolke et al. (2006). Monofilaments ranged in a geometric order of 12 filaments between 0.25 and 512 mN. The method of limits was used to determine the detection threshold with a series of stimuli presented to participants with their eyes closed. The threshold was determined as the geometric mean of five pairs of “up and down” stimulus presentations alternating from stimulus detection to failure of detection.

Assessment of tactile sensitivity was also undertaken with the “Bumps” device (Kennedy et al. 2011), which consists of a checkerboard-like plate with a smooth surface divided into 12 squares. Each square contains five colored circles of 4-mm diameter, with one randomly selected circle containing a single coin-shaped 550-μm-diameter bump of variable height. Bump height ranged from 26 to 0.5 μm over four plates. Participants were given standard instructions and asked to identify where the raised bump was located in each square, using their index fingertip to scan the plate. As per Kennedy et al. (2011), threshold was determined as the lowest-height bump that could be correctly detected in a series of three consecutive correct detections, so that for a threshold of 2.5 μm bumps of 3 and 3.5 μm also had to be correctly identified. The lowest threshold was taken from two trials across all plates.

To assess functional ability and fine motor skills, two pegboard tasks were undertaken with the right hand. The average number of pegs inserted in 30 s across two trials was recorded for the Purdue Pegboard (Lafayette Instrument; Tiffin and Asher 1948). The number of seconds taken to insert 25 pegs into grooved slots was recorded for the Grooved Pegboard (Lafayette Instrument).

**Precision grip assessment.** The tasks involved a precision grip with the thumb and index finger of a 225-g manipulandum with two parallel smooth aluminum grip surfaces of 40-mm diameter (Fig. 1A). Six axis force torque sensors (Mini 40 F/T transducers, ATI Industrial Automation) were used to measure GF (normal to the grip surface) and LF (tangential to the grip surface) as in Loh et al. (2010). Volunteers were seated with their right hand placed on a table. Talcum powder was applied to the fingers both with and without gloves to keep friction constant (Augurelle et al. 2003).

In the constant-weight series, participants were cued to lift the manipulandum at a 5-cm height and hold it for 5 s before replacing it on the table. A series of 20 trials was undertaken with an intertrial interval of 7 s (end to onset). In the variable-weight series, a pseudorandom sequence of weight changes of the manipulandum occurred. The manipulandum was coupled to a robotic arm (Phantom, Geomagic; as in Van Polanen and Davare 2015) through a hole drilled through the table to enable hidden weight changes, as in Loh et al. (2010). The robot was programmed to provide a light or heavy resistance equivalent to 0.5 and 3 N, respectively, in a pseudorandom order. Participants were cued to lift the manipulandum at a 5-cm height and hold it for 2.5 s before replacing it on the table. Forty-one trials were undertaken (3.5 s intertrial interval; end to onset) so that there were 10 trials of each weight transition condition: light-after-light, heavy-after-light, light-after-heavy, and heavy-after-heavy. To determine slip force and coefficient of friction, participants were asked to perform several trials lifting the manipulandum to a 5-cm height and then slowly releasing grip to allow slip. For each condition, three trials were averaged after completion of practice trials.

**Data acquisition and analysis.** Force data were digitized via a CED power 1401 interface, and data were recorded in Spike2 (version 5.21, Cambridge Electronic Design, Cambridge, UK). Analysis was done by custom-made scripts in MATLAB (MathWorks), and variables measured for each trial included peak grip force (PGF), peak load force (PLF), static GF, preloading phase duration (from onset of GF to onset of LF), loading phase duration (from onset of LF to liftoff of the object), maximum coefficient of correlation between LF and GF profiles from GF onset ± 50 ms, and PGF (GF rate) and PLF (LF rate) rates as the first derivatives of GF and LF (Fig. 1; see also Davare et al. 2006). Slip force was measured as the minimal GF to prevent slippage and determined as the GF at the onset of slippage. Safety margin was determined as the excess static GF above the slip force. The coefficient of friction was calculated as the slip force divided by LF. To determine the coefficient of friction for the index finger, the slip force for the index finger was divided by half the LF at the onset of slippage, assuming that the index finger supported half of the load of the symmetrical manipulandum, as in Kinoshita (1999).

Data from the variable-weight series were analyzed as in Loh et al. (2010). To determine the effects of sensorimotor memory, two ratios were calculated. The effect of a preceding heavy object was determined by the ratio of GF rate of the light-after-heavy trials divided by the light-after-light trials. A ratio of >1 indicates that GF rate for a light object increased in trials preceded by a lift of a heavy compared with a light object. The effect of a light object in the preceding lift was determined by the ratio of GF rate in heavy-after-light trials divided by the heavy-after-heavy trials. A ratio <1 indicates a reduced GF rate of a heavy object with a preceding light object compared with a heavy one. Results are given as means ± SE and were analyzed with SPSS (version 21, IBM) using paired t-tests and Pearson correlation.
coefficients as appropriate. A $P$ value of $\leq 0.05$ was considered significant.

