

1 **Fast Adapting Mechanoreceptors are Important for Force Control in Precision Grip but not**  
2 **for Sensorimotor Memory**

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28 **ABSTRACT**

29 Sensory feedback from cutaneous mechanoreceptors in the fingertips is important in effective object  
30 manipulation, allowing appropriate scaling of grip and load forces during precision grip. However  
31 the role of mechanoreceptor subtypes in these tasks remains incompletely understood. To address  
32 this issue, psychophysical tasks which may specifically assess function of type I fast adapting (FAI)  
33 and slowly adapting (SAI) mechanoreceptors were used with object manipulation experiments to  
34 examine the regulation of grip force control in an experimental model of graded reduction in tactile  
35 sensitivity (healthy volunteers wearing two layers of latex gloves). With gloves, tactile sensitivity  
36 decreased significantly from  $1.9 \pm 0.4\mu\text{m}$  to  $12.3 \pm 2.2\mu\text{m}$  in the Bumps task assessing function of  
37 FAI afferents, but not in a grating orientation task assessing SAI afferents ( $1.6\pm 0.1\text{mm}$  to  
38  $1.8\pm 0.2\text{mm}$ ). Six axis force/torque sensors measured peak grip (PGF) and load forces (PLF)  
39 generated by the fingertips during a grip-lift task. With gloves there was a significant increase of  
40 PGF ( $14\pm 6\%$ ), PLF ( $17\pm 5\%$ ) and grip and load force rates ( $26\pm 8\%$ ;  $20\pm 8\%$ ). A variable weight  
41 series task was used to examine sensorimotor memory. There was a 20% increase in PGF when the  
42 lift of a light object was preceded by a heavy relative to a light object. This relationship was not  
43 significantly altered when lifting with gloves, suggesting that the addition of gloves did not change  
44 sensorimotor memory effects. We conclude that FAI fibres may be important for the online force  
45 scaling but not for the build-up of a sensorimotor memory.

46  
47 **New & Noteworthy:** This manuscript provides insights into the role of cutaneous feedback in object  
48 manipulation and precision grip. Force control during object manipulation relies on prior experience  
49 and anticipation as well as feedback from mechanosensitive afferents. Using a graded model of  
50 experimental tactile dysfunction, we have selectively reduced the sensitivity of FAI, but not SAI  
51 mechanoreceptors and demonstrate that impairment of FAI function leads to selective deficits of  
52 object manipulation whereas it does not perturb sensorimotor memory.

## 53 INTRODUCTION

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

70 Deficits in tactile feedback produce significant functional difficulties, demonstrated in patients with  
71 sensory neuropathies (Nowak and Hermsdörfer, 2004) or experimental reduction of tactile sensation  
72 in healthy volunteers by digital anaesthesia (Monzée et al., 2003; Nowak et al., 2001; Augurelle et  
73 al., 2003; Johansson et al., 1992). While neuropathy and digital anaesthesia underscore the  
74 importance of sensory feedback in force scaling and memory build-up, they lead to a non-selective  
75 degradation of sensory afferent outflow from the finger tip. In the present study, we studied the  
76 functional consequences following selective reduction of the sensitivity of mechanoreceptors,  
77 achieved via wearing two layers of latex gloves.

78 Psychophysical tasks have been developed which may provide a selective readout of FAI and SAI  
79 mechanoreceptor function. Spatial acuity can be determined by the grating orientation task which is  
80 encoded by the activity in SAI mechanoreceptors in primates (Johnson and Philips 1981; Philips and  
81 Johnson et al., 1981). By contrast, the detection of a small elevated dot on a smooth surface or bump-  
82 like stimulus as in braille is signalled by FAI mechanoreceptors (La Motte and Whitehouse, 1986)  
83 and can be assessed by the ‘Bumps task’ (Kennedy et al., 2011).

84 Examination of FAI and SAI firing activity during precision grip via microneurography has provided  
85 correlative evidence that both FAI and SAI afferents are important in grip control but that FAI fibres  
86 are chiefly responsible for controlling grip force scaling (Macefield et al., 1996). However, the  
87 potential contribution of FAI fibres to controlling grip force scaling has not been experimentally  
88 demonstrated. We examined the hypothesis that the potentially selective reduction of activity in one  
89 mechanoreceptor (FAI) pathway leads to an impairment of online force scaling but not sensorimotor  
90 memory.

