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Mental Rotation of Digitally-**Rendered Haptic Objects**

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80 Sensory substitution is an effective means to rehabilitate many visual functions after 81 visual impairment or blindness. Tactile information, for example, is particularly useful for 82 functions such as reading, mental rotation, shape recognition, or exploration of space. 83 84 Extant haptic technologies typically rely on real physical objects or pneumatically driven 85 renderings and thus provide a limited library of stimuli to users. New developments in 86 digital haptic technologies now make it possible to actively simulate an unprecedented 87 range of tactile sensations. We provide a proof-of-concept for a new type of technology 88 (hereafter haptic tablet) that renders haptic feedback by modulating the friction of a 89 90 flat screen through ultrasonic vibrations of varying shapes to create the sensation of 91 texture when the screen is actively explored. We reasoned that participants should 92 be able to create mental representations of letters presented in normal and mirror-93 reversed haptic form without the use of any visual information and to manipulate 94 95 such representations in a mental rotation task. Healthy sighted, blindfolded volunteers 96 were trained to discriminate between two letters (either L and P, or F and G; 97 counterbalanced across participants) on a haptic tablet. They then tactually explored 98 all four letters in normal or mirror-reversed form at different rotations (0°, 90°, 180°, 99 and 270°) and indicated letter form (i.e., normal or mirror-reversed) by pressing 100 101 one of two mouse buttons. We observed the typical effect of rotation angle on 102 object discrimination performance (i.e., greater deviation from 0° resulted in worse 103 performance) for trained letters, consistent with mental rotation of these haptically-104 rendered objects. We likewise observed generally slower and less accurate performance 105 with mirror-reversed compared to prototypically oriented stimuli. Our findings extend 106 107 existing research in multisensory object recognition by indicating that a new technology 108 simulating active haptic feedback can support the generation and spatial manipulation 109 of mental representations of objects. Thus, such haptic tablets can offer a new avenue 110 to mitigate visual impairments and train skills dependent on mental object-based 111 112 representations and their spatial manipulation.

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Keywords: haptic, object, multisensory, mental rotation, sensory substitution, low vision, vision impairment

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Mental Rotation of Digitally-Rendered Haptic Objects

INTRODUCTION

In everyday life, vision supports crucial functions that enable 117 us to successfully interact with our environment, such as 118 manipulation of objects as well as spatial orientation and 119 navigation in space. These functions depend on the correct 120 acquisition and maintenance of mental representations of 121 our environment and the objects within it. In sighted 122 individuals, vision typically predominates these functions and 123 spatial abilities more generally (e.g., Welch and Warren, 124 1980; Knudsen and Knudsen, 1989; Schutz and Lipscomb, 125 2007). However, visual impairments affect nearly 300 million 126 people globally, with another \sim 36 million suffering from 127 complete loss of vision (World Health Organization, 2000). Q11 128 This calls for effective rehabilitation methods, including sensory 129 substitution approaches. 130

Studies in visually impaired individuals document the 131 extensive neuroplasticity of both non-visual functions, as well 132 as within visual cortices. For example, visual deprivation 133 enhances tactile acuity not only in sighted individuals (Pascual-134 Leone and Hamilton, 2001; Merabet et al., 2007; Norman 135 and Bartholomew, 2011), but also in blind and visually 136 impaired patients (Goldreich and Kanics, 2003; Lederman 137 and Klatzky, 2009). It is now well-established that cross-138 modal plasticity can promote functions that are supported 139 predominantly by vision. Tactile information has been most 140 widely utilized to date to train functions such as reading 141 (e.g., Braille) and exploration of space (e.g., white cane). 142 Specifically, object geometry and form judgments based on 143 haptics have been demonstrated to activate visual areas along 144 the so-called dorsal pathway (Prather et al., 2004; Sathian, 2005). 145 Furthermore, visual areas have been found to be activated 146 during Braille reading in functional imaging studies (Sadato 147 et al., 1996, 1998, 2002; Burton et al., 2002; Amedi et al., 148 2003). Sathian et al. (1997) were the first to demonstrate, 149 via hemeodynamic imaging, that discrimination of orientation 150 of tactile gratings activates the same extrastriate areas as 151 those observed active during visual orientation discrimination. 152 This cross-modal functional recruitment of nominally visual 153 cortices for tactile perceptual functions most likely results 154 from cross-modal plasticity operating via the interplay between 155 unisensory and multisensory neurons (Amedi et al., 2001; Kitada 156 et al., 2006). More generally, there is now convergent and 157 consistent evidence for visual cortex activation during tactile 158 perception in both blind and sighted individuals (reviewed in 159 Lacey and Sathian, 2014). 160

