Speech-in-Noise Auditory Training and The Medial Olivocochlear Efferent System

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Abstract

The medial olivocochlear system is an important system that mediates efferent control over the outer hair cells of the cochlea (Boothalingam, Allan, Allen, & Purcell, 2019). It has been shown to play a role in varying aspects of hearing, such as signal-in-noise perception (Lilaonitkul & Guinan, 2009; Robertson, 2009; D. W. Smith & Keil, 2015). Importantly, the connection between speech-in-noise auditory training and the changes seen in speech-in-noise perception and how these relate to the medial olivocochlear system are fundamentally important (Bhattacharya, 2020; de Boer & Thornton, 2008).

This study aimed to build on a previous study by further evaluating the relationship between an auditory training programme and its effects on speech-in-noise perception and medial olivocochlear system activity (Bhattacharya, 2020). Additionally, this study aimed to evaluate the relationship between the changes in speech-in-noise perception following the auditory training programme and changes in medial olivocochlear activity to identify the mechanisms underlying these changes. Speech-in-noise perception was measured using Word Recognition-in-Noise and Quick Speech-in-Noise Tests, whereas medial olivocochlear system activity was measured through Distortion Product Otoacoustic Emissions and Auditory Brainstem Responses.

The findings of this study showed an improvement in speech-in-noise perception ability for participants who underwent the auditory training programme. Furthermore, there was a suppression identified in DPOAE and ABR wave I response amplitudes when measured with the presence of a medial olivocochlear reflex elicitor. However, the findings of this study did not reflect any significant changes in medial olivocochlear system activity following the training programme or any significant relationship between the changes in speech-in-noise perception and medial olivocochlear system activity.

This led to the conclusion that the improvements seen in speech-in-noise perception with auditory training could have been mediated by alternative mechanisms, or there could be an involvement of the medial olivocochlear system that was undetected. Importantly, this study identifies that perceptual improvements seen with auditory training and medial olivocochlear activity are a result of complex interconnections between multiple structures, and therefore, require further research to develop certainty regarding these mechanisms. These findings are generally consistent with the previous study on this topic (Bhattacharya, 2020).

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Glossary of Abbreviations

ABR – Auditory Brainstem Responses

AEP – Auditory Evoked Potentials

AN – Auditory Nerve

AVCN – Antero-Ventral Cochlear Nucleus

BBN – Broadband Noise

CAS – Contralateral Acoustic Stimulation

CF – Characteristic Frequency

CN – Cochlear Nucleus

dB – Decibels

dB SPL – Decibels Sound Pressure Level

DCN – Dorsal Cochlear Nucleus

DNLL – Dorsal Nucleus of the Lateral Lemniscus

DPOAE – Distortion Product Otoacoustic Emissions

Hz – Hertz

IAM – Internal Auditory Meatus

IC – Inferior Colliculus

IHCs – Inner Hair Cells

kHz – Kilohertz

LL – Lateral Lemniscus

MEM – Middle Ear Muscle

MET – Mechanoelectrical Transduction

MGB – Medial Geniculate Body

MNTB – Medial Nucleus of the Trapezoid Body

MOC – Medial Olivocochlear

MOCR – Medial Olivocochlear Reflex

MSO – Medial Superior Olive

OHCs – Outer Hair Cells

OAE – Otoacoustic Emissions

QuickSIN – Quick Speech-in-Noise

PVCN – Postero-Ventral Cochlear Nucleus

SIN – Speech-in-Noise

SNR – Signal-to-Noise Ratio

SOC – Superior Olivary Complex

VCN – Ventral Cochlear Nucleus

VNLL – Ventral Nucleus of the Lateral Lemniscus

VNTB – Ventral Nucleus of the Trapezoid Body

WINT – Word Recognition-in-Noise Test

WRT – Word Recognition Threshold

Introduction

The human auditory system is a complex system that allows for the perception of auditory stimuli. The auditory system is composed of multiple structures that play a role in the eventual perception of sounds (Alberti, 2006). These structures include sensory hair cells, the higher processing centers such as the primary auditory cortex, as well as the ascending and descending pathways that regulate and mediate important auditory information (Alberti, 2006). One specific efferent pathway that holds importance to this study is the medial olivocochlear (MOC) system. The MOC system innervates and regulates outer hair cell (OHC) activity (Boothalingam et al., 2019). These OHCs are responsible for mediating the cochlear active process, which is believed to amplify the incoming sound, aid in frequency discrimination and provide compressive non-linearity. These functions are important in maintaining the sensitivity of hearing and are fundamentally important in ensuring efficient and accurate perception of hearing (Hudspeth, 2014). The regulation of OHCs by the MOC system results in a reduction in the gain of the cochlear amplifier, which has been suggested to play an important role in hearing (Ciuman, 2010).

These roles include protection from overstimulation/ noise trauma, signal-in-noise perception and sound localization. Multiple studies have evaluated these roles in humans and animal models (Ciuman, 2010; de Boer, Thornton, & Krumbholz, 2012; Lopez-Poveda, 2018; Robertson, 2009). The findings of these studies are typically contradicting, which suggests the need for further research in this field. However, an important role of the MOC system that is focused on in this study is signal-in-noise perception. The MOC system is believed to improve signal-in-noise perception through varying mechanisms (Lilaonitkul & Guinan, 2009; Robertson, 2009; D. W. Smith & Keil, 2015). One such mechanism is termed anti-masking and is discussed in more depth in further sections (Robertson, 2009). Furthermore, to evaluate the role of the MOC system in hearing, it is vital to be able to measure MOC system activity. This can be measured by analyzing distortion product otoacoustic emissions (DPOAE) as well as auditory brainstem responses (ABRs) (Lilaonitkul & Guinan, 2009; Lopez-Poveda, 2018). The latter is fundamentally important to this study, as will be shown throughout this research.

There is also an important connection between signal-in-noise perception and auditory training. Auditory training is a process that an individual can go through which aims to train the individual's auditory skills to aid in improvement. Studies have shown there to be improvements in speech-in-noise (SIN) perception with auditory training (Besser & Launer, 2020; Ferguson, Henshaw, Clark, & Moore, 2012; Henshaw & Ferguson, 2013). Furthermore, the idea of plasticity is also fundamentally important. Studies have shown there to be plasticity in various auditory structures, including the MOC system. This is important as it shows how factors such as auditory training can result in changes in the processing of certain stimuli (Anderson & Kraus, 2013; Brown, Kujawa, & Liberman, 1998; Illing, Kraus, & Michler, 2000).

Previous research has been conducted that shows a relationship between SIN perception and auditory training relating to MOC system activity (de Boer & Thornton, 2008). However, the amount of research present in this field is scarce, with contradicting evidence in some studies (Bhattacharya, 2020; de Boer & Thornton, 2008; de Boer et al., 2012). This indicates the need for further research in this field to evaluate these relationships. An important idea to understand is the physiological mechanisms that underlie the improvements seen in SIN perception with auditory training and MOC system activity. A key study conducted by Bhattacharya (2020) found there to be an improvement in individuals' SIN perception ability with a SIN auditory training programme. This study also evaluated MOC system activity, which was shown to have no significant change over the training period. This study was also not able to reflect a relationship between SIN perception and MOC system activity (Bhattacharya, 2020). Therefore, this current study will build on this previous study by investigating whether additional measures of MOC activity (namely ABR wave I responses) are able to reflect changes in MOC system activity following the auditory training programme and if they are able to identify a relationship between MOC activity and the changes seen in SIN perception, indicating the mechanisms underlying these changes.

This study aims to evaluate the involvement and underlying connection of the medial olivocochlear reflex (MOCR) to training-induced changes in SIN perception. This study will evaluate whether changes seen following an auditory training programme can be explained and/or correlated to MOCR related activity as measured through varying assessments. Additionally, this study will also aim to identify whether the auditory training programme affects the activity of the MOCR and affects SIN perception ability. Therefore, this study will be building directly on the previous study conducted on this topic (Bhattacharya, 2020).

This study will begin by discussing and reviewing literature surrounding various topics on the auditory system. This will provide a background to the study conducted. This will be followed by the aims and hypotheses of this study, as well as the methodological approach used. The findings and results of this study will then be described, followed by an in-depth discussion of the findings. Finally, a summary and conclusion to this study will be discussed.

Review of Literature

1. Anatomy and Physiology of the Human Ear

The human ear is a fundamental organ responsible for hearing and balance. When considering the sense of hearing, the ear is responsible for collecting, detecting and analyzing sound, which is achieved through sensory transduction (Alberti, 2006). Sensory transduction is the process of converting sound-driven mechanical activation into electrochemical activation, which involves the central auditory nervous system. This process is essential to the perception of sound as it travels from the periphery to central brain structures (Alberti, 2006; Nava & Lasrado, 2021). The human ear can be separated into three substructures: the external, the middle and the inner ear (Nava & Lasrado, 2021).

1.1. Outer Ear

1.1.1. Anatomy

The outer or external ear consists of the pinna and the ear canal and possesses the primary function of collecting and delivering sound into the ear. The pinna is made up of cartilage and is covered by skin with multiple anatomical structures such as the helix and the tragus (Alberti, 2006). These structures are physiologically essential and aid in varying aspects of sound perception. The ear canal extends to the tympanic membrane and is comprised of cartilage and bone (Alberti, 2006; Nava & Lasrado, 2021). The outer two-thirds of the ear canal is made up of cartilage, whereas the inner one-third is comprised of bone. The outer portion of the ear canal contains sebaceous glands and sweat glands, which work to produce cerumen (ear wax) (Alberti, 2006). This, in combination with the tiny hairs found in this portion of the ear canal, primarily function as a protective mechanism particularly against foreign objects. The bony portion of the ear canal directs sound to the tympanic membrane, which can pass the sound into the middle ear system by being set into motion (Alberti, 2006). Therefore, through these anatomical structures of the outer ear, sound can be collected and delivered into the ear to eventually be processed and perceived.

1.1.2. Physiology

Aside from possessing the role of transmitting sound to the tympanic membrane, the outer ear also possesses additional physiologically important functions, including sound localization and amplification of sound pressure at the tympanic membrane (Alberti, 2006). As the sound is funneled from the pinna into the narrower ear canal, sounds are amplified particularly between 2000 Hz and 4000 Hz, which results in a greater sensitivity of the ear to these sounds. This is due to the resonance of the ear canal (Alberti, 2006). This is particularly important when considering speech as this frequency range (approximately) is identified to be important for speech signals. Furthermore, the outer ear also plays a vital role in localizing sounds in space (Alberti, 2006). Humans use a combination of binaural and monaural cues to localize sounds, which can become difficult if one set of cues is absent. This can be the case where binaural cues such as interaural intensity and interaural level differences are used solely and do not provide sufficient evidence into locating the source of the sound (Scharine, Letowski, & Sampson, 2009). This phenomenon is referred to as the cone of confusion, where binaural cues do not provide enough information about the source of the sound, particularly in the front-back axis and regarding the elevation of the sound in space. Therefore, the pinna and its contribution as part of the head-related transfer function can aid in localizing sounds (Scharine et al., 2009). This is achieved through varying representations and patterns of the incoming signal in the sound spectra because of the way the sound waves interact with the individual's pinna. These characteristics can be analyzed by the auditory system to aid in the localizing of sounds in space (Scharine et al., 2009).

1.2. *Middle Ear*

1.2.1. Anatomy

The middle ear is an air-filled cavity that is found between the tympanic membrane and the oval window, which is an opening to the inner ear (Alberti, 2006). The middle ear can be separated into two parts: the epitympanic recess and the tympanic cavity (Nava & Lasrado, 2021). The front end of the tympanic cavity has the opening of the Eustachian tube, which connects the middle ear to the back of the nose. This tube holds multiple functions, one such being to equalize the pressure between the middle ear space and the ambient environmental pressure (ear canal pressure) (Alberti, 2006). Within the mastoid process are mastoid air cells that are found posteriorly to the epitympanic recess and aid in some aspects of pressure changes within the middle ear space (Alberti, 2006). The middle ear also houses the ossicular chain. This is a chain of three small bones that aid in conducting and transferring sound from the tympanic membrane to the inner ear (George & Bordoni, 2021). These bones include the malleus, incus and stapes. The malleus is attached to the tympanic membrane on one end and articulates with the incus on the other, forming the incudo-malleolar joint, which in turn is attached to the stapes (George & Bordoni, 2021). The connection between the incus and stapes forms the incudo-stapedial joint. The stapes itself is embedded into the oval window, which provides an opening into the inner ear (George & Bordoni, 2021). The movement of these ossicles resulting from incoming sound sets into motion sound driven movement within the inner ear that eventually results in the perception of sound. Also present in the middle ear are multiple ligaments that hold these ossicles in place (George & Bordoni, 2021).

This is accompanied by the stapedius and tensor tympani muscles which innervate the stapes and malleus, respectively. These are believed to play a protective role against loud sounds by increasing the stiffness in the ossicular chain and attenuating the incoming sound so that it does not cause damage to the ear (Mukerji, Windsor, & Lee, 2010). The Middle Ear Muscle (MEM) reflex is believed to work through ascending information in the auditory nerve synapsing with interneurons in the ventral cochlear nucleus (VCN). These interneurons (either directly or indirectly) project onto MEM reflex motoneurons found near the motor nuclei of the facial or trigeminal nerve (Mukerji et al., 2010). From here, neurons project and innervate the stapedius and tensor tympani muscles. Both crossed and uncrossed pathways exist where the ipsilateral VCN can project to both ipsilateral and contralateral motor nuclei of the facial or trigeminal nerve (Mukerji et al., 2010).

