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Functional selectivity in sensory-deprived cortices

Giulia Dormal[1,2] and Olivier Collignon[1,3]

[1]*Centre de Recherche en Neuropsychologie et Cognition, Université de Montréal, Montreal;* [2]*Institut de Neuroscience, Université Catholique de Louvain, Belgique; and* [3]*Centre de Recherche du CHU Sainte-Justine, Université de Montréal, Montreal, Canada*

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Dormal G, Collignon O. Functional selectivity in sensory-deprived cortices. *J Neurophysiol* 105: 2627–2630, 2011. First published March 23, 2011; doi:10.1152/jn.00109.2011.—In a recent study, Lomber, Meredith, and Kral (2010) investigated crossmodal reorganization in congenitally deaf cats. They demonstrated that specific regions of the auditory cortex are responsible for distinct supranormal visual performances following early auditory deprivation. These exciting results are considered in light of recently increasing research suggesting that crossmodal plasticity associated with early sensory deprivation follows organizational principles that maintain the functional specialization of the colonized brain regions.

crossmodal reorganization; early sensory deprivation

IN THE PAST TWO DECADES, INCREASING evidence has demonstrated the impressive ability of the brain to rewire its components as a function of experience. Recognizing the dynamic nature of cortical circuitry is crucial in understanding how the nervous system adapts after sensory deprivation. As such, several studies have demonstrated that deafness or blindness leads to massive crossmodal recruitment of the cortices deprived of their natural inputs (Bavelier and Neville 2002). Crucially, these neuroplastic changes are believed to be the underlying cause of superior abilities in the remaining modalities of sensory-deprived individuals.

Recently, Lomber et al. (2010) tested this hypothesis in congenital deaf cats and further demonstrated that specific regions in the deaf auditory cortex are responsible for distinct aspects of enhanced visual performances. The authors first showed that congenitally deaf cats displayed superior abilities compared with hearing controls in specific visual psychophysical tests, namely, localization within the peripheral visual field and visual motion detection. In the visual localization task, the cats were trained to localize visual targets appearing in the front of the head or in peripheral positions up to 90° in the left and in the right visual space. In the motion detection task, they were trained to select between two fields, the one in which the dots were moving. In a second set of experiments, different portions of the auditory cortices of both groups of animals were individually deactivated using cooling loops to test their functional involvement in the superior visual abilities observed in the congenitally deaf cats. Four bilateral regions were targeted according to their known involvement in specific auditory functions in the hearing brain. The primary auditory cortex was chosen because it is the first relay for the auditory information, whereas the posterior auditory cortex (PAF) and the dorsal zone of the auditory cortex (DZ) were selected because of their role in auditory spatial localization (Malhotra and Lomber 2007). Finally, the anterior auditory field (AAF) was included as a control area since it is known to be responsible for auditory pattern but not auditory spatial processing in the hearing brain (Lomber and Malhotra 2008). Lomber et al. (2010) demonstrated that the superior visual performances in peripheral visual field localization and motion detection were separately and selectively altered in the deaf cats when specific portions of the dorsal auditory cortex were transiently deactivated. Essentially, a double dissociation was evidenced: while deactivation of PAF altered peripheral localization performance without affecting motion detection thresholds, deactivation of DZ resulted in the opposite profile. Importantly, none of these manipulations altered visual performance in the hearing cats.

