

HUMANS USE A LOCAL CODE FOR TACTILE PERCEPTION

Arindam Bhattacharjee^{1,2}, Christoph Braun^{3,4,5} and Cornelius Schwarz^{1,2}

- 1 Werner Reichardt Center for Integrative Neuroscience, Systems Neuroscience
- 2 Hertie Institute for Clinical Brain Research, Dept. Cognitive Neurology
- 3 MEG Center
Eberhard Karls University, Tübingen, Germany
- 4 Department of Psychology and Cognitive Science
- 5 Center for Mind/Brain Sciences
University of Trento, Italy

Running title: Local coding in tactile perception

With 29 text pages and 4 figures

Character counts (with blanks): Title 46, Total 37.823

Word counts: Abstract 237

Correspondence: cornelius.schwarz@uni-tuebingen.de (C. Schwarz)

Classification: Biological Sciences, Neuroscience, Psychological and Cognitive Sciences

Keywords: human, fingertip, psychophysics, tactile system, tactile coding

1 **Abstract**

2 Humans are classically thought to use either spectral decomposition or averaging to identify
3 vibrotactile signals. These are general purpose 'global' codes that require integration of the
4 signal over long stretches of time. Natural vibrotactile signals, however, likely contain short
5 signature events that can be detected and used for inference of textures, instantaneously,
6 with minimal integration, suggesting a hitherto ignored 'local code'. Here, by employing
7 pulsatile stimuli and a change detection psychophysical task, we studied whether humans
8 make use of local cues. We compared three local cues based on instantaneous skin position
9 and its derivatives, as well as six global cues, calculated as summed powers (with
10 exponents 1,2, and 3) of velocity and acceleration. Deliberate manipulation of pulse width
11 and amplitude (local+global) as well as pulse frequency (global) allowed us to disentangle
12 local from global codes. The results singled out maximum velocity, an instantaneous code,
13 as a likely and dominant coding variable that humans rely on to perform the task. Comparing
14 stimuli containing versus lacking local cues, demonstrated that performances exclusively
15 using global cues are rather poor compared to situations where local ones are available as
16 well. Our results are in line with the notion that humans not only do use local cues but that
17 local cues may even play a dominant role in perception. Our results parallel previous results
18 in rodents, pointing to the possibility that quite similar coding strategies evolved in whisker
19 and finger tactile systems.

20 **Significance statement**

21 The brain is believed to select coding symbols in sensory signals that would most efficiently
22 convey functionally relevant information about the world. For instance, the visual system is
23 widely believed to use spatially local features, like edge orientation, to delineate a visual
24 scene. For the tactile system only global, general purpose coding schemes have been
25 discussed so far. Based on the insight that moving contacts, characteristic for active touch,
26 feature short-lived stick-slip events, frictional movements that transfer fair amounts of texture
27 information, one should expect the brain to use a temporally local code, extracting and
28 instantaneously analyzing short snippets of skin movement. Here, we provide the first
29 analytical psychophysical evidence in humans that this indeed is the case.

30 **Introduction**

31 A sensory signal can transmit information about the world using either local or global
32 variables. A classical dispute in vision research was between one view that early vision
33 essentially is a set of global linear filters (Campbell and Maffei, 1974) and an opposing view
34 that interpreted neurons as local feature detectors (Barlow, 1972; Hubel and Wiesel, 1968).
35 In research on the tactile sense, local coding was rarely considered – at least for pure
36 temporal coding of texture (roughness). Global coding schemes like spectral decomposition
37 and finding the ‘best frequency’, as well as signal averaging to come up with ‘intensity’,
38 dominated the thinking in tactile research of finger/hand related perception (LaMotte and
39 Mountcastle, 1975; Luna et al., 2005; Yoshioka et al., 2001). However, insight from tribology
40 and recent research in whisker-based sensation and perception raised the possibility that
41 vibrotactile signals contain local features (i.e. short-lasting events) that can be extracted and
42 these features contain large amounts of texture information (Schwarz, 2016) (Fig. 1A). In the
43 whisker system, evidence supporting local codes come firstly from biomechanical studies
44 describing prominent stick-slip movements (Oladazimi et al., 2018; Ritt et al., 2008; Wolfe et
45 al., 2008), secondly from neuronal coding on the ascending tactile pathway, revealing that
46 neuronal spikes respond to local features in the tactile stimulus (Chagas et al., 2013; Jones
47 et al., 2004; Maravall et al., 2007; Petersen et al., 2008), and finally from perceptual studies
48 showing that pulsatile whisker deflections, devoid of local cues, are poorly discriminated
49 (Gerdjikov et al., 2018, 2010; Waiblinger et al., 2015a, 2015b). Evidence pointing to this
50 direction are also available in the fingertip system. Papillary ridges have been shown to
51 undergo complex shear during lateral movement (Delhaye et al., 2016), the sensory
52 consequences of which may reach perception (Barrea et al., 2018). Further, characteristics
53 of vibrotactile signals as well as skin deformation when tapping support the possibility that
54 tactile signals are processed and perceived instantaneously (Johansson and Birznieks,
55 2004; Lawrence et al., 2000; Pruszynski and Johansson, 2014; Weber et al., 2013).

56

57 Here we used psychophysics based on pulsatile fingertip skin indentation to demonstrate for
58 the first time, that humans use local codes. The experimental idea was that the change of
59 single pulses' waveform without changing pulse frequency is a manipulation of local and
60 global variables, whereas manipulation of pulse frequency without waveform changes is a
61 manipulation of global variables (Waiblinger et al., 2015a) alone. Our results strongly
62 indicate that humans do use a local code and may even use it as the dominant code in
63 addition to the classic global ones.

64 **Results**

65 We established a Yes/No change detection task. In each trial two 500 ms long pulse trains,
66 concatenated in a seamless way, were presented as vertical indentations to the left index
67 fingertip of participants (Fig. 1BC). After experiencing a single presentation of such stimuli,
68 participants indicated whether they perceived (Yes/No) a stimulus change in the middle of
69 the stimulus presentation (Fig. 1C; black stimulus [4th from top]: correct response – No; all
70 other exemplary stimuli: correct response - Yes).

71 *Experiment 1*

72 Our first aim was to elucidate systematic performance deficits with deliberate manipulation of
73 pulse width and amplitude (as shown in the four upper stimuli of Fig. 1C). In this experiment
74 the pulse frequency of all the trials was kept constant at 90 Hz, and thus, did not provide any
75 cue of stimulus change. In principle, the local changes to pulse waveforms can bring about
76 changes in the global intensity variable as well. The amount of these possible changes,
77 however, depends very much on how intensity is defined. In the literature a variety of
78 intensity definitions have been used, such as linear integration ('mean speed'), or non-linear
79 integration ('power') of different kinematic derivatives (position, velocity, acceleration). In
80 fact, an accepted standard measure of intensity does not exist. Therefore, instead of using
81 one fixed intensity definition, we decided to use an array of them. Since in principle there are
82 infinite ways of defining intensity – we opted for an array of definitions that firstly vary the
83 code's characteristics in a systematic way across the stimulus space; presumably, one of
84 the coding definitions would capture specific performance deficits in stimulus space related
85 to the sought-after unknown coding variable. Secondly, we incorporated a non-linear
86 element (taking the signal to the power of >1 before summation) in the definition of intensity
87 that systematically varies the emphasis of local features within the vibrotactile signal. This
88 was done to address the possibility that local coding could be realized by a mathematical

89 integration with non-linear preprocessing as well (as opposed to the truly local,
90 instantaneous feature extraction that we portrayed above).

91 Intensity was thus defined as the sum (or equivalently as the mean) of the first and second
92 stimulus derivative (i.e. velocity and acceleration) taken to the powers 1, 2, or 3. This choice
93 satisfied the spread in stimulus space. Keeping each of those intensities constant (under the
94 assumption that only pulse amplitude and width are varied), yielded an array of so-called
95 'iso-lines' fanning out from the origin (no change) into relevant sections of the space
96 spanning possible stimulus changes (tagged 'stimulus space' for short throughout this
97 report; Fig 1D). To illustrate the stimulus space, the extreme stimulus changes (in the
98 corners of the stimulus space) are marked with a star and the respective waveforms can be
99 looked up in panel C. Thick lines represent iso-lines that keep one of the local variables
100 constant (maximal pulse position, velocity, and acceleration, colored black, gray and pink,
101 respectively) while thin lines represent iso-lines of global variables (shades of green:
102 velocity-based; shades of blue: acceleration-based). It is important to note that two of the
103 local iso-lines overlapped with global ones ('maximum position' with 'mean speed', and
104 'maximum velocity' with 'mean absolute acceleration'). (These overlaps required extra
105 experiments to disentangle them – cf. experiment 2 below).

