

RESEARCH ARTICLE

Somatosensory Crossmodal Plasticity in Superior Colliculus of Visually Deafferented Rats

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Abstract

Terminal fields of a certain pathway result denervated if the regeneration after the lesion of the pathway fails. If the lesion happened in a young animal, terminal fields of other nervous pathways that are spatially coincident or are close to the denervated field, growth of axon collaterals or reactive synaptogenesis could take place and reinervate deafferented neurons. In that way these denervated neurons can be recruited for functional compensatory responses and can convey information to areas that result enriched with additional inputs to be processed. The present paper reviews the plastic reactions that take place in the superior colliculus, a mesencephalic layered structure, after the neonatal suppression of its visual afferents that terminate in its superficial layers. The postlesional reactive ascending growth of somatosensory afferents that in control animals innervate intermediate and deep collicular layers invade the superficial layers and connect with visually deafferented cells that result recruited for descendent collicular responses and to send sensory information to the visual cortex via the colliculo-geniculate pathway. In that way in neonatally deafferented animals, somatosensory information gains additional territory to be processed. Two somatosensory connections to the superior colliculus will be discussed in this review. One ascending from the cuneiform nucleus and the other descending that originates in the barrel cortex.

Somatosensory ascending connections

Origin and distribution

The rat SC is a mesencephalic, layered structure involved in orientation, approach and escape behaviour (1, 2, 3, 4). Whereas the superficial collicular strata (stratum zonale SZ, stratum griseum superficialis SGS, stratum opticum SO) are mostly devoted to visual functions, the intermediate and deep strata (stratum griseum intermedialis SGI, stratum griseum intermedialis SAI, stratum griseum profundum SGP, stratum albus profundum SAP) contain multimodal neurons that display a wider range of activities in response to somatosensory, auditory and visual stimuli (5, 6, 3). Somatosensory ascending afferents terminate in the intermediate and deep collicular layers. There share territories with descending sensory connexions coming from the barrel cortex. Those carrying sensory information of the receptors located below the neck made relay stations in the dorsal column nuclei - gracile and cuneate- and in their way to the contralateral ventroposterior lateral thalamic nucleus send collaterals to the intermediate and deep strata of the superior colliculus. Direct injections of anterograde tracers into these nuclei allow to visualize the axons of this sensory afferents. Whereas the GrN (gracile nucleus) concentrates its efferents into the posteromedial collicular sectors, axons emerging from the CuN (cuneiform nucleus) are organized into two groups: one medial smaller and one external, more considerable, externally located (7). The axons of the external contingent are distributed in dense plexuses that extend

from the periaqueductal grey matter until the upper levels of the intermediate stratum griseum.

.At posterolateral collicular levels cuneate-collicular fibres reach the upper parts of the intermediate stratum griseum, in close contact with stratum opticum. The alignment of visual and somatosensory maps that occur in the superior colliculus, made possible that the lower temporal visual field represented in the superficial collicular layers is topographically aligned with maps corresponding to the upper limb (8).

Poslesional plasticity

After neonatal visual deafferentation a series of plastic changes affecting afferents to the superior colliculus occur (10, 11, 12, 13, 15, 16, 17, 18). Among them, it has been demonstrated that collicular afferents from the CuN change their normal territory in intermediate collicular strata and ascend to contact neurons located in the more superficial visual strata (11). Whereas fibres coming from the GrN do not show any detectable morphological change, fibres from the CuN undergo an expansion toward overlying stratum opticum (SO) and SGS but conserving the topography in the rostrocaudal and lateromedial axes of the unlesioned adult animal (Figure 1). Electrophysiological data show that these reactive terminals activate many neurons located in the visually deafferented SGS and SO (11, 19, 20). In this way somatosensory information is made accessible to the visual cortex through the colliculo-geniculo-cortical pathway (11). There is therefore a selective capacity of

somatosensory fibers to grow in response to enucleation changes according to the

body region from which they relay information.