*1.2.2. **Physiology***

Physiologically an important function the middle ear possesses is that of acting as a transformer. Due to the impedance difference between the air found outside the ear and the fluid in the inner ear, the sound pressure without the middle ear would not have sufficient energy to effectively move the fluids within the inner ear (Qing & Mao-li, 2009). This could approximately result in a 30-40 dB hearing loss. Therefore, the transformer function provided by the middle ear is essential to the perception of sound (Qing & Mao-li, 2009). This is achieved through multiple factors, such as the difference in surface area between the tympanic membrane and the oval window (larger surface area of the tympanic membrane compared to the oval window) and the lever-action that is produced by the ossicles, which leads to an amplification of sound pressure (Qing & Mao-li, 2009). This allows for the sound to effectively be transmitted into the inner ear.

Similarly to the outer ear, the middle ear also provides resonance at certain frequencies, which is believed in the literature to be at approximately 1 kHz (Homma, Du, Shimizu, & Puria, 2009). This is in part due to the stiffness and mass of the tympanic membrane as well as the ossicular chain and can affect how certain frequencies of sounds are transferred (Sundar, Chowdhury, & Kamarthi, 2021).

Furthermore, another important physiological role of the middle ear is the MEM reflex or acoustic (stapedial) reflex (ASR). As explained above, the MEM reflex is activated when loud sounds are detected by the auditory system (Mukerji et al., 2010). These are believed to be sounds approximately 70-90 dB above the hearing threshold of an individual (Sundar et al., 2021). Although the tensor tympani muscle is believed to be associated with this reflex, the stapedius muscle is the dominant mediator in humans, whereas the tensor tympani muscle is potentially involved with other roles such as the startle response. The ASR is believed to play a protective role in humans by preventing damage related to intense acoustic stimuli (Mukerji et al., 2010). It is also believed to be important in speech discrimination by preventing low frequencies (typically found in background noise) to mask speech signals. Lastly, the ASR is noted to be important in preventing loud acoustic stimuli originating from the individual from being disturbing or damaging. This can include bodily functions such as speaking (Mukerji et al., 2010).

However, studies have shown the function of the ASR to be restrictive in instances where the loud acoustic stimulus is prolonged for approximately ten seconds or more (Mukerji et al., 2010; Ünsal et al., 2016; Xu, Cheatham, & Siegel, 2015). This is particularly relevant to this research as studies have identified a potential overlap with the ASR and medial olivocochlear reflex (MOCR) exerting suppressive effects on otoacoustic emissions (OAEs) with contralateral broadband noise stimulation. However, ASR effects are believed to exist during the early durations of the stimulus as compared to the MOCR, which is considered in this research (Xu et al., 2015).

1.3. Inner Ear

1.3.1. Anatomy of the Cochlea

Housed within the temporal bone is the bony labyrinth, which works to protect the structures that are key for our sense of balance and hearing (Alberti, 2006; Musiek & Baran, 2017b). The bony labyrinth is made up of the cochlea, semi-circular canals and the vestibule. Found within are membranous structures such as the cochlear duct, semi-circular ducts and the utricle and saccule (Bruss & Shohet, 2021; Musiek & Baran, 2017b). This is referred to as the membranous labyrinth and also contains fluids necessary for sensory transduction. Aside from the cochlea, the structures named are key for providing information about the angular, linear and static position of the head and help maintain balance (Alberti, 2006; Bruss & Shohet, 2021).

The cochlea is found in the petrous area of the temporal bone and is located medially to the middle ear (Musiek & Baran, 2017b). There are two openings into the inner ear; one such opening is the oval window which opens into the scala vestibuli and in which movement of the stapes sets into motion the perilymph, which is a type of fluid found within the cochlea. The other opening is the round window which opens into the scala tympani and is covered by a fibrous membrane and works to move at the same time but in the opposite direction as the oval window (Alberti, 2006; Musiek & Baran, 2017b). This allows for the fluids within the cochlea to be displaced to allow for sensory transduction to occur, which would otherwise be difficult as the fluid could be in ways incompressible (Alberti, 2006). The cochlea has a snail shell shape with approximately 2.2 to 2.9 turns in humans. Centrally to the cochlea (cochlea wraps around the modiolus) is a structure named the modiolus that houses blood vessels and nerve fibres (Musiek & Baran, 2017b). The osseous spiral lamina is a structure that also wraps around the modiolus from the base to the apex of the cochlea. The lower shelf of the spiral lamina supports and acts as a point for the basilar membrane and the cochlear duct to attach to. Whereas the upper shelf acts as a support and attachment point for the tectorial membrane (Musiek & Baran, 2017b).

Within the cochlea are three compartments, the scala vestibuli, scala media (cochlear duct) and the scala tympani. The cochlear duct is separated from the other compartments by two structures known as the basilar membrane and the Reissner's membrane (Alberti, 2006; Musiek & Baran, 2017b). The basilar membrane seperates the cochlear duct from the scala tympani and is connected to the spiral ligament found on the outer wall of the bony cochlea and to the osseous spiral lamina. The Reissner's membrane seperates the cochlear duct from the scala vestibuli (Musiek & Baran, 2017b). Although these compartments are separated, the scala tympani and scala vestibuli interact at the helicotrema. The fluids found within these compartments also differ (Alberti, 2006). The scala vestibuli and scala tympani house perilymph, whereas the scala media contains endolymph. Perilymph is low in potassium (K+) and high in sodium (Na+) compared to endolymph which is high in K+ and low in Na+ (Bruss & Shohet, 2021; Musiek & Baran, 2017b). This is physiologically important as the K+ is important for sensory transduction in the hair cells, and therefore, is named the endocochlear potential. Research suggests that the stria vascularis is the main contributor of the K+ concentration found in the endolymph (Musiek & Baran, 2017b).

1.3.1.1. ***<u>The Organ of Corti</u>***

The organ of Corti is a very important sensory structure as it contains the sensory cells and nerve fibres essential for sensory transduction. The organ of Corti is found on the basilar membrane, with the tectorial membrane being found above it (Musiek & Baran, 2017b). The tectorial membrane is an important structure as it is believed to interact with the sensory hair cells (particularly the outer hair cells (OHCs)) and is important when considering sensory transduction (Musiek & Baran, 2017b).

However, it is believed that inner hair cells (IHCs) do not interact with the tectorial membrane and operate through a different manner. It is also important to note that the stiffness of the basilar membrane decreases from the base to the apex of the cochlea, whereas the mass increases (Musiek & Baran, 2017b). This is physiologically important for factors such as frequency coding. The organ of Corti also contains a structure known as the reticular lamina, which forms a barrier above the sensory and supporting cells from the endolymph (Musiek & Baran, 2017b). The stereocilia found on the hair cells are believed to penetrate this barrier to be situated in this endolymph, whereas the body of these hair cells is situated in perilymph. Also found within the organ of Corti are supporting cells such as Deiters' cells (Musiek & Baran, 2017b).

1.3.1.2. __Hair Cells__

There are two types of sensory hair cells found within the organ of Corti. These are OHCs and IHCs. There are approximately 3,500 IHCs in humans which are arranged in a single row spanning the length of the cochlea (Musiek & Baran, 2017b). This differs from OHCs which are arranged in rows of three to five. There are approximately 12,000 OHCs in humans. These hair cells have afferent and efferent innervation in the base and stereocilia at the top (Musiek & Baran, 2017b). These stereocilia are arranged in three rows graded in length on the OHCs shaped in a W pattern. Research also suggests there to be a greater number of stereocilia on each OHC towards the base of the cochlea (approximately 150) compared to the apex (approximately 50) (Musiek & Baran, 2017b). The OHCs also contain contractile proteins such as prestin, which are essential for the function of the OHCs relating to electromotility. Contrastingly, the stereocilia found on the IHCs are flat and U-shaped (Musiek & Baran, 2017b). Furthermore, there is also a greater number of stereocilia on each IHC found at the apex (approximately 100) compared to the base (approximately 50-70) (Musiek & Baran, 2017b). Located at the tip of the stereocilia are mechanoelectrical transduction (MET) channels and are connected to tip link filaments (Qiu & Müller, 2018). These tip links connect one stereocilium to another and result in the opening or closing of these MET channels when there is a deflection of the stereocilia in a certain direction. This, in turn, allows for the flow of K+ ions, which is important for sensory transduction (Musiek & Baran, 2017b; Qiu & Müller, 2018).

1.3.1.3. __Afferent Cochlear Innervation__

The auditory nerve (AN) is a key component along the sound transmission and perception pathway. The AN carries information about the timing, frequency and intensity of sound from the cochlea to central brain structures and is essential in the accurate perception of sound (Musiek & Baran, 2017c). The tonotopic arrangement of the AN fibers allows for frequency information to be accurately coded, and therefore, perceived. These AN fibers connect to the hair cells at the terminal buttons and make their way through the habenula perforate to the spiral ganglion, which is where the cell bodies of the AN fibers reside (Musiek & Baran, 2017c). From here, the fibers go through the internal auditory meatus (IAM) to central brain structures. These AN fibers can be separated into type I and type II fibers (Musiek & Baran, 2017c). Type I fibers are believed to account for approximately 90-95% of total AN fibers and primarily innervate the IHCs. The pattern of innervation is referred to as divergent as one IHC is typically innervated by multiple type I fibres (Musiek & Baran, 2017c). Research has suggested for these fibers to vary in properties such as spontaneous firing rates, which can be an important factor when considering intensity coding and loudness perception, a concept known as dynamic range stitching (Wen, Wang, Dean, & Delgutte, 2009). Contrastingly, type II AN fibres account for approximately 5-10% of total AN fibers and primarily innervate OHCs. The pattern of innervation for these fibers is convergent as typically multiple OHCs can be innervated by one type II fiber (Musiek & Baran, 2017c). Research has also suggested a difference in myelination between these two types of AN fibers. This indicates that the primary function of type I fibers is to carry sensory information to the central nervous system to allow for the perception of sound (Musiek & Baran, 2017c). Contrastingly, type II fibres typically carry information regarding the state of the cells and information regarding the active process (Weisz, Glowatzki, & Fuchs, 2009). Importantly, research has suggested that these type II AN fibres potentially play a role in providing sensory input mediating the MOC reflex, which is important for this research. Although this is debated in the literature, compelling evidence supporting this has been found (Froud et al., 2015).

The synapse between the hair cells and AN fibers is referred to as a ribbon synapse. This is due to a high-density ribbon structure that works to have numerous vesicles containing neurotransmitters (NT) in them (Glowatzki, Grant, & Fuchs, 2008; Moser, Brandt, & Lysakowski, 2006). The predominant NT involved in this process is glutamate. These ribbon structures can be found in the presynaptic membrane in a region known as the active zone, whereas the postsynaptic receptors can be found on the AN fibers across the synaptic cleft (Glowatzki et al., 2008; Moser et al., 2006). The ribbon structure ensures quick and sufficient release of NTs across the synaptic cleft onto the post-synaptic receptors to ensure accurate coding and perception of sound can be achieved. This is also important for temporal coding as there can be minimal intervals between varying sound stimuli (Glowatzki et al., 2008; Moser et al., 2006).

1.3.2. *Physiology of the Cochlea*

1.3.2.1. *The Travelling Wave and Passive Mechanics*

When considering the physiology of the cochlea, it is essential to understand the travelling wave and passive mechanic concepts that underlie the coding of sound information. The movement of the stapes at the oval window results in a displacement of cochlear fluids (Musiek & Baran, 2017a). This results in a pressure difference between the scala vestibuli and the scala tympani as the displacement travels the whole length of the cochlea. This difference results in the movement of the basilar membrane upon which sits the organ of Corti (Musiek & Baran, 2017a). This explains the fundamental principle behind the travelling wave (Manley, 2018). The stiffness of the basilar membrane also plays an important role in this concept. The basilar membrane is stiffer at the basal end compared to the apical end (Musiek & Baran, 2017a). This means that different frequencies of sound have different travelling waves that are maximally displaced at different points along the basilar membrane (Manley, 2018). This is typically found with higher frequencies being maximally displaced towards the base and lower frequencies being displaced towards the apex of the cochlea (Alberti, 2006; Musiek & Baran, 2017a).

Frequency and intensity discrimination associated with the travelling wave is also an important concept. It is believed that frequency coding can occur through two ways (Oxenham, 2013b). One of these theories is referred to as temporal coding. This is believed to occur through coding of the oscillation rate of the basilar membrane as a result of the incoming sound (Musiek & Baran, 2017a). However, this is limited to lower frequencies of sound due to limitations by the refractory period of the auditory nerve fibers, meaning it cannot keep up with the oscillations of high frequencies of sound. For these high-frequency sounds, the theory of place coding is important (Oxenham, 2013b). This explains how, due to the characteristics of the basilar membrane including its width and stiffness, the travelling wave reaches a point of resonance specific to the frequency of sound, resulting in an enhanced movement of the basilar membrane. This is believed to be the primary mechanism by which frequency is coded in the peripheral auditory system (Musiek & Baran, 2017a; Oxenham, 2013b).

Importantly, Georg von Békésy's (1960) findings around the travelling wave identified passive mechanics in the cochlea. These indicated linearity in the cochlear mechanics (Manley, 2018). This is because the envelope of displacement along the basilar membrane would be larger with higher intensity sounds. However, these findings did not identify the reasoning behind accurate frequency discrimination in these instances or generally (Musiek & Baran, 2017a). This is because the frequency discrimination was more finely tuned than explained by the passive mechanics shown by the travelling wave alone (Manley, 2018; Musiek & Baran, 2017a). This is where the concept of the cochlear active process is important and is discussed in 1.3.2.4.