In addition to evidence pointing to the involvement of 161 visual cortices in tactile discrimination, spatial functions can 162 also be achieved in a modality-independent fashion, including 163 based solely on tactile information. For example, studies of 164 mental rotation where participants need to judge whether an 165 image is portrayed in its normal or mirror-reversed form 166 demonstrate a typical increase in reaction times (RTs) with 167 increasing rotation of the image (Shepard and Metzler, 1971; 168 Lacey et al., 2007a,b). Marmor and Zaback (1976) showed that 169 the same mental rotation effect occurs with tactile stimuli. 170 This and other findings have led to the belief that spatial 171

properties can be encoded in a modality-independent format172(Lacey and Campbell, 2006), and may thus engage a common173spatial representational system(Lacey and Sathian, 2012;Lee Masson et al., 2016).175

The discovery of modality-independence of spatial 176 representations has opened a new avenue for vision 177 rehabilitation, i.e., tactile-based sensory substitution. One 178 particularly striking example here is the successful use of haptic stimulation of the tongue with the tongue-display unit (TDU) 180 to retrain "tactile-visual" acuity (TDU, Chebat et al., 2007). 181 The TDU is a sensory substitution device (SSD) that converts 182 a visual stimulus into electro-tactile pulses delivered to the 183 tongue *via* a grid of electrodes. Visually impaired individuals 184 were able to discriminate various orientations of the letter E 185 (i.e., the Snellen E test) based solely on stimulation with the 186 TDU (Chebat et al., 2007). While such efforts are impressive, 187 they risk remaining limited in their applications. However, 188 this is at least partially addressed in new technologies for 189 digitization of information, such as tablets digitally rendering 190 tactile information (e.g., Xplore Touch¹). This digitization of 191 information has led to significant improvements in healthcare, 192 including reduced costs and increased accessibility and reliability 193 of treatments (Noffsinger and Chin, 2000; Dwivedi et al., 194 2002). Currently, visually impaired individuals require 195 persistent training for the rehabilitation of visual functions 196 that support basic everyday activities such as cooking, cleaning, 197 and navigating one's environment. This involves numerous 198 hours of work together with therapists. Digitalizing the method 199 of delivery of therapeutic procedures would likely allow 200 visually impaired patients to be more independent and, so, 201 successful, in their training. For one, the therapeutic programs 202 could be created online and then easily downloaded onto 203 a digital device. Second, patients would be able to practice 204 and improve their tactile acuity as well as their form and 205 object perception abilities without the constant presence 206 of a therapist. 207

It is known that spatial operations such as mental rotation 208 can be supported solely by tactile stimuli such as Plexiglas 209 forms or wooden blocks (Marmor and Zaback, 1976; Carpenter 210 and Eisenberg, 1978, for recent reviews see Prather and 211 Sathian, 2002; Lacey et al., 2007a). By contrast, it is unknown 212 whether individuals can create and manipulate mental 213 representations of objects based solely on simulated haptic 214 representations. If spatial functions can be rehabilitated with 215 digital devices, this should substantially improve both the 216 speed and the extent of the recovery and independence of 217 visually impaired patients. Haptic tablets thus promise to 218 open up unprecedented possibilities for recovery of visual 219 functions for blind and visually impaired individuals, due 220 to the ease of delivery of digital information and of the 221 transfer of the learnt information from tablet to veridical 222 environments. Being able to mentally rotate digitally presented 223 haptic objects would serve as an important proof-of-concept 224 for the successful acquisition of a representation of a simulated 225 haptic space. 226

