

# Task-selectivity in the sensory deprived brain and sensory substitution approaches for clinical practice: evidence from blindness

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## Introduction

To what extent is the human brain already defined at birth, and alternatively, how much does the brain change in response to cognitive and sensory experiences? This question has inflamed philosophical debate for centuries, and even today, is still one of the most crucial questions in cognitive neuroscience. In general terms, the most accepted notion that has prevailed over decades is that functional brain specializations arise from evolutionary programming that developed through natural selection. This conclusion was supported by the repeatedly observed anatomical consistency of brain specializations across individuals, not only concerning the division of sensory labor (e.g., the division of the brain into visual, auditory, or somatosensory regions) but even within specific sensory cortices (e.g., the division in the visual cortex between retinotopic mapping in early visual cortices and selectivity for specific visual categories such as faces or body images in higher-order visual cortices).

But then, within the natural selection framework, what is the role of cognitive and sensory experiences? Do they play a role only for evolutionary purposes, i.e., on a time span of thousands of years, or do they also affect brain specializations in the time span of the life of an organism? For many decades, the main assumption in this matter was that cognitive and sensory experiences do play a crucial role during human life, but their role is strongly

constrained by the closure of critical/sensitive periods of development (i.e., an optimal time window in early infancy when the development of a particular sensory system should be pursued in order for the corresponding brain specializations to develop in a typical manner<sup>1</sup>). In other words, the influence of sensory experiences was classically considered to be very minimal during adulthood: if a specific sensory system did not develop during critical periods early in life, it would never properly develop to a level comparable to the control population.<sup>1–7</sup> These conclusions strongly rely on the seminal work by Hubel and Wiesel on kittens visually deprived in one eye at different times after birth and for different time periods.<sup>2</sup> Specifically, Hubel and Wiesel showed that even short periods of monocular deprivation of a few days permanently affected cortical physiology. They also showed that after 3 months of monocular deprivation, deficits in cortical physiology and atrophy in crucial regions of the visual system persisted for years, even though, behaviorally, vision partially recovered in the deprived eye.<sup>2</sup> Later studies on patients who recovered vision during adulthood corroborated these seminal findings by further documenting the lack of a proper development of visual-related brain specializations, even after years of therapy aimed at visual restoration.<sup>8–12</sup>

However, this classical view has been called into question during the last decades, due to accumulating evidence highlighting that the brain still retains a considerable amount of plasticity during adulthood that can be triggered via specific training regimens.<sup>13–18</sup> Numerous studies of this kind showed the remarkable benefits of specific training for the efficient (re-)wiring of the brain in several domains: for the recovery of higher-order abilities such as language, memory, and executive functions mainly in the aging brain<sup>19–24</sup>; for the improvement of specific sets of sensory/cognitive abilities either as a consequence of specific acquired expertise (e.g., in musicians<sup>25–30</sup>) or as a consequence of partial lesions<sup>31,32</sup> or of lesions occurring during adulthood.<sup>33,34</sup> This body of studies then unraveled the lifelong capacity for plasticity in the brain and the crucial role of specific training programs for efficiently triggering it. However, from this perspective, it is still posited that each specific ability/sensory-specific function must be at least partially experienced during critical periods early in development in order for the corresponding brain specialization to emerge (and later in life to be further modifiable by training). In other words, the currently accepted view still postulates that sensory brain regions are strictly sensory-specific in nature (i.e., determined by evolution), and that there is an unalterable link between a given brain sensory region and a sensory-specific computation/cognitive task which must be established during critical periods via sensory-specific experiences.

In this chapter, we will review a series of studies conducted in the last few decades with sensory-deprived adults and specifically, with congenitally blind adults, challenging the classic assumptions on the factors driving sensory brain organization in relation to critical periods of development (see companion chapter by Lomber et al., this volume, for a comprehensive review of studies on congenital and acquired deafness). We will focus in particular on the (re-)organization occurring within higher-order visual cortices deprived of their natural sensory input (vision), describing the mechanisms we propose as underlying the emergence of their organization and redefining the assumptions regarding critical periods based on the available results. We will then discuss the implications of these results and novel frameworks for rehabilitative approaches to sensory restoration with a special emphasis on sensory

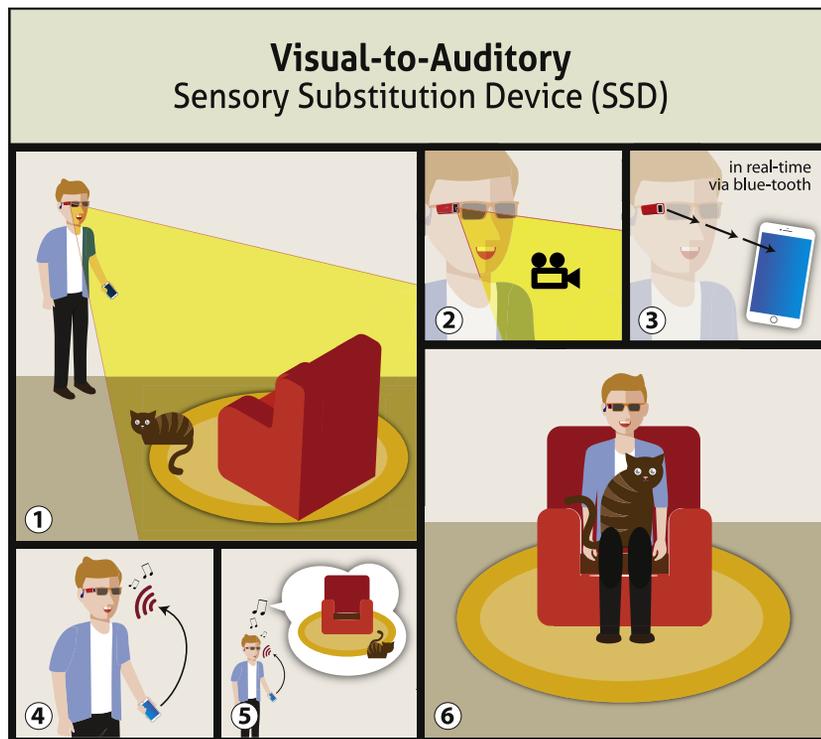
substitution devices (SSDs) and the role of specific training for reshaping/rewiring brain sensory functions. Before diving into this exciting literature, we will introduce the concept of sensory substitution, as we will refer to this throughout the chapter.