1.3.2.2. ***Mechanoelectrical Transduction***

The movement of the basilar membrane upwards (rarefaction waves) and downwards (condensation waves) as a result of stapes displacement means that there is corresponding movement and deflection of the stereocilia found on the hair cells. A rarefaction wave results in the shearing of the stereocilia found on the OHCs with the tectorial membrane, whereas the IHCs are believed to operate slightly differently (Musiek & Baran, 2017a). It is believed that the flow of fluid through the subtectorial space allows for the deflection of stereocilia found on the IHCs. This is because the IHCs are not believed to be in contact with the tectorial membrane. Research has also suggested that IHC stereocilia could also potentially be in contact with a structure known as the Hensen's stripe, which causes the deflection of their stereocilia (Musiek & Baran, 2017a).

A deflection of these stereocilia towards the site of activation (towards the tallest stereocilia) will result in tension between the tip-links and opening of the MET channels. This opening will allow for an influx of Ca2+ and K+ ions into the hair cells resulting in depolarization and ultimate release of NT, resulting in an action potential (AP) along the AN fibers (Hudspeth, 2005; Musiek & Baran, 2017a). The flow of these ions is due to a gradient that is established across the outside and inside of the hair cells. The resting potential outside the hair cell is approximately +80 mV which is relatively greater than the -45 mV to -60 mV found within the hair cell (McPherson, 2018). This gradient allows for the flow of K+ ions into the hair cells upon opening of these MET channels. This depolarization then opens voltage-gated Ca2+ channels, which is important for the release of NT at the base of the hair cell (Hudspeth, 2005; McPherson, 2018). When these hair cells are deflected in the opposite direction, the tension in these tip-links is reduced, resulting in the closure of these MET channels. This results in hyperpolarization. Research suggests that at rest there are a few channels that remain open and ensure a resting discharge exists (Hudspeth, 2005; Musiek & Baran, 2017a).

Although the general mechanism by which these MET channels work is the same for IHCs and OHCs, some properties of these differing hair cells vary. This is especially true for OHCs (Musiek & Baran, 2017a). Aside from providing some sensory input, OHCs play an important role as cochlear amplifiers. Research has shown for OHCs to contract and elongate upon stimulation (Brownell, 2017; Salvi, Eddins, & Wang, 2017). This works to produce a greater displacement and finer tuning of the basilar movement aiding with frequency discrimination (Brownell, 2017). This is believed to operate more so at lower intensities compared to higher intensities of sound. Research suggests that without OHCs, the IHCs could become insensitive and only become activated with at least 50-60 dB of sound (Musiek & Baran, 2017a). The motor protein prestin is believed to mediate the contraction and elongation seen with OHCs. Cl- anions are believed to be important in regulating this response (Salvi et al., 2017). Upon depolarization, the anion is believed to move to the cytoplasmic side of the prestin protein, resulting in contraction of the protein, and therefore, the hair cell. Contrastingly, the movement of the Cl- anion to the extracellular side results in elongation. This allows for the function of the OHC to be carried out (Salvi et al., 2017).

1.3.2.3. __Auditory Nerve Response__

The auditory nerve carries information from the cochlea to central brain structures. It carries important information about the frequency, intensity and timing of sound. The information presented is largely agreed upon in literature regarding the functional aspects of the auditory nerve (Musiek & Baran, 2017c). Eventual perception of the auditory signal is achieved through action potentials being propagated along the auditory nerve fibers through multiple brain structures, until eventually the information is conveyed to the auditory cortex. The coding of information such as intensity and frequency is achieved through careful representation along the pathway (Musiek & Baran, 2017c).

Similarly to the hair cells and specific locations along the basilar membrane, AN fibers each have the lowest threshold for a certain frequency known as the characteristic frequency (CF) that they best respond to. However, increasing the intensity of the stimulus can, in some cases, mean that other frequencies aside from the CF of an AN fiber can be responded to as well (Musiek & Baran, 2017c). Additionally, it is also important to understand the tonotopic arrangement of the AN fibers. Running through the center of the AN is believed to be fibers innervating hair cells in the apex of the cochlea, and each layer of AN fibers outside of this center is believed to innervate more higher frequency areas of the cochlea, moving to the base (Musiek & Baran, 2017c). This tonotopic arrangement is maintained throughout most components of the auditory pathway aiding in frequency discrimination (Langers & van Dijk, 2012).

One way frequency coding can occur is through place coding. This is where specific areas of the basilar membrane represent specific frequencies for which the corresponding AN fibers then carry information regarding that frequency (Musiek & Baran, 2017c; Oxenham, 2013b). This also uses firing rates to establish frequency where AN fibers corresponding to that specific frequency of sound will fire maximally, whereas the fibers surrounding this area will fire at a different level. These different firing responses can then provide information about the frequency of sound (Musiek &

Baran, 2017c). Another way frequency coding occurs is through temporal coding. This is where neural activity is time-locked to the incoming acoustic signal, a concept known as phase-locking (Oxenham, 2013b). However, research argues the ability of AN fibers to phase-lock to high frequencies of sound. Although there is some evidence of AN fibers being able to phase-lock for frequencies up to 5000 Hz, the general consensus is that there are not many fibers that are able to do this (Musiek & Baran, 2017c). Therefore, for high-frequency sounds, it is believed that the volley principle comes into effect. This is where varying AN fibers are able to fire at varying intervals to provide information about higher frequency sounds that would otherwise exceed one AN fibers firing rate. Therefore, research suggests that frequency coding is a result of both place and temporal coding, allowing for the fine frequency discrimination that is achieved (Musiek & Baran, 2017c).

Intensity coding is achieved through varying spontaneous rate fibers that innervate the IHCs. Research suggests for there to be low and high threshold fibers that have high and low spontaneous rates of firing, respectively (Barbour, 2011). As the intensity of the sound stimulus increases, the low threshold fibers fire till they become saturated. From here, the high threshold fibers take over and begin firing (Musiek & Baran, 2017c). Varying fibers with different spontaneous rates and thresholds can take over at different intensities. The varying activity in these fibers can, as a result, code for intensities of sound (Musiek & Baran, 2017c). Research has also suggested the role of adaptation to be important in intensity coding. This is where the AN fibers are able to adapt to the ambient conditions to preserve the dynamic range of hearing (Barbour, 2011). This is also believed to be important in intensity coding. Some research has also highlighted an increase in the number of fibers and the amount of firing undergone by AN fibers as a basis for intensity coding (Ray & Doetsch, 1990; Viemeister, 1988). Although this may be true in some instances, a contradictory study indicated that the number of neighbouring AN fibers that are firing may not, in fact, code for the intensity of sound (McGee & Walsh, 2005). However, the amount of evidence supporting these claims can be considered limited as there is other research highlighting a general agreement in the literature supporting firing rates and total recruitment to also play a role in the coding of intensity (Ray & Doetsch, 1990; Viemeister, 1988).

1.3.2.4. Cochlear Active Process

The cochlear active process (also termed cochlear amplifier) has been an area researched extensively in the literature. It explains a process by which there is an amplification of the movements and vibrations in the basilar membrane that work to provide different functions (Davis, 1983). This amplification has also been noted to overcome the resistance provided by the fluids of the cochlea, further aiding in the sensitivity of hearing (Hudspeth, 2014). The cells that are believed to mediate these effects are OHCs. Due to the electromotility carried out by OHCs, they are able to mediate these amplifications that are seen in the basilar membrane, which aids in hearing sensitivity (Hudspeth, 2014). These OHCs contract upon intracellular depolarization and elongate with hyperpolarization, which mediates this active process function. Contraction results in the basilar membrane being 'pulled further up', which aids in the amplification of the incoming signal (Hudspeth, 2014; Musiek & Baran, 2017a). This cochlear amplifier is believed to improve hearing sensitivity by approximately 40 dB. This further contradicts earlier evidence which suggested a sole passive process in the cochlea, which would not provide the sensitivity to hear low-level sounds (Choi, 2010).

The cochlear active process is believed to amplify the incoming sound, aid in frequency discrimination and provide compressive non-linearity. The amplification of the incoming sound through the movement of the basilar membrane is important to overcome the resistance provided by the fluids of the cochlea (Hudspeth, 2014). Research has shown for the sensitivity of hearing to be less than 1% of normal when there is damage to the cochlea and this active process. Secondly, this active process is fundamental in frequency selectivity and neural tuning curves (Hudspeth, 2014). The activity of the OHCs is believed to increase the movement of the basilar membrane at the CF of the incoming signal. This means that the IHCs that are then stimulated as a result are those that are finely tuned to the specific frequency of sound. This aids in frequency selectivity and discrimination (Davis, 1983; Musiek & Baran, 2017a). Lastly, another important function of the cochlear amplifier is to provide compressive non-linearity (Hudspeth, 2014). Non-linearity in the cochlea indicates that for a given incoming signal, the amount of movement seen at the basilar membrane is not directly proportional to the incoming sound (Musiek & Baran, 2017a; Nizami, 2013). This is believed to provide a protective mechanism to the hearing structures (Musiek & Baran, 2017a). In a linear system, a loud incoming stimulus could result in excessive movement of the basilar membrane, which could damage important structures. Therefore, indicating the importance of non-linearity (Musiek & Baran, 2017a). This works by low-intensity sounds being amplified more through the function of the active process compared to higher-intensity stimuli. These higher-intensity stimuli undergo compression. This works to maintain hearing sensitivity (Musiek & Baran, 2017a; Nizami, 2013). Some research has also indicated a connection between basilar membrane displacement and the recruitment of varying AN fibers, whereby the amplitude of basilar membrane displacement mediates which AN fibers fire (i.e. low-spontaneous and/ or high spontaneous fibers) (Yates, 1990). This further shows the importance of the cochlear active process.

1.3.2.5. ***Otoacoustic Emissions***

An important concept that is explored and used in this research is that of OAEs. OAEs are sounds that are generated from the cochlea, typically as a result of specific stimulation (Kemp, 2002). These sounds travel back out from the cochlea and the middle ear and can be detected by microphones placed in the external auditory canal. These OAEs are believed to originate from the cochlear active process explained above and involve the OHCs (Kemp, 2002). As these OAEs originate from OHCs in the inner ear and travel back through the middle ear. These can be affected by pathologies affecting these compartments of the ear. This can include pathologies such as otitis media with effusion which affects the transmission of these OAEs through the middle ear (Thakur et al., 2013). OAEs are widely used in clinical test batteries and can provide valuable information regarding an individual's auditory system when used in conjunction with other tests. OAEs are also very valuable as a research tool and aid in measuring different aspects of the auditory system (Kemp, 2002).

OAEs can be separated into spontaneous (SOAEs) and evoked (EOAEs) emissions. SOAEs are believed to arise from linear reflections, whereas EOAEs are believed to arise from a combination of reflection and distortion emissions, the latter of which is a form of nonlinear distortion (Shera & Guinan Jr., 1999). Under the category of EOAEs are different types of evoked emissions that can be found; these include transient evoked OAEs (TEOAEs), distortion product OAEs (DPOAEs) and stimulus frequency OAEs (SFOAEs). These differ based on the stimulus used to evoke these OAEs. The main focus of this section will be DPOAEs as this was used in this research (Shera & Guinan Jr., 1999).

DPOAEs are generated when two tones are played into the ear of an individual. These two tones have CFs that overlap on the basilar membrane. The non-linearity generated by the cochlear amplifier creates a distortion product at this overlapping point (Shera & Guinan Jr., 1999). This sound that is created travels back through the middle ear and can be measured in the ear canal. Alongside this, some of this sound also travels along the basilar membrane to its CF and can be heard by the individual (Kemp, 2002; Shera & Guinan Jr., 1999). This travelling of sound along the basilar membrane results in some reflections to be created as a result of nearby impedance perturbations. These also travel back out through the middle ear and in combination with the distortion source can combine to produce the DPOAE that is recorded in the ear canal (Shera & Guinan Jr., 1999). Having said so, of importance are the parameters used when measuring DPOAEs. Therefore, it is important to use the correct frequency separation ratio between the two frequencies (f1 and f2) as well as the level of the primaries to ensure DPOAEs can be measured (Caroline Abdala & Visser-Dumont, 2001). Research suggests that primaries within the range of 55-65 dB SPL provide the greatest accuracy when undertaking these measures. Primary levels that are louder may not, in fact, reflect cochlear amplifier activity, and therefore, may not be accurate (Caroline Abdala & Visser-Dumont, 2001). Furthermore, a frequency separation ratio of 1.2 and a level difference of 10 dB between the two tones is believed to provide the largest amplitudes of DPOAEs. This can be important, especially when undertaking research, as changes can be minimal (Caroline Abdala & Visser-Dumont, 2001). This information was considered when carrying out this research.

Of relevance to this research is the efferent control exhibited by the MOC system on these OHCs, and therefore, the OAEs. This, in turn, provides a measure of the MOC system and the MOCR, which is used in this research (Kemp, 2002; Marshall et al., 2014). This is discussed further in section 3.2.1.2.

2. Auditory Masking

Our normal daily environment exposes individuals to complex listening situations. In most instances, our listening environment is made up of multiple streams of sound, which can encompass both meaningful sounds such as speech stimuli and unwanted sounds such as background noise (Oxenham, 2013a). Therefore, the auditory system must play a role in coding for and separating the important parts of an incoming signal from the unwanted noise. Research has suggested that an important mediator of this is the frequency analysis carried out by the auditory system (Oxenham, 2013a). Having said so, this, in some instances can be difficult due to the amount of noise present in a particular environment. This can be referred to as masking and works to raise thresholds of one sound due to the occurrence of another sound (Oxenham, 2013a). This can make hearing difficult in noisy situations and is a fundamental idea on which this research is based. Of relevance is the idea of using clinical masking to test and evaluate an individual’s ability to perceive SIN. Although this does not provide a direct correlation to the experience of listening in a noisy background, it provides some information that can be useful. When considering auditory masking, this general area can be divided into peripheral masking and central masking. Peripheral masking is any masking that is a result of processes in peripheral auditory structures, whereas central masking refers to physiological processes in central auditory structures (Oxenham, 2013a; Zwislocki, 1971).