91

## 92 **METHODS**

93 12 healthy volunteers were recruited (6 males and 6 females, age  $32.7 \pm 1.3$  years; mean  $\pm$  standard  
94 error of the mean). Ethics approval was obtained from the London City and East National Research  
95 Ethics Service Committee and participants provided written informed consent. The Edinburgh  
96 Handedness inventory (Oldfield, 1971) established all participants as right-handed. Participants  
97 completed all tasks with and without the addition of two pairs of surgical latex gloves appropriate for  
98 their hand size (0.27 mm thick, Biogel Surgeons Gloves, Mölnlycke Health Care, Göteborg,  
99 Sweden). Multiple sizes were available to ensure appropriate fit. Two layers of gloves were chosen  
100 in order to ensure that tactile sensitivity was significantly reduced, as prior studies have identified  
101 elevations in sensory thresholds with multiple layers of latex gloves (Shih et al., 2001). The order of

102 presentation was pseudo-randomised, so that half of the participants completed the tasks without  
103 gloves to begin with while the other half started with gloves on first.

#### 104 **Psychophysical and Behavioural Tasks**

105 All psychophysical tests were undertaken on the distal phalanx of the right index finger. For two  
106 tests the finger was stabilised with adhesive putty to prevent movement.

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

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

120 Assessment of tactile sensitivity was also undertaken using the 'Bumps' device (Kennedy et al.,  
121 2011) which consists of a checkerboard-like plate with a smooth surface divided into 12 squares.  
122 Each square contains 5 coloured circles of 4 mm diameter, with one randomly selected circle  
123 containing a single coin-shaped 550 $\mu$ m diameter bump of variable height. Bump height ranged from  
124 26 $\mu$ m to 0.5 $\mu$ m over 4 plates. Participants were given standard instructions and asked to identify  
125 where the raised bump was located in each square, using their index fingertip to scan the plate. As

126 per Kennedy et al., 2011, threshold was determined as the lowest height bump that could be correctly  
127 detected in a series of 3 consecutive correct detections, so that for a threshold of 2.5 $\mu$ m, bumps of  
128 3 $\mu$ m and 3.5 $\mu$ m also had to be correctly identified. The lowest threshold was taken from two trials  
129 across all plates.

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

### 135 **Precision grip assessment**

136 The tasks involved a precision grip with the thumb and index finger of a 225g manipulandum with  
137 two parallel smooth aluminium grip surfaces of 40mm diameter (Figure 1A). Six axis force torque  
138 sensors (Mini 40 F/T transducers: ATI Industrial Automation; North Carolina USA) were used to  
139 measure grip force (normal to the grip surface) and load force (tangential to the grip surface) as in  
140 Loh et al., 2010. Volunteers were seated with their right hand placed on a table. Talcum powder was  
141 applied to the fingers both with and without gloves to keep friction constant (Augurelle et al., 2003).

142 In the constant weight series, participants were cued to lift the manipulandum at a 5cm height and  
143 hold it for 5 seconds before replacing it on the table. A series of 20 trials was undertaken with an  
144 inter-trial interval of 7 seconds (end to onset). In the variable weight series, a pseudorandom  
145 sequence of weight changes of the manipulandum occurred. The manipulandum was coupled to a  
146 robotic arm (Phantom, Geomagic; as in Van Polanen and Davare, 2015) through a hole drilled  
147 through the table to enable hidden weight changes, as in Loh et al., 2010. The robot was programmed  
148 to provide a light or heavy resistance equivalent to 0.5 and 3 Newtons respectively in a  
149 pseudorandom order. Participants were cued to lift the manipulandum at a 5cm height and hold it for

150 2.5 seconds before replacing it on the table. 41 trials were undertaken (3.5 sec inter-trial interval; end  
151 to onset) so that there were 10 trials of each weight transition condition: light-after-light, heavy-after-  
152 light, light-after-heavy and heavy-after-heavy. To determine slip force and coefficient of friction,  
153 participants were asked to perform several trials lifting the manipulandum to a 5cm height and then  
154 slowly releasing grip to allow slip. For each condition, three trials were averaged, following  
155 completion of practice trials.