## Sensory substitution devices

SSDs aim at conveying the information typically delivered by one sensory modality (e.g., vision) to another sensory modality (e.g., audition or touch) via predetermined algorithms that can be learned by the users through specific training programs.<sup>35–38</sup> At first, the concept of sensory substitution seems very intuitive. For instance, everybody relies on different sensory modalities when visual information is unavailable: we rely on touch when searching for our wallet in our backpack and we rely on our audition to know, for instance, if there are people in a room when the door is closed. What differentiates SSDs from these other strategies is the structured training that users need to undertake in order to learn to interpret the SSD-specific algorithm. The first structured sensory substitution system was probably Braille reading. This technique was originally developed at the beginning of the 19th century by Barbier as a means of writing and reading in the dark for the French military in the Napoleonic era, and then revised by Louis Braille to enable the blind to read by substituting visual letters with tactile dot patterns coding for the letters.<sup>39</sup> This approach was further enhanced in the early 1950s with the development of automatic text-to-braille converters such as the Optacon.<sup>40</sup> A highly interesting effort which is often neglected historically, was the Elektroftalm that attempted for the first time to convey composite visual information, i.e., to electronically transform a visual image into auditory (late 1890s) and tactile (1950s) stimulation using one or several sensors.<sup>41</sup> These early attempts led to the more organized and methodologically sound attempts in the 1970s, by Paul Bach-y-Rita, who is considered the pioneer of the extensive use of sensory substitution for research aimed at visual rehabilitation for the blind population. Bach-y-Rita built his framework for SSD research based on the accepted idea that visual perception mainly takes place in our brain rather than in our eyes.<sup>42</sup> He points out that visual information travels from the retina to the brain in the form of electrical and chemical pulses, and it is the brain that interprets this information as vision.<sup>42</sup> The perception of an image requires much more from the brain than a simple image analysis. Visual perception is based on memory, learning, and interpretation of contextual, cultural, and social factors.<sup>42–44</sup> Thus, he suggests that SSDs are the perfect tools to unravel the extent to which the eyes are essential to vision and the ears are essential to audition.<sup>42</sup> This research question might seem absurd, but it is indeed the problem posed by sensory substitution. Can Braille reading be qualified as vision? Or is it rather a tactile experience that replaces vision?

The biggest challenge that Bach-y-Rita needed to face when building his SSD concerned the choice of the sensory modality he would be using to convey visual information to blind users. Indeed vision has special properties, such as its high informational capacity (or bandwidth), and its capacity for parallel processing, that exceeds those of the other senses.<sup>45</sup> Bach-y-Rita chose to use touch to convey complex visual images, probably because of the possibility to convey tactile information in parallel and the quite obvious skin/retina analogue related to the topographic representation of spatial locations on both sensory organs.<sup>46</sup> The visual-to-tactile SSD that Bach-y-Rita developed is known as “Tactile Vision

Sensory Substitution” (TVSS).<sup>36</sup> He used a camera to capture images and then transmitted them to an electrode grid positioned on the backs of the users, to stimulate cutaneous receptors. Case studies conducted in Bach-y-Rita’s laboratory demonstrated that after extensive training, congenitally blind participants were able to make judgments of distance, grab objects in motion, and even recognize novel objects. Later, this device was adapted to stimulate the tongue. The reason for the choice of the tongue rather than the skin of the back is twofold: firstly, the tongue is embedded in a wet milieu, making possible to use much safer micro-currents for stimulation, and secondly the tongue is a much more sensitive sensory organ with a much higher density of receptors than the back, thus providing much better spatial resolution. However, most research with SSDs, nowadays, relies on the auditory rather than on the tactile modality to convey the missing visual information. This is because users of visual-to-auditory SSD do not need specific materials (i.e., vibrators) to be able to use the device (Fig. 15.1), thus making it a more convenient and easy-to-disseminate approach. In addition, from a more theoretical perspective, the auditory system, compared to the skin,



**FIGURE 15.1** Current visual-to-auditory sensory substitution devices (SSDs). (1–3) Visual images are captured via a camera which is connected via Bluetooth to an app on the smartphone. (4) The app contains the SSD algorithm which transforms the visual image into an auditory soundscape maintaining all the basic features of the visual scene (i.e., shape, size, color, and location of objects). (5–6) After specific training, the users learn to interpret the SSD algorithm and are able to understand the scene in front of them and efficiently and independently interact with the external environment.