2.1. Peripheral Masking

Research conducted by Fletcher (1940) investigated masking and how the frequency components of a masking stimulus affect the stimulus of interest. It has been shown that white noise, which contains energy across a range of frequencies, is able to mask a pure tone stimulus (Yacullo, 2014). However, the research carried out by Fletcher (1940) worked to identify what components of a masking stimulus are important in effecting a particular stimulus of a certain frequency. The findings identified that a narrow band of noise around the frequency that is to be masked is sufficient to mask the stimulus (Moore, 2008; Yacullo, 2014). For speech stimuli, a speech spectrum noise is used. This noise is a broadband stimulus that is filtered to simulate the long-term average spectrum of speech. Due to this reason, speech spectrum noise is more efficient as a masker when compared to white noise (Yacullo, 2014). This outlines the fundamental principles used in clinical masking.

There are also varying mechanisms that have been outlined in the literature that are believed to mediate the effects of masking. One such mechanism is believed to be excitatory masking (Rodríguez et al., 2010). This explains how masking is mediated through the effects of AN fibers and their firing rates. Research explains that a masking stimulus is believed to cause elevations in the firing of AN fibers corresponding to the specific frequency of interest (Delgutte, 1990; Rodríguez et al., 2010). When a signal of interest is played alongside the masking stimulus, this is not able to effectively stimulate the AN fibers by overcoming the discharge rate that is a result of the masking stimulus (Delgutte, 1990; Rodríguez et al., 2010). Another mechanism mediating the masking effects is believed to be suppression. This mechanism works by raising the threshold, meaning that the stimulus of interest can be masked by the masker (Rodríguez et al., 2010). This has been shown through two-tone suppression, whereby presenting two tones together can provide masking effects (Recio-Spinoso, Cooper, Recio-Spinoso, & Cooper, 2013). This requires the presentation of one tone which is not within the CF range of the stimulus of interest (Recio-Spinoso et al., 2013; Rodríguez et al., 2010). However, the envelope of activation of this masking tone is able to overlap with that of the CF of the stimulus of interest. This results in increased activation of OHCs, which are known to saturate at high or increased intensity levels (Delgutte, 1990; Recio-Spinoso et al., 2013; Rodríguez et al., 2010). The result of this is a reduced sensitivity to incoming signals within the certain frequency range resulting in masking (Recio-Spinoso et al., 2013; Rodríguez et al., 2010). These mechanisms are believed to underlie simultaneous masking (Delgutte, 1990; Rodríguez et al., 2010). Though the literature argues that both mechanisms can be involved in masking effects, some evidence suggests varying mechanisms depending on the frequency of the masker in relation to the CF of the stimulus of interest (Delgutte, 1990). Delgutte (1990) identified that masking could potentially be excitatory with masking frequencies near and below the CF and suppressive when masking frequencies are above or below the CF of the stimulus of interest. Though, evidence supporting these claims is typically scarce.

2.2. Central Masking

Masking can also occur as a result of physiological processes in central brain structures as compared to peripheral masking. Central masking can be seen when a masking stimulus presented to the ipsilateral ear can mask a stimulus in the contralateral ear (Zwislocki, 1971). Although this can occur because of 'cross-over' whereby the masking stimulus is at a high-intensity level such that it crosses over through varying mechanisms to effects responses in the contralateral ear. Central masking is believed to operate in situations aside from this (Yacullo, 2014). Research has suggested that the antero-ventral cochlear nucleus (AVCN) and its projections to the medial superior olive (MSO) are significant in mediating the effects of central masking (Zwislocki, 1971).

3. Auditory Pathways

An essential part of the auditory system are the auditory pathways that convey important sensory information from the periphery to central brain structures to allow for the perception of sound. These pathways involve multiple structures which relay information to one another and are known as the afferent pathway (Hackney, 1987). Another key component of the auditory pathway is the efferent pathways. These are pathways with descending innervation that can regulate multiple aspects of the auditory system (Ciuman, 2010). These pathways are believed to be important in factors such as protection of hearing and mediation of signal to noise ratio. Another important function of this pathway is to regulate and control the OHCs, which can be important in some instances. An important component of the efferent pathway is the MSO and its related MOC system (Ciuman, 2010). This is of particular importance in this research due to a significant focus on the MOCR. Therefore, this system will be discussed in greater depth in section 3.2.4.

3.1. Afferent Pathways

The afferent pathway begins at the vestibulocochlear nerve as it passes through the internal auditory meatus. This nerve carries information from both the vestibular and hearing systems (Hackney, 1987). This nerve is comprised of afferent fibers that relay information from the hair cells of the cochlea to the first relay station in the afferent pathway: the cochlear nucleus complex. The cochlear nucleus (CN) itself can be divided into three subdivisions: the anteroventral cochlear nucleus (AVCN), the dorsal cochlear nucleus (DCN) and the posteroventral cochlear nucleus (PVCN) (Hackney, 1987; Moller, 2006). The AN fibers that make up the ascending branch of the cochlear nerve project to the AVCN, whereas the descending branch projects to the PVCN and then the DCN.

Within the subdivisions of the CN are varying types of cells that carry out varying functions (Hackney, 1987; Pickles, 2015). Found within the rostral pole of the AVCN are cells that are considered to be ‘primary-like’. These cells are known as spherical bushy cells. The projections from these cells are believed to travel to the MSO on both sides (via the ventral acoustic stria) and the lateral superior olive (LSO) on the ipsilateral side (Moller, 2006; Pickles, 2015). The AVCN also contains globular bushy cells, which project to the contralateral LSO via the medial nucleus of the trapezoid body (MNTB). Pyramidal cells can be found in the DCN and project to the central nucleus of the contralateral inferior colliculus (Hackney, 1987; Moller, 2006; Pickles, 2015). These are believed to be relayed through the ventral nucleus of the lateral lemniscus (VNLL). These projections typically travel via the dorsal acoustic stria (Moller, 2006). There are also other cells, such as the giant and multipolar cells, which can be found in the DCN. These are also believed to send projections to the ipsilateral inferior colliculus (IC) and the contralateral CN (Hackney, 1987). Alongside this, there are also projections within the cochlear nucleus that aim to assist in the processing of incoming information. This can be seen through projections from the caudal pole of the PVCN from a group of cells known as octopus cells (Hackney, 1987). These cells project to the DCN and can alter and affect afferent fibers that are projecting from the cochlea to the DCN. Additionally, there are connections between the DCN and AVCN as well as the IC, which also aim to regulate complex activity within these areas (Hackney, 1987; Pickles, 2015).

The MSO has projections that travel to the IC ipsilaterally through the lateral lemniscus (LL). Comparatively, the LSO sends projections to the dorsal nucleus of the lateral lemniscus (DNLL) and the IC contralaterally via the intermediate acoustic stria (Moller, 2006; Pickles, 2015). Research has also suggested for there to be connections between the DNLL and the IC on the contralateral side with projections through the commissure of Probst. Whereas the IC on both sides is believed to send projections to either side through the commissure of IC (Moller, 2006; Pickles, 2015).

The medial geniculate body (MGB) can be divided into three nuclei. These include the ventral, dorsal and medial nucleus. The ventral MGB receives projections from the ipsilateral IC and sends projections to the ipsilateral auditory cortex (Pickles, 2015). The specific areas the projections innervate are the tonotopically arranged areas of the auditory cortex. The medial MGB receives projections from the IC as well as multiple other nuclei (Pickles, 2015). This area has the role of integrating information from multiple sensory fields. This area can send projections to varying auditory cortices and the amygdala (Pickles, 2015). The dorsal MGB receives projections from the dorsal cortex of the IC as well as other areas. The projections, in turn, from this area are sent to the non-tonotopic cortical belt around the main parts of the auditory cortex (Pickles, 2015).

The afferent pathway sees a range of divergence and convergence of information as it travels up to the auditory cortex and associated areas. This works to process information to allow for the perception of sound (Hackney, 1987; Pickles, 2015). The tonotopic arrangement seen in the cochlea and the AN fibers is preserved as it travels through the afferent pathway. Within the CN, the innervation of high-frequency information compared to low-frequency information is different (Hackney, 1987). It is believed that higher frequency information typically innervates the dorsomedial areas of the subdivisions in the CN. Whereas the lower frequency information typically innervates the ventrolateral regions (Hackney, 1987). When considering the superior olivary complex (SOC), the bilateral innervation this area receives plays an important role in sound localization. These areas are able to detect and process differences in the intensity and timing of incoming information, which aids in localizing sounds in space (Hackney, 1987). The central nucleus of the IC plays an important role in frequency processing and processing spatial characteristics of sound, whereas the VNLL is believed to be important for analyzing the temporal characteristics of complex signals due to the presence of specialized cells (Pickles, 2015). An important concept that arises when considering the physiology of the afferent pathways is that of varying streams of information that carry information regarding different aspects of auditory processing. Research outlines two such streams: the ventral and the dorsal stream (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Bizley & Cohen, 2013; Pickles, 2015). The AVCN and its projections are believed to be part of the ventral stream, whereas the PVCN and the DCN and their projections are believed to be part of the dorsal stream. These streams of information are believed to converge at the IC, which is a fundamental step in processing information from individual acoustic characteristics to a more complex and integrated perception of the acoustic stimuli. This is further continued in the MGB (Pickles, 2015). The ventral stream is believed to be important in processing information about the auditory space, whereas the dorsal stream is believed to be involved in more complex processing of spectrotemporal characteristics (Bizley & Cohen, 2013; Pickles, 2015). Some research has also suggested another pathway to exist potentially also originating from the DCN. This is known as the non-lemniscal pathway and is separate from the lemniscal pathway that has been discussed thus far (Pickles, 2015). This non-lemniscal pathway is believed to play a role in multimodal integration and reflexes, which is separate from the unimodal auditory processing associated with the lemniscal pathway. This pathway can see projections through the medial and dorsal divisions of the MGB, as explained above (Pickles, 2015).

As the information is further projected through the afferent pathway, the tonotopicity remains, which aids in frequency discrimination and sound perception. There are varying cells present in the auditory cortex that are sensitive to different characteristics of the incoming signal (Pickles, 2015). These can include characteristics such as the location or the frequency of the sound source. This information can be integrated in the auditory cortex and surrounding areas typically through different patterns of neuronal activation (King, Teki, & Willmore, 2018; Pickles, 2015). This can be seen throughout the afferent pathway, which sees varying levels of excitatory and inhibitory activity that modulate responses which ultimately leads to the perception of sound (Pickles, 2015).

3.2. Efferent Pathways

Alongside afferent pathways that carry important sensory information from the periphery to central brain structures. The efferent pathway is an important regulator of incoming information by acting on structures downstream (Pickles, 2015; Robertson, 2009). These efferent pathways are believed to modulate activity that results in the eventual enhancement of stimuli that are to be perceived. These efferent pathways are also known as centrifugal pathways (Bajo & King, 2013; Pickles, 2015). The focus of this section will be on the MOC system due to its relevance to the research conducted. However, a brief evaluation of other efferent pathways will also be discussed.

An important efferent pathway that exists involves connections between the auditory cortex and the IC. These have been termed corticocollicular connections and are believed to modulate the sensitivity to acoustic characteristics such as frequency, intensity and location information for IC neurons (Bajo & King, 2013). Research suggests that activity carried out by these connections is also believed to underlie the effects of learning and experience on auditory perception (Bajo & King, 2013). Pyramidal cells located in layer V of the auditory cortex are believed to be the main cells responsible for these connections, as found through anatomical tracing studies (Bajo & King, 2013; Beyerl, 1978). Furthermore, layer VI has also been shown to exhibit a low level of control over cells found in the IC (Schofield, 2009). In terms of function, some research has also outlined a potential role in auditory segregation played by these corticocollicular connections highlighting the importance of these efferent pathways (Bajo & King, 2013).

Research has also suggested for there to be projections between the auditory cortex and the MGB. Furthermore, important connections also exist between the IC and the SOC as well as the CN (Mellott, Bickford, & Schofield, 2014; Pickles, 2015). Of particular importance are the projections from the differing nuclei found within the SOC, namely the medial superior olive (MSO) and lateral superior olive (LSO) (Ciuman, 2010; Pickles, 2015).

3.2.1. Superior Olivary Complex

The SOC holds important roles in the human auditory system. Research has shown for characteristics associated with sound localization to be processed in these structures (Ciuman, 2010). However, the SOC also plays an important role in maintaining efferent control over the cochlea and related structures. The SOC can be separated into two systems: the LOC system and the MOC system (Ciuman, 2010; Pickles, 2015; Pujol, 1994). The LOC system has efferent fibers which project from neurons in the LSO to the cochlea. This is predominantly on the ipsilateral side (Pickles, 2015; Pujol, 1994). Comparatively, the MOC system has efferent fibers which originate from the MSO and the trapezoid body. These fibers project mainly contralaterally to the cochlea (70% of fibers are believed to project contralaterally) (Pickles, 2015; Pujol, 1994). The fibers from both systems travel within the inferior vestibular nerve and join the cochlear nerve at the anastomosis of Oort (Ciuman, 2010). The lateral efferents are believed to be unmyelinated along the whole pathway and synapse with the dendrites of the afferent fibers innervating the IHCs. Comparatively, the medial afferents are myelinated until they reach the habenula perforata and are believed to synapse with OHCs directly (Ciuman, 2010). The function of this efferent pathway, although complex, is able to regulate both the electromotility and auditory information that is conveyed to higher brain structures (Pickles, 2015; Pujol, 1994).

