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Origins of task-specific sensory-independent organization in the visual and auditory brain: neuroscience evidence, open questions and clinical implications

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Evidence of task-specific sensory-independent (TSSI) plasticity from blind and deaf populations has led to a better understanding of brain organization. However, the principles determining the origins of this plasticity remain unclear. We review recent data suggesting that a combination of the connectivity bias and sensitivity to task-distinctive features might account for TSSI plasticity in the sensory cortices as a whole, from the higher-order occipital/temporal cortices to the primary sensory cortices. We discuss current theories and evidence, open questions and related predictions. Finally, given the rapid progress in visual and auditory restoration techniques, we address the crucial need to develop effective rehabilitation approaches for sensory recovery.

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The origin of task-specific-sensory-independent plasticity

In the last decade or so, task-specific sensory-independent (TSSI) brain organization has rapidly become a firmly established notion in the field of cognitive

neuroscience. A consistent body of data from blind and deaf populations has shown that sensory cortices deprived of their natural sensory input still primarily process the same type of perceptual/computational/categorical information, although it is conveyed by an atypical sensory input (e.g., audition; touch), and in many cases this same task-specific sensory-independent (TSSI) organization can be observed also in the general (healthy sighted or hearing) population [1–7]. Studies using sensory substitution devices (SSDs) which have mainly been conducted with the congenitally blind population, have found that TSSI plasticity can emerge after a relatively short training period designed to teach a different sensory modality (e.g., audition) to interpret some type of information typically processed by vision [8–10,11^{••},12^{••}]. Visual-to-auditory SSDs topographically convert visual images into auditory ‘soundscapes’, which can be interpreted fairly rapidly by users [10]. Studies involving SSD-training have been conducted in adulthood, thus ultimately suggesting the absence of a critical/sensitive period subtending the pairing of a given sensory input (either typical or atypical) with a given task-specific brain region. Thus, if task-specific sensory-independent (TSSI) brain organization is not driven by sensory inputs, what drives its maintenance? Here we analyze results on the basis of the use of two forms of sensory restoration to investigate this crucial issue: sensory substitution devices (SSDs) and cochlear (and to a lesser extent visual) prostheses.

New evidence from our group concerning reading and number processing in the ventral occipito-temporal cortex suggests that a combination of two principles may drive the emergence of its task-specific sensory-independent (TSSI) organization [13^{••}]. The first is known as the biased connectivity principle (BCp), which posits that task-specific recruitment draws on pre-existing cortical connections linking the ventral occipito-temporal cortex TSSI regions to the rest of the networks processing information for a specific computational task (see also [2,10,11^{••},12^{••},14,15]). The second is the shape-feature sensitivity principle (SFSp), which states that task-specific recruitment can emerge from the intrinsic circuitry of the ventral occipito-temporal pathway which may be tuned to the extraction of the specific but invariant shape-features of an object (when a shape is defined as representing the proximity of the component parts of an

object [13^{••}]). In other words, this extraction is expected to occur independently of translation, rotation, size, distance or other variations in the object, and moreover, independently of the sensory modality through which the object-related information is conveyed [13^{••}]. Recent data from our lab and others have supported this claim by documenting both TSSI recruitment in the ventral occipito-temporal cortex regions along with preserved network connectivity organization [11^{••},12^{••},13^{••},16] in blind participants. This was shown using resting-state functional connectivity magnetic imaging, which exploits the assumption that correlations in the activity of different brain regions during resting-state (i.e., without an explicit task) reflect functionally relevant correlations in neuronal firing [17,18]. For instance, we showed that in congenitally blind participants, the visual number form area was recruited in a TSSI-manner after a relatively short SSD training on number identification, and that this recruitment was accompanied by preserved cortical connections between this region and other crucial areas involved in the representation of quantities in the sighted population [11^{••},19,20]. In contrast, in the same group, the visual word-form area showed preserved connections to fundamental areas for language processing ([21,22]; see Figure 1a; see also [10]).