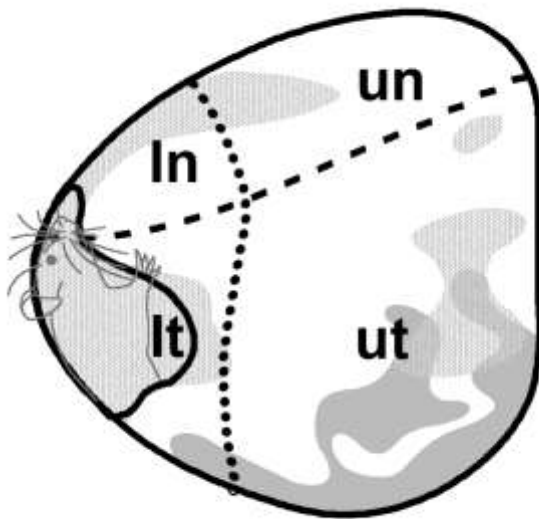


Figure 1: Topographical representation of the somatosensory and visual field maps on the surface of the left superior colliculus. After contralateral visual deafferentation somatosensory afferents corresponding to the external part of the map ascend and connect with superficial cells that make them participate in the motor responses that originate in the colliculus of visally deafferented animals. In, lower nasal; un, upper nasal; lt, lower temporal and ut, upper temporal visual field. Most of the somatosensory maps corresponding to the GrN are located in the ut quadrant (represented in gray), whereas maps of the CuN are located in the ut and lt quadrants respectively (stripped areas).

Several nervous connections are exuberant during early developmental stages and then retract along the postnatal maturation. In this regard, connectivity status seen in the adult after neonatal lesions can be attributed to lack of retraction of early postnatal exuberant connections. As an example, fibers arising from the trigeminal brainstem complex innervate superficial collicular strata during the early postnatal development and subsequently retract (21). The presence of CuN-collicular fibers within deafferented superficial strata may reflect maintenance of normally exuberant collaterals at the time of lesion. CuN-collicular axons may also transiently

innervate superficial strata in neonates, and visual deafferentation at birth could then result in maintenance and even further development of the putative immature exuberant axons innervating visual strata. Alternatively, dorsal expansion of CuN-collicular terminal fields toward deafferented superficial strata suggests that a reaction involving growth of axonal branches and reactive synaptogenesis after the lesion occurs.

Functional consequences

Thus, retinal deafferentation at birth would lead to reactive growth of CuN-collicular terminals, which would tend to occupy territories left vacant by the

eliminated retinocollicular terminals. Ascending fiber redistribution that occurs in the collicular fibers coming from the CuN made possible that somatosensory signals arrive to the superficial collicular neurons that in normal animals receive only visual information. This new connectivity possibilities that superficial collicular neurons can participate in somatosensory circuits. Confirming this possibility Rhoades et al. (1981) have demonstrated that spinal, brainstem, and cortical somatosensory afferents invade superficial collicular layers after neonatal enucleation and that, moreover, many cells of the superficial layers of the neonatally deprived SC respond to somatosensory stimuli (11, 17, 18) in a manner similar to that of somatosensory neurons located in the deeper collicular layers (11). This postlesional plastic reaction is limited only to the lateral collicular region where the topographic somatosensory maps of the forelimb are represented. Descending efferents from this area that are integrated in the behavioural responses (22) result compensatorily reinforced in visually deafferented animals. It is possible that the use of forelimbs for locomotor exploration during postnatal development in enucleated animals would increase electrical activity in the CuN-collicular fibers innervating the lower temporal visual field. Increased activity, together with disappearance of competitive interactions between retinocollicular and CuN-collicular axons, could result in stabilization and even further development of these terminals.

Somatosensory descending connection

Origin and distribution

The vibrissae, which are a significant set of sensing structures located in the face of a series of mammals are represented in the primary rodent S1BF (23). Confirming this, diverse studies have demonstrated that the S1BF undergoes an upregulation of c-fos and other early genes after stimulation of contralateral whiskers (24, 25, 26, 27, 28). This direct cortico-collicular connection originates in the layer V pyramidal neurons, is topographically organized and can be labeled by injecting in the cortex the anterograde tracer BDA. When the BDA injections in the control animals affected the caudally represented barrels, the corresponding terminal fields in the ipsilateral SC were distributed at several levels. Dense fiber plexi appeared in intermediate collicular strata (SGI, SAI) where, according to previous reports (29) formed a patchy organization. The most medial and caudal portions of this terminal field showed weaker labeling. The deeper layers of the SC (SGP, SAP) had a considerable number of BDA-labeled fibers in all cases. A stream of fibers that ran dorsolaterally from the deeper to intermediate strata connected both parts of the terminal collicular fields. When the tracer injections labeled caudal cortical barrels, terminal fields in colliculus were not present in the most medial and caudal regions of the SC. Following BDA injections into the rostral cortical barrels, which represent the rostral microvibrissae rows, the terminal fields were located to the most lateral regions of the SC (figure 2 A,B).