### 156 **Data acquisition and analysis**

157 Force data was digitized via a CED power 1401 interface and data were recorded in Spike 2 (Version  
158 5.21, Cambridge Electronic Design, Cambridge UK). Analysis was done by custom-made scripts in  
159 Matlab (Mathworks, Massachusetts, USA) and variables measured for each trial included peak grip  
160 force (PGF), peak load force (PLF), static grip force, preloading phase duration (from onset of GF to  
161 onset of LF), loading phase duration (from onset of LF to lift-off of the object), maximum coefficient  
162 of correlation between LF and GF profiles from grip force onset  $\pm$  50ms, peak grip force (GF rate)  
163 and load force rates (LF rate) as the first derivatives of GF and LF (Figure 1, see also Davare et al.,  
164 2006). Slip force was measured as the minimal grip force to prevent slippage and determined as the  
165 grip force at the onset of slippage. Safety margin was determined as the excess static grip force  
166 above the slip force. The coefficient of friction was calculated as the slip force divided by the load  
167 force. To determine the coefficient of friction for the index finger, the slip force for the index finger  
168 was divided by half the load force at the onset of slippage, assuming that the index finger supported  
169 half of the load of the symmetrical manipulandum, as in Kinoshita (1999).

170

171 Data from the variable weight series was analysed as in Loh et al., 2010. To determine the effects of  
172 sensorimotor memory, two ratios were calculated. The effect of a preceding heavy object was  
173 determined by the ratio of GF rate of the light-after-heavy trials divided by the light-after-light trials.  
174 A ratio of greater than 1 indicates that GF rate for a light object increased in trials preceded by a lift

175 of a heavy compared to a light object. The effect of a light object in the preceding lift was  
176 determined by the ratio of GF rate in heavy-after-light trials divided by the heavy-after-heavy trials.  
177 A ratio lower than 1 indicates a reduced GF rate of a heavy object with a preceding light object  
178 compared to a heavy one. Results were given as mean  $\pm$  standard error of the mean and analysed  
179 with SPSS (Version 21, IBM) using paired t-tests and Pearson correlation coefficients as appropriate.  
180 A *p* value of less than or equal to 0.05 was considered significant.

181

## 182 **RESULTS**

### 183 **Psychophysical tasks**

184 Sensory thresholds were significantly increased in participants wearing gloves. Bumps detection  
185 threshold (no gloves  $1.9 \pm 0.4 \mu\text{m}$ ; with gloves  $12.3 \pm 2.2 \mu\text{m}$ ;  $P < 0.0005$ ) and monofilament  
186 detection threshold (no gloves  $0.6 \pm 0.07 \text{ mN}$ ; with gloves  $6.4 \pm 1.7 \text{ mN}$ ;  $P \leq 0.005$ ) were elevated  
187 (Figure 2A). However, there were no changes in the ability to undertake the grating orientation task  
188 with the addition of gloves (no gloves  $1.6 \pm 0.1 \text{ mm}$ ; with gloves  $1.8 \pm 0.2 \text{ mm}$ ;  $P > 0.2$ ; Figure 2B),  
189 suggesting that FAI but not SAI mechanoreceptor function was disrupted. In addition, gloves  
190 significantly reduced performance in both the Purdue pegboard (no gloves  $17.0 \pm 0.4$  pegs in 30sec;  
191 with gloves  $14.6 \pm 0.4$  pegs in 30sec;  $P < 0.005$ ) and the Grooved pegboard tasks (no gloves  $52.9 \pm$   
192  $1.3 \text{ sec}$ ; with gloves  $61.1 \pm 2.2 \text{ sec}$ ;  $P < 0.005$ ), suggesting impairment in global manipulative tasks.

193

### 194 **Precision grip: Constant weight series**

195 A series of constant weight lifts was undertaken to test the effect of selective FAI impairment on the  
196 online force scaling within a trial. The addition of gloves increased grip forces, with peak grip force  
197 increased by  $14 \pm 6\%$  and static grip force by  $22 \pm 6\%$  (Table 1; Figure 3). Peak load force was also  
198 increased by  $17 \pm 5\%$  with the addition of gloves. In addition both grip force rate and load force rate  
199 were enhanced, indicating that gloves produced a faster grip. GF rate was increased by  $26 \pm 8\%$  and



200 LF rate by  $20 \pm 8\%$ . However, specific timing phases were not significantly affected by gloves  
201 (Preloading phase: no gloves  $35.0 \pm 5.7$  ms; with gloves  $42.6 \pm 7.8$ ms  $P > 0.2$ ; Loading phase: no  
202 gloves  $92.1 \pm 9.5$  ms; with gloves  $105.0 \pm 26.7$  ms  $P > 0.5$ ) and the synchrony between grip and load  
203 forces was preserved (maximum correlation coefficient: no gloves  $0.91 \pm 0.01$ ; with gloves  $0.91 \pm$   
204  $0.02$ ;  $P > 0.5$ ).