Crucially, additional recent data suggest that the combination of these two principles might account for task-specific sensory-independent (TSSI) plasticity in the deprived occipital cortices in a much more general way. That is, even beyond the ventral occipito-temporal cortex, extending to other occipital regions, such as the lateral occipito-temporal cortex [23], MT+ [24] and the extrastriate body area [12^{••}] which are all located more laterally than the ventral occipito-temporal cortex. For instance, similar to the results obtained in the ventral occipito-temporal cortex [10,11^{••}], we observed in a group of blind participants TSSI recruitment of the extrastriate body area elicited by the perception of SSD-presented body shapes, accompanied by preserved functional connectivity between this region and other areas considered to be integral part of the body-image network in the sighted population, such as the posterior superior temporal sulcus and the temporal–parietal junction ([12^{••}]; see Figure 1a). A recent study showed that the retention of category preference and functional connectivity yield overlapping results in vast areas of the visual cortex of the blind [25^{••}]. Furthermore this study showed that this combination of shape-feature sensitivity principle (SFSp) and biased connectivity principle (BCp) in the blind population also correlated with polymodal activations in the brains of sighted controls, thus additionally supporting the suggestion that both these principles guide visual cortex organization even without visual experience. We further propose that in order for the combination of BCp and SFSp to account for TSSI plasticity in the sensory cortices as a whole, shape-feature sensitivity

principle (SFSp) needs to be generalized to include the emergence of task-specificity in auditory regions (e.g., in deaf humans for sign language; [4,26]), and in auditory and visual regions activated by tasks that do not involve any shape information (e.g., in MT; [24,27], in deaf animals and in blind humans for visual [5] and auditory localization [3]). We term this extended SFSp the ‘task-distinctive feature sensitivity principle’ (TDFSp).

This expanded proposal still leaves several critical questions open (see Box 1). Here we discuss two especially important ones: the generalization of these two principles to the organization of the early sensory cortices, and more practically, the implications of these principles for sensory restoration — could including them in rehabilitative programs help maximize sensory recovery?

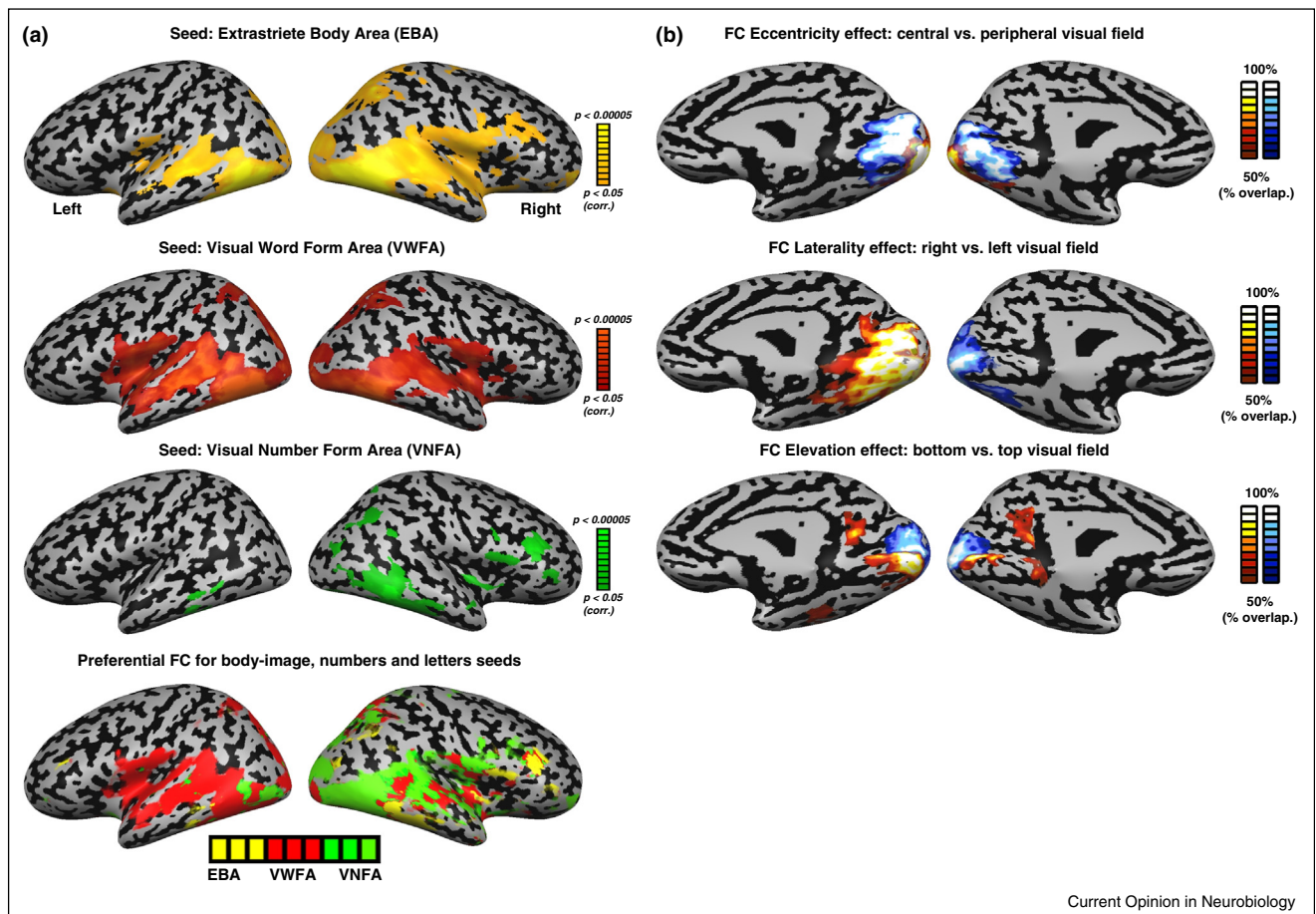
Reorganization of deprived primary sensory cortices

