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Plasticity in Damaged Multisensory Networks

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Additional information is available at the end of the chapter

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Abstract

This chapter opens by discussing functional and anatomical locations as well as neural networks of unimodal senses: vision, somatosensation, audition, gustation and olfaction. How and where these unimodal sensory systems intersect and interact with multimodal sensory processes to provide a holistic view of how experiencing complex external objects and events lead to a single multimodal percept. Reviews of current neuropsychological research on damage occurring within both unimodal and multimodal sensory networks further explain the association between these networks and how they operate together in perception. Current research reviews on cross-modal plasticity reveal the neural changes that occur in multisensory areas following brain damage and the potential benefits of this plastic reorganization of the cortex.

Keywords: plasticity, multisensory networks, neural damage, unimodal, multimodal integration

1. Introduction

When we actively engage and interact with objects in our surroundings, our brains inherit an enormous amount of information pertaining to the complexity of these objects and features of the external environment itself. Information from the environment is initially collected by our multiple senses, and then processed and interpreted before motor interaction are planned and executed, all occurring within an instance. Perception has been traditionally viewed as a unimodal sensory process with the different sensory modalities operating as independent processes. However, it is obvious that multisensory interactions must occur in various perceptual tasks and events in order to allow one to have proper interactions with the environment. There are numerous brain areas and pathways for multisensory interaction that will be briefly overviewed within this chapter.

External environmental information is received through sensory modalities such as vision, somatosensation, audition, olfaction and gustation. Each of these sensory modalities is comprised of an organ that contains specialized receptive cells, with corresponding receptive fields that respond to external stimuli. The stimulation of a neuron's receptive field initiates a response related to the size and shape of the stimulus; this information travels via sensory pathways sent to the corresponding primary receiving areas of the cerebral cortex. In general, sensory pathways are neurons that link the sensory receptors at the periphery with the spinal cord, brainstem, thalamus and cerebral cortex.

It is essential to clarify how individual pathways work in unison in order to understand the neuronal changes that arise from damage within these systems as a whole. Plasticity of the spared senses can shed light on how the brain changes as a result of damage, providing important insight related to time management and rehabilitation for a variety of neuropsychological disorders.

Next, we will discuss how the senses combine in multisensory networks that enhance our sensory experiences and reactions to external stimuli. Various neuroanatomical techniques are documented in the existing literature, which have been used on nonhuman primates to pinpoint key multimodal cortical sites such as the superior temporal sulcus (STS), intraparietal sulcus, posterior insula, parietopreoccipital cortex, frontal brain regions including the prefrontal, premotor and anterior cingulate (AC) cortex [1–4], and subcortical sites including superior colliculus (SC), claustrum, medial pulvinar nucleus of the thalamus, suprageniculate, hippocampus and the amygdaloid complex [5–7]. The exact functions of these areas and their connections with other multisensory networks will be further examined.

Extensive studies on both animals and humans have shown that during the early stages of development, any environmental alteration or disruption of processing in a single sense results in an enormous fluctuation in favor of neuronal plasticity between multiple senses [8–11]. However, less is known about the potential neuronal changes that arise after damage has occurred to multisensory areas later on in life. Thus, this section will discuss research in cases where damage has occurred within multisensory networks and areas involved in polysensory integration. First, we will describe a study on a patient with Balint's syndrome [12], followed by a report on a case study examining the multisensory effects of damage via infarct in the right primary visual cortex [13]; we will then describe a study which looks at patients with hemianopia and/or neglect in a visual detection task [14]. Lastly, we will describe research on plasticity in multisensory dorsal stream networks involved in nonvisual processing of action [15].

Damage to heteromodal or unimodal sensory areas reduces the effects of multisensory integration that give rise to holistic perception. However, spared multisensory networks have shown to be associated with behavioral benefits through cross-modal plasticity, where the spared heteromodal areas attempt to reconnect the multisensory system and bypass injured areas [9, 11, 14–17].

The final sections of the chapter will discuss some of the research on neuroplastic reorganization that we are currently conducting in our laboratory. In one study, we investigated the effects of long-term professional ballet training on tract fractional anisotropy (FA) lateralization and

extent of tract FA. Research indicates that experience and training modulate brain structural parameters including volume and FA [18]; FA is a diffusion tensor imaging (DTI) derived index of water molecule diffusion sensitive to the collective effect of microstructure properties. The effect of long-term ballet training characterized in terms of tract FA lateralization, extent of tract FA and global volume has not been previously reported. We localized these FA parameters in expert dancers relative to controls using DTI, and results indicate that dancers had greater leftward lateralization in the anterior thalamic radiation (ATR), whereas the non-dancers had greater rightward lateralization and that dancers also had higher FA localized to the left cortical spinal tract (CST). Higher dancer FA implies heightened axonal ability to communicate. The large percentages of variability shared by dancer years of training and the structural metrics FA and global volume implicate a substantive impact of dance training on brain structure.