3.2.1.1. Lateral Olivocochlear System

The LOC system has been shown to possess more efferent fibers than the MOC system. There are approximately 1005 efferent fibers as part of the LOC system and 360 MOC fibers (Lopez-Poveda, 2018). It is believed that the LOC reflex is mediated through sound driven activity. Information travels through the auditory nerve and through the PVCN to the LOC neurons, which are activated (Lopez-Poveda, 2018). This results in activation of these LOC efferents, which synapse onto the dendrites of type I afferent fibers innervating IHCs. This, in turn, regulates activity in these type I afferent fibers (Lopez-Poveda, 2018). Research has shown for there to be two types of neurons present in the LSO. These are intrinsic neurons and shell neurons (Ciuman, 2010). Intrinsic neurons are believed to be smaller and run only 10-20% of the total cochlear length. Comparatively, the shell neurons are more diffuse, and research indicates that they can extend up to 80-95% of the total cochlear length (Ciuman, 2010).

The LSO system has a variety of NTs that allows for it to exert its effects on AN fibers. These NTs include acetylcholine (ACh), gamma-aminobutyric acid (GABA), calcitonin gene-related peptide (CGRP), as well as dopamine, serotonin, and specific opioids (Ciuman, 2010; Safieddine & Eybalin, 1992). It is also believed that the lateral efferents can co-localise these NTs. Research has indicated that NTs such as CGRP and ACh are able to enhance neural activity (Ciuman, 2010). This is achieved through a lowering of the resting potential, which works to increase neural activity. Contrastingly, NTs such as GABA and dopamine are able to reduce neural activity by increasing the resting potential (Ciuman, 2010; C G le Prell et al., 2003). These NTs are believed to have inhibitory effects. Therefore, the NTs that are released can affect neural activity, and therefore, this can be a way to modulate activity in the peripheral auditory system (Ciuman, 2010).

The LOC system has been speculated to play a protective role in limiting damage to the cochlea as a result of overstimulation (Pujol, 1994; Robertson, 2009). Research has suggested that enkephalins are an important mediator in this process. Enkephalins are endogenous pentapeptides that act as neurotransmitters and neuromodulators exerting their affects through their various receptors (Pujol, 1994). Enkephalins are believed to reduce the firing in the AN fibers as a way to regulate and protect the important fibers and synapses. A link to tinnitus has also been established where it is believed that enkephalins are potentially responsible for reducing abnormal spontaneous activity seen in AN fibers, which can be seen in tinnitus (Pujol, 1994). However, these findings require further studies and evaluation to find further evidence for these claims. This protective role by the LOC system is also believed to be mediated through dopamine. This is believed to be important in situations of overstimulation (Pujol, 1994). Dopamine is thought to prevent noise-induced excitotoxicity, which is a result of excessive glutamate release at the IHC and AN fiber synapses (Pujol, 1994).

The LOC system is also thought to play a role in the homeostatic regulation of the AN afferent fibers. Through its regulation and mediation, research suggests that the LOC system maintains and controls the excitability of afferent fibers that synapse with IHCs (Robertson, 2009). This is important so that slight changes in electrical potential do not lead to varied spontaneous rates of firing or varied responses by the afferent nerve fibers to incoming sound. Therefore, this regulation ensures that the AN fiber activity is kept regulated to ensure that sensory information can be accurately conveyed (Robertson, 2009). This potential role is, however, not guaranteed. This is because conclusive evidence is yet to be found that supports the idea of afferent fiber activity requiring constant regulation due to any changes in activity (Robertson, 2009). Therefore, further evidence is required.

3.2.1.2. __Medial Olivocochlear System__

The MOC system operates in a similar manner to the LOC system. However, there are significant differences when considering the locations these efferents innervate as well as the role they play in hearing. As these medial efferents can eventually be stimulated by sound, and therefore, alter cochlea functionality, this process has been termed the medial olivocochlear reflex (MOCR) (Boothalingam et al., 2019). Therefore, to understand this reflex, it is important to develop an understanding of the pathways and other physiological mechanisms that are responsible for mediating this reflex.

The MOCR reflex pathway can be divided into two specific pathways: the contralateral and ipsilateral pathways. These pathways differ in the way their projections travel to stimulate the ipsilateral and contralateral cochlea (Lopez-Poveda, 2018). Beginning with the contralateral pathway, stimulating the right ear results in AN fibers firing that has projections to the PVCN. From here, these MOC-reflex interneurons project to the contralateral ventral nucleus of the trapezoid body (VNTB). The final projection is from the VNTB to the cochlea on the left side, innervating the OHCs directly (Lopez-Poveda, 2018). Contrastingly, although the initial part of the pathway is similar in both ipsilateral and contralateral divisions, there are differences that exist. Stimulating the right ear will result in firing in the AN fibers projecting to the PVCN and from here projections to the contralateral VNTB. However, following this, these neurons project contralaterally to cross the midline again and innervate the OHCs in the right cochlea (Lopez-Poveda, 2018). This shows a key difference which has been highlighted to be because of uncrossed and crossed fibers. The contralateral pathway crosses the midline on one occasion and involves the uncrossed efferent fibers. Contrastingly, the ipsilateral pathway crosses the midline on two occasions and involves the crossed efferent fibers (Lopez-Poveda, 2018). Research suggests for there to be approximately 1,500 medial efferent fibers innervating the cochlea on each side. Out of these fibers a greater proportion are believed to be monoaural fibers which are only activated by sound in one ear (de Venecia, Liberman, Guinan, & Brown, 2005). Approximately 2/3 of these monoaural fibers are believed to be activated by sound in the ipsilateral ear, whilst the others are activated by contralateral stimulation. Binaural neurons are also believed to exist in the population of MOC neurons (de Venecia et al., 2005).

The NTs that are believed to be involved at the MOC and OHC synapses are GABA, ACh and CGRP, which are similar to those found at the LOC efferents. However, research has also suggested for there to be an involvement of enkephalins, nitric oxide (NO) and adenosine triphosphate (ATP) (Ciuman, 2010). Some pieces of evidence suggest for ACh to be one of the most important NTs in the MOCR that allow for its effects to be exhibited (Pujol, 1994). Related to this are the nicotinic-like ACh-receptors, which are found in greater quantities in OHCs compared to IHCs. These are located at the synapses between the OHCs and the MOC efferents and are responsible for inducing hyperpolarization in the cell membrane (Ciuman, 2010). These receptors work by allowing Ca2+ entry into the cell when activated by ACh, which allows for a hyperpolarizing Ca2+-sensitive K+

current. This then hyperpolarizes the cell membrane resulting in a change in the activity of the OHCs (Ciuman, 2010). This is particularly true for the cochlear amplifier gain, which is reduced as a result. It is also believed that the Ca2+ influx also affects the motor protein prestin found with the OHCs (Ciuman, 2010). This influx results in elongation of the OHC, which in turn reduces the cochlear amplifier. The MOCR is, therefore, driven by initial acoustic stimulation, which explains how the MOC system can play a role in the protection of key sensory structures from overstimulation (Ciuman, 2010). By reducing the cochlear amplifier, the MOC system effectively reduces the activity and sensitivity of the IHCs to sound. This is because the cochlear amplifier is an important process that allows for sufficient stimulation of IHCs, particularly at low intensities. This, in turn, increases the cochlear sensitivity to sound (Robertson, 2009). These MOC effects can be seen through varying clinical measurements. One such measurement is through OAEs, where amplitudes are shown to decrease due to a reduction in the cochlear amplifier, which also reduces the non-linearity that is seen in the cochlea. Additionally, studies have also observed reductions in auditory brainstem responses (ABR) wave I amplitudes due to MOCR activation (Lopez-Poveda, 2018).

Multiple pieces of research have suggested a suppression observed in OAE measurements when this MOCR reflex has been stimulated and activated. This is believed to occur following stimulation being provided to the auditory system, although typically, this is studied through the provision of contralateral stimulation (Brashears, Morlet, Berlin, & Hood, 2003; Jamos, Kaf, Chertoff, & Ferraro, 2020; Lilaonitkul & Guinan, 2009). The efferent fibers that innervate the cochlea have similar tuning curves to those seen with the AN afferent fibers. These efferent fibers are believed to similarly innervate those OHCs that are located at the CF of the MOC efferent fiber (Liberman & Brown, 1986; Lilaonitkul & Guinan, 2009). This, therefore, shows a frequency-specific innervation and modulation of cochlear activity (Lilaonitkul & Guinan, 2009). However, research has shown that broadband stimulation which is typically delivered contralaterally, has greater effects on OAE suppression in comparison (Lilaonitkul & Guinan, 2009; Lisowska, Smurzynski, Morawski, Namyslowski, & Probst, 2002; Velenovsky & Glattke, 2002). Having said so, varying pieces of research provide contradictory information that explains the potential for ipsilateral broadband stimulation to provide greater MOC activation (Lopez-Poveda, 2018). Though this is inconclusive when considering the evidence, it is important to highlight. Furthermore, there are also claims that bilateral broadband stimulation provides a greater activation of the MOCR reflex when compared to the ipsilateral and contralateral stimuli separately (Berlin, Hood, Hurley, Wen, & Kemp, 1995; Lilaonitkul & Guinan, 2009; Lopez-Poveda, 2018). Therefore, this is an important characteristic that has been considered in this research.

To understand the physiology potentially underlying these affects, it is important to understand the integration of MOC effects across varying frequencies. Research has shown that the MOC effect increases as the bandwidth and the corresponding number of octaves increases (Lilaonitkul & Guinan, 2009). This suggests that increasing the bandwidth results in increased MOC activity, most likely due to activation of fibers in other locations of the cochlea now within the increased bandwidth. This, therefore, indicates the potential integration of MOC effects (Lilaonitkul & Guinan, 2009). Underlying this, studies have attributed these effects to type II AN fibers. Due to mutual synaptic connections between OHCs, type II AN fibers and MOC efferents, it is speculated that these type II AN fibers may play a role in this integration (Lilaonitkul & Guinan, 2009). However, conclusive evidence is yet to be found supporting this. Furthermore, some studies have also highlighted the involvement of central brain structures in allowing for this integration of MOC effects across frequencies in the cochlea (Lilaonitkul & Guinan, 2009). This then aids in understanding potential reasons as to why broadband stimulation results in greater MOC effects. It is believed that broadband stimulation will result in greater stimulation due to a wider range of frequencies being stimulated. This is accompanied by the narrow dynamic range of the low threshold AN fibers, which will result in greater firing. In turn leading to a higher level of MOC activity which will potentially spread across the frequencies due to the integration effects explained above (Lilaonitkul & Guinan, 2009).

Studies have also shown that the MOCR can be measured through ABRs, specifically focusing on the wave I responses. Research has shown for there to be a reduction in wave I amplitudes as a result of MOCR activation (Lilaonitkul & Guinan, 2009; Lopez-Poveda, 2018). This is of particular importance in this research as it is a fundamental aspect of what the research is analyzing. The affects and underlying physiology of the MOCR on ABR wave I responses are discussed further in section 6.1.1. There is currently a limited level of research that has been done investigating these effects (Lilaonitkul & Guinan, 2009). This is particularly true when adding and considering speech-in-noise (SIN) auditory training to the research. Therefore, these effects have been investigated in this research.

4. Roles of the Medial Olivocochlear System

The MOC system has been studied extensively when regarding its role in hearing. The majority of this research, however, has been conducted in animal models, with there being a lack of evidence present in humans supporting some roles of the MOC system (Ciuman, 2010; Lopez-Poveda, 2018). Having said so, the roles this section will cover have been widely suggested in the literature to be important functions of the MOC system. These roles include protection from overstimulation/ noise trauma, signal-in-noise perception and sound localization (Ciuman, 2010; de Boer et al., 2012; Lopez-Poveda, 2018; Robertson, 2009).

4.1. Protection

An important role of the MOC system is its ability to protect key hearing structures in the periphery. Multiple studies have researched the effects of the MOC system in animals, evaluating the protective role carried out by the MOCR (Marshall & Miller, 2015). In relation to this, multiple mechanisms have been highlighted which are believed to mediate these effects. One such mechanism identifies the reduction in the cochlear amplifier that is mediated by the OHCs (Marshall & Miller, 2015). As explained above, MOC efferent activity will reduce these effects, which in turn result in reduced amplification mediated by the OHCs. This means that there is a reduced chance of damage to the cochlea, protecting it from excessive noise (Ciuman, 2010; Marshall & Miller, 2015). However, the underlying physiology shows that the non-linearity of the OHCs means that the cochlear amplifier is mostly active during low-level sounds. Therefore, there must be other mechanisms that explain the protective role for high-level sounds (Marshall & Miller, 2015). Research has shown for there to be a reduction in the endocochlear potential, which is mediated by MOC efferent activity due to an increased flow of current through OHCs. This results in a lowered IHC receptor potential, and therefore, a reduced release of NTs by the IHCs (Marshall & Miller, 2015). Studies investigating AN fiber activity have seen these effects with reduced firing rates. This is also specifically seen in medium and high threshold fibers which are typically active with higher-level sounds (Guinan & Stankovic, 1996; Marshall & Miller, 2015). Furthermore, increased stiffness of the basilar membrane has also been theorized to mediate the protective role of the MOC system. However, the physiology of this process is yet to be understood (Marshall & Miller, 2015).

