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Neuroplasticity in congenitally deaf humans

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RESUMO

A neuroplasticidade é um processo que reflete a capacidade do cérebro de se reorganizar em função de acontecimentos endógenos ou exógenos, incluindo a privação sensorial. O debate acerca de como a neuroplasticidade emerge e quais as estruturas afetadas por este processo encontra-se ainda em aberto. Estudos mostram que em humanos com surdez congénita, o Córtex Auditivo (CA) pode ser cooptado para processar a informação visual. Mas como é que a informação visual é redirecionada para o CA? Neste artigo irá ser apresentada uma revisão dos principais estudos sobre esta questão, enfatizando as hipóteses atuais para explicar as mudanças neuroplásticas observadas em indivíduos com surdez congénita, tanto ao nível neuronal como comportamental. Finalmente, será abordado o papel da língua gestual na neuroplasticidade apresentada por humanos com surdez congénita e apresentadas algumas das principais implicações que estes estudos podem ter para a melhoria da qualidade de vida da pessoa surda.

Palavras-chave: neuroplasticidade; surdez congénita; reorganização sensorial; córtex auditivo.

ABSTRACT

Neuroplasticity reflects the brain's capacity to reorganize itself due to endogenous or exogenous events, including sensory deprivation. The debate on how neuroplasticity emerges and which structures can suffer and regulate neuroplastic changes is still fierce. It has been shown that in congenitally deaf humans the auditory cortex (AC) can be co-opted to process visual input. But how is this visual information rerouted to AC? Here, we will present a review of the main studies concerning this issue and emphasize the extant hypotheses that focus on the neuroplastic changes observed in congenitally deaf individuals at the neural and behavioral level. Finally, we will focus on the role of sign language in the neuroplasticity presented by congenitally deaf humans and present some of the important implications these studies may have on the quality of life in deaf individuals.

Keywords: neuroplasticity; congenital deafness; sensory reorganization; auditory cortex.

INTRODUCTION

Research on sensory deprivation (e.g., deafness or blindness) has always been of great interest to the scientific community as it has been considered a very important model for understanding long-term neuroplasticity. How do deaf and/or blind individuals adapt to their environment, at the behavioral and neural level? Are there fundamental functional and structural changes that compensate for the sensory deprivation they experience? Current evidence suggests that neuroplastic changes happen both within brain regions responsible for the remaining intact senses and within brain regions typically dedicated to the processing of the affected sense (Merabet & Pascual-Leone, 2010). These changes may result in compensatory plasticity, whereby some sensory capabilities are enhanced in the deaf or blind when compared to hearing or sighted individuals (Merabet & Pascual-Leone, 2010). By characterizing the

brain areas that suffer some type of plasticity we can better understand how the information is being processed in those areas and the role of this neural reorganization. Here, we will present a review of several studies concerning plasticity in congenitally deaf subjects, focusing on the plastic changes happening within the deprived cortical sensory areas. We will first address how animal studies have made important contributions to our understanding of how neuroplasticity changes the auditorily-deprived cortex; we will then look into data that is emerging from studies with congenitally deaf human individuals; we will explore how these effects are related to proficiency in sign language; and finally we will exploit how neuroplasticity can impact sensory substitution devices and how this has a major effect on the quality of life of deaf individuals.

Neuroplasticity – comparative studies

Animal studies have clearly shown that the auditory cortex (AC) of congenitally deaf animals processes visual and somatosensory stimuli (e.g., Hunt, Yamoah, & Krubitzer, 2006; Kral, Schröder, Klinke, & Engel, 2003; Meredith & Lomber, 2011; Rebillard, Carlier, Rebillard & Pujol, 1977; Rebillard, Rebillard & Pujol, 1980). In fact, some of these visual responsive neurons present characteristic response patterns typical of neurons within visual cortex (e.g., direction selectivity, location information; e.g., Meredith & Lomber, 2011). Interestingly, however, it has been shown that the primary AC of congenitally deaf animals suffers volumetric reduction (e.g., Wong, Chabot, Kok, & Lomber, 2013), suggesting that these neuroplastic responses are dependent on non-primary sensory areas. Lomber, Meredith and Kral (2010) conducted a study in which the visual skills of congenitally deaf cats and hearing cats were observed, with the aim of identifying visual functions that are optimized in early deafness, and identifying whether these visual functions were dependent on structures within the auditory cortex. In order to test these, the authors used a cooling technique, which allows for temporary deactivation of a specific part of the cortex, and a motion detection task. Lomber et al. (2010) concluded that the performance of deaf cats was far superior to that of hearing cats on detecting motion within peripheral visual fields, whereas other visual acuity tasks showed no significant differences between the groups. As to whether there is a causal relationship between the reorganization of the auditory cortex and visual function in deaf cats, they demonstrated that specific areas within AC that do not include primary AC are causally involved in behavioral compensatory plasticity (Lomber et al., 2010).

