

Other ways of seeing: From behavior to neural mechanisms in the online “visual” control of action with sensory substitution

Michael J. Proulx^{a,*}, James Gwinnutt^a, Sara Dell’Erba^a, Shelly Levy-Tzedek^b,
Alexandra A. de Sousa^{a,c} and David J. Brown^a

^a*Crossmodal Cognition Lab, Department of Psychology, University of Bath, Bath, UK*

^b*Cognition, Aging and Rehabilitation Lab, Recanati School for Community Health Professions,
Department of Physical Therapy & Zlotowski Center for Neuroscience, Ben Gurion University of the Negev,
Beer-Sheva, Israel*

^c*Department of Science, Bath Spa University, Bath, UK*

Abstract. Vision is the dominant sense for perception-for-action in humans and other higher primates. Advances in sight restoration now utilize the other intact senses to provide information that is normally sensed visually through sensory substitution to replace missing visual information. Sensory substitution devices translate visual information from a sensor, such as a camera or ultrasound device, into a format that the auditory or tactile systems can detect and process, so the visually impaired can see through hearing or touch. Online control of action is essential for many daily tasks such as pointing, grasping and navigating, and adapting to a sensory substitution device successfully requires extensive learning. Here we review the research on sensory substitution for vision restoration in the context of providing the means of online control for action in the blind or blindfolded. It appears that the use of sensory substitution devices utilizes the neural visual system; this suggests the hypothesis that sensory substitution draws on the same underlying mechanisms as unimpaired visual control of action. Here we review the current state of the art for sensory substitution approaches to object recognition, localization, and navigation, and the potential these approaches have for revealing a metamodal behavioral and neural basis for the online control of action.

Keywords: Sensory substitution, blindness, prosthetics, object recognition, perception for action, active sensing

Our senses allow us to interact with the world. Vision in particular is adapted to providing information about distant, silent objects by decoding the reflected or emitted light to perceive what objects are and where they are (Marr, 1982). The distinction between recognition and localization maps led on to the discovery of

two processing streams in the visual brain for “where” information in the dorsal stream and “what” information in the ventral stream (Mishkin & Ungerleider, 1982). It has been suggested that these categories should be modified: the “where” category includes perception for action in addition to mere spatial perception, and would more appropriately be termed “how” rather than just “where” (Milner & Goodale, 2008). It is worth noting that, although there is this appar-

*Corresponding author: Michael J. Proulx, Department of Psychology, University of Bath, 2 South, Bath BA2 7AY, UK. Tel.: +44 1225 385963; E-mail: m.j.proulx@bath.ac.uk.

ent dissociation of processing into two streams in the brain, there certainly must be many interactions between the two: one must know what something is to know where it is and how to act upon it. This is apparent in any experience where one simultaneously processes what and where something is while acting upon such information, but also in an extensive line of recent work that has shown that action can impact perception, and vice-versa (Biegstraaten, de Grave, Brenner, & Smeets, 2007; Cressman & Henriques, 2011). The adaptive nature of action, such as hand motion, in response to perceptual information is termed the perceptual online control of action (Gritsenko, Yakovenko, & Kalaska, 2009). Perception for action research provides a dynamic perspective given that one must continually map and re-map the surroundings in a reference frame to accommodate for self-movement and the movement of other objects (Pasqualotto & Proulx, 2012; Pasqualotto, Spiller, Jansari, & Proulx, 2013b).

For example, past research has shown that when hand motion is directed towards a visual target, an initial set of instructions is sent to the muscles controlling both hand and eye motion, and that this information is updated from retinal and extra-retinal signals as the motion occurs to fine tune the trajectory of the hand. This allows one to account for any changes in location of the target (Goodale, Pelisson, & Prablanc, 1986; Sarlegna et al., 2004) and to correct small performance errors (Gritsenko et al., 2009). This fine tuning of motion is termed online control of action and is suggested to be automatic rather than voluntary (Gritsenko et al., 2009). Transcranial magnetic stimulation (TMS) can disrupt individuals' online corrective behavior when placed over the posterior parietal cortex, suggesting it plays an important role in the online updating of motor actions (Gomi, 2008).

The online control of action can occur in the other senses, for example, human can use auditory feedback and even echolocation to direct movements toward a target (Boyer et al., 2013; Thaler, 2013; Thaler, Arnott, & Goodale, 2011; Thaler & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2014). Recent work to develop prosthetics for sight restoration aims to provide "visual" online control through methods of sensory substitution for vision using the other senses. Sensory substitution devices aim to provide various features and dimensions of visual information for the visually impaired by translating visual information into tactile or auditory form

(Bach-y-Rita & Kercel, 2003; Meijer, 1992; Proulx, 2010).

Here we review the research on sensory substitution for vision restoration in the context of providing the means of online control for action in the blind or blindfolded. First we will describe sensory substitution in more detail, and then we will examine how such devices are used for object recognition, localization, and action, including pointing, grasping, and navigation behaviors. We summarize with a review the neural basis for perception through such devices and note the excellent potential to reveal new, underlying neural mechanisms for the online control of action (Levy-Tzedek et al., 2012b).

1. Substituting vision with auditory or tactile perception

Vision has special properties that are challenging to convey to the other senses in that the bandwidth of vision, and the capacity for parallel processing, exceeds that of the other senses (Pasqualotto & Proulx, 2012). Parallel processing is crucial for multisensory integration and thus multisensory perception and learning. This is disrupted in congenital visual impairment because vision provides the best spatial acuity and processing capacity to integrate information from the other senses (Proulx, Brown, Pasqualotto, & Meijer, 2014). The information capacity of the human eye has been estimated to be around 4.3×10^6 bits per second (Jacobson, 1951). This is four orders of magnitude greater bandwidth than estimates of the human fingertip of 100 bits per second (Kokjer, 1987), and other areas of skin estimated even lower, from 5 to 56 bits per second (Schmidt, 1981). The information capacity of the human ear is between these two estimates, and the highest after vision, with a capacity at 10^4 bits per second (Jacobson, 1950). For this reason, although the original tactile-visual sensory substitution systems used the skin of the back or stomach as an analogue of the retina (Bach-y-Rita, Collins, Saunders, White, & Scadden, 1969), the modern version uses more sensitive areas such as the forehead or tongue (Bach-y-Rita & Kercel, 2003). Even so, compared to central vision it is low-resolution.

The first general-purpose auditory sensory substitution system was invented by Meijer (1992) to provide a higher resolution substitution mechanism. Although the skin/retina analogue is obvious in some ways due to

136 the topographic representation of spatial locations on
137 each, the auditory system, compared to the skin, pro-
138 vides a higher informational capacity to convey visual
139 information to the brain. Meijer's invention, "The
140 vOICe" (the middle letters signify, "Oh, I see!") con-
141 verts images captured by a camera into sound through
142 headphones. Each image is translated into sound with
143 a left-to-right scan every one or two seconds with tim-
144 ing and stereo cues representing the horizontal axis,
145 frequency representing the image's vertical axis and
146 loudness representing pixel brightness. The input can
147 take many forms, however is always two-dimensional
148 in nature, with one camera providing sufficient visual
149 information for this. The software can run on Android
150 phones, and can use the phone's camera, or with a web-
151 cam input for a PC. Spy sunglasses, with a webcam on
152 the bridge of the nose, allow the visual input to be near
153 the impaired or blindfolded eyes as a form of monoc-
154 ular vision. There are other auditory approaches to
155 substitution. The Prosthesis for Substitution of Vision
156 by Audition, for example, uses frequency to code for
157 both axes by increasing from bottom to top and from
158 left to right of the converted image, with increased
159 representation of the center of the image as occurs
160 with the fovea (Capelle, Trullemans, Arno, & Veraart,
161 1998).

162 Both of these devices, with extensive training,
163 result in experiences that seem qualitatively similar to
164 vision in some ways. Participants report distal attribu-
165 tion with tactile and auditory substitution for vision,
166 rather than just merely attributing perceptual experi-
167 ence to the stimulated modalities (Auvray et al.,
168 2005). Fascinatingly, a long-term user of The vOICe
169 has acquired blindness later in life, and reports having
170 visual imagery evoked by the device that is reminis-
171 cent of vision, including depth perception and smooth
172 movement (Ward & Meijer, 2010). These findings
173 of distal attribution and visual phenomenology con-
174 verge with theoretical work concerning whether the
175 experience of sensory substitution is more like the
176 sensory modalities which have been substituted or
177 those which are doing the substituting (Hurley & Noë,
178 2003), with some concluding that the experience is
179 an extension of the sensory capacities of the individ-
180 ual to a novel sensory modality domain (Auvray &
181 Myin, 2009). There is a unifying role for sensorimo-
182 tor action for learning to use sensory substitution, and
183 for describing the experience of it (O'Regan & Noe,
184 2001). Although visual information might be trans-
185 formed into sound or touch, interacting with the world

186 in an active, visual-like way will confer something
187 other than just the substituting sensory modality, and
188 possibly even something resembling the substituted
189 modality.

2. Pointing and grasping 190

191 Vision is key for being able to locate silent, distal
192 objects and also the optimal sense to allow sensorimo-
193 tor coordination for directing another person via point-
194 ing or reaching out and grasping accurately objects
195 within arm's reach. A few studies on blind or blind-
196 folded subjects have examined object localization, with
197 two conducted to assess identification as well (Auvray,
198 Hanneton, & O'Regan, 2007; Brown, Macpherson, &
199 Ward, 2011), and one that focused specifically on per-
200 ception for action (Proulx, Stoerig, Ludwig, & Knoll,
201 2008). Over a three week period, participants assigned
202 to use The vOICe practiced with it daily using objects
203 in their own homes. Proulx et al. (2008), in a study on
204 blindfolded subjects, assessed localization with a man-
205 ual search task that required pointing and responding
206 by pressing LED lit buttons. They used a perimetry
207 device constructed with an LED array. An LED would
208 light up and a tone would be emitted by the controlling
209 computer until the light had been pressed. The partici-
210 pants were able to generalize the self-initiated practice
211 at home to the lab test with significant improvements
212 in speed and accuracy. A second experiment exam-
213 ined the localization and grasping of natural objects
214 placed on a large table. Although again, those trained
215 to use The vOICe had significant improvement in locat-
216 ing the objects, the more impressive finding was that
217 the participants had also learned to reach with grasp-
218 appropriate hand configurations (Dijkerman, Milner, &
219 Carey, 1999). Given the challenge of interpreting the
220 sound, created by a two-dimensional, greyscale image,
221 and determining object borders, distance, and size, this
222 finding was surprising. Such performance implied that
223 participants learned to extract information about size,
224 distance, shape, and orientation, and were able to use
225 that information to adjust grasping movements appro-
226 priately to pick up objects of different sizes, shapes,
227 and materials.