A study conducted by Maison et al., (2013) investigated the effects of temporary threshold shifts (TTS) in mice that had MOC activity terminated due to MOC lesions. The results showed a greater loss in afferent AN fibers in mice that did not have MOC activity, indicating the protective role carried out by this system (Maison, Usubuchi, & Charles Liberman, 2013; D. W. Smith & Keil, 2015). Furthermore, the findings of this research have been supported by other studies which found similar results. These results showed a reduced TTS when the MOC system was activated, further contributing to evidence supporting this role of the MOC system (Otsuka, Tsuzaki, Sonoda, Tanaka, & Furukawa, 2016; Rajan, 2000; Rajan & Johnstone, 1988). These findings, however, are in animal models, which means that direct correlations to humans are difficult to make. A few studies investigating the protective role of the MOC system in humans have also been conducted (Otsuka et al., 2016). These studies found that there was a correlation between the level of MOC activity and the TTS. These findings showed an inverse relationship (Wolpert, Heyd, & Wagner, 2014). A study conducted by Otsuka et al., (2016) found similar results in musicians. These findings reflected a similar lower TTS in musicians with a greater level of MOC activity, further providing evidence of the protective role of the MOC system in humans (Otsuka et al., 2016). However, a study by Collet et al., (1991) was unsuccessful in finding similar results. This, therefore, shows the inconclusiveness of the MOC protective role in human studies and shows that more research is required in this field, though it can be speculated that this role exists to some extent in humans (Lopez-Poveda, 2018).

4.2. Signal-in-Noise Perception

An important role carried out by the MOC system is that of improving signal-in-noise perception (Lilaonitkul & Guinan, 2009; Robertson, 2009; D. W. Smith & Keil, 2015). This role is of particular relevance due to this research investigating signal-in-noise perception and evaluating MOC activity alongside this. Multiple studies have been conducted that have evaluated an individual's signal-in-noise performance and have analyzed MOC activity (de Boer et al., 2012; D. W. Smith & Keil, 2015). Furthermore, some research has also been done on potential underlying explanations as to why the effects are seen (D. W. Smith & Keil, 2015). Therefore, this section will cover these pieces of research, providing a basis for this role of the MOC system.

An important concept underlying signal-in-noise perception with MOC activation is antimasking (Robertson, 2009). When there is an incoming stimulus in quiet background situations, research has shown that the firing rates of the AN afferent fibers increase in firing till they reach their point of saturation. This is a typical response in the AN fibers in quiet situations (Winslow & Sachs, 1987). Comparatively, in noisy background situations, a different response is seen. There is increased firing from the afferent fiber in response to the incoming background noise, which results in a reduced maximum firing rate (Winslow & Sachs, 1987). This means that the range of output for the afferent fiber is reduced, which is accompanied by reduced cochlear sensitivity as a result of the incoming noise affecting the OHC response (Winslow & Sachs, 1987). This has also been explained as an increased firing rate and a reduced rate at which fibers saturate, thereby affecting the dynamic range within which afferent fibers can operate (de Boer et al., 2012; Guinan, 2006). These effects, therefore, work to 'mask' the important signals in noise, such as speech (Winslow & Sachs, 1987). Now considering the effects of the MOC system, these characteristics of the AN fibers are altered. In quiet situations, the same nerve fiber has a shifted response in quiet background situations (Winslow & Sachs, 1987). This means that a similar response is seen where there is spontaneous firing at low levels followed by increased firing when the stimulus is at an intensity loud enough to cross the fibers threshold. The AN fiber also becomes saturated at similar levels (Winslow & Sachs, 1987). However, due to MOC activation reducing the cochlear amplifier, relatively louder intensities of sound are required to increase the firing rate in the AN fiber. Comparatively, in noisy background situations, MOC activation results in a reduced firing of the AN fiber in response to background noise, which results in an increased maximum firing rate (Winslow & Sachs, 1987). Additionally, the output range is also improved, which aids in signal-in-noise perception in noise. This is referred to as antimasking and explains the fundamental process behind the improvements seen in SIN perception with MOC activation (Winslow & Sachs, 1987).

Aside from the explanation provided by studies investigating these antimasking effects, there are inconsistencies in the literature regarding evidence supporting this effect in humans. A study conducted by Scharf et al., (1997) found contradicting evidence to show that the MOC system does not, in fact, affect signal-in-noise perception. This study showed that the inactivation of the MOC system did not alter an individual's ability to detect tones embedded in noise. Contrastingly another study provided evidence supporting the antimasking effects by showing a greater ability for individuals to detect signals in noise that correlated to their MOC activity. The MOC activity was measured through OAE suppression with contralateral stimulation (Micheyl & Collet, 1998). Therefore, this shows the inconsistencies in the literature supporting these antimasking effects showing the need for further research to evaluate these effects (Lopez-Poveda, 2018).

Research has also been conducted to evaluate the effects of the MOC system on SIN perception. There is some speculation in the literature that suggests that the effects of the MOC system may be seen to a greater extent when using complex stimuli such as speech compared to pure tones when evaluating the role of the MOC in signal-in-noise perception (de Boer et al., 2012). This was studied by Giraud et al., (1997) who found that individuals with absent MOC systems did not see improvements in SIN performance with contralateral sound. Furthermore, this study also found that there was an improvement in SIN intelligibility, which corresponded to the level of MOC activity. These findings reflected the role of the MOC system in improving signal-in-noise perception (Giraud et al., 1997). Other studies have also found similar results indicating and supporting this role of the MOC system (de Boer et al., 2012; Kumar & Vanaja, 2004). However, there is also evidence present from other studies that contradict this evidence which suggests inconclusiveness in this role (de Boer et al., 2012). This further indicates the need for additional research to provide more evidence in this area.

The speculated mechanisms that underlie these improvements seen in SIN perception with MOC activity are as follows. Research has suggested for MOC activity to play a role in the spectral analysis of incoming information, which contributes to the perception of sound, specifically complex stimuli such as speech (Giraud et al., 1997). This can be seen through poorer frequency tuning in individuals with absent MOC activity, potentially playing a role in stimulus encoding. Furthermore, the MOC efferent fibers are also believed to be important in the intensity coding of speech signals (Giraud et al., 1997). Due to the mechanisms explained above, afferent nerve fibers are more responsive to transient signals in the presence of background noise. This preserves the rate representation of the incoming sound aiding in coding for intensity (Giraud et al., 1997). This can help improve SIN coding, and therefore, perception. Lastly, MOC efferent fibers are also believed to play a role in the temporal analysis of incoming stimuli (Giraud et al., 1997). This is believed to operate through an increased temporal resolution of the basilar membrane and OHCs, which improve the ability to code for speech stimuli. These mechanisms are believed to underlie the improvements seen in SIN perception with MOC activation (Giraud et al., 1997). However, further research needs to be conducted to find evidence supporting these claims.

There is also some evidence supporting a potential involvement of attention in the MOCR. Research suggests that attention can modulate the effects of the MOCR and can, in instances, increase or decrease the level of activity. Therefore, attentional effects have also been speculated to play a role in SIN perception with MOC activity (de Boer et al., 2012).

Importantly, although research has been conducted in this field, to my knowledge, an underlying physiological mechanism has not been identified with evidence that explains and corresponds to the studies showing improvements seen in signal-in-noise perception with MOCR activation. This is particularly true when a period of auditory training has been added to the study design to observe changes in performance that correlate with MOC activity following a training period. Therefore, this research has attempted to evaluate these effects.

*4.3. **Sound Localization***

Another important role of the MOC system is that of aiding in sound localization. This is believed to operate through a similar mechanism to that explained above (Boothalingam, Macpherson, Allan, Allen, & Purcell, 2016). Research has speculated that the antimasking effects exhibited by the MOC system also play an important role in sound localization (Boothalingam et al., 2016). This was supported by studies that found a strong relationship between MOC activity and vertical-plane sound localization in noise (Andéol et al., 2011). However, similarly to above, these findings are also contradicted by evidence suggesting that the MOC system does not affect sound localization as much as claimed by other studies. This was seen through a study conducted by Boothalingam et al., (2016) which found a weak correlation between MOC activity and sound localization. Furthermore, there is also varying evidence suggesting there to be a difference in horizontal- and vertical-plane sound localization and its correlation to MOC activity, further adding to the uncertainty for this role of the MOC system (Lopez-Poveda, 2018). Additionally, a study conducted by Irving et al., (2011) theorized that MOC effects in sound localization might be affected by frequency, and therefore, specific frequencies such as high frequencies may be affected by MOC activity greater than other frequencies. This then would mean that MOC activity would play a role in specific processing, such as with interaural level differences due to their correlation with high frequencies (Irving et al., 2011). However, further evidence is required to evaluate these claims. This, therefore, shows that further evidence is required to evaluate the role of the MOC system in sound localization in humans.

5. Auditory Training

Auditory training is a process that an individual can go through which aims to train the individual's auditory skills to aid in improvement. These skills can vary; however, ultimately, the goal of auditory training is to see improvements in aspects such as speech perception or other communication skills (Besser & Launer, 2020). Typically, auditory training is used as a rehabilitative measure to aid individuals with hearing impairments. Research has shown that these periods of auditory training help improve these individuals' hearing ability (Besser & Launer, 2020). Furthermore, some studies have also shown improvements in other aspects, including working memory and cognition. Therefore, highlighting the usefulness of auditory training as a rehabilitation technique (Besser & Launer, 2020). Auditory training is typically used in individuals with hearing impairments. However, studies have been conducted on individuals with normal hearing, which show similar improvements in hearing ability following a period of auditory training (Karawani, Bitan, Attias, & Banai, 2016). Fundamentally, an important concept discussed in the literature around auditory training is that of cognitive processing. Multiple pieces of research have shown that complex signals such as speech require greater integrated and complex processing (Ferguson & Henshaw, 2015; Karawani et al., 2016). This is particularly true in instances where there is a difficult listening environment, such as one with a variety of background noise. To perceive key stimuli in these environments, complex processing is required, which can involve working memory and attention (Ferguson & Henshaw, 2015; Karawani et al., 2016).

Literature suggests for there to be distinctions between the physiological changes that come as a result of auditory training. There are believed to be bottom-up processing and top-down (cognitive) processing changes (Henshaw & Ferguson, 2013). Studies show that these processes can be affected differently depending on the type of auditory training that is undergone. Auditory tasks with varying phonemes and words typically are shown to aid bottom-up processing, whereas non-auditory tasks such as visuospatial or visual discrimination tasks are believed to improve top-down cognitive processes (Ferguson & Henshaw, 2015). However, research has also shown that training that aids in bottom-up processing may also aid in improvements with top-down processing, which could also explain the improvements seen in SIN perception for individuals after auditory training (Ferguson et al., 2012; Henshaw & Ferguson, 2013).

The effects of auditory training can also vary depending on the stimuli used as well as multiple other factors (Karawani et al., 2016). A study conducted by Burk et al., (2006) has shown that using words embedded in noise as a training stimulus showed improvements in individuals' ability to perceive SIN. However, these improvements were limited to words that were used in training and the improvements were not seen for unfamiliar words or sentences (Burk et al., 2006; Karawani et al., 2016). Therefore, when developing an auditory training programme, it is important to evaluate what effects are to be evaluated and what results are to be expected.

In general, multiple studies have found improvements with varying methods of auditory training in individuals with and without hearing impairment. These improvements have been seen in a range of areas. These include communication skills, perceptual, cognitive, speech processing and SIN perception, among others (Besser & Launer, 2020; Ferguson & Henshaw, 2015; Ferguson et al., 2012; Henshaw & Ferguson, 2013; Karawani et al., 2016).

Auditory training is a key component of this research as it was used to evaluate changes in individuals' SIN perception ability. This, in combination with MOCR measurements was the fundamental component of the research conducted. Therefore, this section will highlight the underlying physiological principles as well as research highlighting auditory-training related effects in centrifugal pathways such as the MOC system.

5.1. Underlying Physiology of Auditory Training

A few studies have investigated the biological mechanisms that underlie the improvements seen with auditory training (Ferguson & Henshaw, 2015). One such study identified the involvement of cortical and subcortical structures and potential connections which underlie the training-induced changes.

This study speculated that auditory training, particularly through programmes such as LACE (Listening and Communication Enhancement), which can involve both peripheral and central structures, can play an important role in strengthening cognitive processes (Song, Skoe, Banai, & Kraus, 2012). Due to the contents of the LACE programmes, a high level of demand is exerted on cognitive processes. This, in turn, then ensures that subcortical processing is similarly strengthened, which works to improve hearing speech in noisy background situations (Song et al., 2012). This works as a loop where strengthened processing is further relayed to cortical structures, which aids in the processing of information. Furthermore, this research also showed that auditory training could improve the coding of pitch-related information (Song et al., 2012). As discussed in earlier sections, pitch and frequency coding are important when perceiving SIN. Therefore, these improvements are believed to underlie the training-induced changes (Song et al., 2012).

Furthermore, neural correlates of auditory training can also be seen through studies conducted on musicians. Musicians go through musical training as a result of repeated exposure to music (Zendel & Alain, 2014). This has been shown through studies investigating musicians' ability to analyze spectral and temporal information in a given stimulus. These findings have reflected significantly better performance for musicians compared to non-musicians at these tasks. Furthermore, some studies have also identified better SIN performance for musicians that is preserved as they age (Parbery-Clark, Skoe, & Kraus, 2009; Zendel & Alain, 2014). Findings have shown that musicians show enhanced brainstem responses compared to non-musicians which further indicates improvements in subcortical processing. Furthermore, this indicates the potential importance of corticofugal pathways in regulating subcortical activity, as was explained above (Kraus & Chandrasekaran, 2010; Zendel & Alain, 2014). Additionally, auditory event-related potentials (ERPs) reflected enhanced object-related negativity (ORN) and P400 responses in younger and older musicians, respectively. These findings reflect an improved ability of musicians to undergo spectrotemporal analyses of incoming stimuli (Zendel & Alain, 2014). This could aid with concurrent sound segregation. Therefore, these studies reflect that the underlying biological mechanisms of auditory training can involve both cortical and subcortical structures as well as corticofugal connections between varying structures (Zendel & Alain, 2014).

