

1 FAST GRIP FORCE ADAPTATION TO FRICTION RELIES ON LOCALIZED
2 FINGERPAD STRAINS

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28 **ABSTRACT**

29 Humans can quickly adjust their grip force to a change in friction at the object-skin interface during
30 dexterous manipulation in a precision grip. To perform this adjustment, they rely on the feedback of
31 the mechanoreceptive afferents innervating the fingertip skin. Because these tactile afferents encode
32 information related to skin deformation, the nature of the feedback signaling a change in friction
33 must somehow originate from a difference in the way the skin deforms when manipulating objects of
34 different frictions. To better characterize the origin of the underlying sensory events, we asked
35 human participants to perform a grip-lifting task with a manipulandum equipped with an optical
36 imaging system. This system enabled to monitor fingertip skin strains through transparent plates of
37 glass that had different levels of friction. We observed that, following an unexpected change in
38 friction, participants adapted their grip force within 370ms after contact with the surface. By
39 comparing the deformation patterns when unexpectedly switching from a high to a low friction
40 condition, we found a significant increase in skin deformation inside the contact area arising over
41 100ms before the motor response, during the loading phase, suggesting that local and partial
42 deformation patterns prior to lift-off are used in the nervous system to adjust the grip force as a
43 function of the frictional condition.

44 **INTRODUCTION**

45 In a seminal paper in the 80s, Johansson and Westling described how efficiently human participants
46 handle objects of different textures and friction (Johansson and Westling, 1984). They observed that
47 when lifting objects, humans scaled their grip force (GF) to the frictional properties of the surface,
48 such that an object with a slippery surface was gripped more firmly than one with a sticky surface.
49 Moreover, it was found that a change in the frictional properties of the object from one trial to the
50 next elicited a GF adaptation that was observable only 100ms after contact with the surface. Such
51 adaptation was cancelled under local anesthesia, underlining the essential role of afferent feedback
52 (Westling and Johansson, 1987; Nowak et al., 2001; Augurelle et al., 2003; Witney et al., 2004). A
53 rapid feedback loop is thus able to take into account tactile afferent information about the surface
54 efficiently (Johansson and Flanagan, 2009; Delhayé et al., 2018).

55 However, the mechanisms underlying such a feedback loop remain unknown. Indeed, since the
56 surfaces used in the aforementioned paper (Johansson and Westling, 1984) had very different
57 textures, it is not clear whether the feedback provided by the afferents was related to the
58 topography of the material, thereby quickly eliciting the recall of a motor memory related to the
59 surface, or if the feedback was directly related to friction, such that the motor system could scale the
60 GF accordingly. Notably, it was later demonstrated that human are able to adapt to changes in
61 friction (Birznieks et al., 1998), even those that are not directly associated with a change in texture
62 (Cadoret and Smith, 1996). In this study, different textures and coatings were used to show that
63 humans adjust the level of GF to the coefficient of friction and not to the texture when lifting objects.
64 These results suggest that the skin deformation during each lifting movement can be used to scale
65 the grip force without necessarily requiring a full slip event.

66 The possibility that humans adjust their grip force quickly based on an estimate of friction is
67 supported by recent imaging studies of fingertip deformation during loading. We and others have
68 shown that localized partial slips take place at the object-finger interface during tangential loading
69 (Levesque, 2002; Tada et al., 2006; André et al., 2011; Delhayé et al., 2014). Partial slips are
70 associated with substantial skin deformation in the contact area (Delhayé et al., 2016) that trigger a
71 strong afferent responses (Delhayé et al., 2021a), and may therefore signal an impending slip.
72 Importantly, reducing friction accelerates the progress of partial slips and leads to an earlier

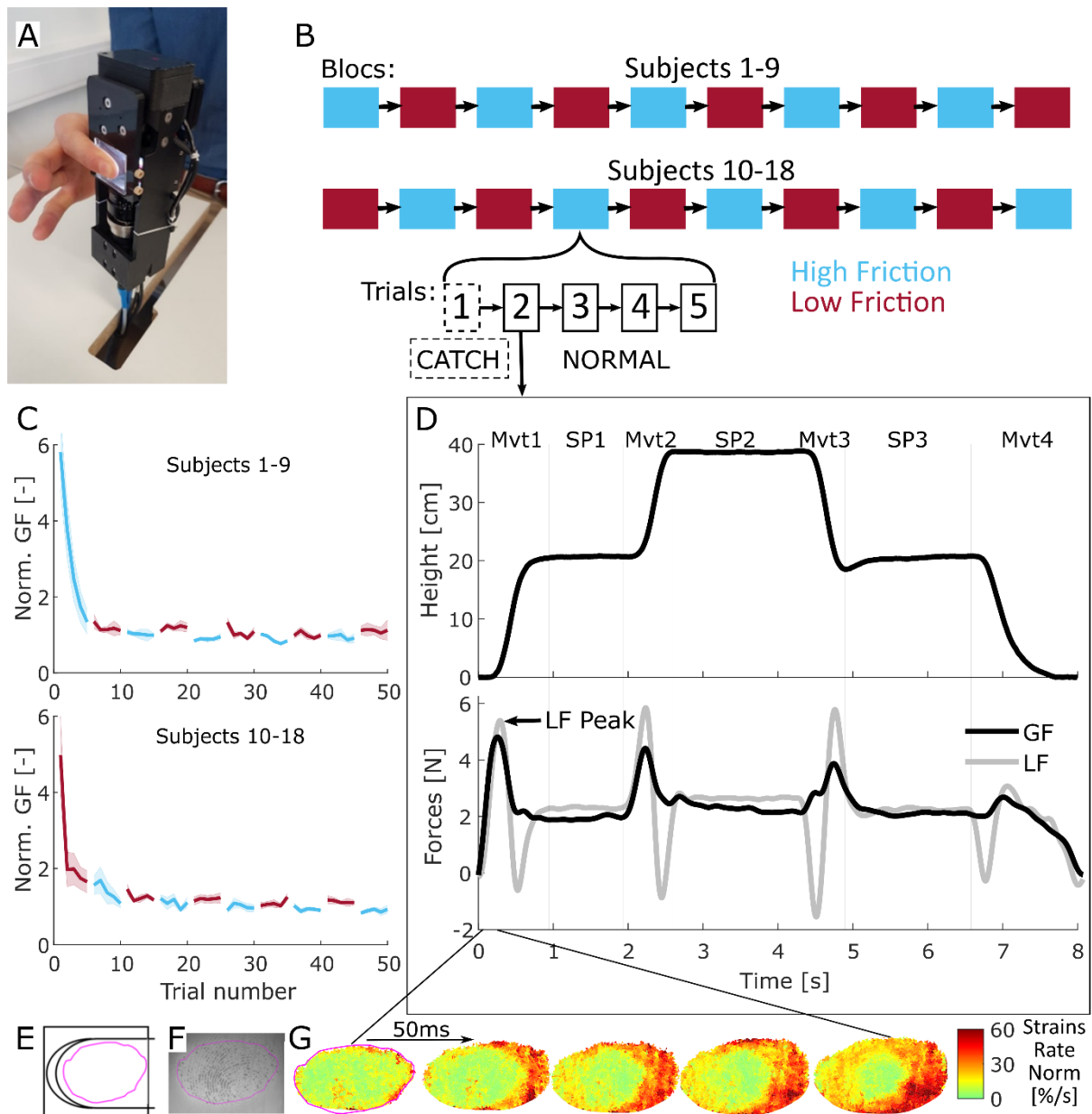
73 discharge of the tactile afferents, which can potentially inform the central nervous system about the
74 upcoming contact instability (Khamis et al., 2014; Delhaye et al., 2021a). Moreover, the perception of
75 tactile slip seems to be induced by skin deformations associated to partial slip, since it is perceived
76 before full slippage and is impeded when the amount of strains is diminished by applying a coating
77 that reduces friction (Barrea et al., 2018). Furthermore, generating artificial skin strains at the
78 contact interface with the object during lifting also lead to an increase in GF (Farajian et al., 2020).

79 Taken together, the aforementioned findings lead us to hypothesize that partial slip, or the
80 associated skin deformations, are a sufficient sensory signal to adjust the GF to the friction condition
81 during active manipulation. To test this hypothesis, we sought to describe and quantify where and
82 when skin deformation associated to partial slip take place following an unexpected change of
83 friction, and if those allow participants to adapt their GF to a change in friction that is not associated
84 with a change in texture. To this end, we asked human participants to repeatedly grip and lift a
85 manipulandum, while the friction was changed unbeknownst to the participant (Fig 1A-B). We found
86 that participants adjusted the GF to a change in friction only 114ms after liftoff (370ms after contact
87 was made with the surface), suggesting that most of the sensory information about the friction
88 change was available before the object started moving. To further understand the mechanisms
89 underlying such adjustments, we imaged, at the same time, the contact area between the index
90 finger and the object. We used those images to track the skin strains resulting from partial slip (Fig
91 1F-G), and reveal a localized strain contrast after friction changes very early in the trial, i.e. before
92 liftoff. Our findings thus support the hypothesis that humans make use of localized strain patterns to
93 adjust the GF to unexpected changes in friction.