The animal model then strongly suggests there to be cross-modal neuroplasticity that has behavioral signatures regarding the way deaf animals process visual information, especially for stimuli appearing in the periphery. Moreover, these changes may not be so strong within the primary cortex, and are causally dependent on other auditory areas.

The case of congenital deafness in humans

Data from studies with congenitally deaf humans are in line with what has been shown in the animal literature. It has been consistently shown that deaf individuals are better on some visual tasks than hearing individuals (Bavelier & Hirshorn, 2010; see also Bavelier & Neville, 2002; Bavelier, Dye, & Hauser, 2006). For instance, Neville and Lawson (1987a, b) showed that the deaf, when compared to hearing individuals, are faster at detecting motion in

peripheral visual locations and show an increase in visual evoked potentials in response to visual stimuli located in the periphery. Proksch and Bavelier (2002) also suggested that deaf individuals have greater attentional resources in the peripheral visual field. In fact, there is a broad agreement on the idea that deaf individuals, compared to hearing individuals, have greater processing accuracy within the peripheral visual field, and perhaps some of these results are due to heightened attentional resources under deafness.

These behavioral profiles have been related to neural responses that may support them. Finney, Fine and Dobkins (2001) measured neuronal activity in auditory areas of individuals with early deafness and of hearing individuals under visual stimulation. Using functional Magnetic Resonance Image (fMRI) the authors found that deaf, but not hearing individuals, demonstrated stronger activation on the right AC for visual stimulation, particularly in Brodmann area 41, which is located in the primary AC. Also using fMRI, Almeida et al. (2015) found that the AC of congenitally deaf humans can code information typical of the visual cortex. More specifically, the authors found that under congenital deafness the right hemisphere AC holds precise information about the location of a stimulus in the visual field, a predominantly visual feature. Finally, it has also been shown that the AC of congenitally deaf humans suffers volumetric reduction (e.g., Shibata, 2007).

Human studies are then, and for the most part, in line with what has been shown in the animal literature, suggesting that the AC of deaf individuals processes information from the remaining senses. In fact, recent data suggests that the functional organization of the AC may follow, albeit crudely, organizing principles that are native of other sensorial regions. Interestingly, and contrary to animal studies, human studies may be suggestive of a stronger involvement of primary AC in the neuroplastic changes present.

The path of visual information in congenital deafness - seeing with your ears

One outstanding question in the study of neuroplasticity under congenital deafness concerns how visual information reaches the AC. In order to try clarifying this question, Bavelier and Neville (2002) proposed four types of mechanisms: changes in local connectivity, changes in subcortical connectivity, changes in cortico-cortical feedback and changes in long-range cortico-cortical connectivity. Studies using deaf cats demonstrated that afferent projections to auditory cortex remain the same in both deaf and normal cats (Heid, Jähn-Siebert, Klinke, Hartmann, & Langner, 1997; Stanton & Harrison, 2000), meaning that cortical auditory areas may possibly continue to receive input from subcortical areas. In fact, studies using newborn ferrets in which retinal cells were redirected into the subcortical auditory pathway (i.e., the medial geniculate nucleus – the principal auditory thalamic nucleus), demonstrated that the response patterns to visual stimulation in primary AC are similar to the ones observed in primary visual cortex (Sur, Garraghty, & Roe, 1988; Roe, Pallas, Hahn, & Sur, 1990). That is, changes in subcortical connectivity can be, in part, responsible for the neuroplastic changes typically observed in the deaf. Studies with congenitally deaf humans are more vague regarding this question: although it has been consistently shown that the deprived sensory system is neuroplastically reorganized, it is not clear which brain structures and/or processes can be responsible for passing the “novel” sensory information to the AC. Future work should focus on changes in anatomical and functional connectivity from subcortical relay areas and the AC under congenital deafness as a proxy for understanding the route of visual information to the AC under congenital deafness.