205

### 206 **Precision grip: Variable weight series**

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

### 218 **Slip force and safety margin**

219 We controlled for friction by using talcum powder and confirmed that the addition of gloves  
220 decreased the coefficient of static friction by 33% as in prior studies (no gloves  $0.27 \pm 0.01$ ; with  
221 gloves  $0.21 \pm 0.02$ ;  $P < 0.005$ ). However, the friction range was similar between conditions (no gloves  
222 friction range  $0.19 - 0.34$ ; with gloves friction range  $0.12 - 0.28$ ). Slip force was increased by the  
223 addition of gloves (no gloves  $3.6 \pm 0.2$  N; with gloves  $4.7 \pm 0.3$  N;  $P < 0.001$ ). There was a trend  
224 towards increased safety margin but this was not significant (no gloves  $5.0 \pm 0.4$  N; with gloves  $5.7$

225  $\pm 0.7$  N;  $P > 0.05$ ). The safety margin as a percentage of grip force also did not increase (no gloves  
226  $43 \pm 2\%$ ; with gloves  $47 \pm 3\%$ ;  $P > 0.2$ ). To determine if changes in friction were partially  
227 responsible for the elevation of grip force, the extent of change in peak grip force was correlated with  
228 the extent of change in friction. While these variables were significantly correlated (correlation  
229 coefficient = 0.747;  $P < 0.005$ ; Figure 4), the direction of association (positive rather than negative  
230 correlation) was not consistent with a role of friction in driving an increase in grip force. Participants  
231 who experienced the greatest reduction in friction between bare hands to gloves had smaller (rather  
232 than larger) increases in grip force with the addition of gloves. There was no correlation between the  
233 peak grip force and friction values in either the gloves or no gloves conditions.

## 234 **DISCUSSION**

235 The present study utilised graded experimental tactile dysfunction to identify patterns in  
236 psychophysical and precision grip parameters associated with graduated sensation loss. Sensory  
237 thresholds were significantly elevated for tasks associated with FAI function but not for tasks relying  
238 on SAI mechanoreceptors. Accordingly, peak grip and load forces were elevated, as were maximum  
239 grip force and load force rates, but timing parameters were unaffected. In addition, there was no  
240 indication that the addition of gloves affected programming of fingertip forces based on the  
241 sensorimotor memory of the previous lift.

### 242 **The role of mechanoreceptors in precision grip**

243 Four types of mechanosensitive receptors have been identified in human glabrous skin, with the type  
244 I afferents - fast adapting (FAI) and slowly adapting (SAI) – present in high density in the fingertip  
245 (Johansson & Vallbo, 1979). The grating orientation task has been linked to SAI afferent activity,  
246 with strong responses to periodic gratings identified in monkey mechanoreceptive afferents (Johnson  
247 and Philips 1981; Philips and Johnson et al., 1981). Conversely, it has been demonstrated that the  
248 response to braille or bump-like stimuli is mediated by FAI afferents (La Motte and Whitehouse,

249 1986; Kennedy et al., 2011). In monkey mechanoreceptors, the number of FAI afferent impulses and  
250 the receptive field sizes of individual FAI afferents increased with bump height (LaMotte and  
251 Whitehouse, 1986). Similarly, in human fingertip skin biopsies, there was a correlation between  
252 Meissner corpuscle density and bump detection threshold (Kennedy et al., 2011).