¹http://www.hap2u.net

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To this end, the present study investigated whether 229 participants would be able to successfully mentally rotate 230 representations of letters in their normal and mirror-reversed 231 forms, experienced solely via digitally-rendered haptic feedback. 232 We focused on the distinction of letter forms (i.e., normal 233 vs. mirror-reversed), because judgments of letter identity 234 (for example the distinction between a letter and a number) 235 do not necessarily implicate mental rotation (White, 1980). 236 We hypothesized that normally-sighted participants should 237 show the prototypical mental rotation effect, with steadily 238 decreasing accuracy (and increasing RTs) with increasing 239 240 angular disparity from the prototypical upright letter orientation, 241 which would translate into a main effect of angle. Moreover, we expected that participants would show better performance 242 with letters in their normal form compared to mirror-243 reversed letters, due to the well-investigated effect of stimulus 244 245 familiarity on mental rotation (White, 1980; Bethell-Fox and Shepard, 1988; Prather and Sathian, 2002), illustrated 246 by a main effect of letter form, due to the mentioned effect 247 of stimulus familiarity. We also expected a main effect of 248 training, meaning that participants would perform better with 249 letters which they had trained with, compared to letters that 250 were untrained. 251

MATERIALS AND METHODS

Participants

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256 All participants provided written informed consent to 257 procedures approved by the cantonal ethics committee in 258 accordance with the Declaration of Helsinki. We tested 17 adults 259 (12 women and five men; age range 25–37 years, mean \pm stdev: 260 28.9 \pm 3.5 years), who volunteered for our experiment. 261 Participants reported normal or corrected-to-normal vision. 262 No participant had a history of or current neurological or 263 psychiatric illness. Handedness was assessed via the Short Q11 264 Form of the Edinburgh Handedness Inventory (Oldfield, 1971). 265 Two of our participants were left-handed, while the remainder 266 were right-handed. We also asked our participants about their 267 experience playing a musical instrument, due to evidence 268 of increased cortical representation of the hands of musical 269 instrument players (see e.g., Elbert et al., 1995). Nine participants 270 were active instrument players (i.e., actively played instruments 271 at the time of the testing session), five had formerly played 272 instruments (i.e., during childhood, adolescence and early 273 adulthood, however they were not actively practising at the time 274 of testing), and three played no instruments.

276 Apparatus

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277 Haptic stimulation was delivered via a tablet with a 278 TFT capacitive 7-inch touchscreen with a resolution of $1,024 \times 600$ pixels. The screen of the tablet is controlled by 279 a Raspberry Pi 3 based system, and the operating system is 280 Raspbian (Linux). The processor of the tablet is a Broadcom 281 ARMv7, quadcore 1.2 GHz and it has 1 Go RAM and Rev C 282 283 WaveShare. The tablet comes with a haptic creation tool, which is a software that allows for user control of haptic textures. 284 Several other APIs based on C++ or Java are installed, such as 285

library tools that allow the implementation of haptics on other applications. Figures in jpeg format were re-coded in haptic format using a kit written in C++. For more technical details describing the rendering of the haptic feedback, see Vezzoli et al. (2016, 2017) and Rekik et al. (2017). 290

Stimuli

Stimuli consisted of four capital letters—L, P, F and G—created 293 in Paint (see e.g., Carpenter and Eisenberg, 1978; see also 294 Figure 1). We chose these capital letters as their mirror-image 295 counterparts do not confuse, as compared to for example 296 lower-case "d," whose mirror image is "b" and "b," whose mirror 297 image is "d" (Corballis and McLaren, 1984). Moreover, these 298 letters have previously been used in mental rotation tasks (Cohen 299 and Polich, 1989; Rusiak et al., 2007; Weiss et al., 2009), including 300 tasks with tactile objects (e.g., Carpenter and Eisenberg, 1978). 301 The letters were resized to always be presented centrally on the 302 screen of the haptic tablet, which has a pixel resolution smaller 303 than that used to generate the images. Letters were then rotated 304 to 0° , 90° , 180° and 270° and mirrored in Matlab. Letter size was 305 935×509 pixels. With regard to the image to haptic conversion, 306 the letters appeared centrally on a white background. White 307 pixels did not result in a texture on the finger. All non-white 308 pixels were then coded with the same haptic texture, which was 309 created using the hap2u pre-installed Texture Editor software. 310 The ultrasonic vibration was adjusted to have a square shape, as 311 this offers the most intense and quick reduction of the friction 312 of the screen under the finger, thus conferring a rather sharp 313 and pointy sensation, in contrast to a sinusoidal-shaped wave, 314 which would confer a rather smooth perception. The period of 315 the window of one square ultrasonic signal was chosen to be 316 3,500 µm (which is considered a "coarse" texture, see Hollins 317 and Risner, 2000), and the amplitude was set at 100%, meaning 318 roughly 2 µm (as the friction reduction hits a plateau at this 319 value, see e.g., Sednaoui et al., 2017). 320 321