**RESULTS**

**Psychophysical tasks.** Sensory thresholds were significantly increased in participants wearing gloves. Bump detection threshold (no gloves $1.9 \pm 0.4$ $\mu$m, with gloves $12.3 \pm 2.2$ $\mu$m; $P < 0.0005$) and monofilament detection threshold (no gloves $0.6 \pm 0.07$ mN, with gloves $6.4 \pm 1.7$ mN; $P \leq 0.005$) were elevated (Fig. 2A). However, there were no changes in the ability to undertake the grating orientation task with the addition of gloves (no gloves $1.6 \pm 0.1$ mm, with gloves $1.8 \pm 0.2$ mm; $P > 0.2$; Fig. 2B), suggesting that FAI but not SAI mechanoreceptor function was disrupted. In addition, gloves significantly reduced performance in both the Purdue Pegboard (no gloves $17.0 \pm 0.4$ pegs in 30 s, with gloves $14.6 \pm 0.4$ pegs in 30 s; $P < 0.005$) and the Grooved Pegboard (no gloves $52.9 \pm 1.3$ s, with gloves $61.1 \pm 2.2$ s; $P < 0.005$) tasks, suggesting impairment in global manipulative tasks.

**Precision grip: constant-weight series.** A series of constant-weight lifts was undertaken to test the effect of selective FAI impairment on the online force scaling within a trial. The addition of gloves increased GFs, with PGF increased by $14 \pm 6\%$ and static GF by $22 \pm 6\%$ (Table 1; Fig. 3). PLF was also increased by $17 \pm 5\%$ with the addition of gloves. In addition, both GF rate and LF rate were enhanced, indicating that gloves produced a faster grip. GF rate was increased by $26 \pm 8\%$ and LF rate by $20 \pm 8\%$. However, specific timing phases were not significantly affected by gloves (preloading phase: no gloves $35.0 \pm 5.7$ ms, with gloves $42.6 \pm 7.8$ ms, $P > 0.2$; loading...
Table 1. Precision grip parameters

<table>
<thead>
<tr>
<th></th>
<th>No Gloves</th>
<th>Gloves</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak grip force, N</td>
<td>10.3 ± 0.8</td>
<td>11.5 ± 0.8</td>
<td>≤0.05</td>
</tr>
<tr>
<td>Peak load force, N</td>
<td>1.6 ± 0.08</td>
<td>1.9 ± 0.1</td>
<td>≤0.005</td>
</tr>
<tr>
<td>Grip force rate, N/s</td>
<td>13.2 ± 1.9</td>
<td>15.7 ± 1.7</td>
<td>≤0.05</td>
</tr>
<tr>
<td>Load force rate, N/s</td>
<td>3.2 ± 0.2</td>
<td>3.8 ± 0.3</td>
<td>≤0.05</td>
</tr>
<tr>
<td>Static load force, N</td>
<td>1.2 ± 0.07</td>
<td>1.3 ± 0.1</td>
<td>&gt;0.20</td>
</tr>
<tr>
<td>Static grip force, N</td>
<td>8.6 ± 0.4</td>
<td>10.4 ± 0.7</td>
<td>≤0.01</td>
</tr>
</tbody>
</table>

Values are means ± SE.

Phase: no gloves 92.1 ± 9.5 ms, with gloves 105.0 ± 26.7 ms, P > 0.5, and the synchrony between GF and LF was preserved (maximum correlation coefficient: no gloves 0.91 ± 0.01, with gloves 0.91 ± 0.02, P > 0.5).

Precision grip: variable-weight series. A series of lifts of objects of variable weight was undertaken to examine the effect of selective FAI impairment on the trial-to-trial buildup of sensorimotor memory. We quantified the anticipatory planning of fingertip forces based on the previous lift. There was a 20% increase in GF rate for light-after-heavy compared with light-after-light trials, indicating that the previous lift of a heavy object affected the GF rate. This is comparable to previous studies (Johansson and Westling 1988; Loh et al., 2010). These values were unchanged by the addition of gloves, indicating that anticipatory planning of force was unaffected by the addition of gloves (GF rate ratios: no gloves 1.2 ± 0.03, with gloves 1.2 ± 0.04; P > 0.2). Similarly, the GF rate for heavy-after-light trials was reduced by ~11% compared with heavy-after-heavy trials, and there was no difference with the addition of gloves (GF rate ratios: no gloves 0.89 ± 0.02, with gloves 0.86 ± 0.03; P > 0.2), indicating that the impairment of FAI mechanoreceptors did not disrupt GF ratios with variable weights.