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

262 Accurate force control during precision grip of objects with forefinger and thumb requires detailed  
263 information from mechanoreceptors. Microneurography of the median nerve during precision grip  
264 has demonstrated both FAI and SAI afferent activity in the initial response (Westling and Johansson,  
265 1987). FAI afferents quickly adapt, but SAI afferents continued static discharge, and both afferent  
266 types burst when the object is released (Westling and Johansson, 1987). While both FAI and SAI  
267 afferents are involved in grip control, FAI afferents are primarily responsible for conveying  
268 information about object properties from initial contact (Johansson and Flanagan, 2009). In addition,  
269 FAI fibres convey information about coarse spatial features, responding to dynamic mechanical  
270 events, while SAI convey fine spatial detail and sensitivity to edge contours (Bensmaia et al., 2006).  
271 FAI afferents have a major role in scaling GF and LF during precision grip (Macefield et al., 1996)  
272 and have an important role in encoding friction (Johansson and Westling, 1987). While less densely

273 innervated in the fingertip, FAII afferents signal at object lift off and set down during precision grip,  
274 while SAII encode the application of static forces during object lifting, although with less sensitivity  
275 (Johansson and Flanagan, 2009).

276

277 Results from the present study suggest the importance of FAI afferents in GF and LF scaling, which  
278 was disturbed by the addition of gloves. However microneurographic recordings would be necessary  
279 to confirm the role of FAI mechanoreceptors in precision grip and determine how partial reduction in  
280 tactile information affects different afferent subtypes. Further, traditional views of the complete  
281 segregation of mechanoreceptor afferents have been challenged and it is increasingly recognised that  
282 cortical integration is multimodal, involving inputs from multiple receptor types (Saal and Bensmaia,  
283 2014). Accordingly the contributions of FAI and SAI afferents to grip control may overlap and  
284 involve complex interactions with other afferent subtypes (Johansson and Flanagan, 2009).

285

### 286 **Experimental Modulation of Sensory Impairment**

287 Digital anaesthesia has been utilised as an experimental model of tactile dysfunction, typically  
288 producing increased grip force and safety margin (Augurelle et al., 2002; Johansson et al., 1992;  
289 Nowak et al., 2003; Monzée et al., 2003). Temporal coupling of grip and load forces is typically  
290 preserved with anaesthesia (Augurelle et al., 2002; Nowak et al., 2003), although in some studies  
291 timing phases have been altered (Johansson et al., 1992; Monzée et al., 2003). During digital  
292 anaesthesia, a higher safety margin was explained as due to a lack of cutaneous feedback to provide  
293 updates (Augurelle et al., 2002). In the present study, safety margin was not significantly increased,  
294 suggesting that the level of sensory impairment provided by the gloves was not sufficient to interfere  
295 with updating of sensorimotor memory.

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

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

314 While changes in friction were identified with gloves, these changes were not consistent with the  
315 effects of gloves on grip force, suggesting that gloves rather than friction were predominantly  
316 modulating grip force. Further, prior studies have demonstrated a disconnect between friction and  
317 grip force modulation, with altered coefficients of friction with gloves not solely responsible for  
318 changes in grip force (Willms et al., 2009). In addition, Kinoshita (1999) demonstrated increased  
319 friction with rubber gloves without talc, and also demonstrated increased grip force in this  
320 experimental setting. Shih et al. (2001) also identified tactile deficits, increased peak grip and load

321 force and decreased coefficient of friction with gloves. However, while there was no difference  
322 between one, two and three layers of gloves in terms of friction, grip and load forces demonstrated  
323 successive changes, suggesting that altered friction was not directly responsible for changes.  
324 Interestingly, during digital anaesthesia the required adjustments of grip force to friction are  
325 disrupted (Augurelle et al., 2002), suggesting that cutaneous sensation is required for accurate  
326 assessment and reaction to frictional changes (Westling and Johansson, 1984). As mentioned  
327 previously, FAI function may be critical for accurate frictional assessment (Johansson and Westling,  
328 1987; Cole et al., 1999), which may contribute to the discrepancy between grip force modulation and  
329 friction in the present study.

### 330 **Conclusions**

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

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346 **Abbreviations**

347 GF Grip force

348 LF Load force

349 PGF Peak grip force

350 PLF Peak load force

351 FAI Type 1 fast adapting mechanoreceptors

352 SAI Type 1 slowly adapting mechanoreceptors

353

354 **FIGURE LEGENDS**

355 **Figure 1 A** Illustration of precision grip experiment, with the manipulandum and direction of grip

356 and load forces shown. **B** Grip-lift profile demonstrating modulation in grip force (red) and load

357 force (blue) over time, with the preloading phase marked between times 1 and 2 and the loading

358 phase between times 2 and 3. **C** Cross-correlation coefficient between grip and load force profiles

359 plotted against the time lag (ms) between grip and load force profiles. The plot demonstrates the

360 maximum cross-correlation coefficient and the time lag at the maximum coefficient. **D** Grip force

361 rate (red) and load force rate (blue) profiles, plotted as the first derivatives of grip and load force.