228 Research investigating the relevance of device input
229 location has revealed how action for perception might
230 work in non-visual ways. In the work by Proulx
231 et al. (2008) the camera that served as the visual
232 input capturing device for The vOICe was located

233 near the eyes in the form of a small camera in spy
234 sunglasses as a form of monocular vision. However
235 the camera need not be located near the eyes, nor
236 kept relatively static in this way. Brown, Macpherson,
237 and Ward (2011) found that different tasks benefitted
238 from different camera locations. Although Proulx et al.
239 (2008) used a head-mounted camera to mimic eye-
240 sight, Auvray et al. (2007) used a handheld webcam
241 for their experiment. Brown et al. (2011) compared
242 experiments that required either object localization or
243 identification with each camera position. They found
244 an interaction of task by camera location: localization
245 performance was superior with the glasses-mounted
246 camera, identification performance was superior with
247 the handheld camera. This finding implies that a senso-
248 rimotor account of learning and perception (O'Regan
249 & Noe, 2001) applies to sensory substitution devices
250 for the processing of "where/how", that is perception-
251 for-action, but not necessarily for perception for object
252 recognition ("what"). Even if using a different sense
253 modality such as hearing, one can mimic standard
254 perceptual-motor contingencies that are used in normal
255 localization as revealed by having the image input
256 near the eyes. It is important to note that the partici-
257 pants in the Brown et al. (2011) study were blindfolded,
258 but sighted individuals. It would be interesting to see
259 whether this result extends to not only the late, adven-
260 titiously blind who have had visual perceptual-motor
261 experience, but also to the congenitally blind who have
262 not had such experience. In this way the role of visual
263 experience in development, versus innate perceptual-
264 motor mechanisms, could be assessed similar to other
265 work on the role of visual experience for cognition
266 (Pasqualotto, Lam, & Proulx, 2013a; Pasqualotto &
267 Proulx, 2012, 2013; Pasqualotto et al., 2013b; Proulx,
268 Brown, Pasqualotto, & Meijer, 2012; Proulx et al.,
269 2014).

270 These initial studies examining reaching and
271 grasping movements guided by The vOICe sensory
272 substitution device were ecologically valid in many
273 ways, but did not have the ability to measure fine-
274 grained differences in timing and accuracy. A device
275 that has the same basic structure as The vOICe, with
276 the addition of synthesized musical instruments as
277 a feature to represent color, is called the EyeMusic
278 (Levy-Tzedek, Hanassy, Abboud, Maidenbaum, &
279 Amedi, 2012a). These researchers examined the abil-
280 ity of blindfolded sighted individuals to perform fast
281 and accurate reaching movements to targets presented
282 by the EyeMusic, and compared them to visually

283 guided movements. Participants were required to reach
284 rapidly to a target. Surprisingly, participants were able
285 to perform the task nearly as accurately with the device
286 as with seeing after just a short period of training.
287 One limitation, however, is that the participants were
288 given a potentially unlimited amount of time to
289 listen to the object location before the fast reaching
290 movement was required. This delay before initiating
291 the movement illustrates the effortful, conscious
292 nature of using sensory substitution without extensive
293 training, particularly in comparison to the ability of
294 the visual system to process information rapidly and
295 in parallel.

296 The crossmodal transfer of information from
297 sensory substitution to vision (more as a version of
298 sensory augmentation) was examined in an another
299 study by Levy-Tzedek et al. (2012b) that also used
300 The vOICe derivative, the EyeMusic. This study used
301 a version of an online control of action visuomotor
302 rotation task (Krakauer, Pine, Ghilardi, & Ghez, 2000;
303 Novick & Vaadia, 2011). Participants used a joystick
304 to control a cursor on a computer screen. Their goal
305 was to move the cursor from a starting position to
306 a target presented on the screen. The location of the
307 target was alternately portrayed using vision or SSD.
308 After several trials, the relationship between their hand
309 movement and the location of the cursor was altered,
310 such that the cursor movement was diverted by 30
311 degrees compared to the actual hand movement. In this
312 condition, in order to have the cursor reach the target,
313 they had to perform a skewed movement, 30 degrees
314 away from the actual target location (for example, in
315 order to reach a target that is 30 degrees away from the
316 vertical, they would have to move their hand along the
317 vertical). Importantly, the feedback suggesting that the
318 motor command needs to be altered was provided only
319 via the visual modality. No rotation cues were given
320 via sensory substitution. They found that participants
321 were quick to alter their hand movements appropri-
322 ately, and that the adaptation to this rotation transferred
323 rapidly from the visual trials to the SSD trials. After-
324 effects (that is, movement of the hand and the cursor
325 in the opposite once rotation was removed) were
326 found independent of the sensory modality (vision
327 or sensory substitution via audition) that presented
328 the targets. This implies that the underlying neural
329 representation of spatial information used for online
330 action might be independent of the sensory modality
331 with which the target is acquired. Interestingly, they
332 found transfer between vision and sensory substitu-

333 tion with very little training, and with no conscious
334 awareness of the presence of rotation, as reported by
335 the participants.

336 The PSVA, prosthesis for substitution of vision by
337 audition (Capelle, Trullemans, Arno, & Veraart, 1998),
338 has also been used in localization studies. Recall that
339 while The vOICe scans an image from left to right to
340 create the sound, the PSVA provides a simultaneous
341 coding of the entire image with frequency and as a
342 result requires intentional movement to make sense
343 of the image similar to “active sensing” such as
344 using eye movements to perceive an image. The
345 studies described thus far with The vOICe required
346 participants to compute depth to accurately locate and
347 grasp the objects. A study with the PSVA investigated
348 the problem of depth perception from monocular cues.
349 Renier et al. (2005a) had participants locate items in
350 depth using natural corridor cues in a simple, simulated
351 setting. The participants were able to report accurately
352 the depth relations between the objects in the display,
353 though it would be of great interest to extend this work
354 to employ reaching and grasping as well. The authors
355 reported that all early blind participants knew that
356 relative size was a depth cue having heard how sighted
357 people described daily observations. This knowledge
358 is crucial for the task because the acquisition of object
359 identity through haptics is size invariant because
360 any object that can be touched is perceived as its
361 three-dimensional size. This knowledge has also
362 been reported in studies of visual-to-tactile sensory
363 substitution (Segond, Weiss, Kawalec, & Sampaio,
364 2013). Early or congenitally blind participants still
365 have more difficulty using this knowledge than those
366 who had visual experience previously. Learning to
367 “see” through the other senses might require not
368 only active experience (Proulx, 2010), but perhaps
369 visual experience as well for full functioning or at
370 least for the efficient acquisition of the new perceptual
371 motor contingencies (Pasqualotto & Proulx, 2012). In
372 fact, the initial studies with the Tactile Vision Sensory
373 Substitution system found that participants needed
374 to manipulate the camera themselves in order to
375 experience distal attribution of the scene, and that the
376 same did not occur if the camera was manipulated by
377 the experimenter. Therefore they needed to experience
378 perceptual-motor contingencies via active sensing
379 themselves through an interaction with the object
380 and this form of tactile sensation that represented
381 the image (Bach-y-Rita, Collins, Saunders, White, &
382 Scadden, 1969).

3. Spatial navigation 383

384 Among the other senses, the auditory system has
385 superior temporal processing (David J. Brown &
386 Proulx, 2013), and as a result most studies have focused
387 on visual-to-auditory sensory substitution devices for
388 representing object information with high acuity and
389 fidelity in both the spatial and temporal domains
390 (Haigh, Brown, Meijer, & Proulx, 2013). One study
391 also examined the use of The vOICe for spatial navi-
392 gation despite the fact that image acquisition with this
393 device occurs infrequently. Navigation clearly requires
394 online perception and correction to avoid obstructions,
395 yet The vOICe samples the environment with an image
396 every 1-2 s. Such snapshots of the visual world might
397 not be enough to allow for truly online corrections
398 to movements, and this would be exacerbated with
399 moving obstructions. Brown et al. (2011) had par-
400 ticipants using The vOICe walk a short route that
401 contained four obstacles. Participants required over
402 five minutes to complete the task; they demonstrated
403 improvement of over one minute with eight trials of
404 practice.

405 Does navigation require the higher resolution
406 afforded by auditory devices rather than tactile ones?
407 Visual navigation certainly utilizes lower-resolution
408 peripheral vision and perhaps a simpler representation
409 better suits an online task such as full body navigation
410 through a space. This is a domain where visual-to-
411 tactile sensory substitution would excel. Devices like
412 the Tongue Display Unit (TDU), a 10 × 10 matrix of
413 1-mm electrodes placed on the tongue, and convey-
414 ing image information via tactile stimulation, provide
415 constant stimulation and updating of the image input,
416 and, like the PVSA, require movement for accurate
417 localization and identification of objects (Matteau,
418 Kupers, Ricciardi, Pietrini, & Ptito, 2010). The res-
419 olution of tactile devices is lower than that of an
420 auditory device like The vOICe. Yet, as noted, nor-
421 mal obstacle avoidance utilizes peripheral vision, with
422 lower resolution compared to the fovea due to a com-
423 bination of having fewer cone cells and the cortical
424 magnification factor that favors foveal vision (Loschky,
425 McConkie, Yang, & Miller, 2005). Peripheral vision
426 is also a primary contributor for magnocellular pro-
427 cessing which, like the representation provided by the
428 TDU, is selective for contrast (the TDU has only a
429 black and white, not greyscale, representation) and
430 motion (Livingstone & Hubel, 1988). Thus having a
431 sensory substitution device that provides a better repre-

432 presentation of contrast and motion might better integrate
433 with the neural mechanisms used for spatial naviga-
434 tion. Moreover assessing the importance of contrast
435 and motion for navigation with sensory substitution
436 would reveal whether these are the crucial computa-
437 tional aspects independent of sensory modality, and
438 thus metamodal.