Procedure and Task

Participants were tested in a sound-attenuated, darkened room 323 (WhisperRoom MDL 102126E). Subjects were blindfolded and 324 wore noise-canceling headphones (Bose model QuietComfort 2), 325 in order to block any residual light and the sounds of the 326 ultrasonic vibrations produced by the tablet. None of the 327 participants had any prior visual or haptic exposure to the 328 stimuli used in the paradigm, minimizing any cross-modal 329 facilitation (Lacey et al., 2007a,b). The participant's task was 330 a two-alternative forced choice that required discrimination 331 of normal and mirror-reversed letters via a mouse click (left 332 mouse press for the normal form, right mouse press for the 333 mirrored form; same for all participants). Participants were 334 instructed to use a finger from their dominant hand for tablet 335 exploration, and the non-dominant one for responses. The 336 task was to feel the letter on the haptic tablet for 30 s, 337 recognize the letter, and if needed, to mentally rotate the 338 letter to the 0° form, in order to decide whether the normal 339 or the mirror-reversed form had been presented. We used 340 explicit instructions, since it has been reported that this is 341 not a determinant of whether a mental rotation effect is 342

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observed (reviewed in Prather and Sathian, 2002). Stimuli were 372 presented for a duration of 30 s. Next, participants had 20 s 373 for responding, and were instructed to respond as quickly 374 and as accurately as possible. After the response, the next 375 trial was initiated and was preceded by an inter-trial interval 376 randomly ranging between 500 and 1,000 ms. Each participant 377 completed three blocks of training, each comprising 16 trials 378 (two per condition; informed by a pilot study). Participants 379 were trained on pairs of two letters—either L and P or F and 380 G—that they were assigned in a counterbalanced manner across 381 individuals. We grouped these letters given their perceptual 382 closeness, which allowed a progressive learning procedure. We 383 decided to focus the training on a particular letter pairing in 384 order to investigate skill transfer to new, untrained stimuli. 385 Participants were first trained to explore the tablet screen via 386 lateral sweeps [(Stilla and Sathian, 2008), see e.g., (Lederman 387 and Klatzky, 1993) for a discussion of which tactile exploration 388 strategies are particularly appropriate to disclose specific object 389 characteristics, and (Hollins and Risner, 2000) for a discussion 390 of how dynamic vs. static exploration affects coarse (>100 μ m) 391 as compared to fine texture discrimination], using only one 392 finger at a time. Subjects were allowed to change the finger 393 they used for exploration, due to a common complaint about 394 adaptation of their tactile sensation during the pilot experiments 395 or during the training blocks. However, they were not allowed 396 to change the hand used for exploration. Subjects were then 397 taught how to discriminate horizontal from vertical lines, and 398 finally, how to discriminate between the two letters that they were 399

trained on. The experimenter gave subjects verbal instructions and feedback throughout the training session. The testing phase comprised four blocks of 32 trials, making 128 trials in total per participant (i.e., eight trials per each condition, in total 16 conditions). During the experiment, participants were allowed to take regular breaks between blocks of trials to maintain high concentration and prevent fatigue. Stimulus delivery and behavioral response collection were controlled by Psychopy software (Peirce, 2007).

Behavioral Analysis

Data were pre-processed in Matlab and analyzed in R (R Core 440 Development Team, 2017) and SPSS (IBM Corp, 2017). First, 441 we excluded all trials with RTs longer than 15 s (5% of trials), 442 as well as missed trials (2.5% of trials), which were trials where 443 a response was not given within 20 s. We then excluded any 444 remaining outlier trials on a single subject basis (i.e., for each 445 subject and condition), applying a mean ± 2 standard deviations 446 criterion to their RTs (2.7% of trials, see Ratcliff, 1993; Field et al., 447 2012). Accuracy was then calculated. RT data were not further 448 analyzed, since responses were only provided after stimulus offset 449 followed by a subsequent cue. Data from three participants were 450 excluded due to very low accuracy for the 0° condition (<50%). 451 We compared Accuracy with a $2 \times 2 \times 4$ repeated measures 452 ANOVA with factors Training (trained/untrained), Condition 453 (normal/mirror) and Angle (0°, 90°, 180°, 270°), after not having 454 found a significant deviation from the Normal distribution and 455 from homoscedasticity. 456