106 Moreover, our array of (global) intensities was designed to cover as well different degrees of
107 emphasis on local features. To visualize what that means we demonstrate an arbitrary signal
108 containing a shallow local feature in the upper left corner of figure 1E. The signal is
109 differentiated along rows, and is taken to increasing powers along columns. From this
110 demonstration one can easily appreciate that low derivative / low power signals (e.g.
111 $speed = |velocity|^1$) de-emphasize local features, whereas high derivative / high power
112 signals increasingly emphasize them (e.g. $absolute\ cubic\ acceleration = |acceleration|^3$).

113 Armed with this analytic stimulus design, we set out to measure psychophysical
114 performance of 10 participants on stimulus changes located on the iso-lines depicted in

115 figure 1D. The reference stimulus is located at the origin of the coordinate system spanning
116 changes in pulse amplitude and width (pulses of 40 μm amplitude and 5882 μs width). The
117 comparison stimulus (seamlessly concatenated to the reference stimulus) was picked in
118 each session from a different iso-line (15 equidistant pulse widths between 4167 (easy) and
119 5882 μm (difficult)). Each session comprised 840 trials with 50% no change stimuli
120 (comparison = reference = 5882 μm) and 50% change stimuli (comparison \neq reference, i.e.
121 30 trials per 14 pulse widths). We refrained from testing global variables based on stimulus
122 'position' because the iso-lines for position-based intensities are located in a part of the
123 stimulus space where human ability of detection of change was superb whenever a stimulus
124 differed ever so slightly from the reference (in the second quadrant, where amplitude
125 increased and width decreased, Fig. 1D). This stimulus area, thus, provided little
126 experimental leverage to gain insights into the tactile codes used (the respective preliminary
127 experiments are not shown).

128 The typical performance of a single participant is shown in figure 2A. It can be seen that the
129 participant shows a remarkably well isolated deficiency centered on the iso-line of maximum
130 velocity (gray). This observation generally held true in all ten participants. Comparing effect
131 sizes of the thresholds obtained from all ten participants on the maximum velocity iso-line
132 compared to all other iso-lines showed that the poorest performance was located around the
133 iso-line of maximum velocity (AUC comparing to 7 iso-lines in the order listed in Fig. 1D:
134 [0.98, 0.82, 0.53, 0.5, 0.83, 0.91, 0.90]; corresponding p values in t-tests were [0.015, 0.044,
135 0.624, ~, 0.357, 0.049, 0.055]; $n=[10,9,9,\sim,9, 10, 10]$). The best fit logistic functions to the
136 pooled data from ten participants and the respective thresholds are shown in Figure 2BC. It
137 is worth mentioning that in general the psychophysical test was subjectively described as
138 'demanding' by all participants. In fact one person failed on the task (producing no
139 psychometric fit passing $p=0.5$ in any of the sessions) and was excluded from all the
140 analyses. Two other persons dropped out after a few sessions without giving reasons for
141 their decision. Reflecting the challenging nature of the task we observed a consistently high

142 false alarm rate of [0.12, 0.18, 0.16, 0.14, 0.09, 0.04, 0.07] on the 7 iso-lines as listed in
143 figure 1D.

144 *Experiment 2*

145 So far an unambiguous conclusion about the role of local vs. global variables in mediating
146 the poor performance close to the maximum velocity iso-line cannot be reached because the
147 ‘maximum velocity’ iso-line was congruent with that of the global variable ‘mean absolute
148 acceleration’. To disentangle local from global variables, here we implemented the
149 procedure of experiment 1 with an additional manipulation of pulse frequency (pf ; cf. the
150 bottom two stimuli in Fig. 1C). Pure changes of pulse frequency (4th stimulus from the top in
151 Fig. 1C) do not affect instantaneous variables, because the pulse waveform is identical.
152 They do however change the iso-lines of all global variables, which shift downward toward
153 larger decrements in pulse amplitude to balance out the presence of additional pulses. The
154 shift introduced by a change in pulse frequency $\Delta pf = 15 \text{ Hz}$ is demonstrated by the move
155 from the blue [$\Delta pf = 0$] to red [$\Delta pf = 15 \text{ Hz}$] curves in Fig. 3A. The thick gray line is the
156 ‘maximum velocity’ iso-line, which does not move when the Δpf cue is added.

157 Pulse frequency is a cue in itself - independent from the abovementioned instantaneous
158 kinematics (local) and intensity (global). In fact, as mentioned above, frequency is the
159 second candidate variable, next to intensity, for global coding. Therefore, pulse frequency
160 would be expected to change the detection rate by itself; however, this effect should be the
161 same for all iso-lines. Our choice of $\Delta pf = 15 \text{ Hz}$ (reference value 90 Hz, comparison value
162 105 Hz) balances a low perceptual effect (mean increment of the probability to report a
163 ‘change’ 0.15, SD 0.08; as measured in experiment 3) with a large-enough shift of the iso-
164 line to capture eventual differences in performance. Figure 3B demonstrates the
165 performance of the same participant as shown in figure 2A on stimuli from the three iso-lines
166 depicted in Fig. 3A. The effect of pure global stimuli (frequency and intensity) is reflected in
167 the difference between the blue and gray line. It shows a non-significant mean change in the

168 threshold from 1101 μs (SD 194 μs) ($\Delta pf = 0$) to 1272 μs (SD 270 μs) ($t=-2.084$, $n=8$,
169 $p=0.08$; $\text{AUC}=0.13$). However, the performance on the shifted iso-line of ‘ Δpf + mean
170 absolute acceleration’ (red) is significantly improved to a mean change of threshold of 764
171 μs (SD=368 μs , $t=2.868$, $n=8$, $p=0.024$; $\text{AUC}=0.99$). Figure 3C shows the logistic fits for the
172 pooled performance from all 9 participants. In summary, we found that poor performance
173 was pegged to the local ‘maximum velocity’ iso-line, and did not move together with the
174 global ‘mean absolute acceleration’ iso-line.

175 *Experiment 3*

176 The participants in experiment 2 were in addition tested on pulse trains that exclusively
177 changed in Δpf (cf. the gray stimulus in the schematic of Fig. 1C; only data from 8 of 9
178 persons are reported here as from the 9th we did not get any logistic fit that crossed a
179 probability of correct responses of 0.5). Figure 4A presents the logistic fit to the pooled trials
180 of this population. The success of 8 out of 9 participants to detect pulse frequency changes
181 demonstrates that humans in principle are able to use global variables as a basis for their
182 decision. The drop out of one participant and the subjective difficulties observed in others,
183 however, raised the question, how well the successful participants were able to use them,
184 and how their performance compared to situations in which they had additional access to
185 local cues. To this end we scaled the performance on experiment 3 (Δpf cue and respective
186 intensity cues, thick red lines in figure 4B) and those obtained in experiment 1 (intensity cues
187 and local cues, colored lines in figure 4B) to each of the 6 variants of intensity (one variable
188 per sub-panel). In the vast majority of these direct comparisons the performance measured
189 in experiment 1 was shifted to the left and showed far lower thresholds of respective
190 intensive variables as compared to the Δpf stimuli used in experiment 3. That is, generally,
191 the performance when only global cues were present was rather poor compared to the
192 performance with access to the same intensity variable and additional local ones. While this
193 held true for all almost all intensity variables, it was also clear that the definitions using
194 higher derivative and powers seem to fare better in this comparison. In the plot of ‘mean