94 RESULTS

95 Participants performed a series of grip and lift trials using a custom-made manipulandum held in a
96 precision grip (Fig 1A). Following an auditory cue, they were instructed to grip and lift the object
97 vertically to reach a target (movement, “Mvt1” in Fig 1D), and then hold it stationary for one second
98 (static phase, “SP1”). This task was followed by three point-to-point movements (Mvt2- 4, and SP2-3,
99 also paced by auditory cues, not analyzed here). After each experimental block consisting of five
100 trials, the participants were asked to sit on a chair with their back turned away to the experimental
101 set-up, and the experimenter quickly interchanged the surfaces without the participants noticing (Fig
102 1B). Two sets of glass plates having different levels of friction were used (see *Methods*). We defined
103 the first trial following a surface change as a “catch trial”, since it included an unexpected change in
104 friction, and the other four trials were called “normal trials”. The first two blocks were considered to
105 be “training blocks” as the participants’ GFs decreased significantly during those for all participants
106 and were thus excluded from the data analysis (Fig 1C).

107 The manipulandum was equipped with force sensors that allowed us to monitor the GF and the load
108 force (LF, acting vertically and due to the object weight and inertia). A typical point-to-point
109 movement was accompanied by two LF peaks, related to the acceleration and deceleration phases of
110 the movement (Fig 1D). Note that each upward LF peak was paired with a GF peak. We synchronized
111 all trials at the instant of the first LF peak. During the static phases, LF remained fairly constant (2.2N,
112 the object’s weight) as did GF.



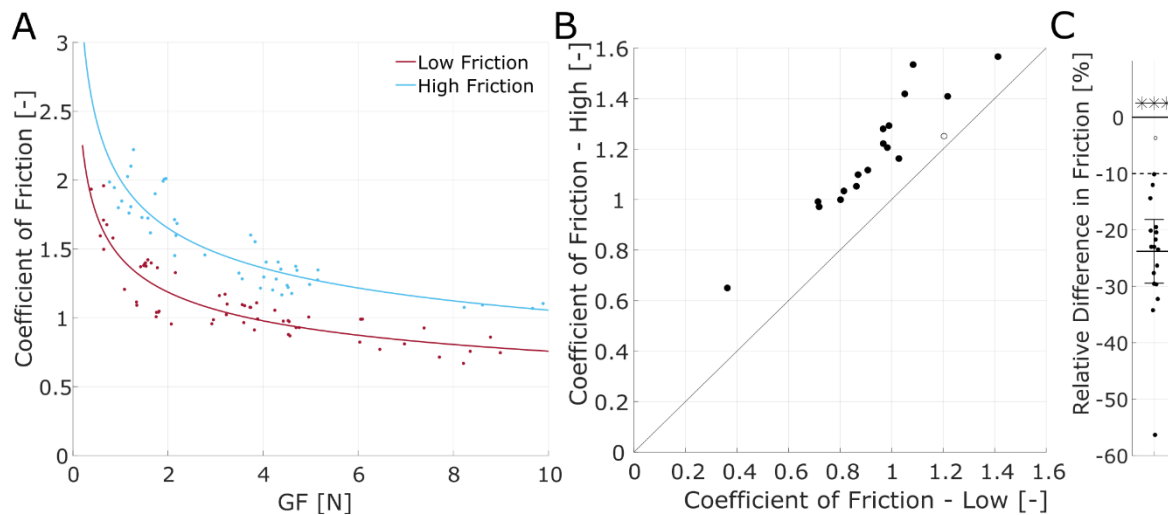
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114 **Figure 1: Experimental setup, experimental procedure, and typical trial.** **A** Participants held the manipulandum in a
 115 precision grip with both fingers applied on transparent glass plates. The device includes sensors allowing the measurement
 116 of the forces applied by both fingers as well as an imaging system allowing the recording of the index fingertip skin. **B**
 117 Participants performed ten blocks of five trials. Transparent plates with high and low friction properties were interchanged
 118 between each block. Half of the participants started with the high friction material. The first trial of each block is called
 119 "CATCH" trial, as opposed to "NORMAL" trials. **C** Group mean of the GF of the first SP for participants who started with the high friction material for the top graph and for participants who started with the low friction material for the bottom one. GF is normalized according to the procedure described in *Methods*. The shaded areas show the standard error of the mean.
 120
 121 **D** Evolution of the vertical position of the manipulandum and the forces applied during a typical trial. It consists of four
 122 fast movements (Mvt) with static phases (SP) in-between. Note that the second LF peak of each movement is due to the
 123 participant having to slow down the manipulandum because of the inertia of the system. The LF during the second static
 124 phase is slightly higher due to a larger portion of the cable being positioned under the device at this height. **E** Position of
 125 the index finger and area of contact with the glass. All strains in this study are displayed as if they were observed through
 126 the glass during the manipulation. The distal side is on the left. The pink curve delimits the contact area. **F** Typical image.
 127 Only the index finger was monitored. **G** Heat maps of the norm of the skin strain rates obtained from a pair of consecutive
 128 images, as described in (Delhaye et al. 2016). This sequence shows deformations during the first 200ms of a typical first
 129 movement (Mvt1 in panel C). Strains are observed at the periphery of the contact area. The central stuck zone remains
 130 undeformed.
 131

132 The index fingertip contact with the object's surface was monitored through the glass plates using a
133 high-speed, high-resolution camera (Fig 1E-F). Image processing techniques allowed us to track
134 fingerprint movements and evaluate surface skin strains during the lift movement (Fig 1G, (Delhaye
135 et al., 2014, 2016), see *Methods*). The rate of change of skin strains resulting from LF increase during
136 the lift of the manipulandum were observed at the periphery of the contact area (Fig 1G). In most
137 trials, the center of the fingertip remained stuck and non-deformed, except when full slip was
138 reached (87 times out of 633, or equivalently 14% of trials). The contact area was an approximately
139 ellipsoidal shape and increased over time following a logarithmic increase consistent with previous
140 observations (André et al., 2011). On average, the contact area reached 85% of its maximum value
141 200ms after the time of contact and had usually reached its maximum value 340ms after initial
142 contact (value reached: $94.4 \pm 5\%$ of the maximum value, $\text{mean} \pm \text{std}$). This time corresponded to an
143 average of 30ms prior to liftoff.

144 *Consistent difference in friction between smooth transparent materials*

145 First, we verified that the two materials showed a consistent difference in their coefficient of friction.
146 To that end, the friction between the fingertips, index and thumb, and the two sets of plates was
147 measured at the end of the experiment to reduce potential cues about the different materials that
148 could have been used during the manipulation task. Note that all participants except three reported
149 that they did not notice that different materials were used. Following ((Barrea et al., 2016), see
150 *Methods*), we characterized the coefficient of friction over a range of GFs relevant to our experiment
151 (see Fig 2). The data were obtained for both fingers of all participants (and are reported in Supp Fig 1
152 for the index and Supp Fig 2 for the thumb) and fit with a negative power law. We observed that the
153 coefficient of friction of the low friction glass remained lower than the one of the high friction glass
154 across all levels of normal force tested, as shown in Fig 2A for a typical participant. From the fits
155 obtained for each participant, we summarized the coefficient of friction by a single value, being the
156 average coefficient of friction over the range of 1 to 5N (which spans the levels of GF used in this
157 study, see e. g. Fig 1D), and across fingers. Overall, the friction was always higher in the case of the
158 high friction material and the average relative difference was larger than 20% (paired t-test,
159 $t(17)=10.0696$, $p<0.001$) (Fig 2B-C). Given that we aimed to observe behavioral adaption to changes
160 in friction, we required a sufficient difference between materials and set a lower bound to a relative
161 difference of 10%. Accordingly, one participant was removed from all subsequent analyses because
162 the relative friction difference was too low (only 2%, less than the 10% required, see the unfilled dot
163 in Fig 2B-C, participant S1 from Supp Fig 1-2). In summary, then, the two flat and transparent
164 materials used in this study showed a consistent difference in friction, on average 23% across
165 participants.