Slip force and safety margin. We controlled for friction by using talcum powder and confirmed that the addition of gloves decreased the coefficient of static friction by 33% as in prior studies (no gloves 0.27 ± 0.01, with gloves 0.21 ± 0.02; P < 0.005). However, the friction range was similar between conditions (no gloves friction range 0.19–0.34, with friction range 0.12–0.28). Slip force was increased by the addition of gloves (no gloves 3.6 ± 0.2 N, with gloves 4.7 ± 0.3 N; P < 0.001). There was a trend toward increased safety margin, but this was not significant (no gloves 5.0 ± 0.4 N, with gloves 5.7 ± 0.7 N; P > 0.05). Safety margin as a percentage of GF also did not increase (no gloves 43 ± 2%, with gloves 47 ± 3%; P > 0.2). To determine whether changes in friction were partially responsible for the elevation of GF, the extent of change in PGF was correlated with the extent of change in friction. While these variables were significantly correlated (correlation coefficient = 0.747, P < 0.005; Fig. 4), the direction of association (positive rather than negative correlation) was not consistent with a role of friction in driving an increase in GF. Participants who experienced the greatest reduction in friction between bare hands and gloves had smaller (rather than larger) increases in GF with the addition of gloves. There was no correlation between the PGF and friction values in either the gloves or no-gloves condition.

DISCUSSION

The present study utilized graded experimental tactile dysfunction to identify patterns in psychophysical and precision grip parameters associated with graduated sensation loss. Sensory thresholds were significantly elevated for tasks associated with FAI function but not for tasks relying on SAI mechanoreceptors. Accordingly, peak GF and LF were elevated, as were maximum GF and LF rates, but timing parameters were unaffected. In addition, there was no indication that the addition of gloves affected programming of fingertip forces based on the sensorimotor memory of the previous lift.
Role of mechanoreceptors in precision grip. Four types of mechanosensitive receptors have been identified in human glabrous skin, with the type I afferents—fast adapting (FAI) and slowly adapting (SAI)—present in high density in the fingertip (Johansson and Vallbo 1979). The grating orientation task has been linked to SAI afferent activity, with strong responses to periodic gratings identified in monkey mechanoreceptive afferents (Johnson and Phillips 1981; Phillips and Johnson et al. 1981). Conversely, it has been demonstrated that the response to braille or bumpy stimuli is mediated by FAI afferents (Kennedy et al. 2011; Lamotte and Whitehouse 1986). In monkey mechanoreceptors, the number of FAI afferent impulses and the receptive field sizes of individual FAI afferents increased with bump height (Lamotte and Whitehouse 1986). Similarly, in human fingertip skin biopsies, there was a correlation between Meissner corpuscle density and bump detection threshold (Kennedy et al. 2011).

In the present study there was a dissociation between psychophysical tasks. The Bumps task was significantly impaired, while the grating orientation task was not affected, suggesting that the gloves may have selectively reduced FAI afferent activity. The bumps threshold has been demonstrated to be independent of pressure or velocity (Lamotte and Whitehouse 1986). While physical cues to orientation may affect grating orientation threshold (Van Boven and Johnson 1994), to reduce the risk of movement the finger was immobilized with adhesive putty. There was a wider range in variability in bumps performance in participants wearing gloves than with bare hands; however, substantial variability in bump detection has also been identified in patients with sensory neuropathy (Kennedy et al. 2011), suggesting that there may be a range of responses to altered sensation.

Accurate force control during precision grip of objects with forefinger and thumb requires detailed information from mechanoreceptors. Microneurography of the median nerve during precision grip has demonstrated both FAI and SAI afferent activity in the initial response (Westling and Johansson 1987). FAI afferents quickly adapt, but SAI afferents continue static discharge, and both afferent types burst when the object is released (Westling and Johansson 1987). While both FAI and SAI afferents are involved in grip control, FAI afferents are primarily responsible for conveying information about object properties from initial contact (Johansson and Flanagan 2009). In addition, FAI fibers convey information about coarse spatial features, responding to dynamic mechanical events, while SAI fibers convey fine spatial detail and sensitivity to edge contours (Bensmaia et al. 2006). FAI afferents have a major role in scaling GF and LF during precision grip (Maceyfield et al. 1996) and have an important role in encoding friction (Johansson and Westling 1987). While less densely innervated in the fingertip, FAI afferents signal at object liftoff and set down during precision grip while SAI afferents encode the application of static forces during object lifting, although with less sensitivity (Johansson and Flanagan 2009).