195 cubic absolute acceleration' (dark blue), two of the curves obtained in experiment 1 showed
196 even slightly higher thresholds than the ones obtained in experiment 3. This is summarized
197 in figure 4C, which plots the relative thresholds obtained in experiment 3 (red stars) and
198 experiment 1 (dots colored with respect to the global variable, same colors as in panel B) on
199 one and the same scale (note that abscissa scales in the sub-panels of Fig. 4B differ as they
200 are individually normalized to the highest value obtained in experiment 3). In summary,
201 relative thresholds yielded by different intensity variables are all similar, a fact that shows
202 that none of these variables stands out in its importance for perception. Moreover, the
203 perceptual effects of intensity variables, particularly the definitions based on lower
204 derivatives and power, are far inferior compared to local cues, as experiment 3 (changes in
205 intensity and pulse frequency) typically resulted in far higher thresholds than those obtained
206 in experiment 1 (changes in intensity and instantaneous kinematics). This was so, despite
207 the fact that participants might have additionally exploited pulse frequency cues from stimuli
208 in experiment 3, which were not present in experiment 1. Finally, it can be appreciated that
209 intensity definitions that are based on the higher kinematic derivative (i.e. acceleration) and
210 higher power (i.e. power of 3) achieved thresholds that are on par with local variables. This
211 chimes well with the fact that these higher order definitions of intensity are increasingly
212 dominated by local features (demonstrated in Fig. 1E). We interpret this match as indicating
213 that our array of intensity definitions exhausts the range of possible formulations that truly
214 represent global features.

215 **Discussion**

216 In this study, we present novel psychophysical evidence that humans use local
217 instantaneous codes in addition to the classical integrative global codes for tactile
218 discrimination. Using manipulations of pulsatile skin-indentation stimuli, we found that taking
219 ‘maximum velocity’ out of the pool of available cues led to poor performance on a Yes/No
220 psychophysical change detection task. Finally, performance on pulse frequency changes
221 (engaging exclusively global coding mechanisms), was found to be significantly inferior
222 when comparing them to performance on sets of stimuli that contained the same changes in
223 global parameters but in addition allowed access to local ones. This last finding speaks in
224 favor of the notion that humans not only use local codes, but that they may even rely on
225 them as the dominant source of information feeding tactile perceptual decisions.

226 *Is it appropriate to use pulsatile stimuli to disentangle local from global coding?*

227 Classically, sinewave stimuli have been used to disentangle ‘intensity’ (sine amplitude) from
228 ‘frequency’ (sine frequency) (LaMotte and Mountcastle, 1975). This approach, however, only
229 allowed addressing global codes because changes in sine amplitude and/or frequency
230 would always concomitantly change the instantaneous signal value, i.e. local coding
231 variables. Thus, for the quest to find out whether local vs global codes are used, the usage
232 of simple sinusoidal stimuli is prohibitive. In order to investigate local features, stimuli need
233 to be manipulated locally in the time domain (Waiblinger et al., 2015a, 2015b). Pulsatile
234 stimuli are an attractive tool for this purpose as they are midway between sinusoids and
235 broad band stimuli featuring spectra that contain a perceptually important peak of power at
236 the base frequency (i.e. the pulse frequency) and allow for simple and systematic changes
237 of individual (local) pulses. Moreover, by introducing, eliminating, or shifting pulses around in
238 time one can easily introduce changes in global cues (frequency, intensity) while keeping
239 local ones (pulse waveform) identical (Gerdjikov et al., 2018). However, there are two major
240 problems with this strategy. Firstly, the success in isolating local changes hinges on the

241 definition of the global code. Certain changes of pulse waveforms may change one global
242 variable but not another. Part of the problem is that in the literature, intensity codes have
243 never been standardized – for instance many studies used signal power (squared sum, e.g.
244 Hipp et al., 2006), others used a simple sum of the absolute signal (e.g. Arabzadeh et al.,
245 2003), etc. We addressed this problem by testing not only one possible intensity code but
246 defining a whole array of them. The iso-lines of our selection of intensity variables cover a
247 large part of the stimulus space (Fig. 1D). Additionally, our strategy to calculate intensity
248 based on different powers of the signal helps to formulate global codes that do or do not
249 emphasize local features (low vs. high derivatives/powers) (Fig. 1E). In fact, our intensity
250 variable that most strongly emphasizes local features, ‘mean cubic absolute acceleration’,
251 yields performance estimates that begin to match the ones obtained with true
252 (instantaneous) local codes (Fig. 4BC), indicating that our sample of intensity codes entirely
253 covers the space spanned between (true) local coding, global coding with emphasis on local
254 features, and (true) global coding without that emphasis. This seems important because (in
255 principle) infinite other definitions of intensity are possible, which, however, are likely to be
256 close to one of our present definitions in terms of iso-line location and bias toward reporting
257 local features.

258 The second issue with pulsatile stimuli is their spectral composition. Any modification of
259 pulse waveform (as done in experiment 1) will keep the signal’s base frequency but will
260 introduce wide ranging spectral changes at higher harmonics. It follows that what we call
261 ‘local coding’ in the time domain relates to differences of spectral patterns at higher
262 harmonics, and therefore is ‘global’ in the frequency domain. From these consideration two
263 aspects are noteworthy: First, our terms ‘local’ and ‘global’ strictly pertain to the time domain,
264 where a pulse is local and a single frequency (like the base frequency) is global. Second,
265 our results cannot be easily compared to studies that use definitions of ‘frequency coding’
266 based on more than single spectral elements(e.g. Manfredi et al., 2014), because frequency
267 coding defined that way may in fact involve a fair amount of local coding in the time domain.

268 There are several hints that in primates and rodents the base frequency of a pulsatile code
269 plays a minor role for tactile perception. Rats show exactly the same performance in
270 detecting changes of pulsatile stimuli irrespective of whether intensity or pulse frequency is
271 changed (Waiblinger et al., 2015a). In rat primary somatosensory cortex spike counts relate
272 better to tactile discriminations than timing of spikes (Gerdjikov et al., 2018). Monkeys
273 perform frequency discrimination on pulsatile stimuli independent of the rhythmicity of pulses
274 (Salinas et al., 2000), and humans perceive frequency based on the longest gap between
275 bursts of pulses irrespective of the absolute number of pulses (at least in lower frequency
276 ranges; Birznieks and Vickery, 2017). Our experiments add to the view that spectral analysis
277 may play a rather inferior role in tactile perception. Our quantitative comparison of
278 performance obtained with pure pulse frequency changes in comparison to stimuli
279 containing local cues (Fig. 4), demonstrated the inferiority of base frequency cues to
280 determine perception.

281 *What is the functional advantage of a local code?*

282 The search for local coding is motivated by the assumed presence of frictional movements in
283 objects that engage in moving contact (Schwarz, 2016). Moving contact is at the heart of
284 tactile processing, as palpation movements are indispensable for the perception of fine
285 textures (Hollins et al., 2001; Hollins and Risner, 2000; Skedung et al., 2013). Prototypical
286 expressions of frictional contact are stick-slip events - short lived elastic deformations of the
287 contacting materials coming about by sticking to surface elements, storing energy in elastic
288 deformation, and releasing them quickly into sudden slips when frictional force is overcome
289 by the driving movement of the contact (Schwarz, 2016). In the rodent vibrissa-based tactile
290 system, frictional slips have been shown to exist (Arabzadeh et al., 2005; Ritt et al., 2008;
291 Wolfe et al., 2008), and to encode texture information (Oladazimi et al., 2018; Wolfe et al.,
292 2008). Primary sensory cortex in these animals has been shown to be selective for slip-
293 based tactile inputs (Jadhav et al., 2009). Stick-slip events are short-lived and therefore local
294 in character, meaning that any tactile information they store is immediately available. An