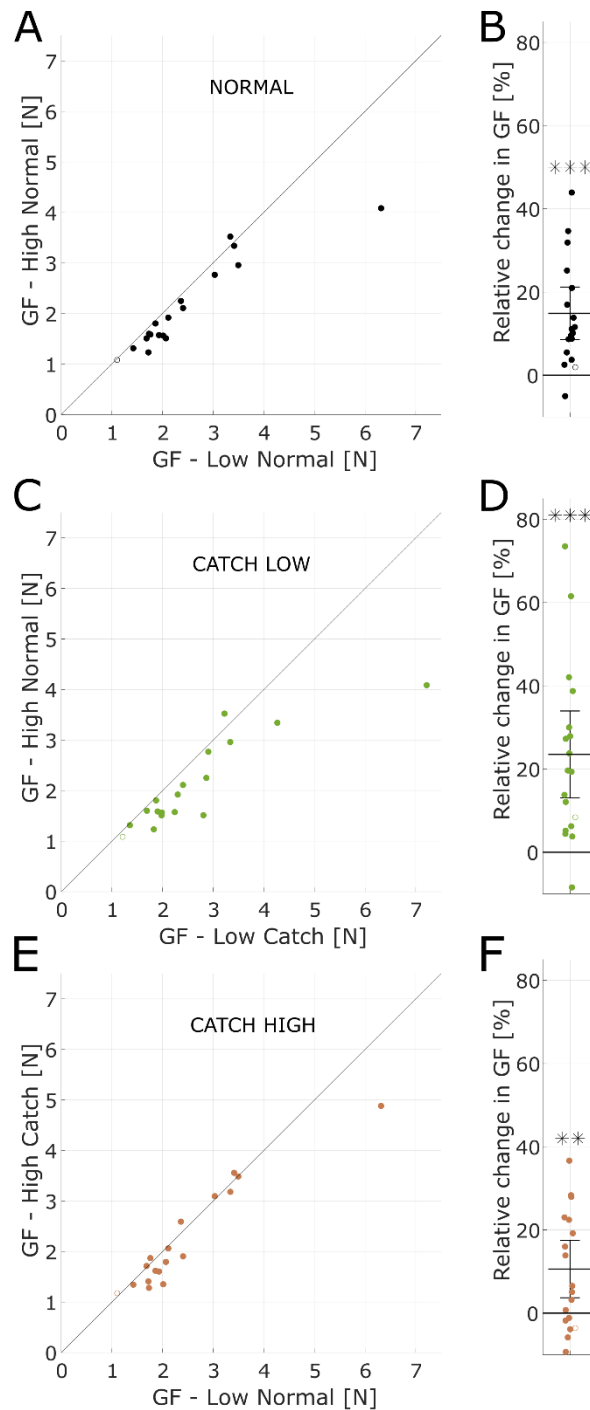


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167 **Figure 2: Consistent difference of friction.** **A** | Coefficient of friction of the index finger as a function of grip force for a
168 typical participant obtained using the method described in (Barrea et al. 2016). **B** | Mean coefficient of friction of both
169 materials over the observed manipulation range (1-5N) for each participant (n=18). **C** | Difference in friction of the materials
170 over the manipulation interval (1-5N), relative to the mean of the values of the coefficient of friction of both materials. The
171 brackets show the 95% confidence interval of the mean. The dashed line indicates the level of sufficient difference in
172 friction between materials for a participant to be included in the study. In panels B | and C |, one point corresponds to one
173 individual participant and the data were averaged across both fingers and the empty circle shows the participant that was
174 removed from the following analysis because of a difference of friction smaller than 10%.

175 *The grip force is adjusted to friction*

176 Next, we sought to assess whether the different materials elicited different gripping behavior. First,
177 we tested if participants could adapt to the difference in friction by using a consistently higher GF for
178 the lower friction during the normal trials, i.e. those not following an unexpected change in friction.
179 We found that indeed, most of the participants used a higher level of GF for the lower friction as
180 averaged over the three static phases (Fig 3A), even though the level of GF varied widely across
181 participants. Overall, the relative difference was statistically significant and close to 15 % (Fig 3B,
182 mean $14.87 \pm 12.7\%$, paired t-test, $t(16)=4.8224$, $p < 0.001$). Thus, participants spontaneously adjusted
183 the GF level to the friction condition. Moreover, the relative GF difference was of the same order of
184 magnitude as the relative friction difference. We observed that the participant that was removed
185 from the analysis because of a lack of difference in friction showed no significant difference in
186 behavior across the friction conditions (diff=2%, as measured by the average level of GF during the
187 static phases of normal trials).



188

189 **Figure 3: GF adaptation to friction during the static phases.** **A** | Mean value of the GF for each material during the static
190 phases of normal trials for all participants (n=18). **B** | Change in the mean value of the GF from the high to low friction
191 material during the static phases of normal trials, relative to the mean value of the GF in both friction conditions. The
192 brackets show the 95% confidence interval of the mean. **C, D** | Same as A, B |, except the static phases of the high friction
193 normal trials are compared to the first static phase of the low friction catch trials, which directly follow. The bar delimited
194 with hashed lines indicates the catch trials. **E, F** | Same as C, D |, except the static phases of the low friction normal trials are
195 compared to the first static phases of the high friction catch trials, which directly follow. For D | and F |, the percentage of
196 change is relative to the mean of the values of normal and catch trials. The participant that is removed from the study due
197 to a low difference of friction is shown with an empty circle and is not included in the means and confidence intervals
198 shown.

199 *Catch trials show GF adjustments within the first movement*

200 Having observed that there was indeed a GF adaptation to friction for normal trials, we then tested if
201 a change in friction elicited a quick adjustment of the GF, as observed in the first static phase of the
202 catch trials. To that end, we compared the static GF after the first movement (SP1, Fig 1D) of the
203 catch trials to the static GF experienced and learned during the normal trials of the preceding block
204 of trials associated with the material with different frictional properties. The catch trials could be of
205 two types: (1) low friction catch trials, following an adapted exposure to high friction, were referred
206 to as “catch-low”, and (2) high friction catch trials, following an adapted exposure to low friction,
207 were referred to as “catch-high”.

208 For the “catch-low” trials, which required an urgent increase in GF because the drop of friction
209 increased the risk of slip and drop of the object, we found that the GF was already higher during the
210 first static phase (Fig 3C-D, paired t-test, $t(16)=4.5486, p<0.001$). The adaptation was close to 20%,
211 thus already of the same magnitude as the adaptation learned throughout many trials (Fig 3B). Then,
212 we looked at the “catch-high” trials, for which the urgency was lower since the experienced surface
213 friction increased and therefore the risk of slippage was lower than for the directly preceding trials.
214 We also found that the GF changed after only one movement, although the relative difference of GF
215 was about 10% on average, thus not as large as for the catch trials in the other direction. Although
216 this difference was not observed for all participants, it was statistically significant (Fig 3E-F, paired t-
217 test, $t(16)=3.1527, p<0.01$).

218 In brief, participants adapted the GF to the friction condition, and this adaptation was already
219 present at the end of the first movement following a catch trials, and for both directions of the
220 changes in friction.

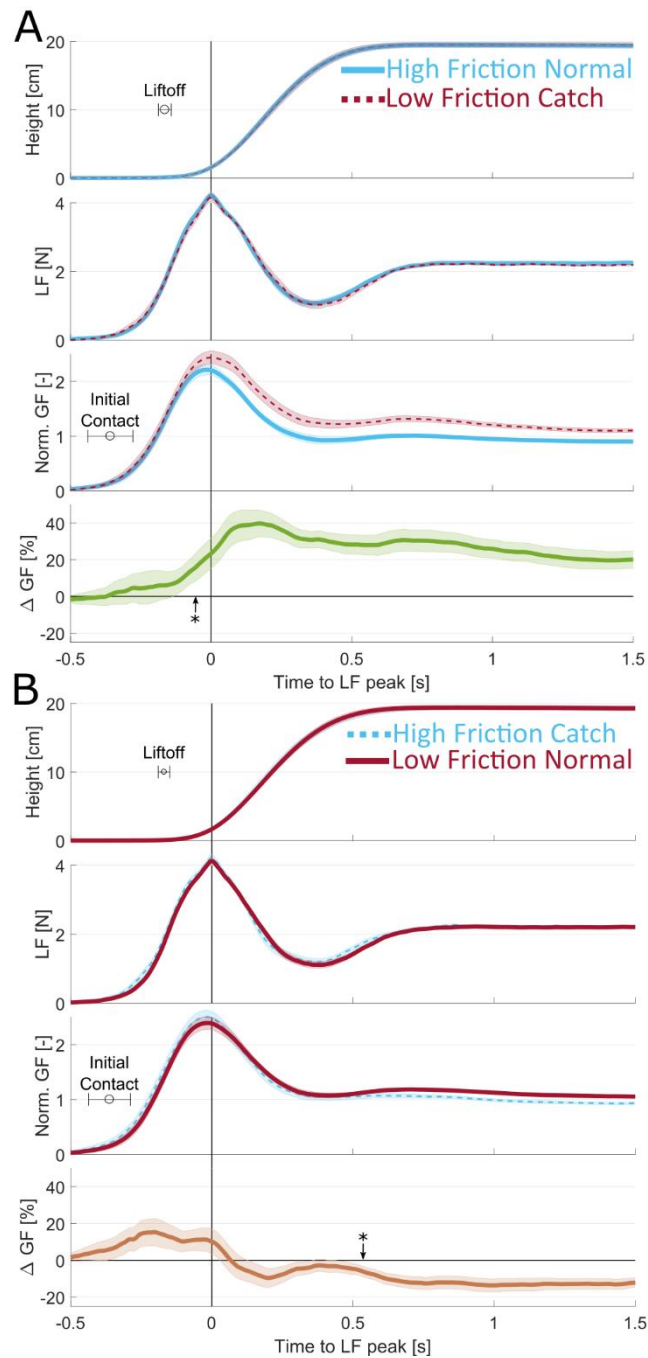
221 *Grip force adjustments start close to the time of liftoff of catch trials*