In another study, we investigated the structural and functional plasticity associated with dance expertise in a cross-sectional pilot study, comparing ballet dancers to controls. Using functional magnetic resonance imaging (fMRI), whole-brain functional activation maps of dancers and controls were compared, while they engaged in motor imagery of dance movements. Anatomically the results reveal that dancers exhibited greater cortical thickness in areas such as the inferior occipital gyrus, inferior frontal gyrus and superior temporal gyrus. We also found years of dance training to be positively correlated with cortical thickness in various regions, including the fusiform gyrus and parahippocampal gyrus. These preliminary results suggested that dance expertise is associated with a functional reorganization that corresponds to reduced activity reported in other motor expertise groups.

Lastly, our lab has investigated the impacts that dance intervention has on people with Parkinson's disease (PwPD) and healthy controls. Dance has been shown to have a positive effect on motor functioning in PwPD, but less well understood are the effects of dance on mood and associated brain activity observed within PwPD. Our aim was to examine the effects of dance on both motor and nonmotor functioning and correlate these potential effects to onsite recordings of resting state electroencephalogram (rsEEG) within the alpha rhythm (6–12 Hz), collected immediately before and after a single dance class. Precisely, we aim to examine and potentially construct brain-related plasticity mechanism(s) as a function of dance. As expected, the preliminary results show an overall improvement in motor impairment after a single dance class in PwPD. We also found differential effects of dance on negative and positive mood for both PwPD and HC. Finally, we show an increase in global alpha power after a single dance intervention. These findings imply that dance promotes changes in affect through its overwhelming positivity, use of imagery, use of imagination, the presence of music and a sense of bonding through partner work. These results are of importance as their implications may allow researchers to better correlate and understand the positive behavioral and physiological benefits of dance for PD, and perhaps can aid in the implementation of dance as a form of rehabilitation for PwPD. We are currently leading a follow-up study examining the results of participation in multiple dance classes overtime in conjunction with our ongoing rsEEG research, which will provide an account for the observed neural changes in global alpha power.

Taken together, these investigations on neural plasticity following dance will supplement the earlier studies discussed in the section on damaged multisensory networks. They provide compelling evidence that plasticity occurs in both healthy and clinical populations following learning, exposure to training and greater experience with a particular task.

2. Unimodal and multimodal sensory systems

2.1. Visual perception

The eye is considered the primary sensory organ for the modality of vision. All external information from both eyes has to travel to the very back of the brain, the primary visual receiving area known as the occipital lobes, before it begins to the process toward conscious vision. Libet's famous study, deriving from direct stimulation of the somatosensory cortex (postcentral gyrus), suggests that at threshold intensity for a sensation, visual information can guide actions within one-fifth of a second (200 ms) and that takes about half a second (500 ms) for us to see an object consciously [19, 20].

Most neurons from the retina and lateral geniculate nucleus (LGN) of the thalamus terminate onto the striate cortex (area V1) where initial cortical processing of all visual information first occurs in the perceptual process. Two retinal ganglion cells exist and create two separate pathways, magnocellular (M) and parvocellular (P). M and P pathways become segregated within the LGN, where the bottom two layers consist of M cells, and the upper four layers are made up of P cells. Neural signaling is converted faster by the M cells for the functions of visual motion perception and eye movements, whereas P cells contribute more toward object recognition and face recognition and thus represent more constant stimulus presence. The M and P pathways remain segregated beyond the striate cortex where the M pathway continues along the dorsal stream of the cortex and the P pathway along the ventral stream of the extrastriate cortex (V2) [21]. The dorsal stream passes through area V2, then area V4, and leads to the posterior parietal cortex (PPC), Brodmann's areas 5 and 7, and the middle temporal area (MT). Research on monkeys has shown that MT is responsible for motion processing, representation of object location, control of the eyes and arms for action and is thus referred to as the "where pathway" [21, 22]. Ventral stream begins at V1 then travels through V2-V4 and finally terminates in the inferior temporal area (IT). The ventral stream is devoted to fine analysis of the visual scene and to the perception of color, features and form on an object and is thus referred to as the "what pathway" [21, 22].

Finally, there is still unsatisfactory evidence as to whether these two separate systems converge onto a mutual pathway that explains the neurological basis of visual perception. One way to explore this further is to examine multimodal processing areas and their association with each of the senses.