295 efficient decoding system making use of stick-slip events is supposed to have evolved under
296 time-accuracy constraints, and thus, must be assumed to be local itself, i.e. make use of
297 tactile information immediately after the reception of slip-based tactile signals. In support of
298 this notion, manipulations of pulsatile whisker deflections in a psychophysical study, have
299 provided strong evidence in favor of local coding in rats' tactile system (Waiblinger et al.,
300 2015a). In the fingertip system evidence about frictional movements is more scant, but by no
301 means negligible: Papillary ridges undergo complex shearing deformations at the onset of a
302 finger movement (Delhaye et al., 2016), and friction has been shown to be a determinant of
303 roughness estimation – most of all for the discrimination of microscopic surface elements
304 (Verrillo et al., 1999). Research on prehension has unearthed unequivocal evidence that
305 sudden slip movement does occur in the skin, and is readily detected by humans to adjust
306 grip forces (Johansson and Westling, 1987). Finally, so-called rate hardness (an
307 instantaneous measure of change of force and speed when tapping surfaces) relates tightly
308 to hardness perception suggesting that it may be based on local elements of the tactile
309 signal as well (Han and Choi, 2010; Lawrence et al., 2000). On the anatomical level, the
310 presence of papillary ridges in glabrous skin, beset by saliently structured rows of ridge-
311 associated Meissner corpuscles and Merkel cells (Cauna, 1954) has rarely been attempted
312 to be incorporated into a functional hypothesis (Gerling and Thomas, 2008). Biomechanical
313 generation of stick-slip in ridges, and specific reception of these by the mentioned rows of
314 ridge-associated receptors is a hypothesis that may help to unearth such functional links in
315 the future. Currently, these are mostly indirect evidences speaking in favor of local coding,
316 but due to lack of more detailed investigations it seems difficult to dismiss local coding as
317 playing a critical role in fine texture perception in primates (Schwarz, 2016). Nevertheless,
318 on the behavioral level, no evidence directly supporting this notion was available so far. Our
319 present results are the first to provide systematic observations that can begin to fill this gap
320 and demonstrate that kinematic features of vibrotactile signals represent a perceptually
321 powerful coding object.

322 **Methods**

323 *Participants*

324 We recruited a total of 13 neurologically-healthy (self-reported) participants (age:20-35
325 years, median 27 years; 5 female). Two participants withdrew from the study without
326 providing any reason. Our participant recruitment advertisement discouraged all individuals
327 from participation if they were diagnosed with dyslexia (because it adversely affects tactile
328 acuity, (Grant et al., 1999; Laasonen et al., 2001), diabetes (which could result in peripheral
329 neuropathy and action potential conduction delays, (Hyllienmark et al., 1995), learning
330 disabilities, nervous system disorders, or had any calluses or injury to the left index fingertip
331 (the tested finger). Based on questions modified from the Edinburgh Handedness Inventory
332 (Oldfield, 1971), we classified 12 participants as right handed. The study was approved by
333 our institutional research ethics board; all the participants signed the informed consent form
334 and were paid for their participation in the study.

335 To identify the stimulus feature that the participants used to perform the perceptual tasks, we
336 required the participants to perform well so that we could generate their psychometric
337 function for each task (see subsection perceptual task). If any participant performed poorly
338 on any task (session) and failed to generate a viable psychometric function for those tasks
339 (passing 50% correct), we ran them again on those specific tasks. Three participants
340 completed the study in a single attempt, 4 participants redid 1 out of 7 tasks, and 3
341 participants redid 2 out of 7 tasks. One participant was disqualified from the study because
342 total percent correct for all 7 sessions using stimuli from the 7 iso-lines in experiment 1 was
343 less than 50%. The data of the disqualified participant and the participants who withdrew
344 from the study are not included in the results section of this study.

345 *Vibrotactile stimulation*

346 We applied passive vibrotactile stimuli (i.e. no finger movement) to the distal pad of the left
347 index finger, using a plastic circular disc of 2.9 mm diameter attached to a galvomotor
348 (Cambridge Technology, Massachusetts; model 6220H). The galvomotor was driven by a
349 custom made amplifier, which reproduced highly precise displacements. We calibrated the
350 displacements of the galvomotor using a laser distance estimator that is sensitive to
351 displacements at the micron resolution. We used Matlab (Natick, USA) to generate the
352 stimulus waveform and control the galvomotor movement by passing voltage waveforms
353 through an analog output channel digitized at 40,000 samples per second at 12 bit resolution
354 via a National Instruments PCI-MIO-16E-1 I/O board.

355 Participants' arm rested on a platform which could be raised or lowered depending on the
356 participants' comfort. To prevent finger movements, the index finger was clamped in a finger
357 housing using a cleft as a rest for the finger nail - in addition to a double-sided tape that
358 affixed the plane of the fingernail to the ceiling of the housing. Once the testing finger was
359 securely positioned, we used a tri-axis micromanipulator to adjust and attach the galvomotor
360 to the distal pad of the left index finger such that the circular disc area was completely
361 covered by the fingertip skin. During the experiment only the testing region of the fingertip
362 touched the circular disc, we ensured that no other part of the galvomotor touched any part
363 of the participants' finger. We asked participants to trim the nail of their testing finger to
364 prevent any possibility of their nail touching any part of the stimulator. The arm platform as
365 well as the galvomotor platform were separate from each other and seated on an anti-slip
366 and anti-vibration mat. The depth of indentation was defined as the position in which during
367 very slow movement toward the skin the participants would first report touch-down. Using a
368 micromanipulator the galvomotor was then proceeded to the null position at a depth of 1
369 mm. From there the stimulus pulses further indented the skin.

370 Pulsatile stimuli were constructed by using one period sinusoids (waveform of a sinusoid
371 extracted from one of its minima to the next) as done before (Gerdjikov et al., 2010). Two
372 manipulations were performed to change pulse width and amplitude. For pulse width, the
373 sinusoids used for this procedure ranged in frequency between 170 and 240 Hz in steps of 5
374 Hz, resulting in 15 pulse waveforms that varied in pulse width between
375 $1^{\circ}\text{s}^{\circ}/^{\circ}170^{\circ}\text{Hz}^{\circ}=\text{4167}^{\circ}\mu\text{s}$ and $1^{\circ}\text{s}^{\circ}/^{\circ}240^{\circ}\text{Hz}^{\circ}=\text{5882}^{\circ}\mu\text{s}$. The pulse amplitude ranged between
376 20 and 40 μm . A third manipulation left pulse waveform untouched but changed pulse
377 frequency, i.e. the inverse of interpulse intervals. Pulse frequency of the reference stimulus
378 was always 90 Hz. It changed in 5 Hz steps to values up to 135 Hz. The stimulus was a
379 seamless concatenation of two pulse trains both 500 ms in duration. The first, called
380 reference stimulus, was a train at a pulse frequency of 90 Hz, a pulse amplitude of 40 μm ,
381 and a pulse width of 5.882 ms. The second train of pulses was either the same as the
382 reference stimulus (i.e. 'no change') or one that was altered into one or several of the above-
383 mentioned manipulations (i.e. 'change')- see Figure 1C (the traces are to scale but for
384 purposes of visualization the traces contain only a few pulses pre- and post-change).

385 *Perceptual tasks and psychophysics procedure*

386 The participants were instructed to indicate in a Yes/No fashion their decision about the
387 absence or presence of the perceived stimulus change. This was done by pressing one of
388 two buttons (Yes/No) on a wireless presenter clicker with their right hand. The intertrial
389 interval started after the participant's response and lasted 5 s. After each block of 280 trials
390 (140 'no change' trials), the participants took a minimum of 2 minutes break in which they
391 were encouraged to stand up and walk around. Participants received feedback after each
392 trial which was delivered through wireless headphones. In addition, after each 280 trial-block
393 participants saw their performance as total percent correct for that block. During experiment
394 2 and 3, white noise was played out loud next to the tactile stimulator. Following the
395 completion of experiment 2, when asked, none of the participants was aware that the
396 pulsatile frequency (along with the pulse width and amplitude) of the target stimuli changed.

397 *Statistical analysis:*

398 To each participant's performance (proportion reported "change") in each task, using the
399 dedicated analysis software *psignifit* (Wichmann and Hill, 2001), we fitted a mixture model
400 cumulative normal psychometric function of the following form:

$$P(x) = \gamma + (1 - \delta - \gamma)p(x)$$

401 where $p(x)$ is the sigmoid modelled as cumulative gaussian – which includes the threshold
402 (i.e. the mean) and width (i.e. the SD) parameters, γ parameter is false alarm (lower
403 asymptote), and δ parameter is the lapse rate (upper asymptote). The *psignifit* algorithm
404 computed the maximum likelihood of each psychometric function generated from the
405 combination of each of the above-mentioned parameters. By marginalizing over the γ , δ , and
406 width parameters *psignifit* yielded a posterior probability density function (PDF) over the
407 threshold parameter(θ), i.e. where the psychometric functioned crossed 50% correct. For
408 each participant's point estimate of their performance on each iso-line, we chose the
409 stimulus value corresponding to the mode of the threshold PDF.