222 Since we observed that the GF was already adjusted to the friction level after the first movement of
223 catch trials, we investigated the temporal evolution of the GF during these catch trials to determine
224 when the changes in GF evoked by the change in frictional properties arise (Figure 4). The
225 participants produced movements with very similar kinematics across conditions, as shown by the
226 height and LF curves, which could not be distinguished across conditions (Fig 4, top two rows of
227 panels A and B). We observed that GF curves of the catch trials progressively diverged from those of
228 the normal trials (Fig 4A-B, third row). In these graphs, the GF were normalized according to their
229 average values during the first static phase for each subject (values reported in Supp Fig 3).

230 For the “catch-low” trials (Fig 4A), we found that the GF difference reached statistical significance
231 very early, just after liftoff (114 ± 23 ms delay), or 50ms before the peak of LF (Fig 4A, bottom row).
232 This timing corresponded to 308 ± 80 ms after initial contact. This difference was substantial, as it
233 peaked on average at 40% with respect to GF during the first static phases of the normal trials.

234 For the “catch-high” trials (Fig 4B), the difference in GF reaches statistical significance later in the
235 movement (540 ms after the peak of LF, 709 ± 20 ms after liftoff, and about 902 ± 74 ms after initial
236 contact) and is relatively smaller at the end of the first movement, as seen previously (Fig 3). Note
237 that participants tended to apply a slightly higher level of GF at the very beginning of the contact of
238 catch trials no matter the sign of the friction change, which might be explained by the short break
239 between blocks. This systemic increase of the GF at the start of new blocks regardless of the actual
240 friction condition suggests that participants were not able to anticipate the friction for the catch
241 trials.

242 In summary, we showed that GF reaches a level that is significantly different from the level of the
243 normal trials during the first lift following a change in friction, around the time of liftoff for the
244 “catch-low” and a bit more than half a second later for the “catch-high” trials.



245

246 **Figure 4: Adaptation to friction during the first movement of catch trials** A| Evolution of object height, LF, GF and GF
247 difference as a function of time for the first movement of catch-down trials for all participants (n=17). Trials are
248 synchronized to the LF peak. Lines are averages across participants and shaded areas are the standard error of the mean. 0s
249 indicates the time of the maximum of Load Force. Blue is for high friction and red is for low friction. Thick continuous traces
250 are normal trials and dashed lines are catch trials. GF normalization values are reported in Supp Fig 3. The star shows the
251 time of the statistically significant difference between GF curves ($p < 0.05$). The lower panel shows catch minus normal trials.
252 B| Same as A for the catch-down trials.

253

254 *Subtle contrast in skin strain rate before liftoff are cues for GF adjustments*

255 Looking at the Δ GF traces (Figure 4A-B, bottom rows), we can observe an upward inflection for
256 “catch-low” trials, and a downward inflection for “catch-high” trials, happening around the LF peak
257 and suggesting that the corrective behavior kicks in around that time. To probe the timing of the
258 reaction of the participants to the change in friction, we thus looked at the rate of change in GF (see
259 Fig 5A).

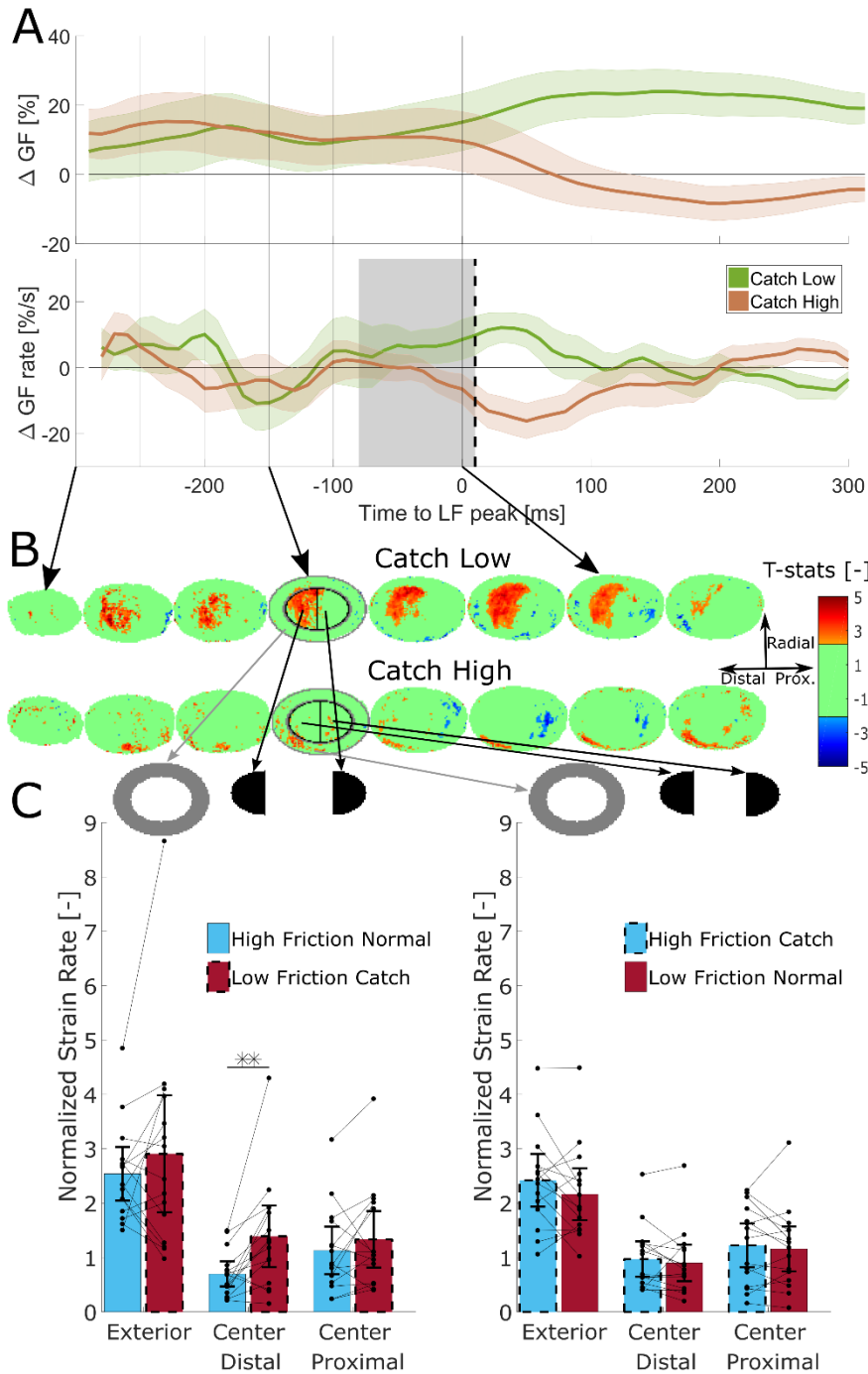
260 In Fig 5A, we first show the catch-low and catch-high Δ GF traces zoomed in a 600ms time window
261 centered on the LF peak, which appeared to be the instant of inflection of the curves. The time
262 derivatives of those curves are also shown below in Fig 5A. Note that in this figure, in contrast to Fig
263 4, we excluded the data from two participants having consistently poor image quality and we also
264 only included the trials in which the images reached high-quality standards (84% of trials among the
265 remaining participants, see *Methods* for more details). As observed in Fig 5A, the two Δ GF traces
266 followed very similar trends just after contact and started to diverge around the LF peak. We found
267 that the Δ GF rates start to diverge significantly 10ms after the time of peak LF (or 370 ± 76 ms after
268 initial contact or 176 ± 21 ms after liftoff), suggesting that online corrections to friction arise around
269 this moment. Note that this is also approximately the time when the Δ GF rates become statistically
270 significantly positive, or negative, for the “catch-low” trials, or the “catch-high” trials, both 20ms
271 after the LF peak.

