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3 **Title: Creating a neuroprosthesis for active tactile exploration of textures**

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37

38 **Abstract**

39

40 Intracortical microstimulation (ICMS) of the primary somatosensory cortex (S1) can

41 produce percepts that mimic somatic sensation and thus has potential as an approach to

42 sensorize prosthetic limbs. However, it is not known whether ICMS could recreate active texture

43 exploration—the ability to infer information about object texture by using one's fingertips to scan

44 a surface. Here we show that ICMS of S1 can convey information about the spatial frequencies

45 of invisible virtual gratings through a process of active tactile exploration. Two rhesus monkeys

46 scanned pairs of visually identical screen objects with the fingertip of a hand avatar, controlled

47 via a joystick and later via a brain-machine interface, to find the one with denser virtual gratings.

48 The gratings consisted of evenly spaced ridges that were signaled through ICMS pulses

49 generated when the avatar's fingertip crossed each ridge. The monkeys learned to interpret

50 these ICMS patterns evoked by the interplay of their voluntary movements and the virtual

51 textures of each object. Discrimination accuracy across a range of grating densities followed

52 Weber's law of just-noticeable differences (JND), a finding that matches normal cutaneous

53 sensation. Moreover, one monkey developed an active scanning strategy where avatar velocity

54 was integrated with the ICMS pulses to interpret the texture information. We propose that this

55 approach could equip upper-limb neuroprostheses with direct access to texture features

56 acquired during active exploration of natural objects.

57

Introduction

Sensory neuroprostheses offer the promise of restoring perceptual function to people with impaired sensation [1,2]. In such devices, diminished sensory modalities (e.g., hearing [3], vision [4,5], or cutaneous touch [6-8]) are reenacted through streams of artificial input to the nervous system, typically using electrical stimulation of nerve fibers in the periphery or neurons in the central nervous system. Restored cutaneous touch, in particular, would be of great benefit for the users of upper-limb prostheses, who place a high priority on the ability to perform functions without the necessity to constantly engage visual attention [9]. This could be achieved through the addition of artificial somatosensory channels to the prosthetic device [1]. Such an approach would endow persons suffering from limb loss [10-12], paralysis [1,13] or somatosensory deficits with the ability to perform active tactile exploration of their physical environment and aid in dexterous object manipulation [14-17].

Previously we demonstrated that motor and sensory functions could be simultaneously enacted though a bidirectional neuroprosthetic system, called a brain-machine-brain interface (BMBI)[18]. In that demonstration, the active exploration enabled by our BMBI-driven neuroprosthesis used a limited and fixed set of ICMS temporal patterns to generate artificial sensory inputs that mimicked the sense of flutter-vibration. However, it remained unclear whether the same approach could generalize to allow the use of natural haptic exploratory procedures, where a person identifies the texture of objects and materials by scanning them with the fingertips.

Normal haptic exploration of objects involves several stereotypic procedures, such as static contact for temperature sensation, holding for weight, enclosure for gross shape, pressure for hardness, contour following for exact shape and lateral fingertip motion for texture [19]. Here we developed a neuroprosthetic paradigm for restoring the sensation of fingertip motion against texture. We hypothesized that ICMS pulses generated by exploratory movements over virtual

83   gratings and delivered to primary somatosensory cortex (S1) would allow discrimination of

84   texture coarseness.

Results

86   *Active texture encoding*

87   Two rhesus monkeys (monkey M and monkey N) were chronically implanted with

88   multielectrode cortical arrays [18] (Supplementary Fig. S1). These animals explored virtual objects

89   on a computer screen using a realistic upper-limb avatar (Supplementary Fig. S2), which they

90   operated manually with a joystick (Fig.1a) or using a BMI. On each trial, a pair of rectangles

91   appeared either on the left or on the right side of the screen. The rectangles were visually

92   identical, but each was associated with an invisible tactile grating whose properties were

93   signaled by charge-balanced ICMS pulses applied to S1 (a region exhibiting left forearm

94   receptive fields for monkey M and left lower-limb receptive fields for monkey N). Each grating

95   consisted of evenly spaced vertical ridges, which were invisible to the monkeys. The spatial

96   frequency of the ridges, f, ranged from 0.5 to 4.0 ridges/cm; an untextured object with no ridges

97   ($f = 0$ ridges/cm) was also presented on some trials.