410 Next, to estimate the population mean for each iso-line, we implemented a Bayesian
411 Hierarchical analysis (see Tong et al., 2016). We represented the participants' threshold as
412 normally distributed over the whole stimulus range (pulse width from 5882 down to 4167 μ s)
413 with unknown mean μ and standard deviation σ (ranging between 0.5 and 30). The
414 probability of a participant's data given (μ , σ) can be written as:

$$p(d_i|\mu, \sigma) = \int_{5.882-4.167\text{ms}}^{i=\text{stimuli}} p(d_i|\theta)p(\theta|\mu, \sigma)d\theta$$

415 Here, the first term in the integrand is proportional to the threshold PDF of each participant
416 (acquired from *psignifit*), because we assume a uniform prior over all possible values of θ

417 (i.e. 5882 to 4167 $^{\circ}$ μ s). Thus, the likelihood of joint distribution of each (μ, σ) of complete
418 dataset ' D ' including all 10 participants can be represented as:

$$p(D|\mu, \sigma) = \prod_{i=1}^{10} p(d_i|\mu, \sigma)$$

419 Finally, we marginalized over σ and obtained a PDF of the population mean; we report the
420 mode of this distribution as the mean of the population along with the Bayesian 95%
421 confidence interval.

422 *Experiment 1:* This experiment exclusively used changes in pulse waveform and set the
423 pulse frequency to 90 Hz throughout. We tested each participant on stimuli changes drawn
424 from 7 iso-lines shown in Fig. 1D (seven sessions were performed, testing one iso-line per
425 session). A session contained 420 'change' and 420 'no change' stimuli. The iso-lines
426 contained stimuli from which we extracted 3 local (maximum position, velocity and
427 acceleration) and 6 global (intensity) variables. The terms are given in Fig. 1D (the
428 integration window was always the entire 500 ms stimulus, therefore we use sum and mean
429 of the variable inter-changeably). In two instances an iso-line was found to be congruent with
430 another ('maximum position' / 'mean absolute velocity' and 'maximum velocity' / 'mean
431 absolute acceleration'); hence, 7 iso-lines were tested. In one iso-line session the
432 presentation was three blocks of 280 trials each, which contained all 'change' stimuli (140)
433 and the same number of 'no change' stimuli trials in pseudorandom order.

434 *Experiment 2:* The aim here was to disentangle performance on the 'maximum velocity' iso-
435 line from that of the 'mean absolute acceleration' iso-line, using additional changes of pulse
436 frequency (Fig. 3A). The change in pulse frequency was set to 15 Hz (i.e. from 90 to 105
437 Hz), a value that was far sub-threshold for all participants (see results). Otherwise the
438 experimental conditions were as described for experiment 1.

439 *Experiment 3*: Here stimulus changes were exclusively based on changes in pulse
440 frequency (Δpf). There were 9 ‘change’ stimuli and one ‘no change’ stimulus’, yielding 540
441 trials per session (30 trials per stimulus). Otherwise conditions were the same as for
442 experiment 1.

443 **Acknowledgements**

444 This research was supported by a grant from the Deutsche Forschungsgemeinschaft
445 (SCHW577/14-1).

446 **Author contributions statement**

447 AB designed and conducted experiments, analyzed data and wrote the paper. CB designed
448 the experiments and wrote the paper. CS designed the experiment, analyzed data, and
449 wrote the paper.

450 **Competing financial interest statement**

451 No interests declared.

452 **Data availability statement**

453 The datasets generated during and/or analyzed during the current study are available from
454 the corresponding author on reasonable request.

455 References

- 456 Arabzadeh E, Petersen RS, Diamond ME. 2003. Encoding of whisker vibration by rat barrel
457 cortex neurons: implications for texture discrimination. *J Neurosci* **23**:9146–9154.
- 458 Arabzadeh E, Zorzin E, Diamond ME. 2005. Neuronal encoding of texture in the whisker
459 sensory pathway. *PLoS Biol* **3**:e17.
- 460 Barlow HB. 1972. Single units and sensation: a neuron doctrine for perceptual psychology?
461 *Perception* **1**:371–394.
- 462 Barrea A, Delhayé BP, Lefèvre P, Thonnard JL. 2018. Perception of partial slips under
463 tangential loading of the fingertip. *Sci Rep* **8**:1–8. doi:10.1038/s41598-018-25226-w
- 464 Birznieks I, Vickery RM. 2017. Spike Timing Matters in Novel Neuronal Code Involved in
465 Vibrotactile Frequency Perception. *Curr Biol* **27**:1485-1490.e2.
466 doi:10.1016/j.cub.2017.04.011
- 467 Campbell FW, Maffei L. 1974. Contrast and spatial frequency. *Sci Am* **231**:106–115.
468 doi:10.1038/scientificamerican1174-106
- 469 Cauna N. 1954. Nature and functions of the papillary ridges of the digital skin. *Anat Rec*
470 **119**:449–468. doi:10.1002/ar.1091190405
- 471 Chagas AM, Theis L, Sengupta B, Stüttgen MC, Bethge M, Schwarz C. 2013. Functional
472 analysis of ultra high information rates conveyed by rat vibrissal primary afferents. *Front*
473 *Neural Circuits* **7**:190. doi:10.3389/fncir.2013.00190
- 474 Delhayé B, Barrea A, Edin BB, Lefèvre P, Thonnard J-L. 2016. Surface strain
475 measurements of fingertip skin under shearing. *J R Soc Interface* **13**:20150874.
476 doi:10.1098/rsif.2015.0874
- 477 Gerdjikov T V, Bergner CG, Schwarz C. 2018. Global Tactile Coding in Rat Barrel Cortex in
478 the Absence of Local Cues. *Cereb Cortex* **28**:2015–2027. doi:doi:
479 10.1093/cercor/bhx108
- 480 Gerdjikov T V, Bergner CG, Stüttgen MC, Waiblinger C, Schwarz C. 2010. Discrimination of
481 vibrotactile stimuli in the rat whisker system: behavior and neurometrics. *Neuron*
482 **65**:530–40.
- 483 Gerling GJ, Thomas GW. 2008. Fingerprint lines may not directly affect SA-I
484 mechanoreceptor response. *Somatosens Mot Res* **25**:61–76.
485 doi:10.1080/08990220701838996
- 486 Grant AC, Zangaladze A, Thiagarajah MC, Sathian K. 1999. Tactile perception in
487 developmental dyslexia: a psychophysical study using gratings. *Neuropsychologia*
488 **37**:1201–1211.
- 489 Han G, Choi S. 2010. Extended rate-hardness: A measure for perceived hardness. *Lect*
490 *Notes Comput Sci* **6191 LNCS**:117–124. doi:10.1007/978-3-642-14064-8_18
- 491 Hipp J, Arabzadeh E, Zorzin E, Conradt J, Kayser C, Diamond ME, Konig P. 2006. Texture
492 signals in whisker vibrations. *J Neurophysiol* **95**:1792–1799.
- 493 Hollins M, Bensmaia SJ, Washburn S. 2001. Vibrotactile adaptation impairs discrimination of
494 fine, but not coarse, textures. *Somat Mot Res* **18**:253–262.
- 495 Hollins M, Risner SR. 2000. Evidence for the duplex theory of tactile texture perception.
496 *Percept Psychophys* **62**:695–705.