272 The different responses of participants to catch-low and catch-high trials suggest that a sensory
273 signal informative about the frictional properties of the material originated prior to this time. We
274 further needed to take conduction delays into account, which for tactile-motor responses are close
275 to 90ms on average. Accordingly, we drew a grey box that encompasses the 90ms before the instant
276 of significant difference to indicate the minimal interval of time needed for the sensory feedback to
277 reach the central nervous system and trigger a motor response (Pruszynski and Johansson, 2014;
278 Pruszynski et al., 2016; Crevecoeur et al., 2017). Thus, to trigger a motor reaction observable just
279 after the LF peak, a sensory signal must be readily observed before the beginning of this grey box (i.e.
280 80ms before LF peak).

281 Accordingly, we evaluated the skin strain associated to partial slip during a period encompassing
282 300ms before the LF peak until 100ms after (see Supp Fig 4). In the same manner as for the GF, we
283 report here the contrast between the catch and the normal trial, looking for a difference that might
284 have triggered a corrective behavior. In Fig 5B, we report the differences in strain rate norm between
285 the different conditions (catch-low, top row and catch-high bottom row), as expressed in the form of
286 a t-value, obtained from paired t-tests performed for each pixel over the whole fingertip contact area
287 (see *Methods*). Red zones show the parts of the fingertip where strain rates were significantly higher
288 for the catch trials, i.e. where a significant excess of strain rate was observed, whereas blue zones
289 show parts of the contact having a significantly lower strain rate for catch trials. Green zones depict
290 insignificant differences ($t(14) < 2.145$, $\alpha = 0.05$). Strains were first normalized according to their
291 average value at the time of peak LF (see *methods* for more details and Supp Fig 3 for normalization
292 values). This normalization procedure was performed because subjects showed markedly different
293 average levels of strains.

294 For “catch-low” trials shown in the top row of Fig 5B, a zone of excess strain rate norm in the distal
295 part of the center of the fingertip starts appearing 250ms before the maximum of LF and is
296 consistently observed until the LF peaks. This excess disappears progressively when participants start
297 to adapt their GF to the level of friction and when the general level of strain rate becomes small.
298 Conversely, some smaller zones in the periphery show lower levels of strain rates. Thus, surprising
299 the participant with a material with a friction lower than for the previous trials generates a

300 consistently higher level of strain rates deeper inside the contact areas while leaving the periphery
 301 less strained at some places. This striking observation is valid over the span of several hundred
 302 milliseconds and can thus be taken into account by participants when adjusting their GF.



303

304 **Figure 5: Differences in skin strains preceding the force adaptation** **A** | Mean difference of GF and mean difference of GF
 305 rate between catch and normal trials. Only participants for whom the images were of sufficient quality are included (n=15).
 306 0ms indicates the time of the maximum of Load Force. Shaded areas are the standard error of the mean. The vertical
 307 dashed line indicates the time when the differences of Grip Force rates are statistically significantly different from each
 308 other (10ms). The grey zone indicates the time during which tactile information was too close to the motor reaction to
 309 contribute to detecting the friction condition. **B** | Heat maps of the t-statistics of the differences in strains between catch
 310 and normal trials. The t-statistic is set to zero when the difference is not statistically significant and the corresponding p-
 311 value is smaller than 0.05. The red color indicates more strains in the case of the catch trial and the blue color more
 312 deformations in the case of the normal trial. The first line compares normal high friction trials to catch-low friction trials and
 313 the second line compares catch-high friction trials and normal low friction trials. **C** | Average value of the strain rate norm at

314 -150ms normalized w.r.t. the value at the peak of LF, in the different zones of the fingertip indicated in Fig 5B. The brackets
315 show the 95% confidence interval of the mean. The bars delimited with hashed lines indicate the catch trials. One point
316 corresponds to one individual participant.

317 For the “catch-high” trials shown in the bottom row of Fig 5B, we do not observe any large zone of
318 difference in strain rate norm. Some patches in the more central part tend to show lower levels of
319 strains rate norm. The sensory signal is less contrasted in the case of “catch-high” trials suggesting
320 that the GF decrease might be an automatic slow decrease following a light GF excess applied
321 because of a new block. A typical “catch-high” and “catch-low” trials are provided in the
322 supplementary video. These show that the strain rate reaches higher level deeper in the surface of
323 contact in the case of “catch-low” trials.

324 The findings are quantified in fig 5C where we arbitrarily defined different zones in the fingerpad,
325 using two ellipses with the smaller one having radii 2/3 as large as the larger one, and quantified the
326 average level of strain rates for each participant at 150ms before the peak of LF and thus
327 approximately 160ms before the first signs of adaptation to the new friction condition. For the
328 exterior part of the ellipse, although the level of strain rate is the highest, there is no statistically
329 significant difference between the two conditions (paired t-test, $\text{diff}=-0.36\pm 1.4$, $t(14)=-1.02$,
330 $p=0.3257$). For the central proximal half part of the ellipse, the level of deformation is lower and
331 there is still no statistically significant difference of level of strains between the two conditions
332 (paired t-test, $\text{diff}=-0.2\pm 0.66$, $t(14)=-1.12$, $p=0.251$). It is only for the central distal half part of the
333 ellipse that we observed that the amount of strain rate norm was almost twice as high for the low
334 friction catch trials as for the normal high friction trials. This difference is large, consistent among
335 participants and statistically significant (paired t-test, $\text{diff}=-0.69\pm 0.8$, $t(14)=-3.37$, $p=0.0046$). We
336 performed the same analysis for the catch-high trials, but observed no statistically significant
337 differences, as can be seen in the right panel of Fig 5C (Exterior ellipse, paired t-test, $\text{diff}=0.26\pm 0.62$,
338 $t(14)=1.59$, $p=0.1343$. Interior proximal, paired t-test, $\text{diff}=0.065\pm 0.4$, $t(14)=0.6$, $p=0.5609$. Interior
339 distal, paired t-test, $\text{diff}=0.0705\pm 0.35$, $t(14)=0.78$, $p=0.4497$).

340 As the observed deformation contrasts take place before the grey zone defined earlier, they can
341 contribute to the information used by the participants to adapt their GF to the condition of friction.

342 In summary, we observed the onset of a motor response resulting from the friction change
343 approximately at the moment of the LF peak and this online GF correction was consistent with a
344 sensory signal resulting from an increase in the deformations closer to the central parts for the
345 contact area happening over 100ms before the motor response. This subtle but essential sensory
346 signal, therefore, explains GF adaptation to changes in friction.

347 DISCUSSION

348 This is, to our knowledge, the first study that quantifies how fast humans can adjust their GF to a
349 change in friction in the case of flat transparent surfaces. We demonstrate that this adjustment can
350 be based on a local strain pattern that takes place in the contact area with the manipulated object
351 and signals an insecure grip. Specifically, we show that when confronted with lower friction than
352 expected, skin strains advance deeper and faster in the contact area. The differences in skin strains
353 with respect to a normal trial are already significant very early after the initial increase of the load
354 force, and more than 100ms before the motor response, which is a reasonable delay to explain it
355 (Macefield and Johansson, 2003; Crevecoeur et al., 2017). These differences are present over a
356 period of time of several hundred of milliseconds and can thus constitute a warning signal that allows
357 the central nervous system to adjust the GF to the friction condition.