provides a higher informational capacity (bandwidth) to convey visual information to the brain.<sup>46</sup> Indeed, the informational capacity of the human eye has been estimated to be around  $4.3 \times 10^6$  bits per second.<sup>47</sup> This is four orders of magnitude greater bandwidth than the estimated bandwidth of the human fingertip—100 bits per second,<sup>48</sup> and of other areas of skin for which the bandwidth estimated was even lower, from 5 to 56 bits per second.<sup>49</sup> The information capacity of the human ear is the highest after vision, with a capacity of  $10^4$  bits per second.<sup>50</sup> In addition, audition has a much wider spectrum than vibration. These factors, in turn, allow the more rapid presentation of more detailed visual images in audition compared to touch. Examples of visual-to-auditory SSDs are the VOiCe<sup>38</sup> or the EyeMusic,<sup>35</sup> which transform visual images into what are called auditory soundscapes maintaining all the basic features of visual stimuli in a scene, such as their shapes and exact spatial locations (Fig. 15.1). Training with visual-to-auditory SSDs was shown to be effective in teaching blind users to perform a variety of “visual” tasks such as object recognition and localization,<sup>51,52</sup> as well as navigation in real and virtual environments,<sup>53,54</sup> among many other tasks<sup>39,55</sup> (Fig. 15.1). Additionally, visual-to-auditory SSDs have been successfully used for teaching inherently visual concepts to blind users such as color perception<sup>35</sup> or visual parsing<sup>56</sup> and were also proven effective to permit users to perform visual acuity tests at a level above the threshold for legal blindness.<sup>57,58</sup>

In this section, we provided an overview on the considerations behind the invention of SSDs and described the main results obtained in the context of visual rehabilitation. Throughout the rest of the chapter, we will discuss other uses of SSDs, for example, for uncovering the properties of our sensory brain organization and for maximizing sensory restoration outcomes.

## Crossmodal plasticity in cases of sensory deprivation

The term crossmodal plasticity generally refers to the recruitment of a deprived region of sensory cortex (e.g., the visual cortex in case of blindness or the auditory cortex in case of deafness) by the intact sensory modalities (e.g., audition or vision). This notion emerged from seminal studies reporting high metabolic/electroencephalographic (EEG) activity in the deprived sensory cortices of adults who became either blind or deaf early in life. The results suggested that deprived cortices in blind adults were not silent but were activated by a variety of tactile and auditory stimuli.<sup>59–64</sup> Similar results were also obtained in the deprived auditory cortices of deaf adults by visual inputs.<sup>65–68</sup> These intriguing results prompted a series of studies aiming at investigating the organizational properties of these crossmodal activations which will be discussed in the next sections.

### **Task-selective sensory-independent organization in the deprived higher-order “visual” cortices**

Perhaps the most groundbreaking result in the past decades regarding the properties of crossmodal activations in the deprived sensory cortices is the finding that most of the known category-selective regions in the deprived higher-order visual cortices maintain their

category-selective functionality (e.g., to process objects, letters or numbers), albeit recruited by the spared sensory modalities (task-selective sensory-independent [TSSI] recruitment; see for reviews<sup>69,70</sup>). These results have been obtained in studies using functional magnetic resonance imaging (fMRI), conducted mainly with congenitally blind participants. Specifically, this body of studies reported TSSI recruitment by auditory and/or tactile inputs, respecting the broad division of labor between ventral (what) and dorsal (where) “visual” pathways<sup>71</sup> as well as specific category-selective specializations in both “visual” pathways, such as spatial localization<sup>72,73</sup>; motion detection<sup>74</sup>; tool and object perception<sup>75</sup>; reading<sup>52,76</sup>; number identification<sup>77</sup>; and body image perception.<sup>78</sup> This body of work ultimately suggests that the brain is organized along the lines of flexible task machinery, rather than sensory-specific machinery as classically conceived.<sup>79</sup> In addition, several of these studies documented, in congenitally blind participants who showed TSSI recruitment in their “visual” cortices, the preservation of functional connectivity patterns between specific category-selective “visual” regions and the other brain regions known to be involved in the same computation in the sighted brain.<sup>77,78</sup> For instance, it has been shown that number identification via audition recruited, in congenitally blind participants, the right number form area (NFA) in the ventral “visual” stream.<sup>77</sup> Additional analyses showed that these same participants had preserved functional connections between their NFA and other nodes that are known to be part of the numeral processing network in the control population, such as the right intraparietal sulcus.<sup>77</sup> Importantly, some of the most convincing results among the studies discussed above, including the latter work,<sup>77</sup> were obtained using visual-to-auditory SSDs. What is unique about using SSDs to investigate brain organization is that, during SSD training programs, users learn a new sensory pairing between a “visual” category (e.g., body shape recognition) and a sensory modality (e.g., audition) which had never been used to perform this specific task before.<sup>52,75,77,78</sup> Thus, the finding that TSSI recruitment of “visual” category-selective regions emerged in congenitally blind adults following relatively short SSD training showed that higher-order “visual” regions are incredibly flexible for the activating sensory modality. Indeed, the SSD training programs implemented in the studies reviewed above, reporting TSSI recruitment in the congenitally blind brain, lasted between 10 and 50 hours.<sup>52,75,77,78</sup> This observed flexibility refutes the idea, that in order for typical specializations to emerge, the pairing between a specific computation and a specific sensory input absolutely needs to take place during critical periods of development early in life.

Overall then, the classic account of the brain as strictly sensory-specific in nature cannot explain the set of findings documenting TSSI recruitment of deprived visual cortices in congenitally blind adults. Thus, if sensory-specific input does not drive the emergence of our sensory brain organization, what are the mechanisms underlying such organization? Based on all the available results, it was recently suggested that TSSI organization arises from a combination of two principles that are not mutually exclusive: a sensitivity to task-distinctive features that is invariant to the input sensory modality (e.g., body shape perception in the extrastriate body area [EBA] independent of the sensory modality used as input) and the preservation of large-scale anatomical and functional (partly innate?) connectivity patterns (e.g., the connections between EBA and all the other brain regions associated with body shape perception<sup>80–82</sup>).