- 497 Hubel DH, Wiesel TN. 1968. Receptive fields and functional architecture of monkey striate
498 cortex. *J Physiol* **195**:215–243.
- 499 Hyllienmark L, Brismar T, Ludvigsson J. 1995. Subclinical nerve dysfunction in children and
500 adolescents with IDDM. *Diabetologia* **38**:685–692.
- 501 Jadhav SP, Wolfe J, Feldman DE. 2009. Sparse temporal coding of elementary tactile
502 features during active whisker sensation. *Nat Neurosci* **12**:792–800.
- 503 Johansson RS, Birznieks I. 2004. First spikes in ensembles of human tactile afferents code
504 complex spatial fingertip events. *Nat Neurosci* **7**:170–7. doi:10.1038/nn1177
- 505 Johansson RS, Westling G. 1987. Signals in tactile afferents from the fingers eliciting
506 adaptive motor responses during precision grip. *Exp Brain Res* **66**:141–154.
507 doi:10.1007/BF00236210
- 508 Jones LM, Depireux DA, Simons DJ, Keller A. 2004. Robust temporal coding in the
509 trigeminal system. *Science (80-)* **304**:1986–1989.
- 510 Laasonen M, Service E, Virsu V. 2001. Temporal order and processing acuity of visual,
511 auditory, and tactile perception in developmentally dyslexic young adults. *Cogn Affect*
512 *Behav Neurosci* **1**:394–410.
- 513 LaMotte RH, Mountcastle VB. 1975. Capacities of humans and monkeys to discriminate
514 vibratory stimuli of different frequency and amplitude: a correlation between neural
515 events and psychological measurements. *J Neurophysiol* **38**:539–559.
516 doi:psychophysics; monkeys; haptic; vibration; tactile; vibro-tactile; frequency;
517 amplitude; integrated measure
- 518 Lawrence DA, Pao LY, Dougherty AM, Salada MA, Pavlou Y. 2000. Rate-hardness: a new
519 performance metric for haptic interfaces. *IEEE Trans Robot Autom* **16**:357–371.
520 doi:10.1109/70.864228
- 521 Luna R, Hernandez A, Brody CD, Romo R. 2005. Neural codes for perceptual discrimination
522 in primary somatosensory cortex. *Nat Neurosci* **8**:1210–1219.
- 523 Manfredi LR, Saal HP, Brown KJ, Zielinski MC, Dammann 3rd JF, Polashock VS, Bensmaia
524 SJ. 2014. Natural scenes in tactile texture. *J Neurophysiol* **111**:1792–1802.
525 doi:10.1152/jn.00680.2013
- 526 Maravall M, Petersen RS, Fairhall AL, Arabzadeh E, Diamond ME. 2007. Shifts in coding
527 properties and maintenance of information transmission during adaptation in barrel
528 cortex. *PLoS Biol* **5**:e19.
- 529 Oladazimi M, Brendel W, Schwarz C. 2018. Biomechanical Texture Coding in Rat Whiskers.
530 *Sci Rep* **8**:11139. doi:10.1038/s41598-018-29225-9
- 531 Oldfield RC. 1971. The assessment and analysis of handedness: The Edinburgh inventory.
532 *Neuropsychologia* **9**:97–113. doi:10.1016/0028-3932(71)90067-4
- 533 Petersen RS, Brambilla M, Bale MR, Alenda A, Panzeri S, Montemurro MA, Maravall M.
534 2008. Diverse and temporally precise kinetic feature selectivity in the VPM thalamic
535 nucleus. *Neuron* **60**:890–903.
- 536 Pruszynski JA, Johansson RS. 2014. Edge-orientation processing in first-order tactile
537 neurons. *Nat Neurosci* **17**:1404–9. doi:10.1038/nn.3804
- 538 Ritt JT, Andermann ML, Moore CI. 2008. Embodied information processing: vibrissa
539 mechanics and texture features shape micromotions in actively sensing rats. *Neuron*
540 **57**:599–613. doi:10.1016/j.neuron.2007.12.024
- 541 Salinas E, Hernandez A, Zainos A, Romo R. 2000. Periodicity and firing rate as candidate

- 542 neural codes for the frequency of vibrotactile stimuli. *J Neurosci* **20**:5503–5515.
- 543 Schwarz C. 2016. The slip hypothesis: Tactile perception and its neuronal bases. *Trends*
544 *Neurosci* **39**:449–462. doi:doi: 10.1016/j.tins.2016.04.008
- 545 Skedung L, Arvidsson M, Chung JY, Stafford CM, Berglund B, Rutland MW. 2013. Feeling
546 small: exploring the tactile perception limits. *Sci Rep* **3**:2617. doi:10.1038/srep02617
- 547 Tong J, Ngo V, Goldreich D. 2016. Tactile length contraction as Bayesian inference. *J*
548 *Neurophysiol* **116**:369–379. doi:10.1152/jn.00029.2016
- 549 Verrillo RT, Bolanowski SJ, McGlone FP. 1999. Subjective magnitude of tactile roughness.
550 *Somatosens Mot Res* **16**:352–360. doi:10.1080/08990229970401
- 551 Waiblinger C, Brugger D, Schwarz C. 2015a. Vibrotactile discrimination in the rat whisker
552 system is based on neuronal coding of instantaneous kinematic cues. *Cereb Cortex*
553 **25**:1093–106. doi:10.1093/cercor/bht305
- 554 Waiblinger C, Brugger D, Whitmire CJ, Stanley GB, Schwarz C. 2015b. Support for the slip
555 hypothesis from whisker-related tactile perception of rats in a noisy environment. *Front*
556 *Integr Neurosci* **9**:53. doi:10.3389/fnint.2015.00053
- 557 Weber AI, Saal HP, Lieber JD, Cheng J-W, Manfredi LR, Dammann JF, Bensmaia SJ. 2013.
558 Spatial and temporal codes mediate the tactile perception of natural textures. *Proc Natl*
559 *Acad Sci* **110**:17107–12. doi:10.1073/pnas.1305509110
- 560 Wichmann FA, Hill NJ. 2001. The psychometric function: I. Fitting, sampling, and goodness
561 of fit. *Percept Psychophys* **63**:1293–1313.
- 562 Wolfe J, Hill DN, Pahlavan S, Drew PJ, Kleinfeld D, Feldman DE. 2008. Texture coding in
563 the rat whisker system: slip-stick versus differential resonance. *PLoS Biol* **6**:e215.
- 564 Yoshioka T, Gibb B, Dorsch AK, Hsiao SS, Johnson KO. 2001. Neural coding mechanisms
565 underlying perceived roughness of finely textured surfaces. *J Neurosci* **21**:6905–6916.
- 566
- 567

568 **Figure legends**

569 **Fig. 1.** Definition of local coding and methods. **A.** The difference of local vs. global in the
570 time domain of a vibrotactile signal. Local coding is defined as focusing on short-lived events
571 in the vibrotactile signal, which can be extracted and analyzed (near-) instantly (golden
572 bracket). Global coding on the other hand is an integrative mechanism, analyzing a long
573 stretch of the vibrotactile signal using averaging or frequency decomposition (black bracket).
574 **B.** In this study skin indentation of an actuated disk of 2.9 mm diameter at the fingertip of the
575 left index finger was used. **C.** Participants received pulsatile stimuli consisting of single-
576 period sinusoids separated by zero movement. They were instructed to indicate detection an
577 abrupt change (orange) in either pulse waveform (Δ amplitude, Δ width; experiment 1, upper
578 four stimuli), pulse frequency (Δpf , experiment 3, 5th stimulus), or both (experiment 2, 6th
579 stimulus). The stimulus containing no change (4th stimulus, all black) was presented in all
580 experiments in 50 % of the trials. All traces are to scale and demonstrate the extremes of the
581 stimulus space used (see stars in panel D and Fig.3A). The changes shown are: amplitude:
582 from 40 to 20 μ m; width: from 5882 to 4167 μ s; pulse frequency: from 90 Hz to 135 Hz.
583 Note, for demonstration purposes only a few pulses around the change are shown. **D.**
584 Definition of coding variables and stimulus space. Stimulus space spanning the change of
585 pulse waveforms presented in experiment 1 is shown. Abscissa: change of pulse width,
586 Ordinate: change of pulse amplitude. The reference stimulus ('no change') is at (0|0). Stimuli
587 located on the nine iso-lines shown do not change the coding symbol indicated on the left
588 (color of line and coding symbol matches). Iso-lines of intensity variables (global) are
589 indicated by thin lines. Shades of green indicate velocity-based, while shades of blue
590 indicate acceleration-based variables. Instantaneous kinematic variables (local) are plotted
591 using thick lines. Note that two pairs of iso-lines (curly brackets) are congruent. Asterisks on
592 the corners mark the extreme stimulus changes demonstrated in C. **E.** Intensity variables
593 integrate long signal stretches. However, non-linear elements in their definition as well as

594 differentiation, can change the weights with which local features enter the value of a global
595 variable. An arbitrary velocity signal and respective first derivative (accel=acceleration) is
596 shown in the upper row and taken to different powers (1,2, and 3; along columns). Higher
597 derivative / higher power intensity formulations are increasingly dominated by local features
598 in the signal.