358 We observed that the levels of skin strains varied greatly from participant to participant, as can be
359 seen by the strain rates normalization values in Supp Fig 3. We have shown similar levels of variation
360 of skin strains in a previous study where participants had to perform oscillations in a precision grip
361 (Delhaye et al., 2021b). We can also observe in that study that a larger amount of skin strains is
362 linked to a lower stick ratio and that the stick ratio also varied greatly between participants. The stick
363 ratio was also measured in a study where participants had to perform a grip-lifting task (Tada et al.,
364 2002). The authors hypothesized that humans control the level of GF to maintain a constant amount
365 of partial slip (~40% of the contact area) when lifting objects of known friction and weight, but they
366 mentioned in their paper that the validness of this hypothesis has to be verified, as only three
367 participants were tested. It is worth noting that humans perceive slippage at very different levels of
368 partial slip in a passive setting (Barrea et al., 2018). The variability in the levels of strains and stick
369 ratio during manipulation and the variability in partial slip between participants seem to point
370 towards strategies of manipulation that vary from person to person. This requires further inquiring,
371 by performing experiments with tasks of different nature, with varying friction and weight of the
372 manipulated object. A characteristic of our results is the asymmetry of the participants' behavior
373 between "catch-high" and "catch-low" trials (Fig 4). Although the motor reaction seemed to be
374 triggered at the same time in both conditions (Fig 5A), it took more time to reach a level of GF that
375 was adapted to friction in the catch-high condition. It is worth noting that a short reaction time in the
376 catch-low condition is critical: it is urgent to increase GF since not correcting it could lead to a
377 dramatic slip and drop of the object. In contrast, the excessive GF in the catch-high trials only results
378 in a temporary slight excess of energy expenditure, which does not require to act quickly. The
379 difference in urgency to adapt GF between conditions is observed in the differences of strains (Fig 5
380 B-C), where a surprisingly low level of friction caused significant differences in strains whereas a
381 surprisingly high level of friction did not.

382 Although we characterized the friction between the fingers and the manipulated object by a constant
383 scalar value per participant-condition pair (Fig 2B-C), this is clearly a gross approximation of a very
384 complex phenomenon. The tribology of the skin is complex and varies significantly at different
385 temporal and spatial scales (Pataky et al., 2005; Adams et al., 2013; Van Kuilenburg et al., 2015). One
386 aspect of this complexity is related to the complex geometry and mechanics of the finger: the
387 fingertips are composed of several layers, from the bone in the interior of the fingertip to the
388 epidermis in the exterior. The epidermis of the glabrous skin is characterized by the presence of
389 ridges and furrows that form the fingerprints and present a complex topography (Choi et al., 2021).
390 This complex geometry and mechanics is likely to impact the friction on a trial to trial basis,
391 depending on how the finger contacts the object. Another aspect of the complex tribology of the skin
392 is that it evolves over time: Sweat pores are present at the surface of the skin and produces humidity
393 at the interface that heavily impacts the level of friction when gripping a material, which changes
394 over the course of several seconds (André et al., 2010; Yum et al., 2020). The occlusion phenomenon
395 defines humidity evolution and plasticization of the skin when in close contact with the material for a
396 few seconds (Adams et al., 2013). The level of friction thus varies during a single trial as moisture
397 varies due to occlusion. In our experiment, the moisture level is however probably partially
398 maintained when trials are close enough from one another. Thus, in the context of this study, the
399 differences in friction measured between materials, which could vary widely between participants,
400 are to be considered as approximations of their actual values, which can vary during manipulation.
401 However, it is clear that the difference in friction between materials was consistent and sufficient to
402 generate coherent adaptation of GF during the overall experiment.

403 Several of our senses are used when performing a task as difficult as fine object manipulation. Our
404 sense of touch in particular is very important. It sends critical information to the central nervous

405 system to adjust GFs to various parameters of the manipulation such as friction. We have shown that
406 when gripping and lifting small objects, the skin strains depended on the level of friction at the
407 interface of the contact. The localized differences in skin strains between conditions during the
408 loading phase were consistent with the timing of the first signs of adaptation of the GF and were
409 sufficient to explain them. We have quantified and described those skin strains and measured the GF
410 modulation, which started less than 500ms after the initial contact.

411 METHODS

412 *Participants*

413 Eighteen volunteers (5 females; ages 20-65) participated in the experiment. All of them provided
414 written informed consent to the procedures and the study was approved by the ethics committee at
415 the host institution (UCLouvain, Brussels, Belgium).

416 *Apparatus*

417 At rest, the device was standing on a table with a hole to allow the passage of the cables coming
418 from the bottom of the device. Its weight (540g) was partially compensated by a counterweight
419 (320g) attached to a system of pulleys. The device is described at length in a recent
420 publication (Delhaye et al., 2021b). Succinctly, forces were measured under each fingertip using two
421 six-axis force and torque sensors (ATI Mini27 Ti, ATI-IA, Apex, NC, USA). From those measurements,
422 the GF and LF were computed, as described in *Data Analysis*. The position was measured using an
423 optical distance sensor (DT20-P224B, SICK Sensor Intelligence). The position and forces were sampled
424 at 200 Hertz with a NI-DAQ card (NI6225, National Instruments).

425 A custom optical system allowed to image the index fingerprints in contact with the glass (Fig 1F).
426 Because of constraints in the design of the manipulandum, it was only possible to monitor one side,
427 as the light is emitted by an array from the side where the thumb is, blocking its observation. This
428 system is based on the principle of Frustrated Total Internal Reflection and enables a high contrast
429 between the point in contact with the glass and those that are not. Images are recorded at 100 fps
430 with a camera (GO-5000M-PMCL, JAI, monochrome, 2560 x 2048 full pixel resolution). Image size is
431 1696 x 1248 pixels with a resolution of 4096 pixels/mm², which corresponds to an area of 26.5 x
432 19.5mm.

433 Two kinds of glass plates were used to generate different levels of friction. The first set of plates are
434 simple transparent optically flat plates of glass. They are referred to as “high friction”. A process
435 called “glass frosting” was used to alter friction in the second set of plates. In brief, a chemical
436 process was used to imprint a nanoscale pattern on the surface of the glass. With the right set of
437 parameters (height and roughness), this decreased the real area of contact between the finger and
438 the plate and thus the coefficient of friction (Derler et al., 2009; Skedung et al., 2010, 2011; Adams et
439 al., 2013; Wiertelowski et al., 2016; Inamoto and Tomeno, 2019). This nano-structured glass was
440 referred to as the “low-friction” surface. The transparent plates are indistinguishable to the naked
441 eye.

442 *Experimental procedures*

443 Participants stood in front of a table on which the device was positioned. After an auditory cue, they
444 were instructed to grip and lift the device to a height of about 20cm within 0.8s, and then hold it still
445 for 1.5s. They then performed three fast point-to-point movements (0.8s) with pauses (1.5s) in-
446 between. Auditory cues were used to pace each movement. We observed that participants’
447 movements were slightly slower than what was instructed, resulting in slightly longer movements
448 and shorter static phases. The participants were requested (and often reminded during the

449 experiment) to use a minimal amount of GF. Indeed, we observed in a preliminary study that
450 participants tended to use an excessive amount of GF naturally, probably because this device
451 composed of a camera and sensors seems fragile and looks heavy. The glass plates were cleaned with
452 alcohol after each trial. This served the purpose of getting images as clean as possible. Also, this
453 procedure removed sweat that could alter the topography of the glass plates at a microscopic level
454 and thus the level of friction. After each block of five trials, participants were instructed to take a
455 break on the other side of the room, from a location where they could not see the experimenter
456 manipulating the device. During that break, the experimenter interchanged the plates such that the
457 friction was changed from high to low or from low to high. This procedure was quick and took a
458 maximum of 2 minutes. Half of the participants started with the high friction condition and the other
459 half with the low friction. This caused no difference in their adaptation to friction, as measured by
460 the difference in GF between conditions during the first static phase of normal trials (t-test,
461 $t(15)=0.36, p=0.72$). The coefficient of friction was measured for each material at the end of the
462 experiment (see *Friction Measurement*). In total, the experiment lasted between one and a half and
463 two hours for each participant.

464 Friction measurements. We measured the coefficient of friction between the participants' fingers
465 and both materials at the end of the experiment using the method described in (Barrea et al., 2016).
466 Briefly, participants were instructed to rub their index finger and thumb on the glass plates for three
467 periods of fifteen seconds at different levels of normal forces. The approximate range of normal
468 forces for each period was 0 to 2.5N for the first, 2.5 to 6N for the second, and 6 to 10N for the third.
469 The moment of slippage was detected by finding the maximum of the ratio of tangential force over
470 normal force at the start of each rubbing motion. This ratio was measured and was our estimation
471 for the static coefficient of friction corresponding to the normal force applied at that moment. The
472 data were obtained for both fingers of all participants (see Supp Fig 1-2) and fit with a negative
473 power law (André et al., 2009). From the fits, we computed a single coefficient of friction value for
474 each participant and each material for the 1-5N range that corresponded to the approximate range
475 that the participants used for manipulation. The friction was averaged across both fingers. The
476 measurement of the friction was always performed first on the material with which the participant
477 finished the experiment.