439 Second, Weiss, and Sampaio (2005) assessed spa-
440 tial navigation by having the participants use the TDU
441 while sitting, but operating a camera-carrying robot
442 in a three-dimensional maze with a remote control.
443 Although the accuracy and speed of the maze comple-
444 tion were assessed and demonstrated success from
445 the very first attempt, it is difficult to generalize from
446 this to real-world navigation. A more recent study with
447 the TDU (Chebat, Schneider, Kupers, & Ptito, 2011)
448 used a large scale navigation task in a corridor with
449 obstacles, similar to the navigation employed with The
450 vOICe (Brown et al., 2011). Participants were able to
451 successfully navigate the course accurately and con-
452 genitally blind individuals were able to out-perform
453 sighted participants, supporting other work that found
454 route or egocentric spatial knowledge is preferred in the
455 absence of visual experience (Pasqualotto & Proulx,
456 2012; Pasqualotto et al., 2013b). The participants were
457 successful in terms of accuracy, but this study did not
458 provide as much information about the time required
459 to complete the task.

460 Navigation is a major challenge for those who have
461 acquired blindness later in life (Sampaio & Dufier,
462 1988), primarily due to feelings of insecurity in rela-
463 tion to the environment, such as obstacles. Certainly
464 one can learn to depend on different kind of cues to
465 form representations of space for successful naviga-
466 tion (Fortin et al., 2008) and utilize white canes and
467 guide dogs. A recent study assessed two echoloca-
468 tion sensory substitution for vision devices that provide
469 online spatial information through sound, using ultra-
470 sound emitters to detect distance from objects (Kolarik,
471 Timmis, Cirstea, & Pardhan, 2014). They required
472 blindfolded participants to walk through an aperture
473 similar to a doorway, but with varied widths unknown
474 to the user. With vision, movements were rapid and
475 accurate, with no collisions. Two pulse-echo sensor
476 devices were used, similar in function to sonar.
477 The Miniguide translates obstacle distance to hand
478 vibrations. The K-Sonar, due to having a narrower
479 beam, translates the distance of an individual object,
480 the existence of multiple objects, and also provides
481 information that can support identification of objects.

482 There were no significant differences between the
483 two devices used, the K-Sonar and the Miniguide.
484 Although performance was less accurate, with some
485 collisions, and slower, as measured by walking veloc-
486 ity, the study provided a proof of concept that such
487 devices could be of use with further training, consistent
488 with past work with similar devices (Hughes, 2001).
489 For example with an aperture 18% greater in width than
490 the participant, participants had one collision every
491 trial with K-Sonar, or every two trials with Miniguide;
492 movement times were less than 2 seconds with vision
493 but 5 to 8 seconds with Miniguide and K-Sonar respec-
494 tively. With vision, participants rotated their shoulders
495 far less to move through the aperture than those
496 using the devices did. Furthermore the results implied
497 that these echolocation devices rely on multimodal
498 areas for depth processing in the occipito-parietal
499 and occipito-temporal areas (Renier et al., 2005a). As
500 demonstrated by Kolarik and colleagues, sensory sub-
501 stitution devices can provide another means of obstacle
502 detection, and although some studies have exam-
503 ined virtual navigation (Maidenbaum, Levy-Tzedek,
504 Chebat, & Amedi, 2013), further research examining
505 the control of actual action based on information pro-
506 vided via such devices will be crucial for this form of
507 visual rehabilitation.

4. Active sensing 508

509 Perception is necessary for action (Goodale, 2008);
510 likewise, action plays a pivotal role in perception,
511 what has become known as active sensing. Active
512 sensing has been shown to play a vital role in per-
513 ception of various modalities, including the visual,
514 the auditory, the tactile and the olfactory systems
515 (Schroeder, Wilson, Radman, Scharfman, & Lakatos,
516 2010; Wachowiak, 2011), in humans as well as a vari-
517 ety of other species (Nelson & MacIver, 2006). Active
518 sensing is the movement of the sensors for optimization
519 of sensing performance (Mitchinson & Prescott, 2013),
520 and it plays a central role in the process of perception
521 (Ahissar & Arieli, 2012).

522 The studies reviewed here report relatively high
523 success rates for the generation of action under SSD
524 guidance. These results indicate that the SSD users
525 are able to maintain the appropriate calibration of
526 their movements based on SSD feedback, and suggests
527 they are making use of the SSD feedback to fine-tune
528 their movements. Movements of sighted individuals

529 in the absence of visual feedback, have been shown
530 to be miscalibrated, and not corrected based on pro-
531 prioception alone (Levy-Tzedek, Ben Tov, & Karniel,
532 2011; Levy-Tzedek, Krebs, Arle, Shils, & Poizner,
533 2011; Soechting & Flanders, 1989; Wolpert, Ghahra-
534 mani, & Jordan, 1995). It can therefore be concluded
535 that the effective generation of movement is a direct
536 result of successfully deciphering cues from the SSD,
537 rather than relying on proprioceptive cues, or on mem-
538 ory (e.g., from visually experiencing the experimental
539 setup, where applicable).

540 Perception of depth cues plays an important role
541 in generation of a fuller representation of spatial lay-
542 outs, an ability which has been demonstrated when
543 2D images were conveyed via an SSD, such as the
544 PSVA (Renier et al., 2005a). We estimate it would
545 therefore be beneficial to combine input from SSDs
546 that provide image information (e.g., the vOICe) with
547 distance-estimation devices (e.g., the K-Sonar), while
548 actively exploring a scene. Exploratory attempts in
549 this direction have been made using newly available
550 depth sensors such as the Kinect (Gomez, Mohammed,
551 Bologna, & Pun, 2011).

522 5. Sensory substitution as cross-modal 523 “translators”

554 Training on how to use SSDs is a major issue that
555 should be considered, as the choice of a particular train-
556 ing paradigm may affect the ultimate performance.
557 For example, active training has emerged as having
558 particular benefits in recent accounts (Proulx et al.,
559 2008; Ward & Meijer, 2010). This holds true in visual
560 rehabilitation across the board, and applies to training
561 on how to use retinal implants (Dagnelie, 2012) and
562 sight-restoration surgery (Ostrovsky, Andalman, &
563 Sinha, 2006; Putzar, Gondan, & Röder, 2012; Xu, Yu,
564 Rowland, Stanford, & Stein, 2012) as well. Learning
565 to decipher visual information is a long process, and
566 includes learning of principles that are unique to
567 vision, such as 3-D perspective, depth cues, variation
568 of size with distance, transparency, reflection, color
569 and shading effects, for example. These are especially
570 challenging for congenitally blind individuals, who
571 do not have experience with this type of input. An
572 added layer of complexity is the fact that the visual
573 input arriving from a prosthesis or an SSD is often
574 degraded, and harder to make sense of than a high-
575 resolution input (Brown, Simpson, & Proulx, 2014;

576 Haigh et al., 2013). Therefore, a carefully planned
577 training program is of utmost importance. Combining
578 concurrent sensory input arriving from different
579 modalities has been shown to improve perception (for
580 a review, see (Proulx et al., 2014). Therefore, once
581 the users learn how to interpret the signals arriving
582 from the SSD, and make ‘visual’ sense of them,
583 they can then use the SSD in combination with other
584 rehabilitation approaches, e.g., with a visual prosthe-
585 sis, and serve as an interpreter of sorts, which can
586 guide and assist the rehabilitation process of the more
587 invasive approaches.

588 6. Using sensory substitution to reveal the 589 neural mechanisms underlying perception 590 for action: Ventral & dorsal streams in the 591 blind

592 The study of sensory substitution and visual impair-
593 ment can also reveal the neural mechanisms underlying
594 perception for action that supersedes just one sense
595 (Proulx et al., 2014; Ricciardi, Bonino, Pellegrini, &
596 Pietrini, 2014); this is particularly important given that
597 most research in this area falls within the domain of
598 vision. Visual information is segregated into different
599 features early in processing, even at the level of the
600 retina, and later into two parallel cortical pathways,
601 the ventral stream and the dorsal stream, which appear
602 to be functionally segregated, with the former discrim-
603 inating object features and the later handling informa-
604 tion about spatial location (Goodale, 2008). The ventral
605 occipitotemporal “what” pathway extends from the pri-
606 mary visual cortex (V1) through visual area 4 (V4) to
607 inferotemporal areas and then up to the prefrontal cor-
608 tex. The dorsal occipitoparietal “where/how” pathway
609 from V1 leads through the posterior parietal cortex
610 towards the premotor cortex (Striem-Amit, Dakwar,
611 Reich, & Amedi, 2012). The dorsal stream is criti-
612 cal for real time control of action, providing visual
613 guidance for movement (Milner, 2012). The ventral
614 stream supports object, event, and action identification
615 (Goodale, 2008) as well as feature analysis for object
616 identity independent of variance in other features for
617 which identity should be invariant, such as position and
618 orientation (Freeman & Ziemba, 2011). The role of the
619 ventral stream in action, then, is to provide visual infor-
620 mation to enable the identification of a specific object
621 and activate the cognitive systems to plan the action
622 performed towards the object. These streams were pri-

623 marily seen as visual because deficits caused by lesions
624 to these areas cause visual aberrations (Milner &
625 Goodale, 2008).

626 A growing body of research examining perception,
627 action, and cognition in the visually impaired suggests
628 that the brain is not necessarily segregated into sensory-
629 specific areas but instead is metamodal and organized
630 in terms of the tasks, functions, and computations
631 that the areas carry out (Pascual-Leone & Hamilton,
632 2001; Proulx et al., 2012); this is sometimes referred
633 to as supramodal as a synonym for metamodal in the
634 literature (Kupers, Pietrini, Ricciardi, & Ptito, 2011;
635 Kupers & Ptito, 2011; Ricciardi & Pietrini, 2011). This
636 perspective, in contrast with the classical one, classifies
637 brain areas by the form of information processing
638 carried out (e.g., shape recognition) independent of
639 the sensory modality that appears to be employed.
640 First we will review the evidence for the metamodal
641 organization of the brain. Then we will note the natural
642 extension of this form of functional organization to per-
643 ception for action, in much the same way that the dorsal
644 stream has been re-characterized from processing
645 “where” information (Mishkin & Ungerleider, 1982),
646 to being more task-specified as the processing of “how”
647 (Milner & Goodale, 2008) such information can be
648 acted upon.

649 Two examples of cortical regions, first thought to be
650 visual in nature, but later discovered to be metamodal
651 are the fusiform face area (Kanwisher, McDermott,
652 & Chun, 1997) and the parahippocampal place area
653 (Epstein & Kanwisher, 1998) that are now known
654 to respond to the same categories even when only
655 perceived by touch or sound (Ricciardi & Pietrini,
656 2011). An extensive review by Ricciardi and Pietrini
657 (2011) details many sources of evidence for the
658 supramodal, or metamodal, functional architecture of
659 the brain.