599 **Fig. 2.** Experiment 1. Detection of pulse waveform changes. **A.** Data and logistic fits to the
600 performance of one participant on all iso-lines shown in Fig. 1D. Same axes scaling in all
601 sub-panels. **B.** Logistic fits using pooled data of all 10 participants. **C.** Thresholds and 95%
602 confidence intervals expressed as pulse width for all isolines. Performance on ‘maximum
603 velocity’ iso-line is poorest across all participants. Colors match throughout all panels. Thick
604 lines / hollow symbols: iso-lines of local variables; Thin lines / filled symbols: iso-lines of local
605 variables. Statistics see text.

606 **Fig. 3.** Experiment 2. Disentangling the congruent iso-lines related to ‘maximum velocity’
607 and ‘mean absolute acceleration’. **A.** Iso-lines with (gray and red) and without (blue)
608 changes in pulse frequency (Δpf). Iso-lines of local variables do not change with adding
609 pulse frequency cues while those of global variables do. The gray curve is the unchanging
610 iso-line of maximum velocity with and without Δpf . The blue and red curves are the iso-lines
611 of mean absolute acceleration with and without Δpf , respectively. Effectively then, the
612 addition of Δpf disentangles the two isolines. For examples of stimulus waveforms refer to
613 figure 1C. **B.** Data and logistic fits for the same participant shown in figure 2B. **C.** Logistic fits
614 for the population of 9 participants. Poor performance is pegged to maximum velocity. There
615 is a slight non-significant improvement in performance when adding Δpf (blue to gray).
616 However, shifting the mean absolute acceleration iso-line with Δpf improves performance
617 significantly (blue to red). Colors in all panels match. Thick lines: iso-lines and respective
618 performance of local variables; thin lines: same for global variables

619 **Fig. 4.** Performance with and without local cues. **A.** Performance on stimuli using pure
620 global cues. i.e pure pulse frequency changes (Δpf , experiment 3; cf. 5th stimulus in Fig.
621 1C). **B.** Replotting data from A (red lines) and data obtained from the performance on seven
622 iso-lines in experiment 1. Each sub-panel plots the data from 7 iso-lines, scaled according to
623 one of six intensity variables. Each intensity variable in the six sub-panels is normalized and
624 scaled to the maximum of that variable found in the Δpf stimuli. **C.** Thresholds of all logistic
625 fits to the data shown in B, now all normalized to the same scale. Red stars relate to red
626 lines in B (experiment 3, Δpf stimuli), colored dots relate to the lines in B of the same color
627 (experiment 1, pulse waveform changes). Note the descending threshold obtained when
628 basing the performance on increasing power (red stars, green line: velocity-based intensity,
629 blue line: acceleration-based intensity). This comparison across scales suggests that
630 intensity definitions using higher powers (weighing local features higher) increasingly
631 represent performance as true local variables do.

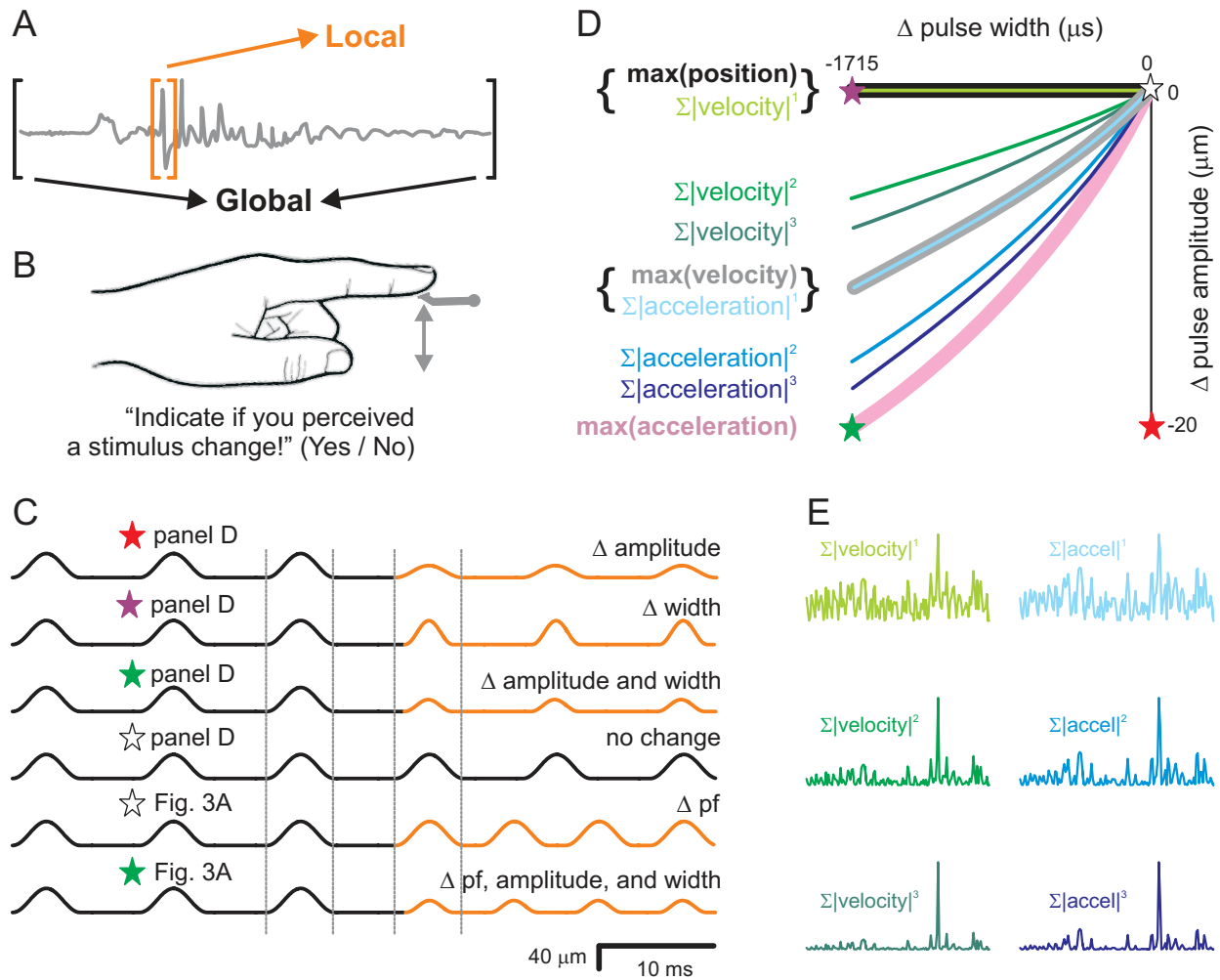


Fig. 1

HUMANS USE A LOCAL CODE FOR TACTILE PERCEPTION
 Arindam Bhattacharjee, Christoph Braun and Cornelius Schwarz