98   The behavioral task required the monkeys to probe the rectangles with the avatar's

99   fingertip, determine which of the two had a higher f, and to hold the avatar over that object for

100 the required interval, 2 s in most cases (Fig. 1b). The artificial sensation was encoded by

101 delivering a charge-balanced ICMS pulse each time the avatar fingertip crossed a ridge in a

102 grating. Thus, the pulse-trains of ICMS delivered on any given trial provided an artificial signal

103 that depended on the interplay between the movements of the avatar and the f of the textures of

104 the explored objects (Supplementary Movie S1). Movements at a constant velocity across a

105 grating with a given f produced an ICMS pulse train with a constant temporal pulse rate (Fig.

106 2a). Movements at a faster velocity across the same grating produced a pulse train with a

107 correspondingly higher pulse rate (Fig. 2b). Irregular movements produced temporally varying

108 ICMS pulse trains (Fig. 2c). The objects' adjacent spacing on the screen encouraged the

109   monkeys to rapidly shift the avatar from one object to the other and determine which one had a

110   denser grating. The monkeys were permitted to explore the objects in any sequence and enter

111   each object multiple times, to accumulate evidence, before making the selection. Accordingly,

112   the monkeys could select an object on the first pass (Fig. 2d,e) or employ several explorations

113   of individual objects (Fig. 2f) before making a final selection. Prior to these experiments, these

114   monkeys participated in other studies [18,20,21] and became proficient in using the joystick and the

115   hand avatar and making decisions using ICMS pulse trains. However, none of the previous

116   experiments employed the particular ICMS encoding rule or the texture scanning paradigm

117   presented in the current study.

118   *Active texture discrimination*

119   Both monkeys learned the task rapidly, reaching high-performance levels (71% of

120   correct trials for monkey N, and 73% for monkey M) after 10 daily sessions of training (Fig.

121   3a,b). The average performance was above chance even in the first training session (64% for

122   monkey N and 56% for monkey M). For monkey M, task difficulty was increased gradually, with

123   a large difference in f introduced early in training, $\Delta f \geq 2$ ridges/cm; $\Delta f < 2$ ridges/cm after 3

124   sessions and the full range from $f = 0$ to $f = 3.5$ ridges/cm and a minimum $\Delta f = 0.5$ by the end of

125   the training. The range for monkey N was $f = 0$ to $f = 3.5$ ridges/cm at the onset of the training

126   and $f = 0$ to $f = 4$ by the end. The minimum difference between textures, $\Delta f,$ was maintained at

127   0.5 for all sessions. Figure 3 c,d shows the behavioral performance after learning (11 and 12

128   recording sessions for monkeys M and N, respectively). Both monkeys performed better on

129   individual trials when presented with larger Δf between the two objects than for smaller Δf, as

130   might be expected. However, we observed an additional scaling of discrimination difficulty that

131   depended on the absolute scale of the spatial frequencies of the objects being compared. More

132   specifically, the psychometric functions for both monkeys were steeper for larger values of $\sum f$,

133   that is, steeper for the larger sum for the two objects being compared (Fig. 4a,b).

134   We quantified this phenomenon by estimating the just noticeable difference (JND), for

135   each presented spatial frequency [22]. We calculated, for each spatial frequency, the probability of

136   choosing a second comparison frequency as a function of the unsigned delta between the

137   standard stimulus and the comparison stimulus (Fig. S3). We found that the JND increased

138   proportionally to f (Fig. 4c), consistent with the Weber–Fechner law [23] and Steven's power law

139   [24]. The results for monkey M could be described by the linear function $JND(f) = 0.47f + $

140   1.06 (R^2 = 0.63); $JND(f) = 0.37f + 0.77$ for monkey N (R^2 = 0.95).