At the behavioral level, the study of Lomber et al. (2010) indicates that visual enhancement associated with auditory deprivation is highly selective. Visual performances in the congenitally deaf and hearing cats did not differ in the psychophysical tasks testing grating and Vernier acuity, orientation discrimination, direction of motion discrimination and velocity discrimination. However, deaf cats were found to have superior localization abilities and lower visual movement detection thresholds. The selectivity of the enhanced visual functions is apparent even within the visual task tested given that the superior abilities demonstrated in the localization task were limited to peripheral locations from 60° to 90°, and these identical superior abilities were reduced after PAF deactivation. Importantly, such selectivity cannot be explained by ceiling levels for central locations (i.e., maximal accuracy) that would preclude the manifestation of superior performances in the deaf cats. These results remarkably match those documented in congenitally deaf humans, who appear to have thresholds equal to hearing controls for brightness discrimination, visual flicker, contrast sensitivity, and direction and velocity of motion, while displaying superior performances in the visual periphery and motion perception in attentional demanding contexts (Bavelier et al. 2006). The interpretation provided by Lomber et al. (2010) for such selectivity is that supramodal functions (i.e., functions that are commonly shared by the auditory and the visual modalities) are the ones most susceptible to perceptual improvement and cortical reorganization after early sensory deprivation. Therefore, spatial localization and motion perception are good candidates, while color and pitch perception, which are modality specific, are not. In the same context, others have previously proposed that peripheral vision may be highly susceptible to improvement in auditory deprivation because it would normally take advantage of the

Address for reprint requests and other correspondence: O. Collignon, Université de Montréal, Département de Psychologie, CERNEC, 90 Vincent d'Indy, CP 6128, succ. Centre-Ville, Montréal (Québec) H3C 3J7 (e-mail: olivier.collignon@umontreal.ca).

convergence of an auditory input to orient attention where the salience of the visual information is weak (Bavelier et al. 2006). Interestingly, superior motion perception abilities in the deaf have been documented when moving stimuli are selectively presented in the peripheral visual field (Neville and Lawson 1987). When crossing a street, deaf individuals might be particularly efficient in detecting moving stimuli in their peripheral field since they lack auditory cues to trigger attention to approaching cars outside of the foveal field. Because the motion detection task in Lomber et al.'s study does not enable disentangling performances in the foveal field from performances in the peripheral field, it is indeed possible that deaf congenital cats outperformed the hearing controls cats in this task using non-foveal vision. Interestingly, when behavioral compensations are observed for the processing of auditory spatial stimuli in blind subjects, they also mainly concern inputs originating in the peripheral auditory field (e.g., Roder et al. 1999). We then suggest that behavioral compensation in sensory-deprived individuals may occur preferentially for supramodal functions, in conditions where the salience of the sensory information is the weakest and where audio-visual convergence is mostly beneficial in non-deprived individuals.

Lomber et al. (2010) also compellingly demonstrated that auditory deprivation triggers reorganization in the auditory cortex. In accordance with these results, a few neuroimaging and electrophysiological studies in early deaf humans have reported activation of primary, secondary, and association auditory regions during the viewing of moving dot patterns and during the processing of stimuli presented in the peripheral visual field (e.g., Finney et al. 2001). However, compared with the literature in visually deprived individuals, crossmodal plasticity in deaf humans has been less extensively explored, probably due to several issues. First, because advances in engineering and surgical implantation techniques have made cochlear implants a standard procedure for the treatment of hearing loss, many deaf individuals are treated for their sensory deficit. Moreover, efficient interactions with deaf individuals require specific communication skills (i.e., sign language), which inevitably leads to more difficult experimental conditions and particularly in the scanner environment where exchanges between the experimenter and the participant cannot easily be made visually. Finally, transcranial magnetic stimulation (TMS), a technique creating reversible "virtual lesions" of a targeted brain region, is not suitable for investigating crossmodal plasticity in the deaf because the localization and orientation of the auditory areas preclude optimal stimulation of these regions. In addition, TMS generates loud noise, which creates a strong confound on performance in a control group of hearing subjects. Related to this last point, no human study to date has demonstrated a causal link between activations in "auditory" regions and visual performances in deaf individuals, suggesting the possibility that such crossmodal reorganization might be a simple epiphenomenon, resulting from nonrelevant neuronal activations. Indeed, the results of Lomber et al. (2010) bring novel and highly convincing evidence that the crossmodal changes observed in deaf individuals are functional by nature. The cooling technique used by the authors is highly advantageous over classical lesion techniques in that it allows transient and selective alteration of individual brain regions while measuring the effects of such manipulations on the animal's behavior. Therefore, such a technique is somewhat comparable to TMS, which has successfully confirmed the functional relevance of the nonvisual recruitment of occipital regions in early blind humans, by demonstrating that local and reversible disruption of occipital activity alters performance in nonvisual processing (Collignon et al. 2007).