660 Striem-Amit et al. (2012) conducted a brain imaging
661 study to examine the functional segregation of the dor-
662 sal and ventral streams in the congenitally blind. Using
663 The vOICE, congenitally blind participants were pre-
664 sented different simple novel shapes in different areas
665 of the “visual” field, and these were transformed into
666 sound. The participants were asked either to identify
667 or locate the shape. This elicited clear differentiation
668 between ventral and dorsal streams, indicating that
669 even with no visual experience, these two streams still
670 encode the tasks they would be expected to perform
671 had it been visual information. To be more specific,
672 shape identity tasks activated the ventral occipital

673 temporal sulcus, which is located in the midst of
674 the ventral stream. In contrast, the localization task
675 preferentially activated auditory regions, such as the
676 supramarginal gyrus located in the inferior parietal
677 lobe, as well as the precuneus, a higher order area of the
678 dorsal stream.

679 Criticisms that are levelled at studies using SSDs
680 are that they usually study highly proficient users of
681 the system, who may have already undergone a plastic
682 change, such as Ptito, Moesgaard, Gjedde, and Kupers
683 (2005) who showed increased occipital cortex acti-
684 vation following SSD training. Striem-Amit et al.’s
685 (2012) study circumvents this limitation by only train-
686 ing participants to use the devices for a maximum of
687 one and a half hours and participants were completely
688 naïve to The vOICE before this training, thus avoiding
689 the problem that brain imaging might be measuring an
690 artificial plastic change rather than what is inherent in
691 the congenitally blind.

692 Furthermore, many studies exploring the use of
693 SSDs in the congenitally blind use familiar, well-
694 practiced stimuli, such as Kim and Zatorre (2011) who
695 trained their participants for five days with the stimuli
696 used for the experiment. This means that potential find-
697 ings were confounded by participants using memory
698 of the stimuli presented in training, rather than shape
699 processing in the occipital region. Striem-Amit et al.
700 (2012) used novel stimuli to ensure that memory was
701 not playing a role in the activation of dorsal and ventral
702 streams, just shape and location processing. The neu-
703 ral correlates of action control and representation has
704 not been only studied using sensory substitution, but
705 there is extensive evidence using standard paradigms
706 in sensory-deprived individuals, further giving sup-
707 port to the metamodal nature of the underlying neural
708 architecture for action (Renzi et al., 2013; Emiliano
709 Ricciardi et al., 2009; Röder, Kusmierek, Spence, &
710 Schicke, 2007).

711 Qin and Yu (2013) postulated that the metamodal
712 nature of the visual cortex could be due to a plastic
713 change in the brain that is caused by the deprivation
714 of visual stimuli. Thus, rather than being inherently
715 metamodal, the visual cortex has been shown to
716 be recruited by other higher functioning processes,
717 such as memory and cognition in the blind (Bur-
718 ton, Sinclair, & Agato, 2012; Renier et al., 2010),
719 and therefore might not be metamodal naturally.
720 Striem-Amit et al. (2012) refute this suggestion by
721 demonstrating this metamodality in the blindfolded
722 sighted as well as the blind, indicating that the meta-

723 modal nature of the two streams is not due to sensory
724 deprivation.

725 This study seems to suggest that a metamodal
726 approach to understanding the brain structure is a
727 more valid approach compared with the standard
728 unimodal model. If the metamodal theory is to
729 be substantiated, more areas of the brain must be
730 demonstrated to be metamodal. Reich, Szwed, Cohen,
731 and Amedi (2011) studied the “visual” word form area
732 (VWFA), a component of the visual cortex, to try to
733 establish whether this area is metamodal. The VWFA
734 in the sighted is activated across writing systems
735 and scripts and encodes letter strings irrespective
736 of case, font or location in the visual field. In this
737 study blind participants were presented with Braille
738 words and nonsense Braille letter strings. The authors
739 used fMRI to investigate whether the VWFA would
740 be activated in response to the tactile letters. The
741 investigators found a striking differentiation between
742 the real Braille words and the nonsense words in
743 the congenitally blind, indicating that the VWFA is
744 activated for reading words regardless of input, plus
745 develops specialization for reading regardless of visual
746 experience, supporting the metamodal theory. Braille
747 reading activating the primary visual cortex in the
748 blind has also been shown by Cohen et al. (1997), thus
749 strengthening the idea that the visual cortex is a meta-
750 modal area of the brain that can be activated by any
751 sensory modality.

752 A further brain area that has been put forward as
753 metamodal is hMT+ (also called the fifth visual area,
754 V5), which encodes for motion. A study by Matteau
755 et al. (2010) found this area was activated when per-
756 ceiving motion using an SSD that rests on the tongue
757 in both the sighted and the blind, again indicating that
758 this area encodes information about motion regardless
759 of sensory input.

760 So far in this review only visual areas have been
761 discussed as being metamodal. For the theory to be
762 substantiated fully, other areas of the brain that have
763 traditionally been considered to be unimodal must be
764 demonstrated to be activated by more than one modal-
765 ity. For example, the auditory cortex would be expected
766 to be activated if a non-audio input was presented that
767 required the same computation as an audio signal.
768 Calvert et al. (1997) used an fMRI with participants
769 with normal hearing. The authors first identified the
770 auditory cortex by playing participants speech through
771 headphones and then asked them to repeat the words
772 back to themselves in their heads. Then they played

773 video of a face silently mouthing numbers, which the
774 participants had to repeat back to themselves in their
775 heads. This lip-reading led to activation in the auditory
776 cortex, despite there being no auditory signal present,
777 indicating that the auditory cortex is also metamodal
778 (Calvert & Thesen, 2004).

779 This is further corroborated by Okada et al. (2010)
780 who presented 20 participants audio input alone
781 compared with audio and an accompanying congruent
782 visual speech input. Audio plus visual led to more
783 activation in the auditory cortex than audio input
784 alone, indicating that areas of the so-called auditory
785 cortex are similarly responsive to visual stimuli, again
786 supporting the idea of the brain as a series of modules
787 that deal with specific computations, rather than being
788 described by the input they receive. Other research
789 suggests similar findings for other “primary” sensory
790 areas, such as the primary olfactory cortex, which
791 has been shown to be responsive to other associative
792 information (Chapuis & Wilson, 2012; Weiss & Sobel,
793 2012). Note that the metamodal, or supramodal, nature
794 of a brain area can be further demonstrated by studies
795 comparing sighted and blind individuals, as this
796 would exclude visual imagery as a potential confound.
797 Indeed many of these areas described have been
798 tested with such an experimental design, and a recent
799 review (Ricciardi et al., 2014) provides examples of
800 such evidence.

801 How might these cortical regions, thought to be pri-
802 mary sensory areas, respond to information provided
803 by other sensory modalities? For example, the visual
804 cortex must be connected to the cochlear nuclei in the
805 brain stem (Recanzone & Sutter, 2008) for there to
806 be activation in this area when presented with images
807 in sound via The vOICe. Two hypotheses have been
808 put forward in explanation of how these, previously
809 thought to be unlinked, peripheral sensors and brain
810 regions are connected. According to the *cortical reor-*
811 *ganization* hypothesis, cross modal brain responses
812 are mediated by the formation of new pathways in
813 the sensory deprived brain (Bronchti et al., 2002). A
814 more compelling argument is the *unmasking* hypoth-
815 esis, which states that loss of sensory input induces
816 unmasking and strengthening of already existing neu-
817 ronal connections (Kupers & Ptito, 2011).

818 The unmasking hypothesis is suggested here to be
819 correct, as blind participants in the Striem-Amit et al.
820 (2012) study showed activation in visual pathways
821 when using an SSD with only minimal training,
822 precluding the idea that the brain had a chance to

rewire itself, instead seeing the connections as extant and unmasked by these types of experiment. This is further substantiated by Striem-Amit et al. (2012) who also showed the same activation in sighted blind-folded participants as in the blind, indicating that it is not a plastic change that occurred due to deprivation of vision.

Furthermore Falchier, Clavagnier, Barone, and Kennedy (2002), using retrograde tracers on cynomolgus monkeys, showed that the primary visual cortex (V1) receives input not only from the visual thalamus but also receives projections from the auditory cortex as well as polysensory areas of the temporal lobe. Further anatomical evidence of multiple other connections projecting to the visual cortex comes from Rockland and Ojima (2003), who showed that areas V1 and secondary visual cortex (V2) receive projections from several parietal and auditory association areas in macaque monkeys. These anatomical explorations in monkeys show that the previously thought of as unimodal areas of the brain are actually connected to other sensory areas directly, rather than just via upstream multimodal association areas, and these data support the idea that the connections are extant in all and are unmasked due to sensory substitution tasks rather than created by the brain following sensory deprivation.

However the debate continues, with evidence coming from Kupers et al. (2006) who used TMS on blind and sighted participants trained to use the tongue display unit (TDU). The TDU is a sensory substitution device that places a 3×3 cm electrode array consisting of 144 gold plates on the tongue, and an electrical pulse is generated by each electrode to correspond to a pixel on the image that is being assessed (Bach-y-Rita & Kercel, 2003; Ptito et al., 2005). When TMS over the occipital cortex was used, blind participants reported somatotopically organized tactile sensations on the tongue, whereas sighted individuals who had also been trained with the TDU did not report this (Kupers et al., 2006). This indicates that a few alternative explanations might be possible. First, that there are differences in the blind that are not found in the sighted, suggesting that instead of there being masked connections between peripheral tactile sensors and the occipital cortex in everyone, there is actually a new connection created between cortex and sensor in the sensory deprived, supporting the cortical reorganization hypothesis. Another option is that the unmasking occurs to a different extent for blind and sighted indi-

viduals. That is, perhaps in the blind brain there is the potential for faster, more efficient unmasking than in the sighted brain.

Based on the evidence presented here, areas of the visual cortex have been demonstrated to be metamodal in nature, such as the dorsal and ventral streams, the VWFA and V5. Further the auditory cortex has been shown to become active when an appropriate computational task is presented to it, despite this task coming in the form of visual input (Calvert et al., 1997). Therefore a system which describes brain structure based on the task or computations that an area performs, rather than the sensory modality that is most often encoded by an area, seems more accurate taxonomy. Previously the brain areas were thought to only be connected to the specific sensory modalities that they computed. However, evidence from lesion studies in monkeys and brain imaging studies in humans have shown that these metamodal areas are in fact linked up to peripheral sensors that were previously not thought to project to them. This leads to the idea that the brain is split into metamodal, computational based modules, that are linked to all sensory inputs and that can process information that is requisite to their computational task, regardless of the modality that this information originates from.