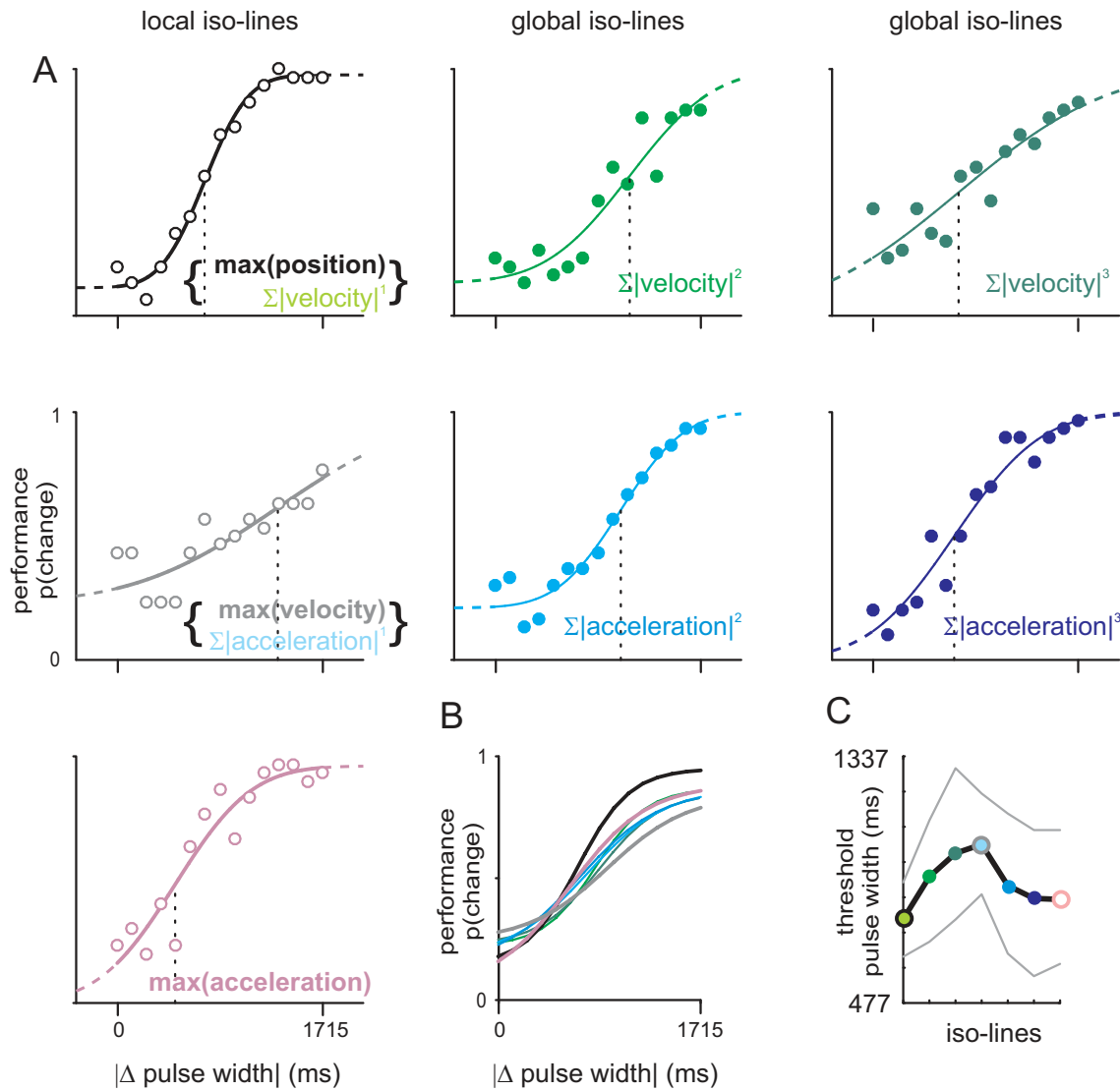


Fig. 2

HUMANS USE A LOCAL CODE FOR TACTILE PERCEPTION
Arindam Bhattacharjee, Christoph Braun and Cornelius Schwarz

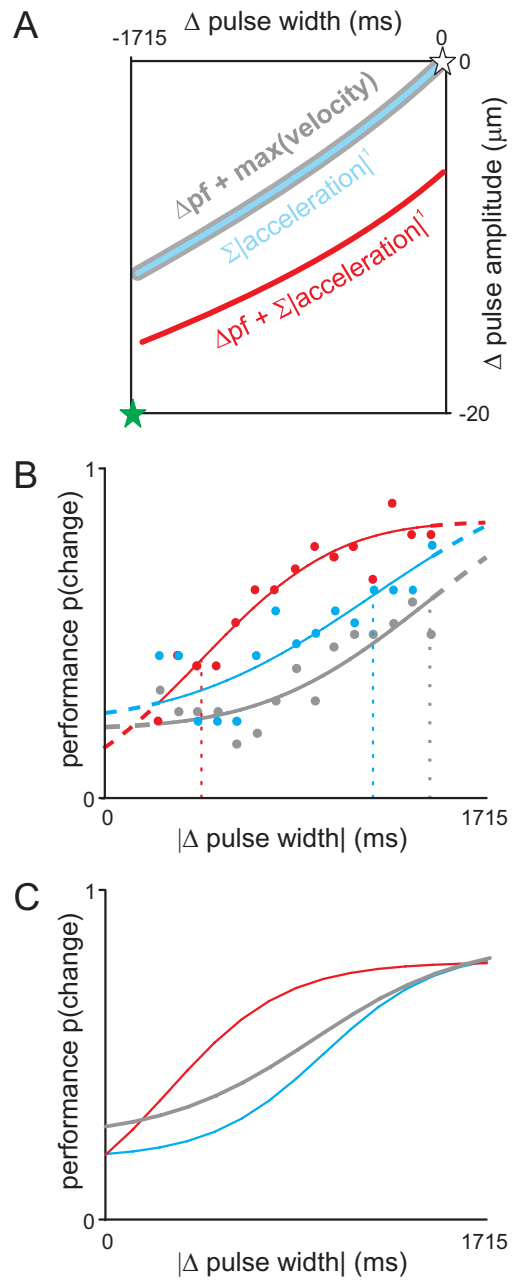


Fig. 3

HUMANS USE A LOCAL CODE FOR TACTILE PERCEPTION
Arindam Bhattacharjee, Christoph Braun and Cornelius Schwarz

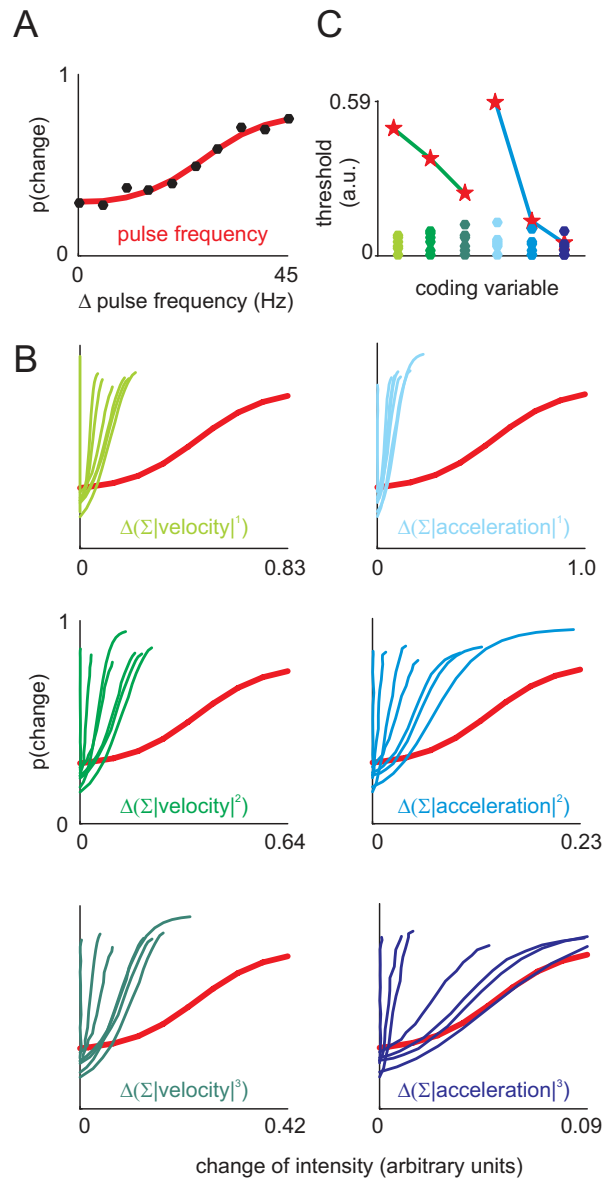


Fig. 4

HUMANS USE A LOCAL CODE FOR TACTILE PERCEPTION
Arindam Bhattacharjee, Christoph Braun and Cornelius Schwarz