2.2. Somatosensory systems

Somatic sensibility has four major modalities that provide us with information of objects in the external world: touch (via physical contact with the skin), proprioception (through the

position and movement of our body), nociception (such as pain and itch) and temperature (such as feeling warmth and cold) [23]. Each of these modalities begins at a somatosensory organ with distinct receptors and pathways that lead to the brain; however, all share common sensory neurons known as the dorsal root ganglia neurons (DRG). Tactile and limb proprioception are transmitted to the ventral posterolateral (VPL) nucleus of the thalamus via the dorsal column of the spinal cord known as the medial lemniscus pathway. These neurons project to the primary somatosensory cortex (SI) in the postcentral gyrus located on the parietal lobe where information is processed regarding the perception of your body and the external environment [24], whereas pain and temperature information terminate in the intralaminar nuclei of the thalamus through the anterolateral pathway [25]. These afferents also project to SI, specifically the dorsal anterior insular cortex and to the anterior cingulate gyrus where both deep pain and dull pain are processed [23].

SI performs the initial stage of cortical processing, and an overlap of information from any of the four somatosensory modalities may intermingle in higher cortical areas leading to complexity in neural responses. SI is subdivided into 4 Brodmann's area: 3a, 3b, 1 and 2. Most of the thalamic afferents project to areas 3a and 3b and these areas in turn extensively innervate their axons to areas 2 and 1 [23]. These four regions are differentiated according to their functionality; areas 3b and 1 receive somatosensory information from areas on the skin, whereas areas 3a and 2 receive proprioceptive information from receptors that belong to muscles and joints [23]. Research on monkeys has shown that much of SI projections innervate a secondary brain region, the secondary somatic sensory cortex (SII), which projects to areas responsible for tactile memory within the temporal lobe [26]. Lastly, Brodmann's area 5 receives input from SI and pulvinar and is known to be responsible for the integration of tactile and proprioceptive information [23]. Projections from the PPC innervate motor areas in the frontal lobe which play a role in the sensory initiation and guidance of movement [23].

2.3. Audition

Auditory perception gives rise to the ability to perceive sound in our environments by detecting vibrations and changes in pressure in the air. The ear is considered the organ for auditory perception; however, it also assists us in determining balance of our bodies [23]. The eighth cranial nerve travels and branches onto the cochlear nuclear complex located within the brainstem. From here, axons project to the inferior colliculus within the midbrain and to the nucleus of the lateral lemniscus located within the pons where further processing of sound occurs [23]. All of these afferents then move to the medial geniculate nucleus of the thalamus and end up in the superior temporal gyrus a part of the primary auditory cortex (Brodmann's areas 41 and 42). Once action potentials reach here, the conscious perception and processing of sound occur.

2.4. Olfaction and gustation

The olfactory system, also known as the sense of smell, aids humans in distinguishing an enormous amount of odors that are categorized into various groups; spicy, floral, burnt, resin, fruit and putrid [27]. Mitral and tufted cells act as relay cells from the olfactory bulb to the

olfactory cortex which is subdivided into five areas: (1) anterior olfactory nucleus (AON), an area responsible for the processing of odors [28]; (2) amygdala for memory associated with specific odors; (3) olfactory tubercle mediating multisensory integration of olfactory information; (4) piriform cortex, responsible for olfactory processing; and finally (5) entorhinal cortex (EC) for preprocessing familiar odors [23]. The latter four parts relay information to the orbitofrontal cortex (OFC) via the thalamus and are an area responsible for decision making for expected rewards or punishments given a certain situation. In addition, the olfactory cortex makes direct connection to the frontal cortex itself for value judgments of odors [23].

Gustatory perception, otherwise known as taste, begins with its essential organ, the tongue. There are a total of five basic tastes that the gustatory system distinguishes, and a combination of these basic tastes gives rise to more complex, established tastes: sour, salty, sweet, bitter and umami [23]. Chorda tympani (cranial nerve VII) innervate the anterior two-third of the tongue and soft palate, the glossopharyngeal (cranial nerve IX) innervates the posterior one-third of the tongue, and lastly, both the vagus (cranial nerve X) and glossopharyngeal nerves innervate the epiglottis and the pharynx [23]. These afferent nerves enter the solitary tract and synapse with secondary neurons in the gustatory area of the medulla [23]. These second order afferent neurons project to the ventral posterior medial nucleus of the thalamus [23]. Finally, they project to the gustatory cortex, between the anterior insula and frontal operculum in the ipsilateral cerebral cortex, to provide conscious perception and discrimination of taste [23].