Is sign language an important factor?

Another important question to consider is the role of sign language in the neuroplastic changes experienced by congenitally deaf humans. A few neuroimaging studies have shown that deaf individuals that are native users of a signed language demonstrate visual responses within AC, suggesting that these responses could be occurring due to the linguistic nature of the stimuli, and not so much to their visual nature. For instance, Petitto et al. (2000), using positron emission tomography (PET), found cerebral blood flow activity in auditory brain regions of deaf signers when processing sign language. Additionally, in an fMRI study, MacSweeney, et al. (2002) found greater activation of the middle/superior temporal and inferior prefrontal regions bilaterally in deaf signers, hearing signers and hearing non-signers groups for audio/signed-visual tasks. This indicates that these areas could be the foundation of language processing, independently from the group status (MacSweeney et al., 2002). These studies pose the question of whether the neuroplastically induced changes present under deafness could be a direct consequence of the multimodal nature of the primary sensory areas (Ghazanfar & Schroeder, 2006). To this point, Emmorey, Allen, Bruss, Schenker, and Damasio (2003), measured whether there were any hemispheric asymmetries in the volume of the Heschl's Gyrus (HG) of both deaf signers and hearing individuals, and found a leftward asymmetry in HG, suggesting that sign language is not responsible for the neuroplastic changes of the AC of deaf individuals. Also, Fine, Finney, Boynton and Dobkins (2005) showed that although deaf individuals who were exposed to American Sign Language (ASL) since birth demonstrated visual responses within AC, hearing individuals with the same fluency with ASL did not demonstrate this, indicating that plasticity is not due to sign language experience. That is, for the most part, the behavioral and neuroplastic changes present in congenital deafness are independent of sign language proficiency.

Thus, sign language appears not to be responsible for the compensatory plasticity and enhanced visual processing that is observed in congenital deaf individuals because these neuroplastic effects are not present in hearing signers. There are, however, neural and behavioral effects that are observed in both deaf and hearing signers, and hence may be heavily dependent on sign language proficiency (e.g., Bavelier & Neville, 2002). For instance, Newman, Bavelier, Corina, Jezzard, and Neville (2002) compared brain activations of subjects who learned ASL before puberty and subjects who learned ASL after puberty. The authors showed that both groups exhibited patterns of neural activation for language processing in the left hemisphere. Nevertheless, only the participants who learned ASL before puberty presented an extensive activation of the right hemisphere, in addition to the left one. These studies show that the right hemisphere could have important implications for the acquisition of a language that depends on visuospatial features and that there are age-related modifications in neuroplasticity (Newman et al., 2002). In fact, some authors have demonstrated that the acquisition of sign language may lead to increased plasticity within the right hemisphere (e.g., Neville et al., 1997; Bavelier et al., 1998; Neville et al., 1998).

DISCUSSION

It is well known that considerable plasticity can take place in individuals who are congenitally deprived of a sense. Work on congenital deafness has demonstrated remarkable changes both in neural processing and in cognitive performance for non-auditory information. For instance, the AC of congenitally deaf animals is co-opted to process visual (and somatosensory) stimuli (e.g., Rebillard et al., 1977, 1980; Hunt et al., 2006; Kral et al., 2003; Meredith & Lomber, 2011). Moreover, putative AC in congenitally deaf humans can be responsive to non-auditory stimulation – Finney and colleagues showed that the AC of congenitally deaf, but not of hearing participants, responds to simple visual stimulation (Finney et al., 2001) – and contain representations of visual field location (Almeida et al., 2015). But how does the visual information reach the AC of congenitally deaf humans? Comparative research has suggested that subcortical projections can be responsible for taking the visual information to the AC of deaf animals (e.g., Sur et al., 1988; Heid et al., 1997; Stanton & Harrison, 2000), but this topic has been much less studied in congenitally deaf humans. Future studies with human participants should be conducted in order to clarify which brain structures and/or processes are responsible for leading the visual information to the AC of congenitally deaf individuals.