Surprisingly, while previous studies documented similar roles for PAF and DZ in sound localization in hearing cats (Malhotra and Lomber 2007; Lomber and Malhotra 2008), it appears that these regions play different roles in the visual modality in deaf cats, with PAF selectively involved in visual localization and DZ selectively involved in visual movement processing. Moreover, one of these studies demonstrated that several regions in the hearing cat's brain (i.e., A1/DZ, PAF, AES) participate in auditory localization since specific deactivation of any of these regions was sufficient to produce deficits in auditory localization (Malhotra and Lomber 2007). Surprisingly, in the study of Lomber et al. (2010), only the deactivation of PAF in the deaf cats produced a significant deficit in visual localization. Particularly, the observation that A1 deactivation did not interfere with any visual tasks in the deaf cats seems to suggest that "higher-level" auditory areas are more susceptible to reorganization than more "primary" sensory regions.

While the involvement of DZ in auditory motion perception in the hearing cat remains to be demonstrated, it appears that at least PAF may retain its functional role despite auditory deprivation. Parallel evidence in literature dealing with blindness has demonstrated that nonvisual recruitment of the occipital cortex follows organizational principles that maintain the functional specialization of the colonized brain regions. For example, the right dorsal occipital regions, which are well known to be preferentially involved in visuo-

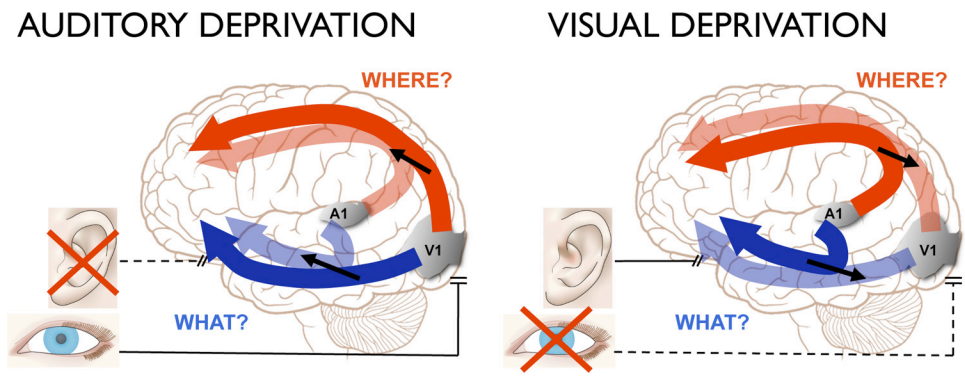

Fig. 1. In auditory and visual cortices, information is believed to be processed along two distinct (but interacting) streams: a dorsal or "where" pathway involved in localization processes and a ventral or "what" pathway involved in identification processes. Recent data, including those of Lomber et al. (2010), suggest that the dual-stream organization might be preserved in the rewired sensory cortices of deaf or blind individuals.

spatial processing in sighted subjects, are selectively activated during nonvisual tasks involving spatial localization in congenitally blind individuals (Collignon et al. 2011). Similarly, hMT+/V5, a region highly specialized for visual motion processing and classically associated with the dorsal stream, responds preferentially to auditory motion in congenitally blind subjects (Bedny et al. 2010). In further accordance with Lomber et al. (2010), when TMS is applied over regions from the right dorsal extrastriate cortex normally involved in visuospatial processing, accuracy significantly drops for auditory spatial localization in the early blind but not in sighted controls, while pitch and intensity perception remain unaffected in either group (Collignon et al. 2007).