Till date, the extent to which a combination of biased connectivity principle (BCp) and task-distinctive feature sensitivity principle (TDFSp) can explain also the reorganization occurring within the deprived *early* sensory cortices remains unclear, but such uncertainty ultimately undermines current interpretations of TSSI brain organization.

There is no conclusive evidence regarding which TSSI computational tasks these cortices should maintain if deprived of their natural input from birth. Hence it is currently impossible to determine whether the TDFSp extends to these cortices. A few studies on early blind populations have reported recruitment of the deprived primary visual cortex (V1) by low-level spatially related features [28,29]. However, such reports are rare and weaker compared to the accumulating evidence of ‘task-switching’ in V1 toward higher cognitive functions in the case of language or memory tasks [30–33], in tasks requiring focused attention [34] or executive control [35]. These results are thought to diverge dramatically from the predictions of TSSI brain organization, because such functions do not typically recruit early visual areas in sighted individuals (but see [36[•]]).

Nonetheless, data collected in the deaf population seems to extend the task-distinctive feature sensitivity principle (TDFSp) to the primary sensory cortex as well. Recent studies consistently report vibrotactile recruitment of the primary auditory cortex (A1) in deaf humans [37–39]. There is no conclusive data as to whether such recruitment is low-level and follows the functional organization of the hearing auditory cortices (i.e., TSSI recruitment). However, the high functional similarity between the computations underlying both types of stimulation (oscillatory pressure patterns translated into frequency

Figure 1



(a) Resting-state functional connectivity (FC) MRI in congenitally blind adults. A lateral view of an inflated cortex overlaid with the connectivity maps. Results of random-effects group analysis (corrected for multiple comparisons) of functional connectivity maps using an EBA seed (top panel — readapted from Striem-Amit and Amedi [12**]), visual word-form area seed (second panel — readapted from Striem-Amit *et al.* [10]), and visual number form area seed (third panel — readapted from Abboud *et al.* [11**]). In the bottom panel a preferential FC map for the three computational tasks (winner — takes-all approach) is depicted. **(b)** Resting-state functional connectivity (FC) MRI-retinotopic organization in congenitally fully blind adults. Results of FC analyses showing preserved retinotopic organization in congenitally blind adults for the three main retinotopic mapping axes: eccentricity (center–periphery; top panel), laterality (left–right; middle panel), and elevation (upper–lower; bottom panel). Data readapted from Striem-Amit *et al.* [45**].