## Does task-selective and sensory-independent organization extend to higher-order auditory regions as well?

Is TSSI recruitment a general principle of brain (re)-organization, or is it specific to the (re)-organization of visual cortices? Unfortunately, when it comes to other deprived sensory cortices (e.g., auditory or somatosensory), evidence for TSSI recruitment is more limited compared to the results obtained with the congenitally blind population. Nonetheless, accumulating evidence from the deaf population supports the findings documented for the blind population, ultimately suggesting that TSSI organization extends beyond visual regions. In the case of congenital deafness, the most elegant evidence regarding the presence of TSSI recruitment of the deprived auditory cortices comes from a series of studies by Lomber's group with congenitally deaf cats showing that deprived higher-order auditory regions maintained their typical computations, albeit being activated by vision<sup>83–85</sup> (see for details the chapter by Lomber et al. in this volume). Evidence in favor of TSSI recruitment in the deprived higher-order "auditory" cortices of deaf humans is less straightforward but is also beginning to accumulate. Indeed, for a long time, the only clear result supporting the task-selective recruitment of deprived auditory cortices in congenitally deaf adults concerned the processing of sign language.<sup>86</sup> It has been repeatedly shown with fMRI that sign language in early or native deaf signers recruits the same auditory regions typically recruited by spoken language both during sign production tasks<sup>87–92</sup> and during sign language comprehension tasks.<sup>91,93–95</sup> These neuroimaging results are corroborated by neuropsychological evidence on selective sign language impairments in deaf adults as a consequence of damage to the left auditory cortex (i.e., the cortex in which spoken language is processed), whereas sign language skills were unaltered after right hemisphere auditory damage.<sup>96–99</sup> All these results suggest that the language network maintains its distinctive large-scale properties independently of the sensory modality used as input (audition or vision). Importantly, these results also provide initial evidence suggesting that the two principles proposed above as underlying TSSI organization in the deprived visual brain (i.e., sensitivity to task-distinctive features and preserved connectivity<sup>82</sup>) might also extend to higher-order "auditory" regions in humans.<sup>80</sup> However, to confirm that these are general principles driving the emergence of the organization of higher-order sensory cortices, more evidence is needed. Apart from language-related activations, evidence for TSSI recruitment in the deprived human auditory cortex started to arise only recently. One EEG study suggests the presence of sensory-independent task-selectivity in early deaf adults for the automatic detection of changes in the environment,<sup>100</sup> a skill that has been primarily ascribed to the auditory system.<sup>101,102</sup> In this study, early deaf and normally hearing adults were tested in a visual mismatch negativity (vMMN) task. vMMN is a well-known electrophysiological marker of sensory expectancy, which is considered to underlie the automatic detection of visual changes in the environment.<sup>103</sup> Source-estimate localization analyses revealed that the early deaf adults, but not adults with normal hearing, recruited their auditory cortices when automatically detecting visual changes.<sup>100</sup> These results provide initial hints in favor of the maintenance of an automatic change-detection functionality within the deprived auditory cortex of early deaf adults.<sup>100</sup> However, this study does not provide conclusive evidence for task selectivity since electrophysiology has rather poor spatial localization and source estimates may not be entirely reliable. In addition, the authors of this study<sup>100</sup> did not test the auditory counterpart of the task, by asking

hearing participants to automatically detect auditory changes and then comparing the resulting auditory MMN source estimate with the one reported for vMMN in the deaf population.

Recently, two conclusive pieces of evidence for sensory-independent task selectivity during perceptual tasks in deaf humans were put forward for visual rhythm sequence perception<sup>104</sup> and for facial identification.<sup>105</sup> Bola and colleagues<sup>104</sup> documented auditory cortex recruitment in congenitally deaf and hearing adults when discriminating visual or auditory rhythm sequences, respectively. In both sensory modalities (vision, audition), the activation for perception of rhythms peaked in the posterior and lateral part of the high-level auditory cortex, i.e., in the same anatomic (auditory) region independently of the sensory modality used as input. Similarly, Benetti and colleagues<sup>105</sup> showed that the region in the auditory cortex which in the control population responds to voice perception is involved in face identity processing in congenitally deaf adults (especially in the right hemisphere). Importantly, the same group also showed, in the same deaf participants, largely preserved connectivity patterns between this task-selective temporal region and occipital regions.<sup>106</sup> This latter result provides corroborative evidence suggesting that indeed preserved connectivity together with sensitivity to task-distinctive features<sup>82</sup> might underlie TSSI organization in higher-order “auditory” regions,<sup>80</sup> as in visual cortical regions (see above). Unfortunately, studies with the deaf population using SSDs to train the auditory-deprived brain to perceive auditory information through visual or tactile sensory channels are still missing. Implementing this approach, however, could allow investigation of the interesting question of whether the flexibility for the sensory modality triggering TSSI recruitment reported for category-selective regions in the deprived visual cortices also extends to the deprived auditory cortices.

Taken together, this body of works suggests that TSSI organization is a general principle characterizing the organization of higher-order sensory cortices, extending beyond visual cortices.

### Does TSSI organization extend to deprived primary sensory cortices as well?

Unfortunately, data regarding the extent to which TSSI organization extends to primary sensory cortices are still quite controversial and not conclusive (for a review see<sup>82</sup>). One of the reasons behind the disparity of findings between primary sensory and higher-order cortices is that while there were clear hypotheses regarding the properties of TSSI recruitment in category-selective regions in higher-order sensory cortices, the hypotheses related to TSSI organization in primary sensory cortices appeared weak. Indeed, primary sensory cortices are the first relay of sensory information in the cerebral cortex and are known to compute basic analyses of sensory features. Thus, among all cortical regions, they are considered the most sensory-specific regions. What sensory-independent and task-selective computation could they perform if deprived of their natural sensory inputs? We propose, that in order to test whether TSSI organization can emerge in these cortices, instead of focusing on specific computations, one must focus on the main and large-scale organizational principle of primary sensory cortices, namely topographic mapping (e.g., retinotopy or tonotopy for visual and auditory primary sensory cortices, respectively). Is topographic mapping, or at least broad topographic division, maintained in the deprived primary sensory cortices? Very interestingly, recent studies demonstrated the maintenance of the large-scale functional