Although, there have been biological mechanisms that have been highlighted in the literature that aim to explain the improvements seen in SIN perception with auditory training. There are a limited number of studies that evaluate and include the MOC system and its potential involvement in the changes seen with auditory training. The findings of these studies also vary, which further provides reasons to continue research in this field to obtain further evidence in this field (Bhattacharya, 2020;

de Boer & Thornton, 2008; Mertes, Johnson, & Dinger, 2019). This is also important as any evidence supporting the involvement, and underlying connection of the MOCR to training-induced changes in SIN perception could have clinical implications that could benefit individuals.

5.2. Auditory Plasticity

An important concept that underlies auditory training is that of plasticity. Plasticity is when there are changes in the processing of sensory information (Anderson & Kraus, 2013). This plasticity usually comes as a result of changes in incoming sensory information or external factors such as periods of auditory training. These changes, therefore, are fundamental in mediating perceptual differences that come as a result of auditory training or other factors (Anderson & Kraus, 2013). This has been shown through studies that have shown plasticity-related changes in individuals having undergone periods of auditory training. A study done by Krishnan et al., (2010) showed that individuals who were speakers of a tonal language showed enhanced coding of pitch compared to those individuals who were non-tonal language speakers. This was further reflected through SIN performance for these speakers, further providing evidence to the information provided in section 5.1 (Krishnan et al., 2010). Additionally, this reflected plasticity in the auditory structures with changes corresponding to the incoming sensory information, which varied across the different groups of individuals (Anderson & Kraus, 2013; Krishnan et al., 2010). Furthermore, another study reflected enhanced coding for fundamental frequency in bilingual speakers compared to those who spoke one language. This further showed the connection between plasticity and changes that come as a result of differing input (Krizman, Marian, Shook, Skoe, & Kraus, 2012). Interestingly, a study done by Gaab and Schlaug (2003) found that musicians showed recruitment and activation of different central structures compared to non-musicians. This was shown through greater activation of the superior parietal lobe, supramarginal gyrus and inferior frontal gyrus. These areas are also known as auditory storage sites. Comparatively, non-musicians saw greater activation of more traditional areas, including the primary and secondary auditory cortices (Gaab & Schlaug, 2003). This reflected the idea of plasticity and varying activation depending on the auditory training as well as the input these individuals had received for certain periods of time (Anderson & Kraus, 2013). Therefore, this shows the importance of plasticity in auditory training.

Corticofugal plasticity has been shown through various studies which have shown altered activity in subcortical structures. This has been shown to be a result of top-down modulation, which works to alter responses, mediating auditory training-related plasticity. This has been discussed in section 5.1.

5.2.1. Plasticity of the Medial Olivocochlear System

Another structure that must be considered when discussing plasticity is the MOC system. This mediates efferent control over the peripheral structures, and therefore, plasticity and auditory training-related changes in this structure are important as they can alter how incoming stimuli are coded for. Multiple studies have been conducted investigating the effects of auditory training on MOC activity (Otsuka et al., 2016). One study found that repeated exposure to sound resulted in increased activity in the MOC efferent fibers reflecting possible plasticity-related changes as a result of auditory training (Brown et al., 1998; Illing et al., 2000). Another study found that those who were exposed to sound for longer periods of time showed smaller PTS (Permanent Threshold Shift – a shift in threshold that does not recover to preexposure levels) compared to those who were not (Kujawa & Liberman, 1999). These studies support the idea of plasticity-related changes that can be seen in the MOC system.

Furthermore, an important idea that has been investigated in literature is that of the input onto the MOC efferents, which controls the descending output on the cochlea and related structures. As explained above, the MOC system receives presynaptic innervation by both descending inputs such as from the IC and ascending inputs from the CN (Romero & Trussell, 2021). Therefore, research has speculated that this control of MOC activity is mediated by both higher-processing centers as well as ascending inputs. Some studies found increased activity from the IC when there was repeated stimulation at the periphery (Romero & Trussell, 2021). This was coupled with reduced ascending activity onto the MOC efferents. This shows that a combination of both descending and ascending information can play an important role in the mediation of MOC efferent activity (Romero & Trussell, 2021). This is also believed to underlie the dynamic and broad range of intensities that the MOC system can operate under. Furthermore, these studies also speculate that these changes in ascending and descending activity could be conditioned to show longer-term plasticity-related changes (Romero & Trussell, 2021). This further shows the plasticity that can exist in the MOC system and how it can be important in mediating the effects of auditory training.

5.3. Auditory Memory

An important characteristic that is relevant to this research is that of auditory memory. When listening to incoming stimuli, some words can be stored in an individual's auditory working memory (Kaiser, 2015; Wojcik, 2013). This is considered to be more of a short-term memory where the stimuli can be forgotten if not properly encoded, consolidated and/ or retrieved (Kaiser, 2015; Wojcik, 2013). Furthermore, there are also connections between working memory and long-term memory (van der Linden, 1998). Research suggests that an individual can retain approximately two seconds of information about an incoming auditory signal, where the stimulus is repeated. This can be lower for those signals or speech that are continually being presented, particularly in those lists of stimuli where the individual is not aware when the list will end (N. Cowan, 2001; Nelson Cowan, 2010). Additionally, when the duration between stimuli is shorter, this is speculated to prevent an individual from accurately remembering the words presented. Furthermore, it is also theorized that multiple lists of words or other stimuli can make it difficult for an individual to be able to discriminate between words presented in different lists, thus making it difficult to remember previous words (Tehan & Turcotte, 2002). This is important as it can affect the results obtained during research that involves using the same stimulus on different occasions. Thus, it was considered when carrying out this study.

6. Auditory Evoked Potentials

Evoked potentials are important tools that are used clinically and in research studies. These are electrical potentials that arise because of a stimulus that is delivered to an individual (Paulraj, Subramaniam, Yaccob, Adom, & Hema, 2015). These potentials and corresponding electrical activity can be recorded by electrodes placed on the scalp/ head or in the ear in some instances. Specifically, a form of evoked potentials are auditory evoked potentials (AEPs). These are potentials that arise following auditory stimulation (Paulraj et al., 2015; Petrova, 2009). These AEPs can be evaluated and assessed to identify problems and lesions along the auditory pathway and can, in some cases, provide information to aid in varying diagnoses (Berger & Blum, 2007; Paulraj et al., 2015). AEPs are generated by stimulating the auditory system with a specific stimulus. This stimulus results in electrical activity and firing in a large number of neurons (Biagio De Jager, 2008). This activity needs to be synchronous and coordinated among the multiple neurons. Additionally, this activity is different compared to the spontaneous activity that occurs when stimulation is not present (Biagio De Jager, 2008). Therefore, this increased and synchronous electrical activity can be measured through the placed electrodes. The resulting activity can be recorded and separated into different groups, typically grouped based on the latency of the activity (Biagio De Jager, 2008). Responses obtained within 10-12 ms of stimulus presentation are referred to as early responses and are comprised of electrocochleography (eCochG) and auditory brainstem responses (ABR) (Biagio De Jager, 2008; Paulraj et al., 2015). The middle latency responses or middle latency AEPs (MLAEPs) typically arise between 10-50 ms of stimulation, whilst the late responses can be seen between 50-300 ms (Biagio De Jager, 2008; Paulraj et al., 2015). The MLAEPs are believed to arise from activity in the thalamus, early auditory cortex and the inferior colliculus. Comparatively, the late responses arise from activity in the auditory cortex and higher brain areas (Biagio De Jager, 2008). These varying responses have different clinical uses and can be used to analyze different aspects of auditory activity/ processing. The stimuli used to elicit these responses can also be varied to evaluate specific processes (Biagio De Jager, 2008; Paulraj et al., 2015). The further sections will provide more detail into ABRs as they hold relevance due to being used in this study.

6.1. Auditory Brainstem Responses

ABRs are very useful clinical tools that aid in multiple aspects of patient management. These are especially used in paediatric populations to provide an insight into the child's hearing status (Biagio De Jager, 2008; Laumen, Ferber, Klump, & Tollin, 2016; Paulraj et al., 2015). This is particularly important as young children can be difficult to test due to uncooperating behaviours and/ or shorter attention spans. Furthermore, infants are not able to undergo other means of diagnostic testing due to an inability to understand and undergo more complex tasks for their age (Biagio De Jager, 2008). Therefore, ABRs can be very beneficial in these populations (Biagio De Jager, 2008; Laumen et al., 2016; Paulraj et al., 2015). Furthermore, the characteristics of ABRs provide information on the integrity of the auditory pathway and can highlight potential sites of lesion as well as aid in varying diagnoses in combination with other test results. Thus, showing the usefulness of ABRs as a clinical tool (Laumen et al., 2016; Paulraj et al., 2015). Furthermore, ABRs are also very useful as a research tool as they can be used to analyze auditory activity in varying conditions (Laumen et al., 2016).

ABRs can be analyzed by assessing varying peaks that arise at different latencies following auditory stimulation. These peaks are typically referred to as waves I through to wave VII (Berger & Blum, 2007; Biagio De Jager, 2008; Petrova, 2009). Wave I activity is believed to arise from neural generators in the peripheral portion of the auditory nerve, whereas wave II activity arises from the distal portion of the auditory nerve and/or the cochlear nuclei. Wave III activity is believed to be generated from the superior olivary complex and the projections to the LL, whereas wave IV responses arise from the LL (Berger & Blum, 2007; Petrova, 2009). Wave V activity is believed to be generated from lower midbrain structures such as the inferior colliculus. Additionally, wave VI and wave VII activity are speculated to originate from subcortical areas and projections to higher cortical areas (Berger & Blum, 2007; Petrova, 2009).

Importantly, the testing parameters that are used to elicit these responses are also important. This is because these parameters can affect how these responses are created, and therefore, affect important characteristics such as latency and amplitudes of responses (Biagio De Jager, 2008). Furthermore, other parameters, such as those that control averaging of responses and artifact rejection etc., are also important as they can affect the reliability and accuracy of results obtained (Biagio De Jager, 2008). Also of importance is ensuring minimal impedance with the electrodes and the amount of noise present in the testing environment. These factors can affect the results obtained (Biagio De Jager, 2008). ABRs that are obtained can have significantly small amplitudes, especially when measured through a far-field recording. Obtaining a near-field recording through the use of an electrode placed in the ear canal of the individual can provide responses with higher signal-to-noise ratios (SNR) and greater amplitudes (Biagio De Jager, 2008). This is particularly true for wave I responses which are particularly important for this research, as will be discussed in section 6.1.1 (Bauch & Olsen, 1990; Biagio De Jager, 2008). Furthermore, varying parameters such as stimulus rate, artifact rejection and high- and low-pass filters, among others, can be used to improve the SNR to ensure reliable and accurate results (Biagio De Jager, 2008).

The stimuli used to evoke these ABRs also plays an important role in determining the responses obtained. Click stimuli deliver a broadband signal that works to stimulate a wide range of frequencies in the cochlea (Biagio De Jager, 2008). However, due to the arrangement of the cochlea, the high frequencies are stimulated before the lower frequencies. The delay is due to the time it takes for lower frequencies to travel along the cochlear partition to the apex of the cochlea (Biagio De Jager, 2008). Comparatively, a chirp stimulus is designed to deliver lower frequencies before the higher frequencies, which works to compensate for this cochlear arrangement. This results in synchronous firing and simultaneous activation of hair cells in the cochlea, resulting in a signal that is typically higher in amplitude (Biagio De Jager, 2008; Elberling & Don, 2008). A specific type of chirp used in studies nowadays is referred to as an LS CE-Chirp. This is designed to accommodate stimulus effects at high intensities (di Scipio & Mastronardi, 2018). Furthermore, the amplitudes and latencies of the responses obtained can also differ depending on the stimulus used (Jamal, Arafat Dzulkarnain, Shahrudin, & Marzuki, 2020). For chirp stimuli, research has shown wave I latencies to be approximately 1.49 ms for normal hearing individuals with an 80 dB nHL stimulus (Jamal et al., 2020; Pani, Sahoo, Chatterjee, & Dutta, 2020). Additionally, the amplitude of wave I responses has been shown to be approximately 0.38 microvolts for the same stimulus (Jamal et al., 2020). There is some variation that can be expected depending on each individual. However, these are suggested to be the normative values (Jamal et al., 2020; Pani et al., 2020). This will be important as we progress further into this research.

6.1.1. Auditory Brainstem Responses and the Medial Olivocochlear Reflex

Research has shown there to be a decrease in the dynamic range within the auditory nerve with noise stimulation. This occurs following an increased baseline rate of firing and early saturation of AN fibers (de Boer et al., 2012). These are believed to be the effects seen with noise stimulation. However, as explained in earlier sections, the MOC system is believed to ameliorate these effects and alter the response of the AN fibers (de Boer et al., 2012). This works to provide a basis for improved signal-in-noise perception, which has been discussed as the antimasking effect. This is theorized to underlie the changes that are seen with MOCR activity and ABRs (de Boer et al., 2012; Lichtenhan, Wilson, Hancock, & Guinan, 2016).

Literature has shown for there to be a connection between ABRs and the MOCR. They have reflected changes in ABR wave I activity as a result of stimulating the MOC system (Lichtenhan et al., 2016). This, therefore, provides a way to evaluate MOCR activity and potentially provide an alternative mechanism that can underlie mediation of the effects of the MOC system. Research has shown for there to be a reduction in ABR wave I amplitudes with contralateral acoustic stimulation. This stimulation is believed to activate the MOCR, thus showing a MOCR related reduction in wave I amplitudes (Lichtenhan et al., 2016). This has been shown through a few studies (Chabert, Magnan, Lallemant, Uziel, & Puel, 2002; Folsom & Owsley, 1987; Lichtenhan et al., 2016). However, the results have been questioned for some studies in regard to their reliability (Lichtenhan et al., 2016). This, therefore, shows further reason to carry out research in this field to accumulate more evidence in this area.