percepts [40]) lends weight to this conclusion. Within a given frequency range, the very same oscillatory pattern can be perceived simultaneously by the peripheral receptors of both sensory modalities (i.e., the basilar membrane of the cochlea and the skin; e.g. [40,41]), suggesting that even deaf people can perceive certain sounds through touch naturally. In fact, through vibrotactile stimulations, deaf individuals can perceive music [42], differentiate timbres [43] and different pitches of voices [44]. These reports in turn suggest that such abilities may depend, in a task-specific manner, on cortical integration of activity across different channels of mechanoreceptors, both auditory and tactile. Future studies should assess the properties of vibrotactile recruitment in the *deaf* A1 more systematically and test whether a similar recruitment is

observed in the *blind* V1 for atypical sensory stimuli sharing functional similarities with visual preferences.

At the same time, studies should also investigate to what extent the biased connectivity principle (BCp) is present within deprived primary sensory cortices. Recent evidence from our lab in congenitally blind adults supports this conclusion by showing retained functional connectivity (FC) patterns mimicking retinotopic organization, a hallmark of the visual cortex structural architecture [45**]. These retained FC patterns were observed for all three main retinotopic mapping axes: eccentricity (center–periphery), laterality (left–right), and elevation (upper–lower), throughout the early and high-level ventral and dorsal streams (see Figure 1b; see also [46,47]). This functional

Box 1 Outstanding open questions and predictions concerning the notion of task-specific sensory-independent (TSSI) organization as emerging from the combination of biased connectivity principle (BCp) and task-distinctive feature sensitivity principle (TDFSp)

1. Would the preserved V1 resting-state functional connectivity result in functional-specific recruitment of the deprived visual cortex as predicted by the task-distinctive feature sensitivity principle (TDFSp)? For instance one hypothesis is that auditory/tactile localization tasks recruit V1 in a retinotopic manner, such that central auditory/tactile localization would recruit central retinotopic areas, peripheral auditory/tactile localization would recruit peripheral areas, etc.
2. Or would TDFSp not entirely generalize to V1 plasticity, given results documenting both retention and divergence in V1 organization in the blind compared to the sighted? For example, one could expect that reading, a task performed foveally by the sighted, would show central-visual-field preferences in the blind [85] when reading Braille, although Braille reading does not elicit V1 activation in the sighted.
3. What are the implications for visual rehabilitation outcomes of the mixed findings documenting both retained and divergent plasticity in deprived V1? To what extent will V1 retained functional connectivity organization be beneficial for sight restoration? And will V1 divergent functional connectivity limit sight restoration efforts?
4. Could divergent V1 activations emerge in the sighted population for the same types of non-visual stimuli, with or without 'unmasking' following short term visual deprivation [1]? If so, this latter result could explain the so-called task-switching toward high-level cognitive functions repeatedly reported in blind populations and reconcile the blind results with the TDFSp predictions.
5. Do biased connectivity principle (BCp) and TDFSp exist from birth or do they need to be established during critical/sensitive periods of development? These questions may already be addressed, in that neuroimaging investigations, although very challenging, are starting to be feasible even in fetuses [86,87].
6. In terms of importance and temporal precedence, does BCp or TDFSp determine task-specific sensory-independent (TSSI) recruitment? If large-scale functional networks connectivity precedes selective tuning to specific shapes and task-distinctive features, the visual word-form area functional connectivity patterns, for example, would exist in blind children before learning Braille and in illiterate blind adults, and perhaps also predict their prospective reading abilities.
7. What is the relative contribution of BCp versus TDFSp in mediating the reorganization occurring within the deprived high-order and *early* sensory cortices? Can different occipital areas be influenced differently by BCp and TDFSp? In higher-order sensory regions, reorganization could be mostly mediated by the BCp, whereas the opposite could be true in early sensory cortices.
8. To what extent does the combination of the BCp and the TDFSp explain the emergence of plasticity in the late blind? Data suggest that at least for certain tasks late-blind plasticity does not follow the predictions of these two principles [14]. Is this true as well for category-selective regions in the occipito-temporal cortex?