connectivity patterns characterizing retinotopic and tonotopic biases in the congenitally blind<sup>107</sup> and congenitally deaf,<sup>108</sup> respectively. However, so far, the functional meaning of these preserved anatomical connections remains unknown. Crucially, these results are quite puzzling for the scientific community, as available results showing crossmodal recruitment of the deprived early sensory cortices, and mainly of the deprived early visual cortices, never hinted at any preserved functional topographic maps. Actually, accumulating evidence suggests “task-switching” in the deprived primary visual cortex toward higher cognitive functions such as language, verbal and episodic memory or numerical cognition,<sup>109–117</sup> focused attention,<sup>118</sup> and executive control.<sup>119</sup> These results are generally described as dramatically diverging from the predictions of TSSI brain organization. This is because such functions do not typically recruit early visual areas in sighted individuals (but see<sup>120</sup>), are not sensory in nature, and are not organized topographically. However, we suggest that functional topographic organizations might emerge independently of the input used, if the information provided carries core “retinotopic” features. This means, for example, that the known eccentricity bias characterizing classic retinotopic mapping might be conceptualized as a TSSI high versus low shape resolution bias. This would predict, for instance, the activation of foveally responsive regions for Braille reading (a task requiring high-resolution shape analyses) in the deprived primary visual cortex.<sup>80</sup> Interestingly, initial support for this prediction comes from the results obtained in the case study of patient S who experienced severe visual acuity reduction due to corneal opacification from the age of six years.<sup>121</sup> Using fMRI, the authors observed that in patient S classic foveally driven regions were recruited by Braille letters, while classic peripherally responsive regions were active during visual processing.<sup>121</sup> Given the low acuity of vision in patient S, this case study suggests, in line with our hypothesis, that the eccentricity bias may indeed be conceptualized as a sensory-independent high versus low shape resolution bias. However, these results were obtained in one participant only, who underwent normal visual development during critical periods. Future studies may further test these intriguing questions in congenitally blind participants, ultimately unraveling whether the whole brain is organized in a sensory-independent and task-selective manner, or if alternatively, there are indeed some constraints in the human brain with respect to specific sensory inputs.

### Task-switching versus TSSI organization in higher-order “visual” cortices

It is important to note that many of the studies reporting task-switching plasticity toward higher-order cognitive tasks, such as verbal memory, semantic and syntactic processing of language, or mathematical reasoning, in the early visual cortices of congenitally blind adults, also reported extensive crossmodal recruitment for these tasks beyond these early regions, across higher-order “visual” regions.<sup>109–112,116</sup> These are the same regions for which TSSI recruitment has been shown. Then, how can these divergent findings be integrated together into a unified framework on sensory reorganization following blindness? Unfortunately, there are not many studies addressing this crucial question. A recent investigation by Kim et al.<sup>122</sup> tested the (re)-organization properties of the visual word form area (VWFA), a region in the “ventral” visual stream repeatedly described as TSSI and responsive to

symbol-to-phoneme conversions<sup>52,76,80</sup> but that was also shown to be recruited by less specific linguistic tasks.<sup>109–112</sup> Specifically, Kim and colleagues showed that the VWFA was responsive to both Braille letters and the grammatical complexity of auditory sentences in congenitally blind adults, whereas in sighted adults it was activated only during reading of print and not auditory sentences.<sup>122</sup> The authors interpreted these results as evidence suggesting that the deprived visual cortex lost its selectivity to specific computations, supporting Bedny's proposal that the deprived visual cortex is pluripotent with the ability to take over a wide range of functions.<sup>115</sup> In other words, Bedny proposes that brain specializations are constrained neither to a specific sensory modality (i.e., the natural selection account) nor to specific sensory-independent computations (i.e., the TSSI account), but rather that they are only constrained by preexistent connectivity patterns and by experience during critical periods early in development.<sup>115</sup> Recently, she further refined her proposal by suggesting that the strongest weight to cortical repurposing is provided by experiences during critical periods rather than by connectivity biases.<sup>123</sup> Specifically, Kanjlia and colleagues tested congenitally blind, late blind, and sighted controls in mathematics and language-related tasks manipulating cognitive load (i.e., all tasks that have been shown to recruit the deprived visual cortex).<sup>123</sup> The authors also acquired resting-state data on the same participants.<sup>123</sup> Their results indicated that, while resting-state functional connectivity between the deprived visual cortex and the rest of the brain was similar in the two blind groups, regional specialization for mathematics and language as well as load-dependent activity across the deprived visual cortices was observed only in congenital blindness.<sup>123</sup> The authors concluded that there are critical periods for the repurposing of the visual pluripotent cortex, i.e., that experiences early in development play a crucial role in determining the properties of cortical specializations.<sup>123</sup>

However, there are numerous studies showing TSSI organization in the deprived higher-order visual cortices.<sup>80</sup> Thus, which of the two organizational principles, namely TSSI or task-switching, is more dominant in shaping the organization of these cortices? A recent study from our laboratory provides initial results in answering this crucial question.<sup>124</sup> Similarly to the work by Kim and colleagues,<sup>122</sup> Sigalev et al. used fMRI to examine the (re)-organization properties of VWFA in congenitally blind,<sup>124</sup> after training on reading letters via an SSD. After SSD training, in congenitally blind participants, the VWFA responded only to SSD-presented words and not during an auditory semantic task.<sup>124</sup> These results suggest that, with the appropriate training, TSSI organization may overcome task-switching plasticity.<sup>124</sup> These findings are not conclusive in this matter as the authors did not test VWFA recruitment by semantics before the SSD training. Nonetheless, this study suggests the interesting working hypothesis that there might be indeed some predispositions to specific sensory-independent computations in the higher-order visual cortices as suggested by the TSSI account for brain (re)-organization. Furthermore, it suggests that such predispositions might be somewhat (re)-awakened or strengthened by task-specific training, even if such training is relatively short compared to the lifelong experience following task-switching in a given region, and even if the training is undertaken during adulthood. Future studies could investigate this issue more systematically, for instance, by performing longitudinal studies during which blind participants are scanned in both task-switching and TSSI-eliciting tasks before and after SSD task-specific learning.