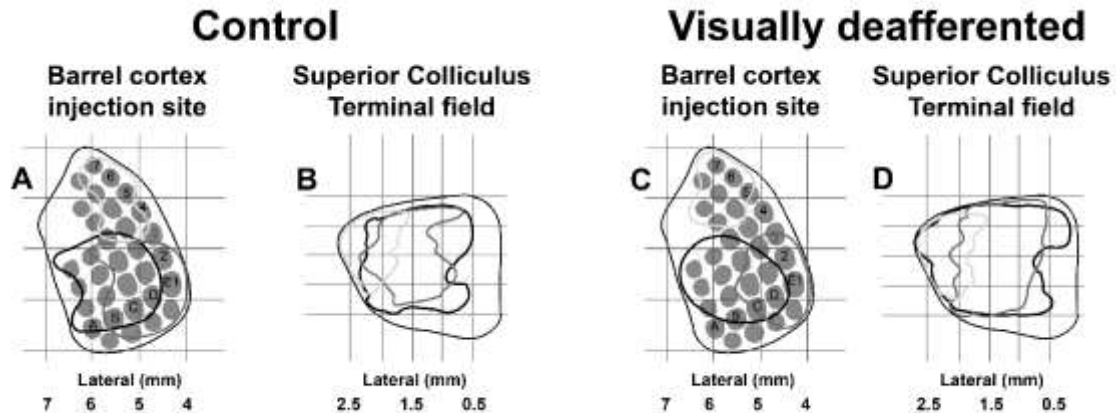


Figure 2: BDA injection sites at the barrel cortex of a control case (A) and the corresponding terminal fields represented on the collicular surface (B); note that the most external terminal fields originated in the most frontal barrel fields. After neonatal visual deafferentiation, similar tracer injections in barrel cortex (C) show that the the most lateral fibers of the collicular terminal fields sprout vertically (striped area in D) and connect with visually deprived neurons of the superficial collicular strata that result recruited for behaviourally relevant responses.

Plasticity after neonatal visual deafferentiation

Neonatal visual deafferentiation does not change the organization of the patches of fibers seen in the SGI of adult animals. However, in the lateral patches, fibers of the tip of the patches send collaterals that grow vertically and reach the SO and upper levels of SGS (figure 2 C,D; figure 3). Therefore the superficial collicular neurons of this lateral sector receive somatosensory information when neonatally visual stimuli were suppressed. Within the rich collicular connectivity, neurons of the superficial strata make

descending local connections with neurons of the intermediate strata (30, 31, 32, 33). And many neurons of the intermediate strata are origin of descending pathways that leave the superior colliculus and connect with troncoencephalic motor neurons (19) that promote orientation motor responses, such as saccades and pinnae and neck movements (2). Therefore, the visual information contributed by superficial collicular neurons to the generation of behavioural motor patterns is substituted by somatosensory information when the retina is neonatally suppressed.