An important aspect of long term neuroplasticity under sensorial deprivation is related to sensory restoration efforts and devices, and ultimately to the quality of life of the deaf individual after sensory restoration. All studies described here have important implications for sensory substitution devices, and particularly in the case of deafness, for the development of cochlear implants. The implementation and efficacy of these devices is dependent of the functional and anatomical (re)organization of the deprived sensory system. These sensory systems, however, show deep reorganization, such that they now respond to and represent information from other senses. If a sensory substitution device is constructed such that it exploits the typical organization of a primary sensory cortex, say be selective to different tones because typically developed auditory cortex is organized by tones (Da Costa et al., 2011), then because that typical organization is, at the very least, perturbed by the processing of non-typical sensory information, these devices may not be optimal solutions. A demonstration of this is that late implementation of cochlear implants typically leads to frustrating sensory experiences (e.g., Tyler & Summerfield, 1996; Sandmann et al., 2012), most probably due to the fact that a novel functional organization of sensory information has taken over and perhaps coexists with the typical organization within the AC of these individuals. As such, considering the types of neuroplastic changes happening within the deprived AC could lead to important improvements in the way auditory processing is restored and ultimately lead to a betterment of the quality of life of implanted individuals.

REFERENCES

- Almeida, J., He, D., Chen, Q., Mahon, B. Z., Zhang, F., Gonçalves, Ó. F., Fang, F., & Bi, Y. (2015). Decoding visual location from neural patterns in the auditory cortex of the congenitally deaf. *Psychological science*, 26, 1771-1782.
- Bavelier, D., Corina, D., Jezzard, P., Clark, V., Karni, A., Lalwani, A., Rauschecker, J., Braun, A., Turner, R., & Neville, H. J. (1998). Hemispheric specialization for English and ASL: Left invariance-right variability. *Neuroreport*, 9, 1537-1542.
- Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: Where and how? *Nature Reviews Neuroscience*, 3, 443-452.