## Beyond the notion of strictly sensory-specific critical periods

All the aforementioned results on TSSI organization highlight that experiences in a specific sensory modality are not essential for the related typical brain specializations to emerge. Indeed, several studies provided robust evidence in this direction by showing, for instance, that “visual” or “auditory” cortices can develop their typical category-selectivity specializations while being activated by an atypical sensory modality. Studies with SSDs further showed the incredible flexibility for the sensory modality inducing TSSI recruitment<sup>52,75,77,78</sup> (for more details see above). Then, how do these results reconcile with the dominant view on the emergence of sensory brain specializations positing an unalterable link between a specific specialized sensory region in the brain and a given sensory-specific function/computation that must be established early in development via sensory-specific experiences? What we would like to stress here is that this classic framework never entirely took into account that every cognitive function/computation has its own specific critical period of development.<sup>125</sup> In other words, we do not deny the existence of sensory-specific critical periods or that they play an important role in cortical development. Rather, we argue that, to achieve the full development of a given cortical area, two types of processes must occur during different critical periods: (1) the development of neural connections underlying proper sensory processing, during sensory critical periods and (2) the development of cognitive/computational units typical of that cortical area, during functional critical periods (e.g., language; object recognition, etc.; see also<sup>70,82,126</sup>). Within this framework, TSSI phenomena may be conceived as possible evidence in favor of the efficient development of a given cognitive/computational unit within its corresponding functional critical period, despite the different sensory modality tuning of that particular unit compared to the control population (see also<sup>39</sup>). Thus, available data on TSSI recruitment, and especially the TSSI results obtained with SSDs, suggest that the two types of critical periods might be independent from each other. Future studies could investigate whether one of the two types of critical periods is more predominant than the other in shaping the development of a given cortical area and related cortical network. Future studies may also investigate how critical periods and their related constraints interact with the proposed principles underlying sensory brain organization (i.e., task-selective distinctive features and preserved connectivity biases<sup>82</sup>). We think the best model to investigate these crucial questions is sensory restoration. In the following section, we will briefly discuss our proposed approach in this direction and we will put forward how we think the results reviewed in this chapter can maximize the outcomes of sensory restoration programs.

### Specific multisensory training as a tool to maximize sensory restoration outcomes

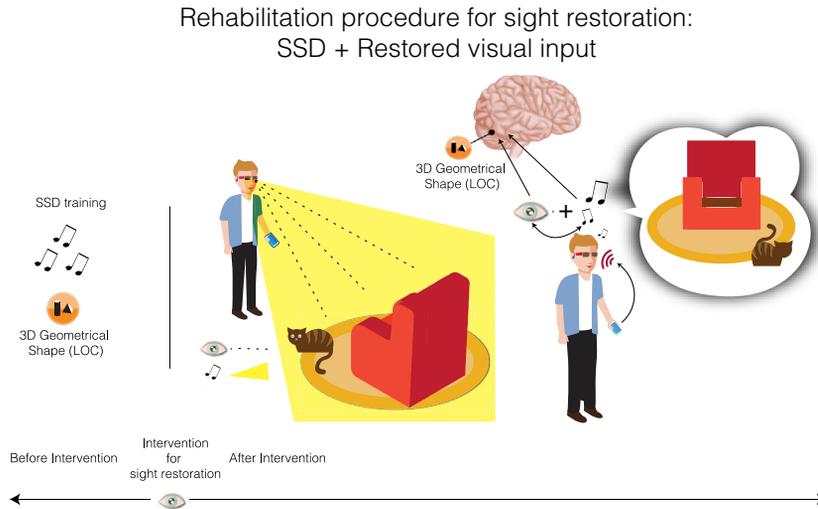
The repeated findings of TSSI recruitment in the deprived sensory cortices together with findings showing TSSI recruitment after short-term training with SSDs (e.g.,<sup>75,78</sup>) pose crucial questions for sensory restoration. Indeed, if sensory cortices still maintain their typical computations while being so flexible for their activating sensory modality, can TSSI brain

organization be exploited to maximize sensory restoration outcomes? Unfortunately, clear results from studies testing this crucial question are still lacking. In our opinion, this is due to the fact that the great majority of the evidence currently available on the efficacy of sensory restoration outcomes has been provided by studies on auditory restoration through cochlear implantation (see chapter by Lomber et al., this volume). Cochlear implants (CIs) are the most established invasive procedure for sensory restoration.<sup>127</sup> However, seminal studies with CI patients reported that patients with poor spoken language recovery had, prior to the surgery, high metabolic activity in response to visual stimulation in their deprived auditory cortex.<sup>128,129</sup> This, in turn, led to the dogma within sensory restoration practices that crossmodal recruitment in the deprived sensory cortex is a negative predictor of sensory restoration.<sup>130</sup> As a result, clinicians suggested that patients avoid, for instance, the learning of a sign language prior to the CI surgery, and the postsurgery training was encouraged to be undertaken in audition alone.<sup>126</sup> We propose, instead, based on results documenting TSSI recruitment, that training within sensory restoration programs should focus on specific computations and use a multisensory approach where the newly restored sensory modality is paired with a familiar and spared one (see also<sup>70,82</sup>).