connectivity (FC) architecture was also observed in people whose eyes did not fully develop in utero (i.e., without any possible visual experience). Thus this architecture appears to be hard-wired and dependent on genetic blueprints, rather than on experience-dependent or even activity-dependent mechanisms [45^{••}]. Further supportive findings were reported by other groups for the retained fine-detailed FC within V1 [45^{••}], and for retained visual

callosal anatomical connectivity [46]. However, consistent with previous studies [3,24,33,48–52] we showed that this retained organization coexisted with some level of divergent organization in FC in the blind [44]. These latter connections varied in accordance with retinotopic division. The *blind* central V1 showed increased FC to the left frontal language areas and their peripheral V1 showed increased FC to the parieto-frontal attention networks. This might indicate distinctive V1 localizations for the two functional roles generally attributed to the *blind* V1; namely, higher-order cognitive functions such as language processing [33,53,54] and non-visual spatial (and also non-spatial) attention [3,14,55,56]. Future studies should further clarify the functional meaning of the findings indicating both the retention and divergence of early visual cortices FC organization, test such connections in tonotopic areas of the deaf population and test their effects on sight/hearing restoration outcomes (see Box 1).

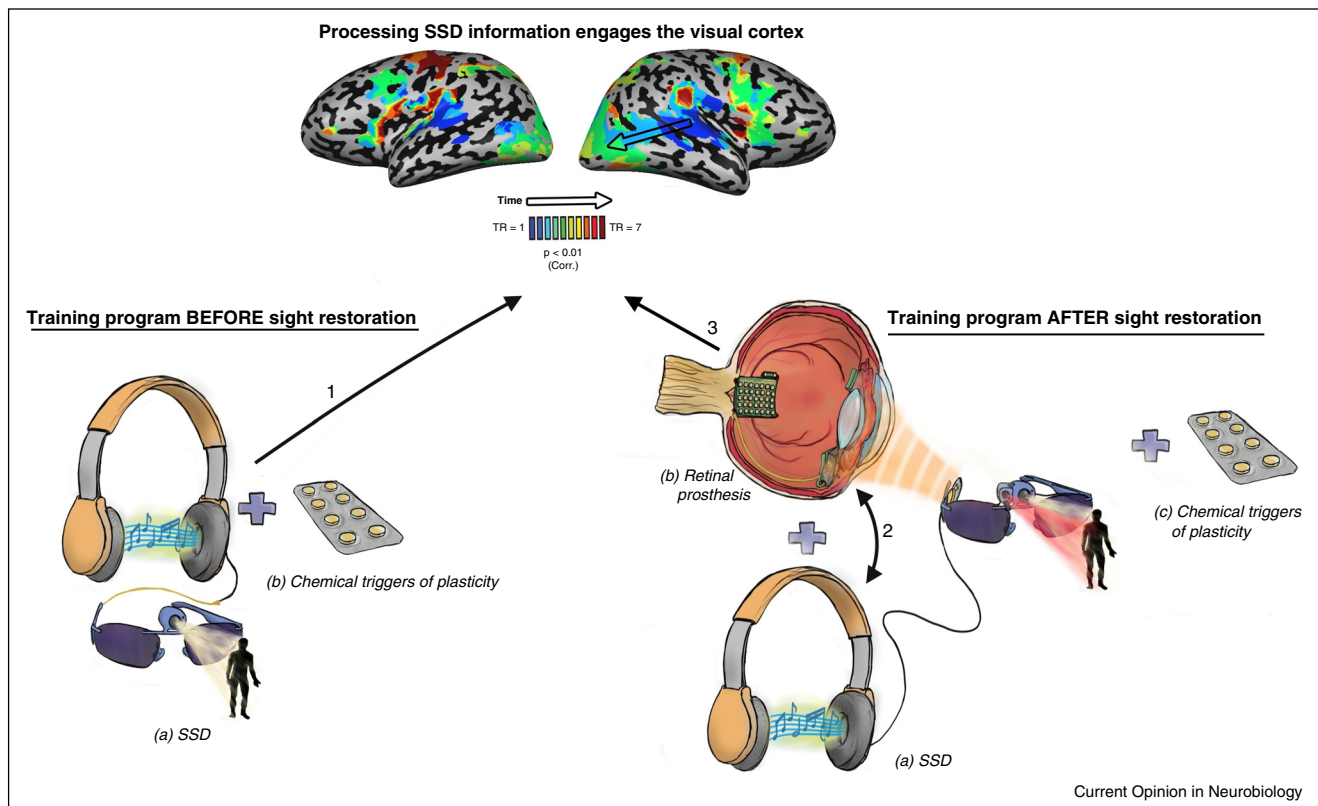
New frontiers for sight restoration

Given the rapid advances in biotechnology in the last decades, it may soon be possible to restore visual input in a variety of ways including retinal implants with increasing levels of resolution (paralleling the more widespread cochlear implants for auditory restoration), stem cell transplants and molecular manipulations [57]. Thus, there is a real need to formulate sight restoration approaches and be able to predict their success from the available evidence, especially since the behavioral outcome of such approaches were quite disappointing so far [57].

A certain number of indications can be gleaned from the few cases of patients who have regained their sight during adulthood [58–60,61[•],62]. While their restored visual abilities are far from optimal, these patients are mainly deficient in high-level visual tasks such as feature binding, object-background segregation, 3D shapes and face processing [59,61[•],63,64]. Since these are precisely the visual abilities that can be learned using sensory substitution devices (SSDs) [10,65], 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 ([65] see Figure 2).

The efficacy of multisensory training has never been systematically tested for sight restoration. However, there is initial encouraging evidence from cochlear implantation. Cochlear implants are now a firmly established procedure for auditory recovery [66]. The classic approach favors rehabilitation programs in audition alone [67]. Recent evidence, though, documents the higher efficacy of multisensory training programs (e.g., audio-visual) compared to unisensory ones (i.e., auditory only) for recovering specific cognitive/computational tasks. For instance, exposure to audio-visual language rehabilitative