The results derived from blind participants supporting a metamodal organization of the brain extend to sighted participants as well. Long-term blindfolding of sighted participants with training in using the vOICe (Proulx et al., 2008) resulted in brain activation similar to that of blind participants in visual cortex but with auditory stimulation (Boroojerdi et al., 2000; Facchini & Aglioti, 2003; Lewald, 2007; Merabet et al., 2008; Pollok, Schnitzler, Stoerig, Mierdorf, & Schnitzler, 2005). Such effects can occur in a matter of days, too, as in a study with five days of visual deprivation and Braille training (Kauffman, Theoret, & Pascual-Leone, 2002; Pascual-Leone & Hamilton, 2001). There is mounting evidence that the visual cortex is functionally involved in auditory and tactile tasks in sighted subjects as well (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Liang, Mouraux, Hu, & Iannetti, 2013; Sathian & Zangaladze, 2002; Zangaladze, Epstein, Grafton, & Sathian, 1999).

Thus far, research using sensory substitution has revealed the metamodal properties of brain areas once thought to be visual in nature. Although such research has targeted both ventral and dorsal streams of processing, those studies examining the dorsal

stream have focused on “where” information in the perceptual sense rather than “how” information in the perception for action sense (Striem-Amit et al., 2012). Much of what is known about the neural basis of perception for action comes from studies of vision. For example, a large body of work has detailed the role of the anterior intra-parietal area (AIP) in macaques for the processing of object shape, size and orientation to guide grasping (Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). A similar region has been found in humans as well (Binkofski et al., 1998), with a number of studies detailing the role of the posterior parietal cortex for the coordination of eye and hand movements when reaching for targets (Desmurget et al., 1999; Van Donkelaar, Lee, & Drew, 2000). Are these vision-specific perception for action areas, or might non-visual information guide hand movements and grasping in these cortical regions? The metamodal hypothesis would have one predict that the task (grasping and hand movements) of AIP define its function, and that any sensory input that provides the necessary spatial information and object features would also evoke such functional recruitment. Sensory substitution would be an ideal approach to examine whether AIP and other areas involved in perception for action are not specific to one sensory modality, vision, but rather allow for precise hand and grasping movements on the basis of any informative sensory modality that provides input.

7. Shared spatial representation across the senses

Spatial information is shared across sensory modalities, such that information obtained via one modality (e.g., vision) is utilized when making movements based on input from another sensory modality (e.g., audition) (Levy-Tzedek et al., 2012b). These findings are in line with evidence from neural recordings showing that the dorsal stream participates in mediation of sensory-motor control, even when the sensory modality is not vision (Fiehler, Burke, Engel, Bien, & Rösler, 2008), suggesting a modality-independent representation of action control.

Several studies have demonstrated (Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994) that direct vision of the target immediately prior to movement significantly increased movement accuracy, whereas a delay between target presentation and move-

ment resulted in deteriorated accuracy; that is to say, the longer participants had to use their cognitive representation of the target, the less accurate were their movements; this line of results was the basis for the suggestion that vision is needed to calibrate the proprioceptive map; and yet, participants in the studies reported here were able to use the auditory or tactile information (possibly to create a ‘visual’-like representation which is the ultimate goal of SSDs for the blind), in some cases without the possibility to perform vision-based calibration between trials, to both plan the movements and improve the accuracy on subsequent trials.

Proulx and colleagues (2014) reviewed these and other results to suggest that the representation of space might not be dependent on the modality through which the spatial information is received. This is supported by brain-imaging studies indicating that areas within the visual dorsal stream, such as the precuneus (Renier & De Volder, 2010) and the right anterior middle occipital gyrus (Collignon, Champoux, Voss, & Lepore, 2011), showed a functional preference for spatial information delivered using the auditory or tactile modalities in congenitally blind and in sighted individuals. These brain areas are also activated when sound encodes spatial information, rather than arriving from different spatial locations, in both sighted and congenitally blind individuals (Striem-Amit et al., 2012). This hypothesis, of a task-specific, rather than a modality-specific structure of brain areas was similarly suggested by research indicating that, during a spatial navigation task with the TDU, congenitally blind individuals were found to recruit the posterior parahippocampus and posterior parietal and ventromedial occipito-temporal cortices, areas that are involved in spatial navigation under full vision (Chebat et al., 2011); similarly, the dorsal pathway has been shown to mediate movement control when only kinesthetic, and no visual information was used to guide actions even when tested in congenitally blind individuals, with no prior visual experience (Fiehler et al., 2008).

It has been suggested that blind individuals tend to rely on a more egocentric, rather than an allocentric frame of reference (Cattaneo, Bhatt, Merabet, Pece, & Vecchi, 2008; Pasqualotto & Proulx, 2012; Pasqualotto et al., 2013b; Röder et al., 2007). As data are accumulated, supporting the hypothesis that the representation of space in the brain is modality-independent, or that very little training is required to create a ‘visual’-

like representation of space using sounds, we suggest that SSDs, by providing detailed spatial information for people with impaired vision, might allow them to employ an allocentric spatial frame of reference when interacting with their environment.

8. Future directions for the online visual control of action through sensory substitution

Here we have reviewed the few studies that have begun to explore how sensory substitution might allow for the online control of action via visual information perceived through sound or touch. One limitation of many of these studies so far is that performance has often been assessed solely in terms of accuracy, with only a few that have also reported response times so that the full efficiency of the behaviors could be assessed.

There are a number of areas where the classic approaches to studying the online control of action can be adopted to address interesting issues with sensory substitution. One fascinating example would be to examine how size illusions via sensory substitution influence perception and action, and whether visual experience is necessary for an illusion to be effective. A crucial test to assess whether there is a clear distinction between perception and action has been whether a size illusion, such as the Müller-Lyer illusion, impacts both perceived size and grasping. Recent research (Biegstraaten et al., 2007), and a comprehensive review (Bruno & Franz, 2009), suggest that there is not necessarily a dissociation between perception and action. This has also been supported by work in other, related areas using illusions and other approaches (Bruno, Knox, & de Grave, 2010; de Brouwer, Brenner, Medendorp, & Smeets, 2014; de Grave, Brenner, & Smeets, 2004; Foster, Kleinholdermann, Leifheit, & Franz, 2012; Franz, Hesse, & Kollath, 2009; Mendoza, Elliott, Meegan, Lyons, & Welsh, 2006). This would be an interesting approach to assess the mechanisms of online control with sensory substitution because the perception of size using other size illusions has also been conducted with sensory substitution. Laurent Renier and colleagues used the PSVA sensory substitution device to assess whether blind and sighted participants would perceive the illusion through interpretation of the sound created by the device (Renier et al., 2005b; Laurent Renier, Bruyer, & Volder, 2006).

In these studies they found that although the sighted and late blind participants perceived the Ponzo illusion and the Vertical-Horizontal illusions just as the sighted do, the early blind participants did not. This has the fascinating implication that visual experience is necessary to have the expectations required to perceive size in a way that is influenced by context. They did not assess perception versus action, and it would be of great interest to assess whether these illusions, perceived through sensory substitution, affect grasping differentially depending on visual experience. Another interesting extension would be to assess the impact of using another sensory substitution approach, such as tactile substitution, on the influence of size illusions. Given the fascinating finding in other work that the online control of action might be sensory modality independent as seen from converging work looking at learning and adaptation with sensory substitution devices (Levy-Tzedek et al., 2012b), there is a lot of potential to use sensory substitution as a means for revealing the underlying mechanisms for the perceptual control of motor action. The next step would be to move beyond the limited data available on online control with full reporting of both response time and accuracy to allow a full assessment of sensory substitution performance. Future work looking at having shifting targets at the time of response initiation and double-step paradigms for reaching to targets (Goodale et al., 1986; Gritsenko et al., 2009) would best allow work on perception for action with sensory substitution to contribute to the fundamental understanding of online control.

Acknowledgments

This work was supported by a grant from the EPSRC to Michael J. Proulx (EP/J017205/1). Partial support was provided by the Helmsley Charitable Trust through the Agricultural, Biological and Cognitive Robotics Center of Ben-Gurion University of the Negev.

References

- Ahissar, Ehud, & Arieli, Amos. (2012). Seeing via miniature eye movements: A dynamic hypothesis for vision. *Frontiers in Computational Neuroscience*, 6.
- Auvray, M., Hanneton, S., & O'Regan, J.K. (2007). Learning to perceive with a visuo-auditory substitution system: Localisation and object recognition with 'the Voice'. *Perception*, 36(3), 416-430.