478 *Data analysis*

479 Forces and position data were filtered with a fourth-order low-pass Butterworth filter with a cut-off
480 frequency of 40Hz. The GF is defined as the mean of the norm of the forces normal to the surface of
481 the object exerted by each finger. The LF is defined as the norm of the sum of the forces applied
482 tangentially to both surfaces by each finger. When comparing dynamics or kinematics between
483 participants as in Fig 3, 4 and 5, an average curve was first computed for each participant by first
484 synchronizing all trials on the maximum of LF for each separate movement. Then, statistics such as
485 the inter-subject mean or standard error of the mean were computed based on these average
486 curves.

487 GF normalization. As participants typically used different levels of GF, a normalization procedure was
488 used when comparing the GF signals across conditions and participants. A GF normalization value
489 was obtained for each participant by taking the mean of GF during the first static phases of all normal
490 trials (except the first two blocks that were excluded because of the learning period). They are shown
491 in Supp Fig 3.

492 Image processing. A previously described image processing pipeline was used to evaluate the skin
493 strains from the raw images (see Delhayé et al, 2014, 2016). This pipeline is only summarized here.
494 First, a custom-made machine learning algorithm was used to detect the area of contact between the

495 finger and the glass plate for each image. This algorithm was trained for each participant separately
496 with manually detected areas of contact for randomly selected images. Then, feature points were
497 selected automatically from several frames of the sequences of images (at the beginning, during, and
498 at the end of each movement). Their position was tracked forward and backward in time from frame
499 to frame using an algorithm of optical flow (Lucas and Kanade, 1981; Shi and Tomasi, 1994). A
500 Delaunay triangulation was then computed and the evolution of the shape of the triangles allowed to
501 measure the local strain rate along three dimensions (vertical, horizontal, and shear strain rate). The
502 norm of the strain rate was calculated as follows:

$$503 \quad \varepsilon_n = \left\| \begin{matrix} \varepsilon_{xx} & \varepsilon_{xy} \\ \varepsilon_{xy} & \varepsilon_{yy} \end{matrix} \right\| = \sqrt{\varepsilon_{xx}^2 + \varepsilon_{yy}^2 + 2\varepsilon_{xy}^2} \quad (1)$$

504 where ε_{xx} , ε_{yy} and ε_{xy} are the horizontal, vertical, and shear strains rates components respectively.
505 This gave a quantitative measure of how the different parts of the fingertips were being deformed,
506 irrespective of the type and directions of these deformations. In this study, we were mostly
507 interested in comparing the amount of strain rate according to the condition of friction and the
508 adaptation of GF rather than the specific description of these deformations (Delhay et al., 2021b).

509 As different participants showed markedly different levels of strains, we normalized the strain rate
510 norm of each participant by the mean value of the strain rate norm across the entire area of contact
511 and trials at the time of maximum LF. The normalization values of the strain rate norm are given
512 together with the normalization value of the GF for each participant in Supp Fig 3.

513 The first images of the contact were difficult to interpret. Indeed, the fingertip skin can be rough and
514 stiff on a small scale, depending on the moisture content of the individual's skin. When it enters in
515 contact with a stiff surface such as glass, the initial real area of contact is low. However, during the
516 first tens of milliseconds of the contact, moisture secreted by the sweat pores hydrates the skin,
517 rendering it softer and elasticizing it. The skin then enters in closer contact with the surface and the
518 real area of contact increases (Pasumarty et al., 2011; Bochereau et al., 2017; Dzidek et al., 2017). As
519 a rapidly changing real contact area not associated with skin deformations was problematic for the
520 interpretation of the results of our image-processing pipeline, we decided to discard the images
521 directly following the time of contact between the skin and the surface from our analysis. We used
522 the first image of the loading phase, defined as the moment when a participant starts applying
523 tangential force to lift the object after the pre-loading phase (Westling and Johansson, 1984) as the
524 first image in our image processing pipeline. This guaranteed that the apparition of moisture would
525 only play a negligible role in our measurement of strains and that the strains caused by the vertical
526 lifting of the object would be included in our analysis.

527 Strain rate summary across participants. To get a summary of strain rates across trials and
528 participants, we first had to project the values from the triangulation used to compute the strains to
529 a standardized structured grid common for all participants. To that end, we first created a reference
530 ellipse with a major to minor axes radii ratio of 3/2. A gridded mesh of size 91x61 was attached to
531 this reference ellipse. Then a least-square procedure was used to fit ellipses on the coordinates of
532 the fingerprint contact area contour for all individual images (Fitzgibbon et al., 1999). Finally, we
533 computed the projection (offset, scaling, and rotation) from the ellipse obtained from the image at
534 the instant of the LF peak to the reference ellipse for each trial and movement. This projection,
535 obtained for each trial and movement, was applied to the center of each triangle for all images to
536 obtain strains on the reference ellipse. The maximum of LF was chosen to compute the projection
537 because this timestamp is used to synchronize the trials. At that instant, the area of contact between
538 the finger and the glass has already plateaued. After having applied this projection, the strain rate
539 norm was averaged for each participant and each condition (i.e. catch/normal and low/high friction).

540 An example of such data for a typical participant is presented in Supp Fig 4. Subsequent statistics on
541 strains across participants were performed on the projected data.

542 Inspection and sorting of trials. As mentioned in *Results*, the first two blocks were considered to be
543 “training blocks” as the participants’ GFs decreased significantly during those for all participants and
544 were thus excluded from the data analysis (Fig 1C). The third block was the first included in our
545 analysis because it was the first for which (1) the grip forces were on average smaller than in the next
546 one in the high friction condition and (2) the grip forces were larger than in the next one in the low
547 friction condition. For some trials, participants placed their index finger outside of the field of the
548 camera or displaced it outside of the field during the trial due to slipping or rolling. Some trials were
549 therefore not included in the analysis. Only the parts of the trials where the finger got out of the field
550 of the camera were removed. After a close inspection of each trial, 99 out of 720 were at least partly
551 removed because the images were unusable during some part of the trial. Those trials were still used
552 for the kinematics and dynamics analysis of Fig 2-4. Also, 15 participants were used for the image and
553 forces analyses of Fig 5 because two participants had very dry skin and the image quality was
554 insufficient to obtain reliable strain data.

555 Full slip trials. To get a different look at our data, we counted the proportion of trials for which a full
556 slip occurred during the first movement, which yielded the following results: a full slip occurred in
557 11.33% of the high friction normal trials, 12.75% of the low friction normal trials, 11.77% of high
558 friction catch trials, and 31.03% of low friction catch trials. A full slip is said to occur when all the
559 feature points whose positions are tracked from frame to frame are measured as moving with
560 respect to the glass. This result is consistent with the differences in strain that are shown in Fig 5 B
561 and C. That is, in some cases, the strain wave reached the central point of the contact. Note that
562 even if full slip occurred for some trials, the extent of slippage was small and was quickly stopped by
563 a corrective GF (slipping distance of the central part of the contact area of 0.19 ± 0.25 mm, mean \pm std,
564 for trials in which the full slip was reached). The full slip trials were included in the strain analysis like
565 all other trials.

566

567 *Statistical analysis*

568 All statistical analyses were performed with MATLAB, using the functions *corr* (for Pearson
569 correlation), *ttest* (for paired t-tests), and *tinu* (inverse of Student's T cumulative distribution
570 function). The test performed, the number of degrees of freedom, and the T-statistics are always
571 mentioned with the p-value. The 95% confidence interval of the means were computed using one
572 mean value per participant and using the following formula:

$$573 \quad CI = \bar{X} \pm Z \frac{s}{\sqrt{n}}$$

574 where CI is the confidence interval, \bar{X} is the average across participants, Z is the inverse of Student's
575 T cumulative distribution function (e.g. $Z=2.12$ for 17 participants), s is the standard deviation and n
576 is the number of participants.