2.5. Multisensory interaction: anatomical and synaptic levels

Objects and situations that we experience in our everyday lives are embedded within rich and complex environment that contain an enormous amount of information. Perceiving, planning and responding to these complex scenarios involve more than a single, isolated sense. Instead a holistic gathering of information across multiple sensory modalities must occur in order to have successful interactions with the external world. This ability to combine sensory information across different modalities enhances both detection and discrimination of external objects [29]. For example, visual sensitivity can be enhanced with the presence of an auditory or tactile stimulus in healthy participants [30]. In this part of the chapter, we will discuss the neural pathways from primary unimodal sensory areas to multimodal association areas involved in sensory integration. After each multimodal description, we will present cases where damage occurred within these areas to provide explanations of their particular functions.

Unimodal association areas discussed above project to multimodal sensory association areas including the parietotemporal and prefrontal cortices, cingulate gyrus, hippocampus and amygdala [23, 31]. In order to plan and compute a movement toward an external object, the multimodal sensory association areas project to multimodal motor association areas where these converging sensory inputs are transformed into planned motor commands or movements [23, 31]. Execution of movement is initiated when the multimodal motor association areas project to premotor (motor preparation) and primary motor (movement execution) cortices [23].

Our knowledge of the nature and localization of neural mechanisms underlying multimodal sensory processing has stemmed from studies involving different animal species while using

a variety of neuroscience techniques. Studies on nonhuman primates using direct cortical recordings have shown convergence of unimodal afferents onto heteromodal cortical sites within the superior temporal sulcus (STS), intraparietal sulcus, posterior insula, parietoprecipital cortex, and frontal regions including the prefrontal, premotor and anterior cingulate (AC) cortices [1–4]. Heteromodal sites have also been found in subcortical structures such as the SC, claustrum, medial pulvinar nucleus of the thalamus, supragenulate, hippocampus and the amygdaloid complex [5–7].

Each multisensory neuron located within the SC contains a map of sensory space corresponding to the senses of audition, vision and tactile sensation. These multimodal sensory maps overlap each other, eliciting activation in the same region of the SC where different sensory modalities innervate the same spatial location on the SC [32]. Research has also shown that multisensory neurons within the SC not only respond to multiple sources of sensory information but are also capable of combining them into an integrated form, when two or more afferent sensory neurons appear in close temporal and spatial proximity. The firing rate of these multisensory neurons sums the impulses for each individual modality and thus increases the firing rate of these cells, in turn resulting in a multimodal neuronal response [33]. In contrast, studies have shown that responses to a stimulus from another sensory modality can substantially lessen a vigorous unimodal sensory response in a different sensory modality [34]. Thus, the SC, both at the population and synaptic level, has shown cross-modal integration mediating attentive and orientation behaviors to external stimuli [33].

Neuroimaging studies in humans have been a bit more convoluted with respect to their findings as the description of the different networks involved in multisensory perception has shown to depend on the type of stimuli being integrated and the demands of the task [35]. Multisensory cortical areas in humans include superior temporal sulcus (STS), intraparietal sulcus (IPS) including the ventral (VIP) and lateral (LIP) intraparietal sulcus, parieto-occipital cortex, posterior insula and frontal regions which include the premotor and prefrontal cortices, parietal cortex and the lateral occipital tactile-visual area [36]. With regard to the subcortical level, multisensory activity has been shown in thalamus [37], ventral and dorsal regions of the cochlear nucleus [38], SC [39] and basal ganglia (BG) [40].

Studies in monkey parietal cortex have shown that area VIP receives multimodal sensory inputs from visual, somatosensory, auditory and polysensory areas [41]; in addition, area LIP connects with areas dealing with spatial vision (visual area MT and the auditory caudomedial) along with the frontal eye field (FEF) [42] and with inferotemporal cortex (ventral visual pathway) [43]. Also, studies on STS show its connection with the visual occipital cortex and with the auditory association area [44]. In addition, the prefrontal cortex receives projections from auditory and visual cortices, essentially playing the role in temporal integration [45]. Lastly, studies on monkeys have shown interconnected multisensory networks in the putamen, VIP, premotor cortex, and parietal area 7b in the perception of visual, tactile and auditory stimuli presented in peripersonal space (a part of external space that is close to the body or a particular body part) [39, 46].

3. Damage in multisensory networks and plasticity

In this part of the chapter, we will introduce patient cases where damage has occurred in particular areas within multisensory networks at both the local brain regions and synaptic levels that will shed light on the mechanisms behind neural plasticity and cortical reorganization.