The existence of separate hierarchical pathways for the analysis of object properties (i.e., the ventral "what" stream) and for the analysis of the spatial relationship between objects (i.e., the dorsal "where" stream) appears as a general principle of functional organization in the visual and auditory cortices (Rauschecker and Scott 2009). Essentially, beyond the dorsal recruitment for spatial localization and motion processes documented in the blind and deaf brain, other studies in the blind provide evidence that ventral occipital regions are activated during identification of a nonvisual input (Reich et al. 2011). This suggests that the dual-stream organization might be preserved in the rewired cortices of sensory-deprived individuals (Fig. 1). In their study, Lomber et al. (2010) did not report evidence that auditory regions commonly considered as involved in the recognition of sound "identity" (i.e., AAF) in hearing cats become responsible for the processing of visual "objects." We postulate that visual functions evaluated by Lomber et al. (2010), such as grating and Vernier acuity, were not susceptible to induce crossmodal recruitment of auditory regions in the congenitally deaf cats because they are visual-specific and therefore might still highly rely on the visual cortices of the deaf cats. Instead, we hypothesize that visual functions normally benefitting from auditory convergence might recruit more ventral regions in the deprived auditory cortex of the deaf. In humans, an example is reading, whereby using Braille leads to specific activations in the visual word form area (VWFA), a region of the ventral visual stream specialized for reading in the sighted brain (Reich et al. 2011).

A crucial question concerns the existence of a sensitive period in order for specific crossmodal organization to occur. One might wonder what would have happened if the cats from the study of Lomber et al. (2010) had lost audition later in life. Assuming an equal period of time in silence, would such specific crossmodal reorganization be observed in the auditory cortices after the full development of the auditory architecture during infancy? While current literature in the deaf is lacking, some studies comparing brain activity in early and late blind individuals suggest that there are sensitive periods for the maintenance of functional specificity in crossmodal plasticity. For example, Bedny et al. (2010) demonstrated that hMT+/V5 responded preferentially to auditory motion in the congenitally blind but not in sighted or late blind participants, nor in a subject who lost vision between the ages of 2 and 3 years old. These results suggest that visual deprivation should occur early in life in order for hMT+/V5 to develop specific crossmodal responses to motion. In summary, while a late onset of sensory deprivation does not rule out the development of general crossmodal changes, early deprivation appears mandatory in order for such crossmodal changes to be functionally specific. Different mechanisms have been proposed to explain crossmodal plasticity in early and late deprivation (Bavelier and Neville 2002). While early deprivation might lead to the maintenance of intermodal connections that are normally pruned in infancy, late sensory deprivation would not preclude the normal developmental synaptic pruning of these extrinsic connections due to the presence of stabilizing sensory input. As such, crossmodal plasticity observed in late deprivation may reflect the strengthening of existing intermodal connections present in non-deprived subjects. As different sensitivity periods exist for different functions within a given modality and as synaptogenesis varies widely between sensory systems, timing of the deprivation might affect each brain system and function differently and specifically. Future studies should therefore explore the effect of auditory deprivation onset on behavioral and cerebral reorganizations occurring in the unaffected senses of deaf individuals.

The study of Lomber et al. (2010) arguably provides one of the most complete and convincing demonstrations that congenital sensory deprivation induces functionally specific crossmodal changes in the cerebral cortex. These results compellingly illustrate how the brain handles plasticity by demonstrating that specific brain areas have evolved to predict particular computations while remaining flexible relative to the sensory input they receive. We therefore postulate that crossmodal recruitment of a sensory-deprived region must find "neuronal niches" in a set of circuits that perform functions that are sufficiently close to the ones required by the remaining senses (Collignon et al. 2011). In the same way the nature of the ground and the climate of a country determine what is cultivated in a specific region, the area of the brain receiving novel input through crossmodal plasticity determines the computational operations that are carried out on these inputs.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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