362 **Figure 2 A** Bumps task threshold ( $\mu\text{m}$ ) for individual participants with and without gloves. **B**

363 Grating orientation task threshold (mm) for individual participants with and without gloves. Mean  $\pm$

364 SEM values for group data are shown with superimposed bar graphs.

365 **Figure 3 A** Grip force profile demonstrating changes (mean  $\pm$  standard error of the mean) in grip

366 force with the addition of gloves (upper curve) compared to bare hands (lower curve) in all

367 participants. **B** Static grip force (N) for individual participants with and without gloves. Mean  $\pm$  SEM

368 values for group data are shown with superimposed bar graphs.

369 **Figure 4** Correlation between change in peak grip force with gloves and changes in friction with

370 gloves, demonstrating that participants displaying reduced friction with gloves also had smaller

371 increases in grip force.

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	<b>No gloves (mean ± SEM)</b>	<b>Gloves (mean ± SEM)</b>	<b>P value</b>
<b>Peak Grip Force (N)</b>	10.3 ± 0.8	11.5 ± 0.8	≤ 0.05
<b>Peak Load Force (N)</b>	1.6 ± 0.08	1.9 ± 0.1	≤ 0.005
<b>Grip Force rate (N/s)</b>	13.2 ± 1.9	15.7 ± 1.7	≤ 0.05
<b>Load Force rate (N/s)</b>	3.2 ± 0.2	3.8 ± 0.3	≤ 0.05
<b>Static Load Force(N)</b>	1.2 ± 0.07	1.3 ± 0.1	> 0.20
<b>Static Grip Force (N)</b>	8.6 ± 0.4	10.4 ± 0.7	≤ 0.01

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376 **TABLE 1 - Precision grip parameters**

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387 **REFERENCES**

- 388 **Augurelle AS, Smith AM, Lejeune T, Thonnard JL.** Importance of cutaneous feedback in  
389 maintaining a secure grip during manipulation of hand-held objects. *Journal of Neurophysiology*  
390 89:665-671, 2003.
- 391 **Bensmaia SJ, Craig JC, Johnson KO.** Temporal factors in tactile spatial acuity: evidence for RA  
392 interference in fine spatial processing. *Journal of Neurophysiology* 95:1783-1791, 2006.
- 393 **Cole KJ, Rotella DL, Harper JG.** Mechanisms for age-related changes of fingertip forces during  
394 precision gripping and lifting in adults. *The Journal of Neuroscience* 19:3238-3247, 1999.
- 395 **Dianat I, Haslegrave CM, Stedmon AW.** Methodology for evaluating gloves in relation to the  
396 effects on hand performance capabilities: a literature review. *Ergonomics* 55:1429-1451, 2012.
- 397 **Flanagan JR, King S, Wolpert DM, Johansson RS.** Sensorimotor prediction and memory in object  
398 manipulation. *Canadian Journal of Experimental Psychology* 55:87-95, 2001.
- 399 **Johansson RS, Vallbo AB.** Tactile sensibility in the human hand: relative and absolute densities of  
400 four types of mechanoreceptive units in glabrous skin. *The Journal of Physiology* 286:283-300,  
401 1979.
- 402 **Johansson RS, Westling.** Roles of glabrous skin receptors and sensorimotor memory in automatic  
403 control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*  
404 56:550-564, 1984.
- 405 **Johansson RS, Westling G.** Signals in tactile afferents from the fingers eliciting adaptive motor  
406 responses during precision grip. *Experimental Brain Research* 66:141-154, 1987.
- 407 **Johansson RS, Westling G.** Coordinated isometric muscle commands adequately and erroneously  
408 programmed for the weight during lifting task with precision grip. *Experimental Brain Research*  
409 71:59-71, 1988.
- 410 **Johansson RS, Flanagan JR.** Coding and use of tactile signals from the fingertips in object  
411 manipulation tasks. *Nature Reviews Neuroscience* 10:345-359, 2009.

412 **Johansson RS, Hger C, Backstrom L.** Somatosensory control of precision grip during  
413 unpredictable pulling loads. III. Impairments during digital anesthesia. *Experimental Brain Research*  
414 89:204-213, 1992.