One study conducted on a patient with a rare affliction known as Balint's syndrome, observed the effects of spatial visuotactile interactions [12]. Balint's syndrome is a very rare neuropsychological impairment resulting from two or more strokes in the parietal lobes in each hemisphere. The symptoms present themselves as a severe disturbance of external space representation with clinical signs of simultanagnosia (inability to perceive the visual field as a whole), oculomotor apraxia (difficulty in fixating the eyes) and optic ataxia (inability to move hand extremities to a specific external object guided by vision) [47]. Within this study, visuotactile interactions were examined during a tactile discrimination task where spatially congruent or incongruent visual cues were simultaneously presented in either the same or the opposite side as the tactile object near the patient's hand. The results for healthy comparison subjects showed that irrelevant visual events elicited a strong and involuntary orientation of spatial attention during concurrent discrimination of tactile stimuli at the same location that was not observed in the Balint's syndrome patient [47]. This finding explains how the posterior parietal cortex (PPC) contributes to spatial processing of exogenous shifts in attention. In the patient with Balint's syndrome, severe spatial deficits were observed affecting the left hemispaces in the visual tasks. More precisely, when stimulating the patient's left hand in the left side of visual space, visuotactile interactions were not modulated by spatially congruent conditions. However, when the right hand was stimulated on the right side of space, performance was affected where improvement in responses occurred when the visual cue was presented on the right side, whereas a visual stimulus near the opposite hand caused an interference [47]. In addition, to dissociate the effects on somatotopic and spatiotopic coordinates, the patient crossed their hands during unimodal tactile discriminations. The results indicated that tactile performance of the left hand was improved when it was crossed over into the right hemispaces, whereas no significant changes were found with the crossed over left hand into the right hemispaces. The results of the study suggested that from the bilateral PPC damage what was lost was the spatial selectivity of the visuotactile effects, the effects produced from the crossing over of the hands suggest a deficit in egocentric spatial coding with respect to the left tactile stimulus. These results indicate the critical role that the PPC has in the integration of both visual and tactile sensory information.

A case study was conducted on a patient with damage to their right primary visual cortex sustaining loss in their left visual hemifield, left hemianopia [13]. In this study, the researchers performed a visual detection task to compare abilities while varying the position of the patient's left arm in space. Variation in the presentation of visual stimuli in space included a baseline condition where the patient's left hand was on their lap, while other conditions presented visual stimuli in various reaching space locations, in locations well out of reach, and lastly a condition where the patient held a tennis racket in their hand in order to extend their reach. The results indicated that the patient's ability to detect visual stimuli in their left blind field was significantly improved with the extension of their contralesional arm into the blind

field [13]. This arm-mediated visual enhancement was restricted to visual stimuli being presented in reaching distance of the hand. Similar results have been reported in cortical activity of VIP and LIP regions in the monkey, regions related to bimodal visuotactile integration of the hand [1]. In humans, these bimodal neurons contain receptive fields that are located directly on the surface of the skin and extend outward into peripersonal space. Thus, any external stimuli approaching the body, for example the hand, will elicit responses in cells that are responsible for that particular receptive field. This recruitment of activity is present even without the person observing the object coming in closer proximity to the hand [15]. Together these findings indicate that the extension of the arm in space enhances visual processing in the presence of degraded visual information.

As mentioned earlier in the chapter, primary visual cortex projects onto several other areas of the brain. Thus, any loss of neurons in the primary visual cortex could be compensated for by the activity of other higher-order visual association areas that remain stimulated by visual input in the presence of damage to V1, such as in hemianopia. In fact, researchers proposed the existence of compensatory synaptic changes for the neuronal loss seen in primary visual cortex where some patients tend to exhibit blindsight. The hypothesis of blindsight is that subcortical pathways bypass the primary visual cortex and directly project onto secondary visual areas such as V5 (for motion detection), thalamus, brain stem, hypothalamus and/or the amygdala (for emotional response). In fact, this hypothesis was confirmed based on anatomical data acquired from fMRI studies where extrastriate activations in the damaged hemisphere of a hemianopic patient were observed during a forced-choice task known to elicit blindsight [48]. The results of this study support the notion of possible changes occurring at the synaptic level between spared and damaged visual networks based on clinical patients.

Another study investigated whether bimodal audiovisual interactions affect visual processing in patients with hemianopia, visuospatial attention deficit (i.e., neglect) and with both conditions presented visual stimuli in the impaired field in two conditions [14]. The patients underwent a visual detection task with unimodal (i.e., vision only) and cross-modal conditions, with the latter presenting a simultaneous auditory stimulus with the visual target that was either spatially congruent or incongruent. The results of the study showed that in patients with hemianopia or neglect, temporally congruent audiovisual stimuli improved the ability to consciously detect the contralesional visual stimuli in comparison with unimodal visual stimuli only. However, these results were not seen in patients that exhibited both hemianopia and neglect [14]. These findings can be explained by considering the functional characteristics of the multisensory neurons found within SC. As described previously, stimuli from multiple sensory modalities interact at close spatial proximity within the SC, which in turn, produces an enhancement of multisensory integration and responses relative to when stimuli are spatially disparate in the environment and SC receptive fields, and there is no integration. The lack of enhancement in patients with both hemianopia and neglect could be explained by the idea that an auditory cue alone can produce improvement in visual detection, but if both hemianopia and neglect are simultaneously present, the effect of the auditory cue may be inhibited. Also, when the lesion was within fronto-temporo-parietal areas (seen in patients with neglect) or to the occipital cortex (seen in patients with hemianopia), both visual and auditory stimuli were integrated. However, in patients with hemianopia

and neglect that have damage to both anatomical areas, the visual and auditory stimuli were not integrated [14].