141   There are a number of strategies that the monkeys could have used to compare the

142   textures. One viable option would be to use a consistent velocity when exploring both objects so

143   that any variation in ICMS pulse rate between the objects would be due to differences in spatial

144   frequency alone. Further analysis revealed that this was not the case. Indeed, both monkeys

145   used a distribution of speeds to sample the gratings (Fig. 5a) and could perform successful

146   discriminations across the majority of their operating range (Fig. 5b)—only having difficulty when

147   moving at very high speeds. Moreover, for the vast majority of trials, the average speeds used

148   to scan the two objects differed, even within the same trial. Monkey M sampled the two objects

149   with the same speed (delta speed < 1 cm/s) on fewer than 3% of trials, a finding that was not

150   explained by the trial outcome (wrong trials: 2.41%, correct trials: 2.82%; Fig. S4). Monkey N

151   used the same scanning speed for each target on only 3.85% of the trials (3.95% of the wrong

152   trials, 3.81% of the correct trials).

153   This variability in arm movements was sufficiently large that, in some cases, the

154   ordinality of spatial frequency of the textures was different from the ordinality of the ICMS pulses

155   rates. An example of one of these apparently paradoxical trials is given in Figure 5c. For this

156   trial, frequency of the right target (F_R = 3.5 ridge/cm) was higher than the left (F_L = 2.5

157   ridges/cm), but the actual ICMS pulse rate delivered for the left target was higher than for the

158   right (left: 200.2 Hz versus right: 103.1 Hz). This occurred because a faster avatar speed was

159   used to explore the left target as compared to the right. Despite this, the monkey was able to

160   accurately choose the target with the higher spatial frequency in this example.

161   We found many of these apparently paradoxical trials (n=1231, 12% of all trials) for

162   monkey N. The majority of these cases corresponded to frequency pairs with high FR+FL (Fig.

163   S5). Monkey N's success rate was significantly above chance for these trials (56.1%, P<0.001,

164   one-tailed binomial test; Fig. 5d). There were fewer of these trials for monkey M (n=329, 6% of

165   all trials). For these trials, monkey M's performance did not reach significance (52.03%, P=

166   0.25, one-tailed binomial test).

167   *Brain-machine-brain interface with active texture discrimination*

168   Finally, we validated our stimulation paradigm in a closed-loop brain-machine-brain

169   interface (BMBI) with monkey M. For this task, the monkey was allowed to move its arms, but

170   the joystick was disconnected; instead the avatar arm—and task performance—was controlled

171   via the decoding of 90 simultaneously recorded right-hemisphere M1 neurons (Fig. 6a). We

172   found that monkey M was able to control the avatar arm to explore the objects with minimal

173   movement of its physical hand as can be seen in the examples shown in Figure 6b. Moreover,

174   when the hand did move, it made smaller movements with lower velocities than the

175   simultaneous movements of the cursor during BMI trials (n=63 trials; Fig. 6c), but the monkey

176   could still control the cursor using cortical activity alone (Supplementary Movie S2). The monkey

177   retained the ability to accurately discriminate between the targets using the BMI; consistent with

178   the non-BMI task, the monkey was significantly above chance in discriminating targets with Low

179    $\sum f$ (76%, P=0.02, one-sided binomial test), but did not reach significance for medium (65%, P=

180   0.09) or high $\sum f$ (40%, P = 0.21; Fig. 6d).

181

182   **Discussion**

183   We have demonstrated a novel encoding strategy for texture representation using ICMS

184   pulses in somatosensory cortex. Using this new approach, two animals were able to

185   discriminate texture coarseness during active tactile exploration. Importantly, for this task, small

186   variations of arm velocity changed the stimulation frequency; the interpretation of the texture,

187   therefore, may have employed a dynamic integration of ICMS stimulation information with arm

188   proprioception feedback or corollary discharge of motor and sensory cortical regions [25]. The

189   apparently paradoxical trials provided evidence for these possibilities: access to the movement

190   command or proprioceptive feedback about the movement is necessary to disambiguate the

191   exafference of the texture from the reafference due to movement.

192   We observed that both monkeys were better at discriminating textures when the overall

193   spatial frequencies were small, consistent with the Weber-Fechner law [26], a phenomenon

194   reported for numerous sensory modalities [27], including touch [28]. Interestingly, this law was

195   previously reported not to hold for the task of discriminating ICMS amplitude in primates [29] and

196   humans [13]. Our task, in contrast, required discriminating ICMS pulse rates, but, as it also used

197   active exploration we cannot rule out the possibility that some aspect of the effect is due to the

198   motor act itself.