- 1113 Auvray, M., & Myin, E. (2009). Perception with compensatory
1114 devices: From sensory substitution to sensorimotor extension.
1115 *Cogn Sci*, 33(6), 1036-1058. doi: 10.1111/j.1551-6709.2009.
1116 01040.x
- 1117 Bach-y-Rita, P., Collins, C.C., Saunders, F.A., White, B., & Scad-
1118 den, L. (1969). Vision substitution by tactile image projection.
1119 *Nature*, 221(5184), 963-964.
- 1120 Bach-y-Rita, P., & Kercel, S.W. (2003). Sensory substitution and
1121 the human-machine interface. *Trends Cogn Sci*, 7(12), 541-546.
1122 doi: S1364661303002900 [pii]
- 1123 Biegstraaten, M., de Grave, D.D., Brenner, E., & Smeets, J.B. (2007).
1124 Grasping the Muller-Lyer illusion: Not a change in perceived
1125 length. *Exp Brain Res*, 176(3), 497-503. doi: 10.1007/s00221-
1126 006-0744-8
- 1127 Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz,
1128 R.J., & Freund, H.J. (1998). Human anterior intraparietal area
1129 subserves prehension: A combined lesion and functional MRI
1130 activation study. *Neurology*, 50(5), 1253-1259.
- 1131 Boroojerdi, B., Bushara, K.O., Corwell, B., Immisch, I., Battaglia, F.,
1132 Muellbacher, W., & Cohen, L.G. (2000). Enhanced excitability
1133 of the human visual cortex induced by short-term light depri-
1134 vation. *Cereb Cortex*, 10(5), 529-534.
- 1135 Boyer, E.O., Babayan, B.M., Bevilacqua, F., Noisternig, M.,
1136 Warusfel, O., Roby-Brami, A. (2013). From ear to hand: The
1137 role of the auditory-motor loop in pointing to an auditory
1138 source. *Front Comput Neurosci*, 7, 26. doi: 10.3389/fncom.
1139 2013.00026
- 1140 Bronchti, G., Heil, P., Sadka, R., Hess, A., Scheich, H., & Woll-
1141 berg, Z. (2002). Auditory activation of "visual" cortical areas
1142 in the blind mole rat (*Spalax ehrenbergi*). *Eur J Neurosci*, 16(2),
1143 311-329.
- 1144 Brown, D.J., Simpson, A.J., & Proulx, M.J. (2014). Visual objects in
1145 the auditory system in sensory substitution: How much infor-
1146 mation do we need? *Multisens Res*, 27(5-6), 337-357.
- 1147 Brown, D., Macpherson, T., & Ward, J. (2011). Seeing with sound?
1148 exploring different characteristics of a visual-to-auditory sen-
1149 sory substitution device. *Perception*, 40(9), 1120-1135.
- 1150 Brown, David J., & Proulx, Michael J. (2013). Increased Sig-
1151 nal Complexity Improves the Breadth of Generalization in
1152 Auditory Perceptual Learning. *Neural Plasticity*, 2013, 9. doi:
1153 10.1155/2013/879047
- 1154 Bruno, N., & Franz, V.H. (2009). When is grasping affected by
1155 the Muller-Lyer illusion? A quantitative review. *Neuropsychol-
1156 ologia*, 47(6), 1421-1433. doi: S0028-3932(08)00419-3 [pii]
1157 10.1016/j.neuropsychologia.2008.10.031
- 1158 Bruno, N., Knox, P.C., & de Grave, D.D. (2010). A metaanalysis of
1159 the effect of the Muller-Lyer illusion on saccadic eye move-
1160 ments: No general support for a dissociation of perception and
1161 oculomotor action. *Vision Res*, 50(24), 2671-2682. doi: S0042-
1162 6989(10)00461-X [pii] 10.1016/j.visres.2010.09.016
- 1163 Burton, H., Sinclair, R.J., & Agato, A. (2012). Recognition memory
1164 for Braille or spoken words: An fMRI study in early blind. *Brain
1165 Res*, 1438, 22-34. doi: 10.1016/j.brainres.2011.12.032
- 1166 Calvert, G.A., Bullmore, E.T., Brammer, M.J., Campbell, R.,
1167 Williams, S.C., McGuire, P.K. (1997). Activation of audi-
1168 tory cortex during silent lipreading. *Science*, 276(5312),
1169 593-596.
- Calvert, G.A., & Thesen, T. (2004). Multisensory integration: 1170
Methodological approaches and emerging principles in the 1171
human brain. *J Physiol Paris*, 98(1-3), 191-205. doi: 10.1016/ 1172
j.jphysparis.2004.03.018 1173
- Capelle, C., Trullemans, C., Arno, P., & Veraart, C. (1998). A 1174
real-time experimental prototype for enhancement of vision 1175
rehabilitation using auditory substitution. *IEEE Trans Biomed
1176 Eng*, 45(10), 1279-1293. doi: 10.1109/10.720206 1177
- Cattaneo, Z., Bhatt, E., Merabet, L.B., Pece, A., & Vecchi, T. (2008). 1178
The influence of reduced visual acuity on age-related decline 1179
in spatial working memory: An investigation. *Neuropsychol
1180 Dev Cogn B Aging Neuropsychol Cogn*, 15(6), 687-702. doi:
1181 10.1080/13825580802036951 1182
- Chapuis, Julie, & Wilson, Donald A. (2012). Bidirectional plasticity 1183
of cortical pattern recognition and behavioral sensory acuity. 1184
Nat Neurosci, 15(1), 155-161. doi: http://www.nature.com/ 1185
neuro/journal/v15/n1/abs/nn.2966.html#supplementary- 1186
information 1187
- Chebat, D.R., Schneider, F.C., Kupers, R., & Ptito, M. (2011). Nav- 1188
igation with a sensory substitution device in congenitally blind 1189
individuals. *Neuroreport*, 22(7), 342-347. doi: 10.1097/WNR.
1190 0b013e3283462def 1191
- Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., 1192
Dambrosia, J. (1997). Functional relevance of cross-modal 1193
plasticity in blind humans. *Nature*, 389(6647), 180-183. doi:
1194 10.1038/38278 1195
- Collignon, O., Champoux, F., Voss, P., & Lepore, F. (2011). Sensory 1196
rehabilitation in the plastic brain. *Prog Brain Res*, 191, 211-231.
1197 doi: 10.1016/B978-0-444-53752-2.00003-5 1198
- Cressman, E.K., & Henriques, D.Y. (2011). Motor adaptation and 1199
proprioceptive recalibration. *Prog Brain Res*, 191, 91-99. doi:
1200 10.1016/B978-0-444-53752-2.00011-4 1201
- Dagnelie, G. (2012). Retinal implants: Emergence of a multidisci- 1202
plinary field. *Curr Opin Neurol*, 25(1), 67-75. doi: 10.1097/
1203 WCO.0b013e32834f02c3 1204
- de Brouwer, A.J., Brenner, E., Medendorp, W.P., & Smeets, J.B. 1205
(2014). Time course of the effect of the Muller-Lyer illusion on 1206
saccades and perceptual judgments. *J Vis*, 14(1). doi: 10.1167/
1207 14.1.4 1208
- de Grave, D.D., Brenner, E., & Smeets, J.B. (2004). Illusions as a 1209
tool to study the coding of pointing movements. *Exp Brain Res*,
1210 155(1), 56-62. doi: 10.1007/s00221-003-1708-x 1211
- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, 1212
G.E., & Grafton, S.T. (1999). Role of the posterior parietal
1213 cortex in updating reaching movements to a visual target. *Nat
1214 Neurosci*, 2(6), 563-567. doi: 10.1038/9219 1215
- Dijkerman, H.C., Milner, A.D., & Carey, D.P. (1999). Motion par- 1216
allax enables depth processing for action in a visual form 1217
agnosic when binocular vision is unavailable. *Neuropsycholo-
1218 gica*, 37(13), 1505-1510. 1219
- Driver, J., & Noesselt, T. (2008). Multisensory interplay reveals 1220
crossmodal influences on 'sensory-specific' brain regions, neu- 1221
ral responses, and judgments. *Neuron*, 57(1), 11-23. doi: 10.10
1222 16/j.neuron.2007.12.013 1223
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of 1224
the local visual environment. *Nature*, 392(6676), 598-601. doi:
1225 10.1038/33402 1226

- 1227 Facchini, S., & Aglioti, S.M. (2003). Short term light deprivation
1228 increases tactile spatial acuity in humans. *Neurology*, *60*(12),
1229 1998-1999.
- 1230 Falchier, A., Clavagnier, S., Barone, P., & Kennedy, H. (2002).
1231 Anatomical evidence of multimodal integration in primate stri-
1232 ate cortex. *J Neurosci*, *22*(13), 5749-5759. doi: 20026562
- 1233 Fiehler, Katja, Burke, Michael, Engel, Annerose, Bien, Siegfried,
1234 & Rösler, Frank. (2008). Kinesthetic working memory and
1235 action control within the dorsal stream. *Cerebral Cortex*, *18*(2),
1236 243-253.
- 1237 Fortin, M., Voss, P., Lord, C., Lassonde, M., Pruessner, J., Saint-
1238 Amour, D. (2008). Wayfinding in the blind: Larger hippocampal
1239 volume and supranormal spatial navigation. *Brain*, *131*(Pt 11),
1240 2995-3005. doi: 10.1093/brain/awn250
- 1241 Foster, R.M., Kleinholdermann, U., Leifheit, S., & Franz, V.H.
1242 (2012). Does bimanual grasping of the Muller-Lyer illusion
1243 provide evidence for a functional segregation of dorsal and
1244 ventral streams? *Neuropsychologia*, *50*(14), 3392-3402. doi:
1245 10.1016/j.neuropsychologia.2012.09.026
- 1246 Franz, V.H., Hesse, C., & Kollath, S. (2009). Visual illusions,
1247 delayed grasping, and memory: No shift from dorsal to ven-
1248 tral control. *Neuropsychologia*, *47*(6), 1518-1531. doi: 10.1016/
1249 j.neuropsychologia.2008.08.029
- 1250 Freeman, J., & Ziemba, C.M. (2011). Unwrapping the ventral stream.
1251 *J Neurosci*, *31*(7), 2349-2351. doi: 10.1523/JNEUROSCI.61
1252 91-10.2011
- 1253 Ghazanfar, A.A., & Schroeder, C.E. (2006). Is neocortex essen-
1254 tially multisensory? *Trends Cogn Sci*, *10*(6), 278-285. doi: DOI
1255 10.1016/j.tics.2006.04.008
- 1256 Gomez, Juan Diego, Mohammed, Sinan, Bologna, Guido, & Pun,
1257 Thierry. (2011). *Toward 3D scene understanding via audio-*
1258 *description: Kinect-iPad fusion for the visually impaired*. Paper
1259 presented at The proceedings of the 13th international ACM
1260 SIGACCESS conference on Computers and accessibility.
- 1261 Gomi, H. (2008). Implicit online corrections of reaching movements.
1262 *Curr Opin Neurobiol*, *18*(6), 558-564. doi: 10.1016/j.conb.
1263 2008.11.002
- 1264 Goodale, M.A. (2008). Action without perception in human vision.
1265 *Cogn Neuropsychol*, *25*(7-8), 891-919. doi: 10.1080/02643290
1266 801961984
- 1267 Goodale, M.A., Pelisson, D., & Prablanc, C. (1986). Large adjust-
1268 ments in visually guided reaching do not depend on vision of the
1269 hand or perception of target displacement. *Nature*, *320*(6064),
1270 748-750. doi: 10.1038/320748a0
- 1271 Gritsenko, V., Yakovenko, S., & Kalaska, J.F. (2009). Integration of
1272 predictive feedforward and sensory feedback signals for online
1273 control of visually guided movement. *J Neurophysiol*, *102*(2),
1274 914-930. doi: 10.1152/jn.91324.2008
- 1275 Haigh, A., Brown, D.J., Meijer, P., & Proulx, M.J. (2013). How well
1276 do you see what you hear? The acuity of visual-to-auditory
1277 sensory substitution. *Front Psychol*, *4*, 330. doi: 10.3389/
1278 fpsyg.2013.00330
- 1279 Hughes, B. (2001). Active artificial echolocation and the nonvi-
1280 sual perception of aperture passability. *Hum Mov Sci*, *20*(4-5),
1281 371-400.
- Hurley, Susan, & Noë, Alva. (2003). Neural Plasticity and Con-
sciousness. *Biology and Philosophy*, *18*(1), 131-168.
- Kanwisher, N., McDermott, J., & Chun, M.M. (1997). The fusiform
face area: A module in human extrastriate cortex specialized
for face perception. *J Neurosci*, *17*(11), 4302-4311.
- Kauffman, T., Theoret, H., & Pascual-Leone, A. (2002). Braille
character discrimination in blindfolded human subjects. *Neu-
roreport*, *13*(5), 571-574.
- Kim, J.K., & Zatorre, R.J. (2011). Tactile-auditory shape learning
engages the lateral occipital complex. *J Neurosci*, *31*(21), 7848-
7856. doi: 10.1523/JNEUROSCI.3399-10.2011
- Kokjer, K.J. (1987). The Information Capacity of the Human Finger-
tip. *Ieee Transactions on Systems Man and Cybernetics*, *17*(1),
100-102. doi: Doi 10.1109/Tsmc.1987.289337
- Kolarik, A.J., Timmis, M.A., Cirstea, S., & Pardhan, S. (2014). Sen-
sory substitution information informs locomotor adjustments
when walking through apertures. *Exp Brain Res*, *232*(3), 975-
984. doi: 10.1007/s00221-013-3809-5
- Krakauer, J.W., Pine, Z.M., Ghilardi, M.F., & Ghez, C.
(2000). Learning of visuomotor transformations for vectorial
planning of reaching trajectories. *J Neurosci*, *20*(23), 8916-
8924.
- Kupers, R., Fumal, A., de Noordhout, A.M., Gjedde, A., Schoenen,
J., & Ptito, M. (2006). Transcranial magnetic stimulation of the
visual cortex induces somatotopically organized qualia in blind
subjects. *Proc Natl Acad Sci U S A*, *103*(35), 13256-13260. doi:
10.1073/pnas.0602925103
- Kupers, R., Pietrini, P., Ricciardi, E., & Ptito, M. (2011). The nature
of consciousness in the visually deprived brain. *Front Psychol*,
2, 19. doi: 10.3389/fpsyg.2011.00019
- Kupers, R., & Ptito, M. (2011). Insights from darkness: What the
study of blindness has taught us about brain structure and func-
tion. *Prog Brain Res*, *192*, 17-31. doi: 10.1016/B978-0-444-533
55-5.00002-6
- Levy-Tzedek, S., Ben Tov, M., & Karniel, A. (2011). Rhythmic
movements are larger and faster but with the same frequency on
removal of visual feedback. *J Neurophysiol*, *106*(5), 2120-2126.
doi: 10.1152/jn.00266.2011
- Levy-Tzedek, S., Hanassy, S., Abboud, S., Maidenbaum, S.,
& Amedi, A. (2012a). Fast, accurate reaching movements
with a visual-to-auditory sensory substitution device. *Restor
Neurol Neurosci*, *30*(4), 313-323. doi: 10.3233/RNN-2012-
110219
- Levy-Tzedek, S., Krebs, H.I., Arle, J.E., Shils, J.L., & Poizner, H.
(2011). Rhythmic movement in Parkinson's disease: Effects of
visual feedback and medication state. *Exp Brain Res*, *211*(2),
277-286. doi: 10.1007/s00221-011-2685-0
- Levy-Tzedek, S., Novick, I., Arbel, R., Abboud, S., Maidenbaum,
S., Vaadia, E., & Amedi, A. (2012b). Cross-sensory transfer of
sensory-motor information: Visuomotor learning affects per-
formance on an audiomotor task, using sensory-substitution.
Sci Rep, *2*, 949. doi: 10.1038/srep00949
- Lewald, J. (2007). More accurate sound localization induced by
short-term light deprivation. *Neuropsychologia*, *45*(6), 1215-
1222. doi: 10.1016/j.neuropsychologia.2006.10.006