Using functional magnetic resonance imaging (fMRI) and psychophysical methods, researchers have investigated action control and space perception in congenitally blind and sighted adults while performing active and passive hand movements without any visual feedback information. Congenital blindness is defined as an absence of vision from the time of birth and can be caused by a number of factors including environment, genetic or improper development [17]. In this study, participants were blindfolded in the fMRI scanner, while they performed kinesthetic guided hand movements in a delayed recognition task. Participants were asked to draw three different line patterns one after the other with a stylus, in their right hand, and maintain a mental representation of their hand movements across a variable delay, while their right hand rested. After the delay, a movement recognition trial was initiated where participants were asked to trace a single probe line pattern and press one of the two buttons with their left hand to indicate whether the last line pattern matched one of the stimulus items [16]. The results indicated that both groups did not differ in their task performance. Interestingly, however, kinesthetically guided hand movements activated the bilateral primary somatosensory cortex, left anterior intraparietal sulcus and the left superior parietal lobe [16]. As explained in the previous section on multisensory integration within the brain, this area is part of the dorsal stream pathway which is responsible for visually guided movements. The fact that this pathway was activated in congenitally blind patients indicates that the functions pertaining to this stream arise even in the absence of visual experience [16]. Sighted participants showed greater activation in areas that are responsible for tactile object localization and processing of spatial coordinates (i.e., precuneus) and pre-supplementary motor area associated with higher-order motor control in comparison with congenitally blind participants. This finding indicates that sighted participants have less experience with in nonvisual movement control creating higher task-related demands on these networks [16]. Unlike the sighted participants, congenitally blind participants rely heavily on their remaining senses to guide their movements, and this is evident in the findings where stronger activation in the extrastriate cortex and auditory cortex was present in congenitally blind participants while performing the kinesthetically guided hand movements. These coactivations imply heteromodal plasticity in the auditory cortex due to visual loss [16]. Taken together, these results suggest that the dorsal stream pathway is not only responsible for visual action directed movements but also for somatosensory guidance of movements and that spared sensory areas may manage the loss of function from the preexisting damaged areas.

In summary, there are a number of studies that indicate the integration of multisensory modalities within particular damaged brain regions. Damage to heteromodal association areas, such as the PPC, and independent unimodal sensory cortices, such as the occipital cortex, indicates how these areas are essential for multisensory integration and the clinical signs that occur postdamage to them, among other polysensory areas described above. Damage to either any of the heteromodal sensory areas or unimodal sensory areas reduces the effects of multisensory integration that give rise to holistic perception. However, spared multisensory networks have shown behavioral benefits by cross-modal plasticity, both at the cortical level and

synaptic level, where spared heteromodal areas attempt to reconnect the multisensory system via bypassing existing injured brain areas thus creating alternative routes in the system.

4. Plasticity research in the lab

In this section of the chapter, we will discuss some of the research on neuroplastic reorganization that we are currently conducting in our laboratory.

4.1. Leftward heightened lateralized fractional anisotropy measures in professional ballet dancers

In one study, we investigated the effects of long-term professional ballet training on tract fractional anisotropy (FA) lateralization and extent of tract FA [49]. Sensorimotor and cognitive training have been associated with altered tract properties as well as altered brain volume. Research indicates that experience and training modulate brain structural parameters including volume and FA [50]. FA is a diffusion tensor imaging (DTI) derived index of water molecule diffusion highly sensitive to the collective effect of microstructure properties, is a putative index of anatomical connectivity and thus is an indicator of microstructural tissue changes.

A single study involving professional ballet dancers and healthy age-matched controls studied whether brain plasticity in either reflex and/or perceptual vestibular processing had discrete neural basis [51]. The authors emphasized that studying brain plasticity while observing changes in gray matter (GM) and white matter (WM) within the vestibular system is of importance as both reflexive and perceptual processing can be assessed while investigating the potential effects of training. Here, the authors correlated GM density and WM microstructure in both groups while simultaneously measuring vestibular psychophysical parameters [51]. Results showed reduction in GM volume in the posterior bilateral vestibular cerebellum negatively correlated with years of dance experience where dancers demonstrated reduced GM volume relative to controls [51]. These results suggested that brain changes within the vestibular cerebellum as a function of dance training affect processing of vestibular perception [51]. Due to the fact that this study reported changes in global volume, our study aimed to investigate changes in FA specifically while secondarily observing global volume changes within dancers and healthy controls.