199   Our tactile encoding scheme was effective for a single channel of independent tactile

200   information—mimicking a single mechanoreceptor localized in the fingertip. This encoding

201   scheme most closely resembles the rapidly adapting (RA) afferents of cutaneous somatic

202   sensation [30]: each pulse of ICMS was triggered by the intersection of the active zone of the

203   avatar fingertip with a ridge on one of the gratings. However, there may be advantages of

204   modeling a more slowly adapting type-1 (SA1) encoding on some additional channels. We

205   believe that our encoding will be naturally extendable to arrays of mechanosensors embedded

206   in the "skin" of a prosthetic limb, with each sensor connected to a channel of microstimulation in

207   sensory cortex. For example, each feature in an object's tactile microstructure could trigger a

208   pulse-train of ICMS that persists for some finite duration. This type of encoding may allow an

209   intuitive representation of the persistence of object-actuator contact interactions or complex

210   representation of natural textures [31]. However, a number of open questions remain, such as the

211 optimal timescale or distribution of timescales for adaptation and whether the degree of

212 adaptation must be matched to the properties of the specific neurons being stimulated. Work in

213 primates [6,32] and rats [33] suggests that the plasticity of the brain will allow even a few channels of

214 stimulation to become effective at providing a rich sensory experience, and complex

215 spatiotemporal coding [34] with enough bandwidth to be clinically useful.

216   In our experiment, monkey N was superior to monkey M in perceiving small differences

217 of texture coarseness. While it is possible that this difference was due to a better

218 comprehension of the task by monkey N, it could also reflect the fact that the stimulation region

219 for monkey N was in the leg area while for monkey M it was in the receptive fields of the same

220 arm used to control the joystick. Therefore, it is possible that interference between feedback

221 from natural somatosensory pathways (hand touching the joystick, proprioception) and S1 ICMS

222 feedback made interpretation more difficult for monkey M. This indicates that further studies are

223 necessary to determine, among other things, the best target in S1 for delivering ICMS that

224 encodes tactile signals for future clinical neuroprosthesis. While delivering sensory feedback to

225 an ethologically meaningful cortical area is likely important for the subject to assimilate any limb

226 prosthesis as a natural appendage [35–37], the use of different somatosensory regions in the

227 cortex may facilitate the sensory-motor integration and tactile acuity. Therefore, we suggest that

228 it may be necessary to deliver artificial sensory feedback to multiple cortical regions

229 simultaneously to achieve the best performance of such limb prostheses.

230   Recently demonstrated clinical neuroprostheses have used modulation of stimulation

231 amplitude (or equivalently, pulse-width) to encode the perception of pressure, force or position

232 [8,10,38,39]. Our approach is complementary—stimulation pulse timing encodes coarse texture—and

233 could be combined with the amplitude encoding approach to convey multimodal percepts of

234 pressure and texture. However some previous animal [40] and human [41] stimulation studies have

235 provided indirect evidence that changes in pulse intensity (amplitude or pulse-width) may be

236 perceptually indistinguishable from changes in pulse rate. Further experiments will be necessary

237   to conclusively determine if this is the case or if there is in fact an extra degree of freedom that

238   can be used to convey clinically relevant prosthetic sensations.

239   Finally, we demonstrated that our encoding strategy could be integrated within a closed-

240   loop BMBI task. While the overall performance of the monkey for the BMBI task was lower than

241   during arm-control, the monkey was still able to discriminate the artificial textures. This, along

242   with the simplicity of our ICMS encoding, suggests that this approach could be used to equip

243   clinical upper-limb neuroprostheses with direct access to the tactile features of the natural world.

244

245   **Online methods**

246   All animal procedures were performed in accordance with the National Research

247   Council's Guide for the Care and Use of Laboratory Animals and were approved by the Duke

248   University Institutional Animal Care and Use Committee.

249   *Subjects and Implants*

250   Two adult rhesus macaque monkeys (*Macaca mulatta*) participated in the experiments

251   (monkeys M and N). Each monkey was implanted with four 96-microwire arrays constructed of

252   insulated stainless steel 304. Each hemisphere received two arrays: one in the upper-limb

253   representation area and one in the lower-limb representation area of sensorimotor cortex.