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Mean accuracy rates are displayed in Figure 2. The 459 $2 \times 2 \times 4$ ANOVA with factors of Training (trained/untrained), 460 Condition (normal/mirror) and Angle (0°, 90°, 180°, 270°) 461 revealed a significant interaction and two main effects. The 462 Angle × Trained interaction was significant ($F_{(1,13)} = 4.912$; 463 $p < 0.05, \eta_p^2 = 0.274$), and there were main effects of Training 464 $(F_{(1,13)} = 5.88; p = 0.03, \eta_p^2 = 0.314)$, with generally higher 465 accuracy scores for trained vs. untrained letters, and Condition 466 $(F_{(1,13)} = 6.02; p = 0.02, \eta_p^2 = 0.317)$, with generally higher 467 468 accuracy scores for normal compared to mirrored stimuli. Given this significant interaction, we carried out separate 469 2×4 ANOVAs (Condition \times Angle) for trained and untrained 470 letters. Untrained letters revealed no interactions or main effects 471 (F < 0.6). By contrast, trained letters exhibited a main effect of 472 Condition ($F_{(1,13)} = 11.46, p < 0.01, \eta_p^2 = 0.470$) and a main effect 473 of Angle ($F_{(3,13)} = 6.625$, p = 0.02, $\eta_p^2 = 0.338$). Trained letters 474 in their normal form had higher accuracy scores compared to 475 trained letters in their mirrored form, and accuracy generally 476 decreased with increasing angular disparity. Performance on 477 untrained normal letters was more similar to performance on 478 479 mirrored letters than to normal trained letters.

¹ DISCUSSION

We provide the first demonstration that digitally-rendered haptic stimuli can support the creation of mental representations of objects that can then be spatially manipulated. Participants' accuracy scores decreased with greater angular disparity of the presented letters from upright, indicating a prototypical mental rotation effect for trained letters (Shepard and Metzler, 1971). Moreover, letters in their mirrored form were less accurately detected compared to letters in their normal form, consistent with the stimulus familiarity effect that has been previously found to influence mental rotation with real visual stimuli (White, 1980). Specifically, normally sighted participants performed significantly better when tested on previously trained compared to untrained letters. This effect was observed for letters presented 514 in their canonical form, and less for letters in their mirrored 515 form. In addition, our results show that a short training session 516 of about 45 min on the haptic tablet was sufficient to significantly 517 increase the ability to correctly identify the correct form of 518 haptic letters. These results extend previous efforts to support 519 rehabilitation of spatial functions using SSDs, and open new 520 avenues for applications of digital haptic technology. 521

Mental rotation of objects created by haptic feedback 522 successfully modulated accuracy of object recognition; increasing 523 angular disparity away from the prototypical orientation linearly 524 reduced recognition accuracy. As expected, performance was 525 significantly higher for normal letters, compared to mirrored 526 letters, and for trained letters, as compared to untrained letters. 527 Accuracy for letters in their normal upright form decreased up 528 to 180°, with a slight increase for stimuli rotated at 270°. Similar 529 results have previously been found in mental rotation tasks with 530 stimuli of different kinds (see e.g., Kosslyn et al., 1998; Hyun and 531 Luck, 2007; Milivojevic et al., 2011; Zeugin et al., 2017), further 532 corroborating that our experimental manipulation was effective 533 and that mental rotation of our haptic letter stimuli indeed 534 took place. The significant interaction between factors Condition 535 and Angle illustrates the fact that mental rotation of familiar 536 stimuli was more successful than for unfamiliar stimuli. To be 537 precise, given that the stimuli were letters, they can generally 538 be considered familiar stimuli, however only letters presented 539 in their normal form can be considered overlearned (White, 540 1980), while letters in their mirrored form can be considered 541 unfamiliar, as individuals are seldomly using mirrored letters 542 in their everyday lives. In addition, the significant effect of the 543 factor Training indicates that with only little training on the task 544 and limited exposure to haptic stimulation before the testing, 545 participants were able to improve their performance, which was 546 not the case for untrained letters. 547

Our findings replicate and extend prior studies of mental 548 rotation based on haptic information. Mental rotation has 549 been studied with Plexiglas letters and objects (Carpenter 550 and Eisenberg, 1978; Hunt et al., 1989), abstract Braille-like 551



right displays results for mirrored stimuli. Red lines refer to trained stimuli, while the blue lines represent untrained stimuli.