The effects of long-term ballet training characterized in terms of tract FA lateralization (calculated by `tbss_sym` script was used [52]), extent of tract FA and global volume have not been previously reported in existing literature and thus was the primary concern for this study. We localized tract FA lateralization and extent of tract FA in expert ballet dancers ($n_{male} = 9$, $M_{age} = 23.00$, $SD = 10.21$) relative to healthy controls ($n_{male} = 5$, $M_{age} = 24.89$, $SD = 1.70$) using DTI. The results indicated that dancers had greater leftward lateralization in the anterior thalamic radiation (ATR), whereas healthy controls had greater rightward lateralization and that dancers also had higher FA localized to the left cortical spinal tract (CST). Refer to **Table 1** for significantly lateralized FA voxels; p -values; and effect sizes (Cohen's d).

Voxels	Max X	Max Y	Max Z	Structures	<i>d</i>	<i>p</i> < 0.10
260	-15	-56	28	JHU: 11% left Ci; JH: 10% left CB WM	2.00	0.052
49	-17	22	41	HOC: 8% left SFG WM	1.89	0.079
48	-21	-55	39	JHU: 3% left ATR	1.83	0.038
29	-18	33	31	JHU: 3% left IFOF; 3% left ATR	2.25	0.059
25	-7	-67	34	JHU: 3% left Ci	2.34	0.069
5	-19	27	33	JHU: 3% left ATR; HOC: 4% WM of left SFG	1.19	0.099
1	-14	47	27	JHU: 29% left FMi; 3% left ATR	1.65	0.100

ATR = anterior thalamic radiation; CB = callosal body; Ci = cingulum; *d* = Cohen's *d*; FMi = forceps minor; IFOF = inferior fronto-occipital fasciculus; ILF = inferior longitudinal fasciculus; SFG = superior frontal gyrus; HCs = healthy controls. Percentages represent the probability identity of a structure as estimated by the HOC = Harvard-Oxford Cortical, JHU = JHU-ICBM White-Matter Tractography and JH = Juelich Histological Atlases; WM = white matter.

Table 1. MNI coordinates of dancer leftward FA asymmetry.

In addition to the FA lateralization found in our expert ballet dancers, we also showed that substantive variability in FA was shared with ballet training (32–35%) implicating a relatively large effect of training on tract alteration and enhanced tract conductivity. Overall, the results of our study imply that higher dancer FA reflects heightened axonal ability to communicate. The large percentages of variability shared by dancer years of training, and the structural metrics FA and global volume implicate a substantive impact of dance training on change in brain structure.

4.2. Functional and neural correlates of dance expertise

In a different study, we investigated structural and functional plasticity associated with dance expertise in a cross-sectional pilot study, comparing ballet dancers to healthy controls [53]. Using functional magnetic resonance imaging (fMRI), whole-brain functional activation maps of dancers and controls, while they engaged in motor imagery of dance movements, were compared. Brain plasticity has been studied through a wide variety of experimental paradigms. With respect to humans, one of the most influential models to study experience-related plasticity has been that of probing the structural and functional changes that occur as a result of motor skill learning and expertise [54, 55] through complex motor skills that take extensive time and practice to learn, focused on expert groups whose motor expertise

is commonly restricted to finger or single limb movements. Thus, there has been a noted lack of studies, particularly in the context of functional neuroimaging, that have investigated the plasticity associated with motor expertise in skills that require whole-body movements [56, 57]. An expert group that may be used to investigate questions on plasticity associated with expertise in complex whole-body movements is that of professional dancers, which were investigated within our current study.

To investigate the above structural and functional neural changes, we had both ($n = 17$) expert ballet dancers ($n_{male} = 11$, $M_{age} = 19.00$, $SD = 1.17$, dance experience $M = 11.25$, $SD = 3.21$ years) and ($n = 5$) controls ($n_{male} = 3$, $M_{age} = 26.00$, $SD = 10.07$, with no self-reported dance experience) perform motor imagery of dance movements while undergoing 8 min of functional neuroimaging. Due to dance being a highly complex motor and cognitive task, both groups were expected to recruit an extensive functional network that included motor-related cortical and subcortical areas, as well as frontoparietal regions during motor imagery [57]. We also investigated the structural correlates associated with dance expertise by comparing cortical thickness between dancers and controls. Various studies have reported motor learning and expertise to be associated with alterations in gray matter, with the common finding being an increase in gray matter in regions believed to be task relevant [58, 59]. Prior to the fMRI scanning procedure, participants received a 20–45 min tutorial on motor visualization, in which they learned the difference between visualizing movements from an internal (kinesthetic motor imagery) and external (visual motor imagery) perspective; this was done to ensure that the participants engaged in the motor imagery task from an internal perspective. Participants were then placed in the MRI scanner and were instructed to visualize themselves dancing to the music from an internal perspective. Scanning followed a block design, consisting of five 60-s-long dance imagery task blocks, interleaved by six 30-s long rest blocks [68].