254   These arrays covered both M1 and S1; only microwires implanted in S1 were used for delivering

255   ICMS in study. For the BMI task, we used recordings from the right hemisphere arm arrays as

256   the monkey manipulated the joystick with the left arm. Within each array, microwires were

257   grouped in two four-by-fours, uniformly spaced grids each consisting of 16 electrode triplets.

258   The separation between electrode triplets was 1 mm. The electrodes in each triplet had three

259   different lengths, increasing in 300-mm steps. The penetration depth of each triplet was

260   adjusted with a miniature screw. After adjustments during the month following the implantation

261   surgery, the depth of the triplets was fixed. The longest electrode in each triplet penetrated to a

262   depth of 2 mm as measured from the cortical surface.

263   *Task*

264   Each monkey sat in a primate chair, faced a computer screen and grasped a joystick

265   with their left hand. The joystick handle contained an optical sensor to indicate when the

266   monkey released it. The monkeys were trained to manipulate the joystick to control the

267   movements of a left upper-limb primate avatar on the screen [18,42].

268   Each trial began with a circular target appearing in the center of the screen. The

269   monkeys held an index finger of the avatar within this target for a random delay randomly drawn

270   from a uniform distribution parameterized from 200 to 2000 ms. After this delay, the central

271   target disappeared, and two rectangular object zones appeared on the screen. These appeared

272   either both on the left side or both on the right side of the screen at a distance of 7 cm from the

273   center. Both objects in the pair had the same width, (6 cm). The spacing between the objects

274   was 0.1 cm.

275   Vertical square-wave gratings were superimposed on each of the objects. These

276   gratings, which were not visible to the monkeys, were aligned on the center of each object and

277   were parameterized by spatial frequency, f. When the index finger of the avatar crossed a single

278   ridge in a grating, a pulse of ICMS was delivered to a pair of electrodes implanted in S1 cortex.

279   In this way, the pattern of ICMS delivered depended on the velocity of the avatar and the

280   intrinsic spatial frequency of each grating. The microstimulator was serviced at 100 Hz, which

281   meant that for sufficiently fast velocities or high spatial frequencies, it could be possible that

282   more than a single ridge was crossed in a 10 ms interval. If this occurred, we delivered N pulses

283   at N*100 Hz, where N was the number of ridges crossed since the last clock cycle. This

284   operation delivered the correct number of pulses at the correct rate, in expectation, at the cost

285   of up to 10 ms of latency.

286   Symmetric, biphasic, charge-balanced, cathode-leading ICMS pulses were delivered in a

287   bipolar fashion across pairs of microwires. The channels selected had clear sensory receptive

288   fields in the left forearm (monkey M: two pairs of microwires) or left lower limb (monkey N: one

289   pair of microwires). For monkey M, the cathodic and anodic phases of stimulation had a pulse

290   width of 105 µs; for monkey N, the pulse phases were each 200 µs. The cathodic and anodic of

291   the stimulation waveforms were separated by a 25 µs interphase interval. The pulse amplitudes

292   were set to the minimal effective current, as found through psychometric measurements

293   separately for each monkey [43].

294   Monkeys received a reward for selecting the object from the pair with the higher spatial

295   frequency, f, drawn from:

296    $$f \in \{0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0\} \text{ ridges/cm}$$

297   with the constraint that both objects did not share the same f on a single trial. Monkey M did not

298   discriminate the gratings as reliably and so was not presented any gratings with the highest

299   spatial frequency, 4.0 ridges/cm. The monkeys indicated their choice by holding the avatar over

300   one of the objects for the hold interval (2 seconds for the hand control and 1 second for the

301   BMBI task). Selecting the object with the higher f triggered the delivery of a fruit juice reward;

302   selecting the object with lower f ended the trial without reward.