Importantly, in line with our proposal, in the CI-related literature, evidence has started to document the higher efficacy of multisensory training programs (e.g., audiovisual) compared to unisensory ones (i.e., auditory only) for recovery of function on specific auditory tasks. For instance, exposure to audiovisual language rehabilitative training (speech-reading therapy, pairing sign language with spoken language) substantially improves auditory linguistic recovery compared to auditory-only training in CI patients.<sup>70,126,131,132</sup> Furthermore, a recent study showed that learning sign language boosts auditory linguistic recovery in early implanted deaf children.<sup>133</sup> Thus, this latter result suggests that the presence of TSSI recruitment (e.g., the recruitment of the classical language network by atypical sensory information, i.e., by vision instead of audition in the case of sign language<sup>89,91</sup>) can facilitate rather than impede the recovery of a given cognitive task/computation by the restored sensory modality.<sup>82,126</sup> Interestingly, recent evidence highlights the incredible potential of multisensory training for maximizing sensory restoration outcomes even for cognitive tasks/computations that most probably were not even learned during infancy.<sup>134</sup> Isaiah and colleagues (2014)<sup>134</sup> showed that in early deaf ferrets who received bilateral CIs in adulthood, an audiovisual specific training was more effective than an auditory one for recovering auditory localization abilities both at the neural and the behavioral level. This result, in turn, further suggests that binding inputs from different sensory modalities during task-oriented training programs, and especially the combination of a familiar modality (e.g., vision) with a novel, newly restored one (e.g., audition) might be a powerful way to restore efficient and task-specific sensory recovery, even in case of interventions occurring in adulthood.

We propose that a similar multisensory approach to training holds a lot of promise in the case of sight restoration as well, making SSDs tools with great potential in this context. Unlike auditory restoration and CI interventions, sight restoration still lacks a unified set of procedures. However, given the incredibly fast advances in biotechnology that characterize our era, we hope that, in the near future, sight restoration may also enjoy more standardized procedures and better expected outcomes. Thus, it is crucial to begin to prepare potential rehabilitation programs to further maximize such outcomes. Within this context, we propose it will be crucial to exploit the documented TSSI properties of “visual” cortices. Indeed, the few

studies documenting sight restoration reported far from optimal recovery results in these patients.<sup>8,135–138</sup> However, these patients are mainly impaired on high-level visual tasks such as feature binding, object-background segregation, and perception of 3D shapes and faces.<sup>136,137,139,140</sup> Since these are precisely the visual abilities that can be learned using SSDs,<sup>52</sup> one logical step is the systematic implementation of multisensory training programs, where SSD input is paired with the restored visual modality to boost the recovery of specific computational tasks<sup>82</sup> (Fig. 15.2). Specifically, candidates for sight restoration might use SSDs prior to the intervention, and learn, for example, to perceive SSD-presented body-shapes, ultimately recruiting the EBA and its related network of processing<sup>78</sup> (i.e., TSSI recruitment). Then, after surgical sight restoration, the SSD stimulation can be paired with visual input, mediating two types of benefits. The familiar SSD input can help to better understand the newly restored visual input. For example, presenting a body shape both through an SSD and through vision simultaneously may help the patient to perceive fine details of the image or bind visual features into a coherent shape. Moreover, such pairing may facilitate a neural network's adaptability and thus allow it to efficiently process its typical sensory input. For instance, in the case of body shapes, it has been shown that SSD-presented body shapes



**FIGURE 15.2** Proposed rehabilitative procedure for sight restoration: sensory substitution device (SSD) paired with restored visual input. This figure shows the visual-to-auditory SSD used to teach processing of visual objects (and the corresponding brain activations) as an example. The same approach could be implemented using a visual-to-tactile SSD as well as being applicable to many other cognitive/computational tasks. Left: Before the intervention for sight restoration, patients can be trained with SSDs to teach the brain to process (typically visual) specific tasks through a sensory modality (e.g., audition) that has never performed such a task, thus activating task-selective and sensory-independent (TSSI) regions and their related network (in the case depicted in the figure, SSD training on object recognition will trigger the activation of the lateral occipital complex (LOC) in the ventral “visual” stream, a TSSI region involved in 3D geometrical shape analyses). Right: After the intervention for sight restoration, patients can pair the newly acquired and developing visual input with a familiar sensory input (e.g., auditory SSD input). Medical or surgical visual restoration and SSDs could be used together to facilitate, strengthen, and complete the visual experience. This pairing aims to exploit TSSI brain organization, and we propose that it may eventually facilitate the adaptability of the visual cortex to process its typical sensory input (vision; Top).

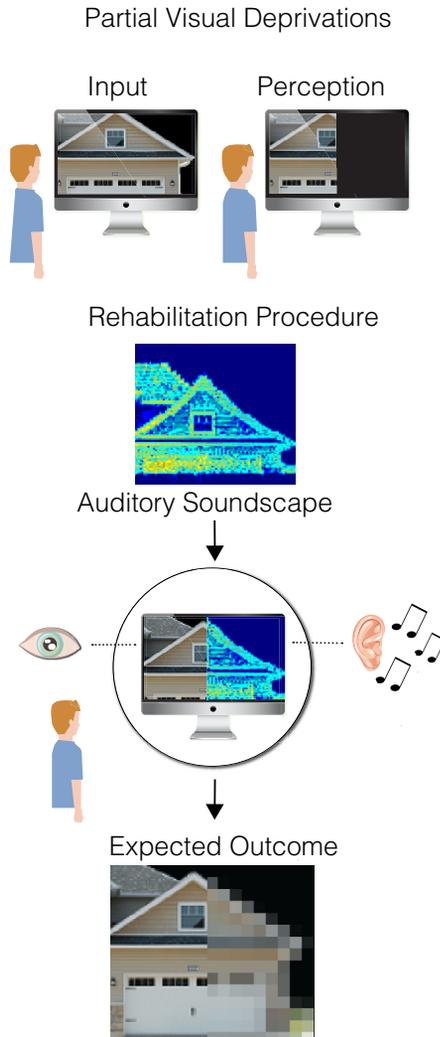
recruit the EBA in a TSSI manner, and that this region is functionally connected to other regions typically involved in body shape processing in the blind population.<sup>78,82</sup> Given the documented flexibility in the activating sensory modality of TSSI cortical regions, pairing an SSD and visually presented body shapes may aid the visual cortex to tune toward specific visual inputs. A similar logic can be applied to basically all the known visual categories and perhaps even for more low-level computations (see, for instance, Fig. 15.2 where this approach is explained for object recognition in the lateral occipital complex [LOC]).