577

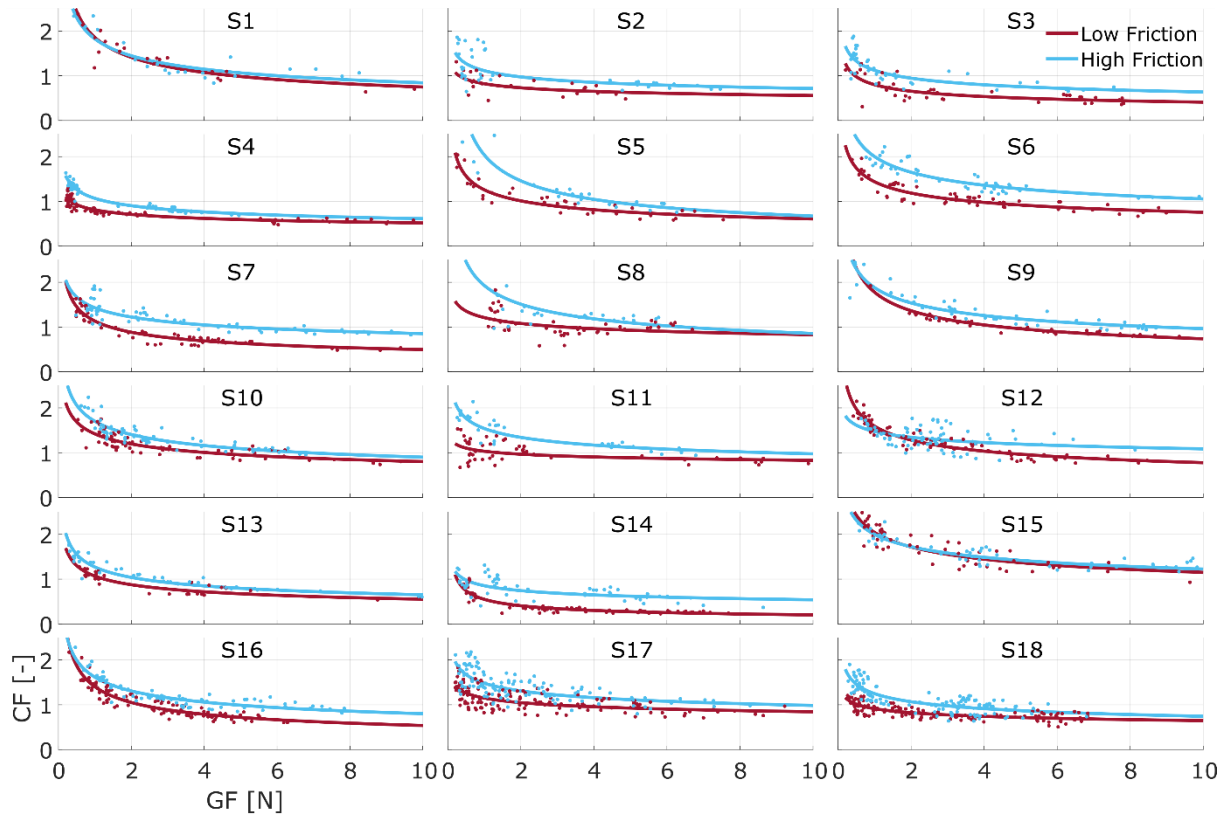
578

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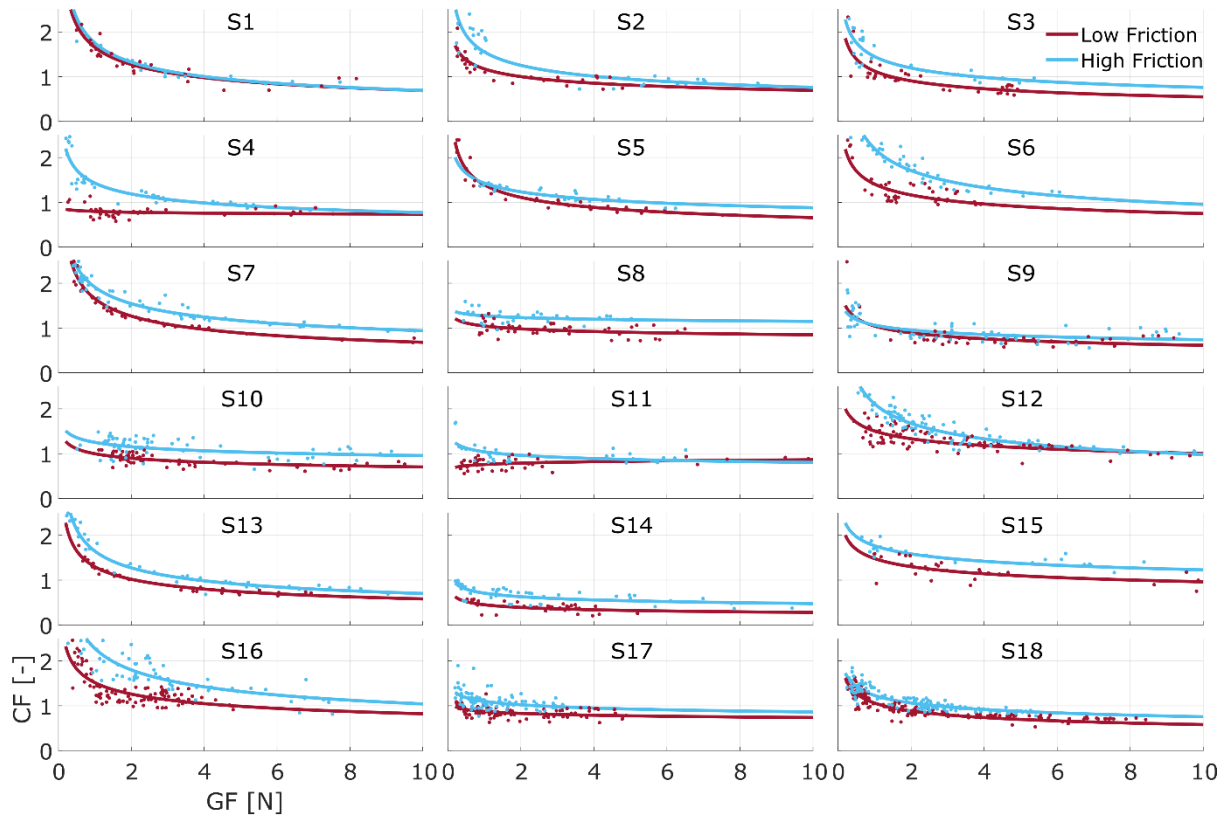
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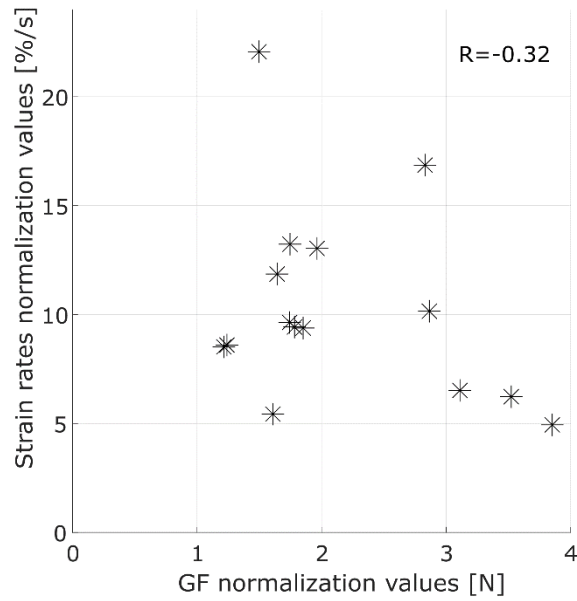
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Supp. Figure 1: Coefficient of friction of the index finger for all participants



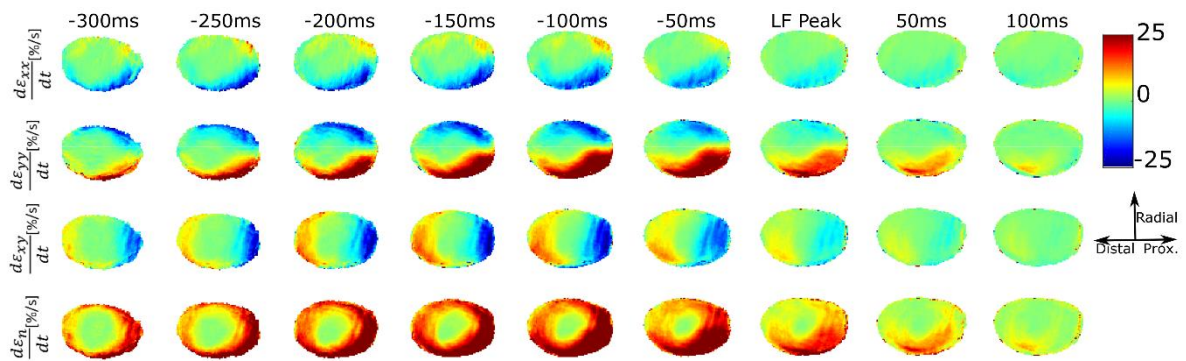
Supp. Figure 2: Coefficient of friction of the thumb for all participants



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690 Supp. Figure 3: Normalization values for the GF and strains

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693 Supp. Figure 4: Averaged strain rate data on the standard grid during the first movement for a typical participant.

694 Compression is shown in red and dilation in blue. The first row shows the horizontal strain rate, the second shows the

695 vertical strain rate, the third shows the shear strain rate and the fourth shows the strain rate norm. The average was

696 computed over all normal high friction trials (n=15) for a typical participant.