- 1337 Liang, M., Mouraux, A., Hu, L., & Iannetti, G.D. (2013). Primary sensory cortices contain distinguishable spatial patterns of activity for each sense. *Nat Commun*, 4, 1979. doi: 10.1038/ncomms2979
- 1338
1339
1340
- 1341 Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240(4853), 740-749. doi: 10.1126/science.3283936
- 1342
1343
- 1344 Loschky, Lester, McConkie, George, Yang, Jian, & Miller, Michael. (2005). The limits of visual resolution in natural scene viewing. *Vis Cogn*, 12(6), 1057-1092. doi: 10.1080/13506280444000652
- 1345
1346
1347
- 1348 Maidenbaum, S., Levy-Tzedek, S., Chebat, D.R., & Amedi, A. (2013). Increasing Accessibility to the Blind of Virtual Environments, Using a Virtual Mobility Aid Based On the "EyeCane": Feasibility Study. *Plos One*, 8(8). doi: ARTN e72555 DOI 10.1371/journal.pone.0072555
- 1349
1350
1351
1352
- 1353 Marr, David. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W.H. Freeman.
- 1354
1355
- 1356 Matteau, I., Kupers, R., Ricciardi, E., Pietrini, P., & Ptito, M. (2010). Beyond visual, aural and haptic movement perception: HMT+ is activated by electrotactile motion stimulation of the tongue in sighted and in congenitally blind individuals. *Brain Res Bull*, 82(5-6), 264-270. doi: 10.1016/j.brainresbull.2010.05.001
- 1357
1358
1359
1360
- 1361 Meijer, P.B. (1992). An experimental system for auditory image representations. *IEEE Trans Biomed Eng*, 39(2), 112-121. doi: 10.1109/10.121642
- 1362
1363
- 1364 Mendoza, J.E., Elliott, D., Meegan, D.V., Lyons, J.L., & Welsh, T.N. (2006). The effect of the Muller-Lyer illusion on the planning and control of manual aiming movements. *J Exp Psychol Hum Percept Perform*, 32(2), 413-422. doi: 2006-04604-015 [pii] 10.1037/0096-1523.32.2.413
- 1365
1366
1367
1368
- 1369 Merabet, L.B., Hamilton, R., Schlaug, G., Swisher, J.D., Kiriakopoulos, E.T., Pitskel, N.B. (2008). Rapid and reversible recruitment of early visual cortex for touch. *PLoS One*, 3(8), e3046. doi: 10.1371/journal.pone.0003046
- 1370
1371
1372
- 1373 Milner, A.D. (2012). Is visual processing in the dorsal stream accessible to consciousness? *Proc Biol Sci*, 279(1737), 2289-2298. doi: 10.1098/rspb.2011.2663
- 1374
1375
- 1376 Milner, A.D., & Goodale, M.A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46(3), 774-785. doi: 10.1016/j.neuropsychologia.2007.10.005
- 1377
1378
- 1379 Mishkin, M., & Ungerleider, L.G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behav Brain Res*, 6(1), 57-77.
- 1380
1381
- 1382 Mitchinson, Ben, & Prescott, Tony J. (2013). Whisker movements reveal spatial attention: A unified computational model of active sensing control in the rat. *PLoS Comp Biol*, 9(9), e1003236.
- 1383
1384
- 1385 Nelson, Mark E., & MacIver, Malcolm A. (2006). Sensory acquisition in active sensing systems. *Journal of Comparative Physiology A*, 192(6), 573-586.
- 1386
1387
- 1388 Novick, I., & Vaadia, E. (2011). Just do it: Action-dependent learning allows sensory prediction. *PLoS One*, 6(10), e26020. doi: 10.1371/journal.pone.0026020
- 1389
1390
- O'Regan, J.K., & Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *Behav Brain Sci*, 24(5), 939-973; discussion 973-1031.
- 1391
1392
1393
- Okada, K., Rong, F., Venezia, J., Matchin, W., Hsieh, I.H., Saberi, K. (2010). Hierarchical organization of human auditory cortex: Evidence from acoustic invariance in the response to intelligible speech. *Cereb Cortex*, 20(10), 2486-2495. doi: bhp318 [pii] 10.1093/cercor/bhp318
- 1394
1395
1396
1397
1398
- Ostrovsky, Yuri, Andalman, Aaron, & Sinha, Pawan. (2006). Vision following extended congenital blindness. *Psychological Science*, 17(12), 1009-1014.
- 1399
1400
1401
- Pascual-Leone, A., & Hamilton, R. (2001). The metamodal organization of the brain. *Prog Brain Res*, 134, 427-445.
- 1402
1403
- Pasqualotto, A., Lam, J.S., & Proulx, M.J. (2013a). Congenital blindness improves semantic and episodic memory. *Behav Brain Res*, 244, 162-165. doi: 10.1016/j.bbr.2013.02.005
- 1404
1405
1406
- Pasqualotto, A., & Proulx, M.J. (2012). The role of visual experience for the neural basis of spatial cognition. *Neurosci Biobehav Rev*, 36(4), 1179-1187. doi: 10.1016/j.neubiorev.2012.01.008
- 1407
1408
1409
- Pasqualotto, A., & Proulx, M.J. (2013). The study of blindness and technology can reveal the mechanisms of three-dimensional navigation. *Behav Brain Sci*, 36(5), 559-560; discussion 571-587. doi: 10.1017/S0140525X13000496
- 1410
1411
1412
1413
- Pasqualotto, A., Spiller, M.J., Jansari, A.S., & Proulx, M.J. (2013b). Visual experience facilitates allocentric spatial representation. *Behav Brain Res*, 236(1), 175-179. doi: 10.1016/j.bbr.2012.08.042
- 1414
1415
1416
1417
- Pollok, B., Schnitzler, I., Stoerig, P., Mierdorf, T., & Schnitzler, A. (2005). Image-to-sound conversion: Experience-induced plasticity in auditory cortex of blindfolded adults. *Exp Brain Res*, 167(2), 287-291. doi: 10.1007/s00221-005-0060-8
- 1418
1419
1420
1421
- Proulx, M.J. (2010). Synthetic synaesthesia and sensory substitution. *Conscious Cogn*, 19(1), 501-503. doi: 10.1016/j.concog.2009.12.005
- 1422
1423
1424
- Proulx, M.J., Brown, D.J., Pasqualotto, A., & Meijer, P. (2012). Multisensory perceptual learning and sensory substitution. *Neurosci Biobehav Rev*. doi: 10.1016/j.neubiorev.2012.11.017
- 1425
1426
1427
- Proulx, M.J., Brown, D.J., Pasqualotto, A., & Meijer, P. (2014). Multisensory perceptual learning and sensory substitution. *Neurosci Biobehav Rev*, 41, 16-25. doi: 10.1016/j.neubiorev.2012.11.017
- 1428
1429
1430
1431
- Proulx, M.J., Stoerig, P., Ludowig, E., & Knoll, I. (2008). Seeing 'where' through the ears: Effects of learning-by-doing and long-term sensory deprivation on localization based on image-to-sound substitution. *PLoS One*, 3(3), e1840. doi: 10.1371/journal.pone.0001840
- 1432
1433
1434
1435
1436
- Ptito, M., Moesgaard, S.M., Gjedde, A., & Kupers, R. (2005). Cross-modal plasticity revealed by electrotactile stimulation of the tongue in the congenitally blind. *Brain*, 128(Pt 3), 606-614. doi: 10.1093/brain/awh380
- 1437
1438
1439
1440
- Putzar, Lisa, Gondan, Matthias, & Röder, Brigitte. (2012). Basic multisensory functions can be acquired after congenital visual pattern deprivation in humans. *Developmental neuropsychology*, 37(8), 697-711.
- 1441
1442
1443
1444