303   The objects could be explored in any sequence. Moreover, objects could be re-explored

304   and re-compared multiple times in a trial. However, the avatar had to pass over both objects at

305   least once per trial. Trials for which only a single object was explored were terminated without

306   reward, even if the correct object was ultimately selected. Trials for which the monkey released

307   the joystick handle at any time, selected the wrong object, made a selection without exploring

308   both objects, or held the avatar outside of either of the objects for 10 s, resulted in the

309   termination of a trial and penalty interval of 2 s for monkey M and 2.5 s for monkey N.

310   We employed correction trials. This meant that after an incorrect trial, the next one

311   repeated with the same object locations and object-frequency identities. These correction trials

312   were used to keep the monkeys motivated and to prevent them from acquiring systematic

313   biases. As the rewarded object was known to the monkeys for correction trials, we excluded

314   these trials from all analyses.

315

316   *BMI decoding*

317   A 10th-order Unscented Kalman filter (UKF) was used for BMI predictions, using

318   methods we previously described [18,44]. The filter parameters were fit using the hand movements

319   made while the task was performed using a joystick. The monkey was permitted to continue

320   moving the joystick, but was only rewarded for target selections made with the brain-controlled

321   cursor.

322

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431

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433   conducted the experiments. JEO, SS, MAL, and MALN analyzed data and wrote the paper.

434

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437

438   **Materials & Correspondence.** The custom code used for the experiments and the data that

439   support the findings of this study is available from the corresponding author upon reasonable

440   request. Requests should be addressed to nicoleli@neuro.duke.edu

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Figure Legends

Fig. 1. **The artificial texture paradigm.** (**a**) A monkey is seated before a display on which an avatar arm and two identical objects are projected. Artificial tactile feedback about the virtual gratings associated with each object is delivered to populations of S1 neurons via temporal patterns of ICMS as the monkey actively scans each object. (**b**) Trials commenced with a random delay interval (1) when the monkey held the index finger of the avatar in the center of the screen. Next, was the exploration interval (2). Two rectangular objects appeared, and the monkey scanned these objects with the index finger of the avatar hand. Each object had an associated virtual grating of vertical lines, which were invisible to the monkey. A pulse of ICMS was delivered to a pair of electrodes in S1 with each crossing of the avatar index finger over a line in one of the gratings. The trial was completed when the monkey indicated its selection (3) by holding the avatar hand over one of the objects for a hold interval. The reward was delivered if the monkey selected the object with the higher virtual grating frequency (inset); selecting the object with the lower grating frequency ended the trial without reward.

Fig. 2. The precise temporal pattern of ICMS delivered on any trial depended both on the intrinsic spatial frequency of each object's virtual grating as well as the velocity with which the monkey scanned each object. For a grating with a given spatial frequency, slow scanning (**a**) would produce a lower ICMS pulse rate than faster scanning (**b**). Irregular scanning (**c**) of a grating produced irregular ICMS pulse trains. All other features of the pulse train (e.g., current amplitude and pulse width) were fixed. (**d-f**). Examples of trials for three values of Δf: (**d**) 3.5 (4.0 vs 0.5) ridges/cm, (**e**) 2.0 (2.0 vs 4.0) ridges/cm, and (**f**) 0.5 (2.0 vs 1.5) ridges/cm, respectively. Traces indicate the x-component of the avatar position (solid lines) and velocity (dashed lines). Gray rectangles indicate the position and horizontal dimension of the

470   objects. Red vertical lines indicate single pulses of ICMS. Trials started with a randomized hold-

471   time (200-2000 ms); a Go cue informed the monkey of the beginning of the exploration interval.

472

473   **Fig. 3**. **Monkeys discriminated spatial gratings based on self-generated temporal ICMS.**

474   (**a-d**) Percentage of trials for which the monkey chose the right-most object, parameterized by

475   the spatial frequencies of the right and left objects, for both monkeys. (**a,b**) The success rate at

476   the first session, and after three and after 10 sessions of training, is reported in parenthesis, and

477   the average percentage of trails for which the right object was chosen when $f_R > f_L$ and when

478    $f_L > f_R$, reported in yellow and blue, respectively.   (**c,d**) The performance for all sessions (11

479   sessions for monkey N, n=10412 and 12 for monkey M, n=5828); monkey M was not presented

480   gratings with 4.0 ridges/cm. Asterisks indicate frequency-pair combinations which were

481   discriminated significantly differently than chance (P<0.05, two-sided binomial test).