415 **Johnson KO, Phillips JR.** Tactile spatial resolution. I. Two-point discrimination, gap detection,  
416 grating resolution, and letter recognition. *Journal of Neurophysiology* 46:1177-1192, 1981.

417 **Kennedy WR, Selim MM, Brink TS, Hodges JS, Wendelschafer-Crabb G, Foster SX, Nolano**  
418 **M, Provitera V, Simone DA.** A new device to quantify tactile sensation in neuropathy. *Neurology*  
419 76:1642-1649, 2011.

420 **Kinoshita H.** Effect of gloves on prehensile forces during lifting and holding tasks. *Ergonomics*  
421 42:1372-1385, 1999.

422 **LaMotte RH, Whitehouse J.** Tactile detection of a dot on a smooth surface: peripheral neural  
423 events. *Journal of Neurophysiology* 56:1109-1128, 1986.

424 **Loh MN, Kirsch L, Rothwell JC, Lemon RN, Davare M.** Information about the weight of grasped  
425 objects from vision and internal models interacts within the primary motor cortex. *The Journal of*  
426 *Neuroscience* 30:6984-6990, 2010.

427 **Macefield VG, Hager-Ross C, Johansson RS.** Control of grip force during restraint of an object  
428 held between finger and thumb: responses of cutaneous afferents from the digits. *Experimental Brain*  
429 *Research* 108:155-171, 1996.

430 **Monzee J, Lamarre Y, Smith AM.** The effects of digital anesthesia on force control using a  
431 precision grip. *Journal of Neurophysiology* 89:672-683, 2003.

432 **Nowak DA and Hermsdorfer J.** Grip force behavior during object manipulation in neurological  
433 disorders: Toward an objective evaluation of manual performance deficits. *Movement Disorders* 20:  
434 11-25, 2004.

435 **Nowak DA, Rosenkranz K, Hermsdorfer J, Rothwell J.** Memory for fingertip forces: passive  
436 hand muscle vibration interferes with predictive grip force scaling *Exp Brain Res* 156:444-450, 2004.

437 **Nowak DA, Hermsdorfer J, Glasauer S, Philipp J, Meyer L, Mai N.** The effects of digital  
438 anaesthesia on predictive grip force adjustments during vertical movements of a grasped object. *The*  
439 *European Journal of Neuroscience* 14:756-762, 2001.

440 **Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory.  
441 *Neuropsychologia* 9:97-113, 1971.

442 **Phillips JR, Johnson KO.** Tactile spatial resolution. II. Neural representation of bars, edges, and  
443 gratings in monkey primary afferents. *Journal of Neurophysiology* 46:1192-1203, 1981.

444 **Rolke R, Baron R, Maier C, Tölle TR, Treede RD, Beyer A, Binder A, Birbaumer N, Birklein**  
445 **F, Bötefür IC, Braune S, Flor H, Hüge V, Klug R, Landwehrmeyer GB, Magerl W, Maihöfner**  
446 **C, Rolko C, Schaub C, Scherens A, Sprenger T, Valet M, Wasserka B.** Quantitative sensory  
447 testing in the German Research Network on Neuropathic Pain (DFNS): standardized protocol and  
448 reference values. *Pain* 123:231-243, 2006.

449 **Saal HP, Bensmaia SJ.** Touch is a team effort: interplay of submodalities in cutaneous sensibility.  
450 *Trends Neurosci* 37:689-97, 2014.

451 **Shih R, Vasarhelyi E, Dubrowski A, Carnahan H.** The effects of latex gloves on the kinetics of  
452 grasping. *International Journal of Industrial Ergonomics* 28:265-273, 2001.

453 **Tiffin J, Asher EJ.** The Purdue pegboard; norms and studies of reliability and validity. *The Journal*  
454 *of Applied Psychology* 32:234-247, 1948.

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

457 **Westling G, Johansson RS.** Factors influencing the force control during precision grip.  
458 *Experimental Brain Research* 53:277-284, 1984.

459 **Westling G, Johansson RS.** Responses in glabrous skin mechanoreceptors during precision grip in  
460 humans. *Experimental Brain Research* 66:128-140, 1987.

461 **Willms K, Wells R, Carnahan H.** Glove attributes and their contribution to force decrement and  
462 increased effort in power grip. *Human Factors* 51:797-812, 2009.

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