Figure 2



Multisensory training program for sight restoration. This figure shows a visual-to auditory SSD used to teach processing of visual body shapes (and the corresponding brain activations) as an example. The same approach could be implemented using visual-to-tactile SSD as well as many other cognitive/computational tasks. Similarly, the figure depicts a retinal prosthesis as an example of a sight restoration system. *Left:* Before sight restoration surgery, patients can be trained with sensory-substitution devices (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 TSSI regions and their related network (top). *Right:* After medical sight restoration, patients can pair the newly reacquired and developing visual input with a familiar sensory input (e.g., auditory SSD input). Medical visual restoration systems and SSDs could be used together to facilitate, strengthen, and complete the visual experience. This pairing may eventually facilitate the adaptability of the visual cortex to process its typical sensory input (top). In the near future, chemical agents that remove molecular breaks in plasticity (chemical triggers of plasticity) may be available to human patients, who can start the treatment a few weeks/months before surgery and after the intervention. This would help set the deprived visual cortex back to its juvenile state, and thus increase its plasticity resources and overcome deficits in the development of the visual system due to early visual deprivation.

training (speech-reading therapy, pairing sign language with spoken language) substantially improves auditory linguistic recovery compared to auditory-only training in cochlear-implant patients [67–69]. Furthermore, a recent study showed that learning sign language boosts auditory linguistic recovery in early-implanted deaf children [70]. Thus, the development of a cognitive skill (e.g., language) even if achieved through an atypical modality, seems to facilitate rather than impede the recovery of this skill in the restored sensory input [67]. The occurrence of task-specific sensory-independent (TSSI) development during childhood is thought to be crucial for efficient multisensory training in sensory restoration programs [67,69]: recently it was claimed that two distinct critical/sensitive periods regulate and predict the success of sensory recovery. One, which we term *task-specific critical/*

sensitive period is related to TSSI components such as, the development of the language-network regardless of the modality used to convey linguistic inputs (sounds or sign language). The second, which we term *modality-specific critical/sensitive period* is related to the maturation of the specific sensory pathways, for instance the development of connectivity enabling processing of auditory sensory inputs [67,69].