- 1445 Qin, W., & Yu, C. (2013). Neural pathways conveying novisual information to the visual cortex. *Neural Plast*, 2013, 864920. doi: 10.1155/2013/864920
- 1447
- 1448 Recanzone, G.H., & Sutter, M.L. (2008). The biological basis of audition. *Annu Rev Psychol*, 59, 119-142. doi: 10.1146/annurev.psych.59.103006.093544
- 1449
- 1450
- 1451 Reich, L., Szwed, M., Cohen, L., & Amedi, A. (2011). A ventral visual stream reading center independent of visual experience. *Curr Biol*, 21(5), 363-368. doi: 10.1016/j.cub.2011.01.040
- 1452
- 1453
- 1454 Renier, L.A., Anurova, I., De Volder, A.G., Carlson, S., VanMeter, J., & Rauschecker, J.P. (2010). Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. *Neuron*, 68(1), 138-148. doi: 10.1016/j.neuron.2010.09.021
- 1455
- 1456
- 1457
- 1458
- 1459 Renier, L., Collignon, O., Poirier, C., Tranduy, D., Vanlierde, A., Bol, A. (2005a). Cross-modal activation of visual cortex during depth perception using auditory substitution of vision. *Neuroimage*, 26(2), 573-580. doi: 10.1016/j.neuroimage.2005.01.047
- 1460
- 1461
- 1462
- 1463
- 1464 Renier, L., & De Volder, A.G. (2010). Vision substitution and depth perception: Early blind subjects experience visual perspective through their ears. *Disabil Rehabil Assist Technol*, 5(3), 175-183. doi: 10.3109/17483100903253936
- 1465
- 1466
- 1467
- 1468 Renier, L., Laloyaux, C., Collignon, O., Tranduy, D., Vanlierde, A., Bruyer, R., & De Volder, A.G. (2005b). The Ponzo illusion with auditory substitution of vision in sighted and early-blind subjects. *Perception*, 34(7), 857-867.
- 1469
- 1470
- 1471
- 1472 Renier, Laurent, Bruyer, Raymond, & Volder, AnneG. (2006). Vertical-horizontal illusion present for sighted but not early blind humans using auditory substitution of vision. *Percept Psychophys*, 68(4), 535-542. doi: 10.3758/BF03208756
- 1473
- 1474
- 1475
- 1476 Renzi, Chiara, Ricciardi, Emiliano, Bonino, Daniela, Handjaras, Giacomo, Vecchi, Tomaso, & Pietrini, Pietro. (2013). The effects of visual control and distance in modulating peripersonal spatial representation. *PLoS One*, 8(3), e59460.
- 1477
- 1478
- 1479
- 1480 Ricciardi, E., Bonino, D., Pellegrini, S., & Pietrini, P. (2014). Mind the blind brain to understand the sighted one! Is there a supramodal cortical functional architecture? *Neuroscience and Biobehavioral Reviews*, 41, 64-77. doi: DOI 10.1016/j.neubiorev.2013.10.006
- 1481
- 1482
- 1483
- 1484
- 1485 Ricciardi, E., & Pietrini, P. (2011). New light from the dark: What blindness can teach us about brain function. *Curr Opin Neurol*, 24(4), 357-363. doi: 10.1097/WCO.0b013e328348bdf
- 1486
- 1487
- 1488 Ricciardi, Emiliano, Bonino, Daniela, Sani, Lorenzo, Vecchi, Tomaso, Guazzelli, Mario, Haxby, James V. (2009). Do we really need vision? How blind people "see" the actions of others. *The Journal of Neuroscience*, 29(31), 9719-9724.
- 1489
- 1490
- 1491
- 1492 Rockland, K.S., & Ojima, H. (2003). Multisensory convergence in calcarine visual areas in macaque monkey. *Int J Psychophysiol*, 50(1-2), 19-26.
- 1493
- 1494
- 1495 Röder, Brigitte, Kusmierik, Anna, Spence, Charles, & Schicke, Tobias. (2007). Developmental vision determines the reference frame for the multisensory control of action. *Proceedings of the National Academy of Sciences*, 104(11), 4753-758.
- 1496
- 1497
- 1498
- 1499
- Rossetti, Yves, Stelmach, George, Desmurget, Michel, Prablanc, Claude, & Jeannerod, Marc. (1994). The effect of viewing the static hand prior to movement onset on pointing kinematics and variability. *Experimental brain research*, 101(2), 323-330.
- 1500
- 1501
- 1502
- 1503
- 1504
- Sampaio, E., & Dufier, J.L. (1988). [An electronic sensory substitute for young blind children]. *J Fr Ophthalmol*, 11(2), 161-167.
- 1505
- 1506
- Sarlegna, F., Blouin, J., Vercher, J.L., Bresciani, J.P., Bourdin, C., & Gauthier, G.M. (2004). Online control of the direction of rapid reaching movements. *Exp Brain Res*, 157(4), 468-471. doi: 10.1007/s00221-004-1860-y
- 1507
- 1508
- 1509
- 1510
- Sathian, K., & Zangaladze, A. (2002). Feeling with the mind's eye: Contribution of visual cortex to tactile perception. *Behav Brain Res*, 135(1-2), 127-132.
- 1511
- 1512
- 1513
- Schmidt, Robert F. (1981). Somatovisceral sensibility *Fundamentals of sensory physiology* (pp. 81-125): Springer.
- 1514
- 1515
- Schroeder, Charles E, Wilson, Donald A, Radman, Thomas, Scharfman, Helen, & Lakatos, Peter. (2010). Dynamics of active sensing and perceptual selection. *Current Opinion in Neurobiology*, 20(2), 172-176.
- 1516
- 1517
- 1518
- 1519
- Segond, H., Weiss, D., Kawalec, M., & Sampaio, E. (2013). Perceiving space and optical cues via a visuo-tactile sensory substitution system: A methodological approach for training of blind subjects for navigation. *Perception*, 42(5), 508-528.
- 1520
- 1521
- 1522
- 1523
- 1524
- Segond, H., Weiss, D., & Sampaio, E. (2005). Human spatial navigation via a visuo-tactile sensory substitution system. *Perception*, 34(10), 1231-1249.
- 1525
- 1526
- 1527
- Soechting, John F, & Flanders, Martha. (1989). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology*, 62(2), 582-594.
- 1528
- 1529
- 1530
- Striem-Amit, E., Dakwar, O., Reich, L., & Amedi, A. (2012). The large-scale organization of "visual" streams emerges without visual experience. *Cereb Cortex*, 22(7), 1698-1709. doi: 10.1093/cercor/bhr253
- 1531
- 1532
- 1533
- 1534
- Taira, M., Mine, S., Georgopoulos, A.P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Exp Brain Res*, 83(1), 29-36.
- 1535
- 1536
- 1537
- 1538
- Thaler, L. (2013). Echolocation may have real-life advantages for blind people: An analysis of survey data. *Front Physiol*, 4, 98. doi: 10.3389/fphys.2013.00098
- 1539
- 1540
- 1541
- Thaler, L., Arnott, S.R., & Goodale, M.A. (2011). Neural correlates of natural human echolocation in early and late blind echolocation experts. *PLoS One*, 6(5), e20162. doi: 10.1371/journal.pone.0020162
- 1542
- 1543
- 1544
- 1545
- Thaler, L., & Goodale, M.A. (2011). Neural substrates of visual spatial coding and visual feedback control for hand movements in allocentric and target-directed tasks. *Front Hum Neurosci*, 5, 92. doi: 10.3389/fnhum.2011.00092
- 1546
- 1547
- 1548
- 1549
- Thaler, L., Milne, J.L., Arnott, S.R., Kish, D., & Goodale, M.A. (2014). Neural correlates of motion processing through echolocation, source hearing, and vision in blind echolocation experts and sighted echolocation novices. *J Neurophysiol*, 111(1), 112-127. doi: 10.1152/jn.00501.2013
- 1550
- 1551
- 1552
- 1553
- 1554
- 1555

- 1555 Van Donkelaar, P., Lee, J.H., & Drew, A.S. (2000). Transcranial mag- 1565
1556 netic stimulation disrupts eye-hand interactions in the posterior 1566
1557 parietal cortex. *J Neurophysiol*, *84*(3), 1677-1680. 1567
- 1558 Wachowiak, Matt. (2011). All in a sniff: Olfaction as a model for 1568
1559 active sensing. *Neuron*, *71*(6), 962-973. 1569
- 1560 Ward, J., & Meijer, P. (2010). Visual experiences in the blind induced 1570
1561 by an auditory sensory substitution device. *Conscious Cogn*, 1571
1562 *19*(1), 492-500. doi: 10.1016/j.concog.2009.10.006
- 1563 Weiss, Tali, & Sobel, Noam. (2012). What's primary about primary 1572
1564 olfactory cortex? *Nat Neurosci*, *15*(1), 10-12. 1573
1574
- Wolpert, Daniel M, Ghahramani, Zoubin, & Jordan, Michael I. 1565
(1995). An internal model for sensorimotor integration. *Sci- 1566
ence*, *269*(5232), 1880-1882. 1567
- Xu, Jinghong, Yu, Liping, Rowland, Benjamin A, Stanford, Ter- 1568
rence R, & Stein, Barry E. (2012). Incorporating cross-modal 1569
statistics in the development and maintenance of multisensory 1570
integration. *The Journal of Neuroscience*, *32*(7), 2287-2298. 1571
- Zangaladze, A., Epstein, C.M., Grafton, S.T., & Sathian, K. (1999). 1572
Involvement of visual cortex in tactile discrimination of orien- 1573
tation. *Nature*, *401*(6753), 587-590. doi: 10.1038/44139 1574

Uncorrected Author Proof