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stimuli (Röder et al., 1997), as well as with haptic versions of 571 the Shepard and Metzler (1971) stimuli (Robert and Chevrier, O12 572 2003). These and other similar works have likewise shown that 573 performance worsens with increasing angular displacement from 574 upright, independently of whether an explicit instruction was 575 576 provided to use a strategy based on mental rotation (reviewed in Prather and Sathian, 2002). By contrast, evidence of mental 577 rotation with tactile stimuli does appear to vary with task. Tasks 578 requiring mirror-image discrimination yield mental rotation 579 580 effects, whereas those requiring identification of isolated stimuli generally do not (Prather and Sathian, 2002). Our study required 581 582 participants to discriminate whether each stimulus was normal 583 vs. mirror-reversed, and we indeed observed a mental rotation effect for trained letters. Our accuracy rates are consistent 584 with, albeit somewhat lower than, what has been reported in 585 sighted participants presented with physical objects (\sim 80%–90% 586 in Marmor and Zaback, 1976; Röder et al., 1997; Robert 011 587 and Chevrier, 2003). However, two important distinctions 588 in our study are the use of digital haptics, and moreover, that 589 participants could only use a single finger to explore the stimulus. 590 Ongoing efforts are working to enhance the haptic perceptual 591 qualia as well as to permit exploration by multiple fingers 592 simultaneously. Such notwithstanding, this limitation may 593 nonetheless help us hone in on specific exploration and haptic 594 learning strategies. Minimally, our results demonstrate that 595 mental representations of haptic objects and their discrimination 596 can be ascertained using information acquired with a 597 598 single digit.

599 To summarize, our results indicate that participants were 600 able to mentally manipulate internal representations of familiar stimuli that they learned solely in a haptic manner, through 601 602 interaction with a digitally created texture. While our results have potential applications in the simulation of tactile sensorial 603 perceptions in virtual reality, we do not have the space to 604 discuss these at length here. Instead, we would like to focus on 605 the important implications that our results have for cognitive 606 models of spatial functions, as well as on the implications for 607 the rehabilitation thereof in patients suffering from impairments 608 due to vision loss. In what follows, we will discuss these latter 609 two points. 610

⁶¹² Implications for Models of Spatial

613 Functions

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614 Our results have implications for current models of cortical mechanisms that decode spatial characteristics of objects. 615 616 Recently, evidence has been accumulating for a decoding 617 mechanism that is modality-independent, with spatial features of objects and spaces being communicated through visual 618 619 (Koenderink et al., 1992; Erens et al., 1993), haptic (Kappers and 620 Koenderink, 1999; Prather et al., 2004; Snow et al., 2014; Lee Masson et al., 2018), and auditory (Amedi et al., 2007, 2002) 621 information alone, as well as through multisensory information 622 (Lacey et al., 2009; Sathian et al., 2011; Lacey and Sathian, 2014; 623 Lee Masson et al., 2016, 2017). Moreover, it was demonstrated 624 625 that multisensory regions, such as V1, IPS, and LOC, specifically encode spatial characteristics such as shape, but not object 626 identity (Amedi et al., 2002). Our results further support 627

such modality-independent models of spatial representations. 628 In particular, it was possible for us to convey the shapes of 629 haptic objects (i.e., letters) to participants through unisensory 630 haptic stimuli. This indicates that spatial features of objects, 631 and, specifically, of object shape, can be decoded from a variety 632 of stimulus formats-be it visual, auditory, or somatosensory. 633 However, sensory impressions coming from haptic and visual 634 information are very different (Rose, 1994), and vision and touch 635 use different metrics and geometries (Kappers and Koenderink, 636 637 1999). Nevertheless, there is substantial neuroimaging evidence showing that vision and touch are intimately connected even 638 if there is no direct, one-to-one mapping (see Amedi et al., 639 2005; Sathian, 2005 for reviews). For one, cerebral cortical 640 areas previously regarded as exclusively unisensory in nature 641 are activated by sensory inputs in a task- and stimulus-specific 642 manner (Lacey et al., 2007a). New evidence also supports 643 high similarities between visual and haptic representations 644 of object perceptual spaces (Cooke et al., 2007; Wallraven 645 et al., 2014; Lee Masson et al., 2016). These results have been 646 further complemented by neuroimaging studies, that helped in 647 corroborating the result of high correlations between perceptual 648 spaces reconstructed using tactile vs. visual information (Snow 649 et al., 2014; Smith and Goodale, 2015). Indeed, clinical cortical 650 lesion studies demonstrate that lesions of visual brain areas, 651 such as the inferior occipito-temporal cortex, or the anterior 652 intraparietal sulcus, are accompanied by tactile agnosia for 653 objects, despite intact somatosensory cortical areas (Feinberg 654 et al., 1986; James et al., 2002). Collectively, our results support 655 a task-specificity, as compared to a stimulus-specificity, of spatial 656 functions. 657