A recent study on deaf ferrets nevertheless challenges the importance of this latter type of critical/sensitive period [71**] and has huge implications for multisensory restoration training. Isaiah and colleagues [71**] showed that in early-deaf ferrets who were fitted with cochlear implants in adulthood, namely after the closure of modality-specific critical/sensitive periods [72,73], an audio-visual

focused training was more effective than an auditory one for recovering auditory localization abilities. This result suggests that binding inputs from different sensory modalities, and especially the combination of a familiar modality (e.g., vision) with a novel, developing one (e.g., audition), might be a powerful way to restore efficient and task-specific sensory recovery, even in case of late interventions.

Thus, now more than ever before, the implementation of multisensory training programs using sensory substitution devices (SSDs) holds promise for sight recovery as well. Candidates for sight restoration might use SSDs before the intervention, and learn for example to perceive SSD-presented body-shapes (i.e., an otherwise typically visual skill), ultimately recruiting the extrastriate body area and its related network of processing [12^{••}]. Then, after medical sight restoration, the SSD stimulation can be paired with visual input, mediating two types of benefits. The familiar SSD input can help better understand the newly restored visual input. For example, presenting a body-shape both through SSD and through vision simultaneously may help the patient perceive fine details of the image or bind visual features into a coherent shape. Moreover, such pairing may facilitate a neural network's adaptability to efficiently process its typical sensory input. For instance, in the case of body-shapes, data have shown that in the blind population SSD-presented body shapes recruit extrastriate body area and that this region is functionally connected to other regions typically involved in body-shape processing [12^{••}]. Therefore, pairing SSD and visually presented body-shapes may aid the visual cortex to sensory tune toward specific visual inputs (see Figure 2). A similar logic can be applied to reading and numbers in the visual word-form area and the visual number-form area, as well as many other tasks and even for more low-level computations [65].

However, this optimistic view and rehabilitation protocol proposed above may not suffice, given evidence of deficient low-level visual information in sight restored adult patients [62,74,75]. This suggests that at least to a certain extent, modality-specific critical/sensitive periods still impact the overall success of sight recovery (see also [76[•]]). Thus, an additional step to improve low-level visual abilities, and ultimately aid rehabilitation, seems needed. Intriguingly, recent evidence with animals indicate that chemical interventions can release molecular 'breaks' of plasticity (involving the balance between inhibition and excitation) and trigger the reopening of modality-specific critical/sensitive periods, thus ultimately resetting juvenile brain plasticity and increasing sensitivity to external inputs ([77^{••},78,79,80^{••},81], see [72]). Treatment on the basis of this approach is being piloted for amblyopia [82,83[•],84], where endogenous permissive neuromodulators are modified to induce plasticity in adults who have had monocular visual deprivation (see

also [80^{••}]). Should this approach prove useful, it may be expanded to people recovering from binocular deprivation, e.g., blindness. In this case, the maintenance of the macro-structural organization of V1 [45^{••},46,85], along with rejuvenating its ability to wire and refine its connections once visual input is restored, may facilitate a vision efficient takeover of the reafferented visual cortex. One groundbreaking possibility to improve sensory restoration outcomes might be to pair SSD-based multisensory training with the reopening of critical/sensitive periods of development (see Figure 2). Although these action paths are only tentative at best and still need systematic testing, their potential convergence may herald a new era in the medical ability to restore lost senses, and to overcome multiple developmental brain challenges.

Conflict of interests statement

Nothing declared.

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