Results from the present study suggest the importance of FAI afferents in GF and LF scaling, which was disturbed by the addition of gloves. However, microneurographic recordings would be necessary to confirm the role of FAI mechanoreceptors in precision grip and determine how partial reduction in tactile information affects different afferent subtypes. Furthermore, traditional views of the complete segregation of mechanoreceptor afferents have been challenged, and it is increasingly recognized that cortical integration is multimodal, involving inputs from multiple receptor types (Saal and Bensmaia 2014). Accordingly, the contributions of FAI and SAI afferents to grip control may overlap and involve complex interactions with other afferent subtypes (Johansson and Flanagan 2009).

Experimental modulation of sensory impairment. Digital anesthesia has been utilized as an experimental model of tactile dysfunction, typically producing increased GF and safety margin (Augurelle et al. 2003; Johansson et al. 1992; Monzée et al. 2003; Nowak et al. 2001). Temporal coupling of GF and LF is typically preserved with anesthesia (Augurelle et al. 2003; Nowak et al. 2001), although in some studies timing phases have been altered (Johansson et al. 1992; Monzée et al. 2003). During digital anesthesia, a higher safety margin was explained as due to a lack of cutaneous feedback to provide updates (Augurelle et al. 2003). In the present study, safety margin was not significantly increased, suggesting that the level of sensory impairment provided by the gloves was not sufficient to interfere with updating of sensorimotor memory.

Several studies have demonstrated the detrimental effects of gloves on manual dexterity (Dianat et al. 2012) and tactile sensation (Shih et al. 2001; Willms et al. 2009). GF and LF increased with increasing glove thickness (Kinosita 1999; Shih et al. 2001; Willms et al. 2009), although timing parameters were not affected, similar to the present study. The present results suggest that even partial reduction in sensation is sufficient to disturb the maintenance of appropriate GF level.

However, prior studies did not examine the impact on sensorimotor memory. In the present study, sensorimotor memory was assessed by comparing peak GF rates between trials using different weights. Peak GF rate occurs during the loading phase—prior to the onset of movement and before current trial information can be updated (Flanagan et al. 2001). Accordingly, the peak GF rate is set without access to cues to object weight and by relying on information obtained from the previous lift (Flanagan et al. 2001). However, these ratios were unaffected by the addition of gloves, indicating that information about the weight of the object from the previous lift was fully available when wearing gloves, despite the modulation in GF. Accordingly, the characteristics of the previous lift had an influence on subsequent lifts despite reduced sensation, suggesting that partial sensory feedback is sufficient to enable this effect. In contrast, GF scaling due to sensorimotor memory can be disrupted by additional sensory feedback such as hand muscle vibration (Nowak et al. 2004), suggesting that sensory feedback disruption can influence sensorimotor memory in some settings.

While changes in friction were identified with gloves, these changes were not consistent with the effects of gloves on GF, suggesting that gloves rather than friction were predominantly modulating GF. Furthermore, prior studies have demonstrated a disconnect between friction and GF modulation, with altered coefficients of friction with gloves not solely responsible for changes in GF (Willms et al. 2009). In addition, Kinosita (1999) demonstrated increased friction with rubber gloves without talc and also demonstrated increased GF in this experimental setting. Shih et al. (2001) also identified tactile deficits, increased PGF and PLF, and decreased coefficient of friction with gloves. However, while there was no difference between
one, two, and three layers of gloves in terms of friction, GF and LP demonstrated successive changes, suggesting that altered friction was not directly responsible for changes. Interestingly, during digital anesthesia the required adjustments of GF to friction are disrupted (Augurelle et al. 2003), suggesting that cutaneous sensation is required for accurate assessment and reaction to frictional changes (Westling and Johansson 1984). As mentioned above, FAF function may be critical for accurate frictional assessment (Cole et al. 1999; Johansson and Westling 1987), which may contribute to the discrepancy between GF modulation and friction in the present study.

Conclusions. Identification of grip-lift profiles associated with different types of sensory dysfunction may assist in providing insights into the role of different subtypes of sensory neurons in object manipulation. While future studies should examine the impact of focal reduction in tactile sensitivity to avoid any effect of gloves on motor performance, the present results further characterize the components of sensorimotor loops involved in force control during skilled grasp. Specifically, our results suggest a potential role of FAI receptors for the online control of force but not for updating internal models about object weight. This model of graded tactile dysfunction may also provide insight into patterns of sensory dysfunction and their effect on precision grip in patient populations.

REFERENCES