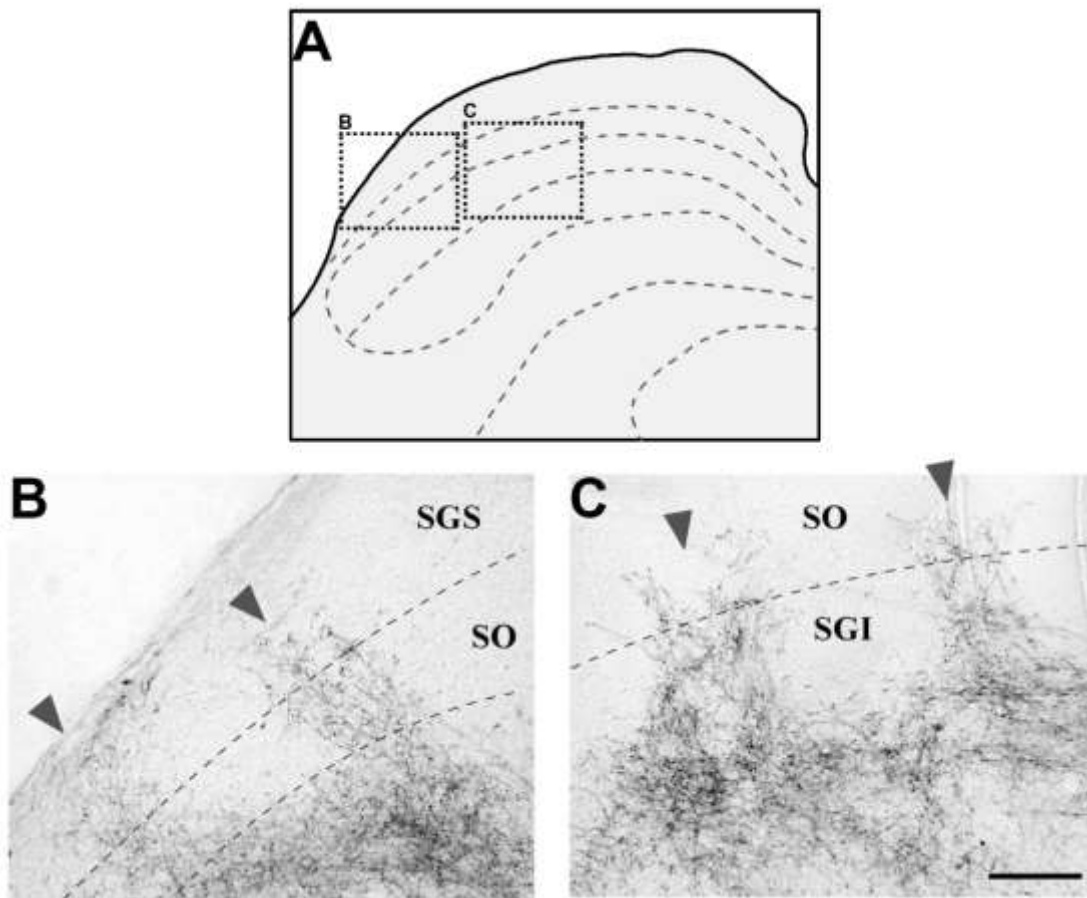


Figure 3: Ascending axonal growths (arrowheads in B) of the lateral terminal barrel field (located in A, B). Fibers grow from intermediate strata and contact superficially located collicular neurons that can result involved in efferent collicular responses. In intermediate areas of the same terminal fields (A, C), growing fibres do not reach the upper levels of the stratum opticum (SO), and do not reach superficial collicular neurons as it happens in the lateral areas. Scale bar: 100µm

Circuitry reorganization and functional consequences.

Neurons in the SGS send axons to the lateral posterior (34) and to the dorsolateral geniculate thalamic nuclei (35). In turn, both of these thalamic nuclei, following the tecto-thalamo-cortical pathway project to the visual cortex (34). In normal conditions, this pathway conveys only visual information, but in neonatally enucleated animals, this pathway could send somatosensory

information (11, 7, 36) to the deafferented visual cortex. Therefore these cortical targets could participate in processing non-visual information. The plastic changes seen here take place mainly in the lateral collicular domains, where rostral vibrissae are represented. The parts of the superficial strata directly above, where axonal sprouting and c-fos expression increases after exploration of enriched environments (36) correspond to the lower visual field representation. To this

collicular quadrant arrive also somatosensory connections from the cuneate nucleus that correspond to the map of the forelimb and neck. The lack of vision in the lower visual field could be compensated by developing new connections related to the body parts used in surface exploration behaviour, such as

the forelimbs and the rostral vibrissae. These results, together with previous data, clearly show that neonatal visual deafferentation elicits crossmodal changes in the central and peripheral intact somatosensory systems, thereby providing a neural basis for behavioural compensation (37, 38).

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