482

483   **Fig. 4. Psychometrics analysis of artificial texture discrimination.** (**a,b**) Discrimination of

484   spatial gratings obeys Weber's scaling for (**a**) monkey N and (**b**) monkey M. Each point

485   represents the percentage of trials for which the monkey chose the right-most object,

486   parameterized by the difference in spatial frequencies for a pair of objects (Δf, f_R-f_L) and the sum

487   of the spatial frequencies (f_R+f_L) for low (less than 2.5 ridges/cm, circles), mid (between 2.5 and

488   5 ridges/cm, diamonds) and high (greater than 5 ridges/cm, triangles) sums. Filled symbols

489   indicate discrimination significantly different than chance (P<0.05, two-sided binomial test).

490   Error-bars indicate 95% confidence intervals. Curves are the sigmoid lines of best fit. (**c**) Just

491   noticeable differences (JNDs) for monkey M (diamonds) and N (circles), as a function of the

492   standard frequency (detail of JND calculation for each standard frequency is shown on Figure

493   S3; for monkey M JNDs for f =1 and f= 1.5 were undefined). Linear fits, the corresponding

494   function and R^2 for each graph.
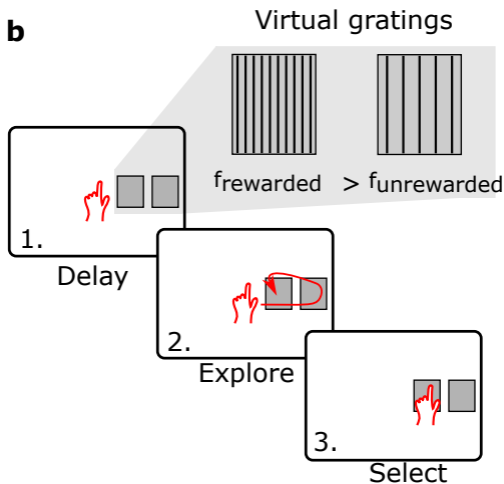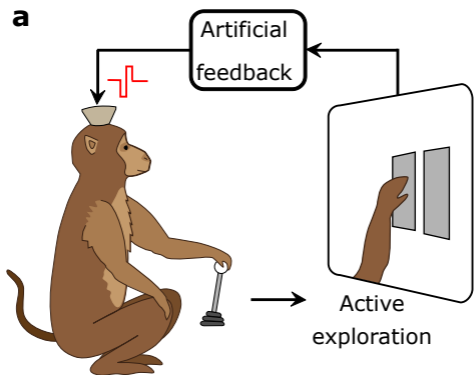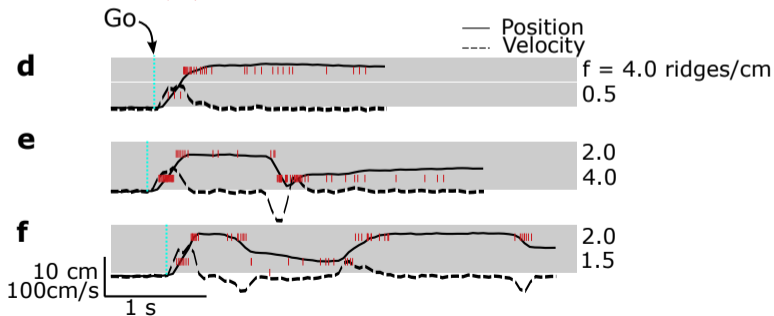
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Fig. 5. Texture perception and arm movement. (**a**) Distribution of per-trial RMS exploration speeds. (**b**) Percentage of trials performed correctly as a function per-trial RMS speed for monkey M and monkey N. Curves are 4th order polynomial fits. Filled symbols indicate discrimination significantly different than chance ($P<0.05$, two-sided binomial test). (**c**) An example of a paradoxical trial with monkey N. First two graphs indicate the x-component of the avatar velocity and the x-position. Gray rectangles indicate the position and horizontal dimension of the objects; their corresponding spatial frequencies were 2.5 and 3.5 ridges/cm, respectively. Vertical red lines indicate single pulses of ICMS. ICMS pulse rate were calculated for bursts of stimulation (a burst of stimulation was considered when the velocity magnitude was maintained above 10 [cm/s]). (**d**) Success rate of the paradoxical trials. The chance level is reported with a black dashed line. Error-bars indicate 95% confidence intervals (one-sided binomial test).