In short, we propose that to maximize the outcomes of sensory restoration procedures, TSSI recruitment of the deprived higher-order sensory cortices by atypical sensory modalities may be beneficial rather than detrimental for proper sensory recovery. We further suggest that the sensory flexibility documented in these cortices may be exploited during training programs for sensory recovery. Specifically, such training programs must be oriented to the recovery of specific tasks and must be multisensory in nature (i.e., pairing the restored sensory modality with a familiar one). We propose such multisensory training can both facilitate the understanding of novel stimuli as well as facilitate the task-selective recruitment of the newly restored sensory cortex by its natural sensory input.

### SSD training as a tool to maximize visual recovery after partial visual loss

While the approach proposed above holds a lot of promise for the future, the patients that can currently benefit from it are very few (e.g., currently there are around 250 patients with retinal prosthesis worldwide). Nonetheless, there are currently over 300 million people worldwide suffering from various types of visual impairments that limit their function.<sup>141</sup> We would like to highlight here that SSDs can be excellent tools not only for those who are blind, but also for recovering function in cases of visual impairments and partial visual loss. SSDs carry the advantage of maintaining many features of visual images such as shape, size, and spatial locations of objects, ultimately making them extremely suitable to be paired and integrated with actual vision. In other words, we propose that visually impaired patients, in addition to blind people, may greatly benefit from SSD training programs aimed at visual rehabilitation and visual recovery. Following a similar logic to the one described in the section above, SSDs can be paired with the residual visual input and allow a more complete understanding of the degraded visual information. This in turn may yield enormous benefits for daily life activities, ultimately boosting the functional independence of this population.

In addition, training with SSDs can also be embedded within specific rehabilitation programs aimed at the visual recovery of patients suffering from visual impairment (Fig. 15.3). Indeed, accumulating evidence suggests that multisensory stimulation may be an effective rehabilitation method for visual impairments acquired in adulthood (e.g., after stroke<sup>142</sup>). The majority of these studies have been conducted with hemianopic patients, i.e., patients with an acquired lesion in the visual structures located in the early visual pathway behind the optic chiasm. Such lesions generally result in visual loss in up to one half of the visual field. This condition, in turn, results in many difficulties in daily life including reading, scanning scenes, and obstacle avoidance, especially relating to the affected portion of the visual field.<sup>143</sup> Several studies documented the greater benefit of multisensory than unisensory training with these patients by showing that the greatest improvement in



**FIGURE 15.3** Proposed rehabilitative procedure for partial visual deprivations. Top: This figure depicts a case of a hemianopic patient who lost his vision in one half of the visual field as an example. The same approach can be used for many other types of visual impairment. Middle: We propose that the rehabilitative procedure should include computerized training programs where visual inputs (in this case objects) are presented together with visual-to-auditory SSD inputs. In this way, the patient is able to complete the missing visual information through the auditory soundscape, ultimately integrating together the information from the two sensory modalities into a unified percept. Bottom: Such multisensory training may lead to better recovery of vision.

visual performance in the affected portion of the visual field was achieved when a visual stimulus was presented together with a coincident sound<sup>144–146</sup> (see also chapter by Stein and Rowland, this volume). We believe that visual-to-auditory SSDs are very promising tools to use for the rehabilitation of these patients. Fig. 15.3 shows an example of such an approach where the auditory-to-visual SSD input is paired with the remaining visual input to boost visual recovery. Specifically, training programs may present stimuli on a computer screen (in the figure we show objects as an example). During training patients integrate the available visual information with the SSD input and achieve a full perception of the presented object. In this way, patients may be helped to recognize objects by being able to perceive them entirely. Furthermore, such pairing may facilitate a neural network's adaptability and thus allow it to efficiently recover the missing visual input, as discussed in an earlier section. Thus, we propose that this multisensory approach may further maximize the outcomes of rehabilitative procedures and functional visual recovery (Fig. 15.3).

Note that the case of hemianopic patients is used here as an example, but the proposed multisensory approach may be suited to implementation for many other types of visual impairments (e.g., peripheral visual impairment in retinitis pigmentosa or central visual loss in macular degeneration).

## General conclusions

In this chapter, we reviewed the current literature on the (re)-organization of sensory cortices following sensory deprivation, mainly blindness. We suggest that the brain may be organized as a task-oriented rather than a sensory-oriented machine as classically conceived. Finally, we propose that this task-oriented and sensory-flexible organization may be exploited during sensory restoration programs to maximize sensory recovery, and more generally, that multisensory training pairing SSD and visual inputs holds great promise to maximize the outcomes of visual recovery. Throughout this chapter, we showed how studies with SSDs played a crucial role in unraveling the incredible sensory flexibility of our brain across the life span. Thus, we can conclude that all the work that was carried on with SSDs after the pioneering studies of Bach-y-Rita in the 1970s corroborated his intuition on the relevance to visual rehabilitation of the fact that we see with our brain rather than only with our eyes. Such a conclusion carries crucial implications for sensory recovery practices, ultimately unraveling novel exciting paths to maximize rehabilitation outcomes.

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