- Bavelier, D., & Hirshorn, E. A. (2010). I see where you're hearing: How cross-modal plasticity may exploit homologous brain structures. *Nature Neuroscience*, *13*, 1309-1311.
- Bavelier, D., Dye, M. W., & Hauser, P. C. (2006). Do deaf individuals see better? *Trends in Cognitive Sciences*, *10*, 512-518.
- Da Costa, S., van der Zwaag, W., Marques, J. P., Frackowiak, R. S., Clarke, S., & Saenz, M. (2011). Human primary auditory cortex follows the shape of Heschl's gyrus. *The Journal of Neuroscience*, *31*, 14067-14075.
- Emmorey, K., Allen, J. S., Bruss, J., Schenker, N., & Damasio, H. (2003). A morphometric analysis of auditory brain regions in congenitally deaf adults. *Proceedings of the National Academy of Sciences*, *100*, 10049-10054.
- Fine, I., Finney, E. M., Boynton, G. M., & Dobkins, K. R. (2005). Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. *Journal of Cognitive Neuroscience*, *17*, 1621-1637.
- Finney, E. M., Fine, I., & Dobkins, K. R. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*, *4*, 1171-1173.
- Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences*, *10*, 278-285.
- Heid, S., Jähn-Siebert, T. K., Klinke, R., Hartmann, R., & Langner, G. (1997). Afferent projection patterns in the auditory brainstem in normal and congenitally deaf white cats. *Hearing Research*, *110*, 191-199.
- Hunt, D. L., Yamoah, E. N., & Krubitzer, L. (2006). Multisensory plasticity in congenitally deaf mice: How are cortical areas functionally specified? *Neuroscience*, *139*, 1507-1524.
- Kral, A., Schröder, J. H., Klinke, R., & Engel, A. K. (2003). Absence of cross-modal reorganization in the primary auditory cortex of congenitally deaf cats. *Experimental Brain Research*, *153*, 605-613.
- Lomber, S. G., Meredith, M. A., & Kral, A. (2010). Cross-modal plasticity in specific auditory cortices underlies visual compensations in the deaf. *Nature Neuroscience*, *13*, 1421-1427.
- MacSweeney, M., Woll, B., Campbell, R., McGuire, P. K., David, A. S., Williams, S. C., Suckling, J., Calvert, G. A., & Brammer, M. J. (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. *Brain*, *125*, 1583-1593.
- Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: the opportunity of change. *Nature Neuroscience*, *11*, 44-52.
- Meredith, M. A., & Lomber, S. G. (2011). Somatosensory and visual crossmodal plasticity in the anterior auditory field of early-deaf cats. *Hearing Research*, *280*, 38-47.
- Neville, H. J., & Lawson, D. (1987a). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study: I. Normal hearing adults. *Brain Research*, *405*, 253-267.
- Neville, H. J., & Lawson, D. (1987b). Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Research*, *405*, 268-283.
- Neville, H. J., Coffey, S. A., Lawson, D. S., Fischer, A., Emmorey, K., & Bellugi, U. (1997). Neural systems mediating American Sign Language: Effects of sensory experience and age of acquisition. *Brain and Language*, *57*, 285-308.
- Neville, H. J., Bavelier, D., Corina, D., Rauschecker, J., Karni, A., Lalwani, A., Braun, A., Clark, V., Jezzard, P., & Turner, R. (1998). Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience. *Proceedings of the National Academy of Sciences*, *95*, 922-929.
- Newman, A. J., Bavelier, D., Corina, D., Jezzard, P., & Neville, H. J. (2002). A critical period for right hemisphere recruitment in American Sign Language processing. *Nature Neuroscience*, *5*, 76-80.
- Petitto, L. A., Zatorre, R. J., Gauna, K., Nikelski, E. J., Dostie, D., & Evans, A. C. (2000). Speech-like cerebral activity in profoundly deaf people processing signed languages: implications for the neural basis of human language. *Proceedings of the National Academy of Sciences*, *97*, 13961-13966.

- Proksch, J., & Bavelier, D. (2002). Changes in the spatial distribution of visual attention after early deafness. *Journal of Cognitive Neuroscience*, *14*, 687-701.
- Rebillard, G., Carlier, E., Rebillard, M., & Pujol, R. (1977). Enhancement of visual responses on the primary auditory cortex of the cat after an early destruction of cochlear receptors. *Brain Research*, *129*, 162-164.
- Rebillard, G., Rebillard, M., & Pujol, R. (1980). Factors affecting the recording of visual-evoked potentials from the deaf cat primary auditory cortex (AI). *Brain research*, *188*, 252-254.
- Roe, A. W., Pallas, S. L., Hahm, J. O., & Sur, M. (1990). A map of visual space induced in primary auditory cortex. *Science*, *250*, 818-820.
- Sandmann, P., Dillier, N., Eichele, T., Meyer, M., Kegel, A., Pascual-Marqui, R. D., Marcar, V. L., Jäncke, L., & Debener, S. (2012). Visual activation of auditory cortex reflects maladaptive plasticity in cochlear implant users. *Brain*, *135*, 555-568.
- Shibata, D. K. (2007). Differences in brain structure in deaf persons on MR imaging studied with voxel-based morphometry. *American Journal of Neuroradiology*, *28*, 243-249.
- Stanton, S. G., & Harrison, R. V. (2000). Projections from the medial geniculate body to primary auditory cortex in neonatally deafened cats. *Journal of Comparative Neurology*, *426*, 117-129.
- Sur, M., Garraghty, P. E., & Roe, A. W. (1988). Experimentally induced visual projections into auditory thalamus and cortex. *Science*, *242*, 1437-1441.
- Tyler, R. S., & Summerfield, Q. A. (1996). Cochlear implantation: Relationships with research on auditory deprivation and acclimatization. *Ear and Hearing*, *17*, 38-51.
- Wong, C., Chabot, N., Kok, M. A., & Lomber, S. G. (2013). Modified areal cartography in auditory cortex following early-and late-onset deafness. *Cerebral Cortex*, bht026.