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Implications for Rehabilitation of Spatial Functions

Our study further validates efforts of rehabilitation of spatial 661 functions through SSDs. Cross-modal and multisensory 662 integration are the drivers of neuroplasticity in visual areas 663 (Kirkwood et al., 1996; Amedi et al., 2004; Merabet et al., 2005; 664 Pascual-Leone et al., 2005; Murray et al., 2015), which promotes 665 a task-selective and modality-independent re-specialization of 666 these cortical structures. Besides the known applications of 667 tactile sensory substitutions such as the Braille alphabet, white 668 cane, or the TDU, our results open new avenues for mitigation 669 of deficiencies of spatial functions in the blind and visually 670 impaired. Indeed, it has been demonstrated numerous times 671 that tactile information can support spatial functions in blind, 672 visually impaired, and sighted subjects (Marmor and Zaback, 673 1976; Carpenter and Eisenberg, 1978; Grant et al., 2000; Ptito 674 et al., 2005; Sathian, 2005; Chebat et al., 2007; Wan et al., 2010; 675 Rovira et al., 2011; Vinter et al., 2012). However, the main 676 innovation introduced by our study is the digital simulated 677 nature of the tactile stimuli. As digital information is easily 678 recoded and reproduced, our results open new exciting venues 679 for increased accessibility of traditionally visual functions, such 680 as reading, navigation, etc., to visually impaired people. 681

In addition, such tactile substitution and multisensory 682 techniques can also be used to retrain spatial functions after sight 683 restoration. Specifically, patients with long-lasting cataracts 684

have deficient depth perception after cataract removal 685 (Hartung, 1962; Gregory, 2003; McKyton et al., 2015), 686 despite normal low-level visual perception. Thus, as auditory 687 information is unable to confer spatial information (Amedi 688 et al., 2002), one could imagine complementing rehabilitation 689 690 programs with tactile spatial information, in order to confer distance relations in a multisensory manner. Another exciting 691 endeavor for further research that we are now also pursuing 692 in the laboratory is the extent to which simulated haptic 693 694 information can support the encoding of entire familiar and 695 new spaces. In short, simulated tactile information has critical 696 implications for applications in rehabilitation regimes. Besides 697 being specifically able to convey spatial relations, as opposed to auditory information, simulated tactile stimuli have the 698 added value of accessibility. This benefit renders tactile tablets a 699 promising solution for the mitigation of complete or partial loss 700 of spatial abilities due to sensory loss or deprivation. 701

CONCLUSION

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We trained normally-sighted participants on a haptic mirrorimage discrimination task, using a new technology that digitally simulates texture. After only a short exposure and habituation to the new sensation, and relatively little training on the task, participants were able to mentally manipulate internal representations of the trained letters. This indicates that spatial functions and attributes such as object shape rely on a modalityindependent mechanism, and that multiple sensory modalities are capable of supporting spatial computations. Furthermore, our results have important implications for research on virtual

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simulated sensorial perception, as well as for neural plasticity and 742 visual rehabilitation, and highlight the merit of restoring visual 743 functions through SSDs. 744

DATA AVAILABILITY

The datasets generated for this study are available on request to 748 the corresponding author. 749

AUTHOR CONTRIBUTIONS

753 RT and MM conceived the study. TR and CC provided essential 754 equipment. RT, J-FK, NT, FA, JR, and MM analyzed the data. All authors contributed to the interpretation of the results and to the 756 writing of the manuscript. 757

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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