Anatomically the results revealed that dancers exhibited greater cortical thickness in areas such as the inferior occipital gyrus, inferior frontal gyrus and superior temporal gyrus ($p < 0.01$). We also found years of dance training to be correlated with cortical thickness in various regions, including positive correlations being reported in the fusiform gyrus and parahippocampal gyrus ($p < 0.01$).

Functionally, controls were found to exhibit significantly greater activity in areas such as superior frontal and medial gyrus, anterior cingulate cortex, hippocampus, precuneus and left cerebellum during motor imagery of dance movements when compared to the expert dancers.

Dance training involves learning and correction of movements, thus leading to the consistent recruitment of regions that are related to functions such as motor control, timing and synchronization, visuomotor imagery, spatial transformations, and action observation and imitation; our results showed cortical differences between dancers and controls in brain regions whose functions are those listed above. It is possible that dancers, who are skilled imaginers due to their training extensively recruit regions such as the precuneus when they are engaged in visual imagery of dance movements. The precuneus in particular has been shown to be implicated in various types of mental imagery tasks, including in motor imagery, where it is believed to be involved in the processing of spatial relationships for body movement control.

These preliminary results suggest that dance expertise is associated with a functional and structural reorganization that corresponds to the reduced activity reported in other motor expertise groups.

Lastly, final studies in the lab investigate the impacts that dance intervention has on people with Parkinson's disease (PwPD) and healthy controls [60–66]. Dance has been shown to have positive effects on motor functioning in PwPD [65, 67], but less well understood are the neural effects and changes of dance on motor skills and nonmotor skills and associated brain activity observed within PwPD. Our aim was to examine the effects of dance on both motor and non-motor functioning and correlate these potential effects to onsite recordings of resting state electroencephalogram (rsEEG) alpha rhythm recordings, collected immediately before and after participation in a single dance class. Precisely, we aimed to examine and potentially construct brain-related plasticity mechanism(s) as a function of dance. We compared changes in motor (using the standardized MDS-UPDRS Part-III), non-motor (using PANAS-X) and rsEEG in both PwPD ($n = 17$; $N_{Males} = 12$, $M_{age} = 68.82$, $SD = 8.95$) and healthy controls ($n = 19$; $N_{Males} = 6$, $M_{age} = 52.78$, $SD = 17.30$) before (PRE) and after (POST) voluntary participation in a single 1.25-h dance class for the dance with Parkinson's program at Canada's National Ballet School (NBS) [60].

As expected, our preliminary results showed overall motor impairment improved after a single dance class in PwPD ($p < 0.001$). We also found differential effects of dance on negative and positive mood for both PwPD and HC ($p < 0.01$). We are in the continual process of data collection and correlating these behavioral effects with rsEEG recordings.

Thus far, these findings imply that dance promotes changes in motor functioning and affects through its overwhelming positivity, use of imagery, use of imagination, the presence of music and a sense of bonding through partner work. These results are of importance as its implications may allow researchers to better correlate and understand the positive behavioral and physiological benefits of dance for PD, and perhaps will aid in the implementation of dance as a form of rehabilitation for PwPD. Currently, we are leading a follow-up study examining these potential results from participation in multiple dance classes overtime. This is in conjunction with our ongoing rsEEG research and will provide a better understanding behind the observed neural changes seen in global alpha power. Further examination of whether the music being played at multiple frequencies would somehow influence these changes in neural alpha band rhythms observed after class is needed to help explain the increases in alpha power observed in our findings.

5. Conclusion and future directions

Overall, it seems reasonable to conclude that in the context of multisensory or unimodal damage or deprivation, the brain recognizes these losses in function and reorganizes to exploit the remaining intact unimodal or multimodal senses at its disposal. The presented set of reviewed literature on plasticity in multisensory networks may have important implications regarding teaching, learning and rehabilitation strategies in persons with damage to the above described

brain areas. These findings indicate that the brain is capable of plastic changes throughout the lifespan, and even in healthy individuals, the brain seems to be always changing as a function of training and expertise.

However, it is essential to make note that plasticity changes are intrinsic properties of the central nervous system, and thus, neural plastic changes do not always lead to a behavioral gain, but instead could be deleterious. Thus, more research should be focused on modulation of neural plasticity for optimal behavioral gain across all different types of individuals.

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