Fig. 6. BMI results (**a**) Same experimental paradigm as in Fig 1a, expect that the control of the avatar arm was done via decoding of motor intention from monkey's motor cortex. The monkey has to hold the joystick during the task, was allowed to move the arm, but the joystick was disconnected (**b**) Examples of two BMI trials and corresponding raster plots. Blue dashed lines report the x projection of the brain-controlled cursor (BMI) and solid black line the monkey's hand movement. ICMS pulses are shown with red vertical lines. Vertical dashed cyan line is the end of the hold time (or onset of exploration), and solid green line is the end of the trial and reward. Raster plots for the trials are grouped between 90 neurons in right hemisphere motor cortex area (R-M1), 47 neurons in right hemisphere sensory area (R-S1) and five neurons in the left hemisphere sensory area. (**c**) The distributions of velocity for the BMI controlled cursor (blue) distribution of the monkey's hand movements (orange). The hand movement was measured via the joystick movement (using the same gain as for hand control trials) and the trial was aborted if the monkey released the joystick handle. (**d**) Percentage success for BMI

522   controlled trials, parameterized by the sum of the spatial frequencies (f_R+f_L) for low (less than

523   2.5 ridges/cm), mid (between 2.5 and 5 ridges/cm) and high (greater than 5 ridges/cm) sums.

524   Error-bars indicate 95% confidence intervals. Filled symbols are statistically different than

525   chance (P<0.05, one-sided binomial test).

526

a Artificial feedback → Active exploration

b Virtual gratings

$f_{rewarded} > f_{unrewarded}$

1. Delay
2. Explore
3. Select

a Slow | 130 μA

100 μs

b Faster

c Irregular

Go

— Position
-- Velocity

d   f = 4.0 ridges/cm
    0.5

e   2.0
    4.0

f   2.0
    1.5

10 cm
100cm/s
1 s

a Monkey N

Session 1 (64%) Session 3 (72%) Session 10 (71%)

Prob. right target for: fR>fL — 80.0% 83.9% 74.3%

Prob. right target for: fL>fR — 38.6% 28.2% 20.8%

f_L (ridges/cm)

c All (11 sessions)

f_R (ridges/cm)

Chose right (%)
0 90

b Monkey M

Session 1 (56%) Session 3 (73%) Session 10 (73%)

64.5% 73.1% 76.5%

47.1% 22.6% 36.0%

f_R (ridges/cm)

f_L (ridges/cm)

d All (12 sessions)

f_R (ridges/cm)

a

b

Chose right (%)

Low $f_R + f_L$
Mid $f_R + f_L$
High $f_R + f_L$

$\Delta,\ f_R - f_L$(ridges/cm)

c

Monkey N

Monkey M

JND = 0.37 f + 0.77
R^2 = 0.95

JND = 0.47 f + 1.06
R^2 = 0.63

JND (ridges/cm)

Standard frquency (ridges/cm)

a

Frequency

- Monkey M
- Monkey N

RMS speed (cm/s)

b

Fraction correct

RMS speed (cm/s)

c

velocity cm/s

1s

x position cm

1s

x position cm

200.2Hz

ICMS pulse rate

f_L: 2.5 ridges/cm

f_R: 3.5 ridges/cm

103.1Hz

0.1s

d

percent correct

Chance

Monkey

N   M

a

Movement decoding

Artificial feedback

Active exploration

c

$\times 10^4$

count

Hand

Cursor

5×10^3

vel [cm/s]

d

% correct

Low   Mid   High

fR+fL [ridges/cm]

b

R²

End hold

Reward

ICMS

BMI

HC

10 cm

1 s

1 s

R-M1

R-S1

L-S1