Another important factor in measuring MOC activity on ABRs is ensuring accurate and correct testing parameters are used. An important consideration is using moderate to high stimulus levels to ensure large amplitudes of the waveforms (Berger & Blum, 2007; S. B. Smith, Lichtenhan, & Cone, 2017). These have been employed in other studies that have evaluated these effects (Berger & Blum, 2007; Lichtenhan et al., 2016; S. B. Smith et al., 2017). Furthermore, aspects such as stimulus rate also need to be considered to prevent adaptation which can affect the ABR results (Buran et al., 2020). For this, a low stimulus rate is recommended, such as a 11.1/s stimulus rate. Other parameters also need to be considered when establishing the testing protocols (Berger & Blum, 2007; Lichtenhan et al., 2016; S. B. Smith et al., 2017).

Some studies have been conducted evaluating the effects of the MOCR on ABRs. These studies have found varying results (Chabert et al., 2002; Folsom & Owsley, 1987; Lichtenhan et al., 2016). This research aims to add additional information to previous studies and investigate a potential correlation between ABR wave I activity and changes in SIN perception following a period of auditory training, as well as any potential connection between ABR wave I activity and auditory training. This study is building on the study conducted by Bhattacharya (2020) and investigates whether ABRs and their related underlying principles can potentially explain and reflect the underlying physiological mechanisms mediating any changes in SIN perception with auditory training and the MOCR.

7. Review of Literature Summary

The literature has provided information covering varying aspects of the auditory system. This includes the outer, middle and inner ear and the underlying anatomy and physiology of these divisions of the human ear (Nava & Lasrado, 2021). Furthermore, aspects such as the afferent and efferent pathways, varying types of masking and principles of AEPs have also been discussed (Ciuman, 2010; Hackney, 1987; Oxenham, 2013a; Paulraj et al., 2015). Importantly, the literature has provided information on the MOC system, including the roles it plays in the human auditory system (Ciuman, 2010; Lopez-Poveda, 2018).

Previously conducted studies have shown that the MOC system plays a role in varying aspects of hearing. These include protection from overstimulation/ noise trauma, signal-in-noise perception and sound localization (Ciuman, 2010; Lopez-Poveda, 2018). Importantly, a common theme among this research is the need for further research to obtain more conclusive evidence supporting these roles in humans.

Previously conducted studies have evaluated the effects of auditory training programmes on SIN perception relating to MOC system activity. However, these studies have found variable results (Bhattacharya, 2020; de Boer & Thornton, 2008; Mertes et al., 2019). Furthermore, studies have also reflected plasticity in the MOC system, therefore, showing how it can be important in mediating the effects of auditory training. Additionally, studies conducted investigating ABRs, and MOC activity have also found results showing suppression of wave I activity, although amongst unreliability in the literature (Chabert et al., 2002; Folsom & Owsley, 1987; Lichtenhan et al., 2016). Therefore, this study aims to build directly on a study conducted by Bhattacharya (2020), which provided future research directions for investigating the physiological mechanisms underlying changes seen in SIN perception with auditory training. This study, therefore, aims to also build on previous research conducted in this field to obtain additional evidence supporting the connection between auditory training and MOC system activity as well as SIN perception. Additionally, finding a connection between MOCR activity (underlying physiological mechanism) and SIN perception is also an important idea investigated throughout this research.

Aims and Hypotheses

Aim One: To obtain additional information on a previous study investigating the relationship between a speech-in-noise auditory training programme and the participants' perception for speech-in-noise stimuli.

> **Hypothesis One (A):** Improvements will be seen in participants' performance throughout the five-day auditory training programme.
>
> **Hypothesis One (B):** Improvements will be seen in participants' ability to perceive speech-in-noise, measured through Quick Speech-in-Noise Test and Word Recognition-in-Noise Test results, at the completion of the auditory training programme when compared to before the programme.

Aim Two: To obtain additional information on a previous study investigating the relationship between a speech-in-noise auditory training programme and medial olivocochlear efferent activity as measured through otoacoustic emissions.

> **Hypothesis Two:** An elevation of medial olivocochlear efferent activity will be seen when measured through contralateral suppression of DPOAE's with broadband noise stimulation, following the auditory training programme.

Aim Three: To investigate the effects of contralateral broadband noise stimulation on medial olivocochlear efferent activity as measured through auditory brainstem responses, focusing on Wave I activity.

> **Hypothesis Three:** An elevation of medial olivocochlear efferent activity will be seen when measured through contralateral suppression of ABR Wave I activity with broadband noise stimulation, as compared to ABR Wave I activity without broadband noise stimulation.

Aim Four: To investigate the relationship between a speech-in-noise auditory training programme and medial olivocochlear efferent activity as measured through auditory brainstem responses, focusing on Wave I activity.

Hypothesis Four: An elevation of medial olivocochlear efferent activity will be seen when measured through contralateral suppression of ABR Wave I activity with broadband noise stimulation, following the auditory training programme.

Aim Five: To obtain additional information on a previous study investigating the relationship between the participants' perception for speech-in-noise stimuli and medial olivocochlear efferent activity as a result of the auditory training programme.

Hypothesis Five: The auditory training programme will result in a positive correlation between improved speech-in-noise perception as measured through Quick Speech-in-Noise Test and/or Word Recognition-in-Noise Test results for participants' and an increase in medial olivocochlear efferent activity as measured through DPOAE and/or ABR Wave I suppression.

Methods

This study was developed to build upon a previously completed study by Bhattacharya (2020). Therefore, the methods used in this study have been kept nearly identical to this previous study. This has been done to evaluate the underlying mechanisms that can potentially play a role in the changes that are seen with auditory training. Furthermore, by keeping the methods the same, this study will be able to obtain additional data on the necessary aims and hypotheses. This is also important as research has shown for there to be contradicting evidence present in the literature. Therefore, obtaining more evidence will be important in eventually establishing a conclusion on the topic (Bhattacharya, 2020; de Boer & Thornton, 2008; Mertes et al., 2019). The study conducted by Bhattacharya (2020) found contradictory information to that found in other studies. Therefore, this study can also evaluate these effects to see if these results were study-specific or if the information indicates differences to the literature. Keeping the same methods, also provides an opportunity for future research to potentially combine datasets to evaluate any potential effects because of a larger sample size.

1. Study Setup

This study was approved by the Auckland Health Research Ethics Committee (Reference: AH2946). Sound treated rooms in the University of Auckland Hearing and Tinnitus Clinics were used to ensure there was minimal background noise during the various testing procedures. This study can be separated and described in four different parts. These parts are a hearing assessment, the baseline measurements or the measurements taken before training, the speech-in-noise (SIN) training programme and the measurements taken after the auditory training programme.

1.1. MOCR Elicitor

The MOCR was stimulated using contralateral acoustic stimulation (CAS). This was used for a variety of measures and was fundamental to the research study. A broadband noise (BBN) stimulus was used to elicit the MOCR. This has been shown to be effective in various studies investigating the effects of CAS on MOCR activity (Lilaonitkul & Guinan, 2009; Lisowska et al., 2002; Velenovsky & Glattke, 2002). Furthermore, the level of the BBN stimulus was set to be 60 dB SPL. This is important as studies have been conducted evaluating the effects of various stimulus levels on MOCR activity. These studies have shown that intensity levels >60 dB SPL potentially activate the middle ear muscle reflex (MEMR) (Marshall et al., 2014). Therefore, to stay clear of these effects on our results, a 60 dB SPL BBN stimulus was used, which has been shown to be effective in eliciting MOCR activity (Marshall et al., 2014).

This elicitor was only used contralaterally for DPOAE and ABR measurements to prevent the noise from affecting the DPOAE stimulus and to keep the elicitor the same when investigating the ABRs. For the SIN auditory training programme and the Word Recognition-in-Noise Test, the BBN stimulus was presented bilaterally. This is because research has indicated that bilateral stimulation results in greater MOC activity compared to other forms of stimulation (Berlin et al., 1995; Lilaonitkul & Guinan, 2009; Lopez-Poveda, 2018).

The BBN elicitor used was created using a computer software called Audacity. Through this software, white noise, which had equal energy across a range of frequencies, was altered to create the BBN used. The white noise was created from frequencies 43 Hz to 22 kHz. From 8 kHz onwards, the software was set to reduce the amplitudes by 48 dB per octave. This was known as a low-pass filter. Additionally, the BBN noise was played through two Dell laptops and a Grason-Stadler Audiostar Pro Audiometer; each coupled to an ER-3A insert phone transducer. This allowed for verification and establishment of the levels required on the volume controls to produce a 60 dB SPL BBN stimulus. For this, a Brüel and Kjær 2250 Sound Level Meter was used, which was coupled with a Brüel and Kjær 4152 Artificial Ear and a Pressure-field Microphone type 4144. This allowed for a 60 dB SPL (LZF weighted) output to be verified.

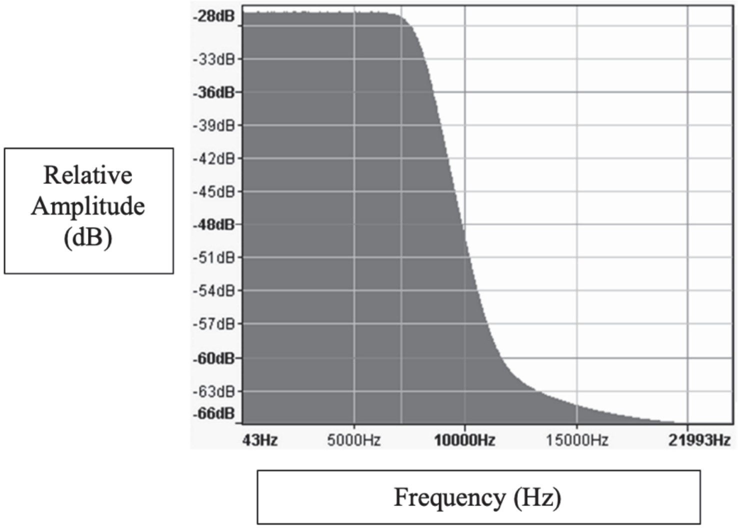


Figure 1: Figure showing the relative amplitudes across varying frequencies for the created BBN elicitor.

1.2. Participants

The participants were recruited based on set inclusion and exclusion criteria. Individuals would be eligible to take part in the study if they were above the age of 16 and had clinically normal hearing. The exclusion criteria included any hearing conditions such as ANSD or APD, abnormal tympanometry results, hearing thresholds that were considered outside of the normal range (>15 dB HL), as well as exposure to loud levels of noise or ototoxic medication which could have effects on hearing. The recruitment process was conducted through printed and verbal advertisements of the study. Each participant was also provided with the Participant Information Sheet and was required to sign a Consent Form to take part in the study.

1.2.1. Control and Treatment Groups

Ten participants were recruited for the study and were randomly allocated into control and treatment groups. Six participants made up the treatment group, and four made up the control group. The control group did not undergo the auditory training programme. This group underwent the Word Recognition-in-Noise Test, the Quick Speech-in-Noise Test, and the DPOAE and ABR measurements on the first and fifth days. Furthermore, they also underwent a hearing assessment. A control group was necessary to evaluate the effects of auditory training. The same methods were used for both control and treatment groups regarding the specific measurements carried out.

2. Part One: Hearing Assessment

The initial part of the study required a clinical hearing assessment to be conducted. This was to ensure the participants had hearing within normal limits and fit the inclusion/ exclusion criteria. An otoscopic examination was conducted as part of this assessment. This was to ensure no visual abnormalities or significant occurrences of cerumen could be detected, which could affect the hearing status of the participants.

This was followed by immittance audiometry. A Grason-Stadler GSI Tympstar Version 2 Middle Ear Analyzer was used for these measurements. For these measurements, a typical audiological process was conducted to ensure there were no contraindications to this testing. For tympanometric testing, a 226 Hz probe tone was used with a sweep rate of 600/200 daPa/sec. The findings of these results were evaluated with normative values established in the literature. The participants were considered to have normal results if the values fell within the normative ranges established (ASHA, 1990). This testing was done in both ears of each participant. The normative values indicate a middle ear pressure between -100 to 100 daPa, an admittance between 0.3 to 1.4 mmho, an equivalent ear canal volume between 0.6 to 1.5 cm^3 and a tympanometric width between 50 to 110 daPa (ASHA, 1990). Alongside this, acoustic reflex thresholds were also obtained using a BBN stimulus. This testing was done for both ears of each participant, and both contralateral and ipsilateral measurements were taken. A threshold was identified at the lowest intensity level that elicited at least a 0.02 mmho change in admittance on two separate occasions (Hunter & Shanaz, 2013). This followed the standard clinical procedure used for ASR measurements which included a check for growth and absence of the reflex at lower intensity levels.

The final part component of the hearing assessment was pure-tone audiometry. A Grason-Stadler Audiostar Pro audiometer was used for this assessment. ER-3A insert earphone transducers were used with 13mm foam tips. The participants were provided with a button to indicate they heard the sound in their ears. Both ears of the participants were tested separately. This was done for frequencies between 250 Hz and 8 kHz. The initial presentation level was 30 dB HL which was decreased by 10 dB HL if the participant successfully heard the tone and increased by 5 dB HL if they did not (Carhart & Jerger, 1959). A screening method was used where the lowest intensity level evaluated was 15 dB HL. Two out of three responses obtained at this level would indicate that the participant had hearing within the normal range (Carhart & Jerger, 1959).

3. Part Two: Baseline or Pre-Training Measurements

3.1. Speech-in-Noise Assessments

3.1.1. Word Recognition-in-Noise Test (WINT)

One of the first tests done as part of the pre-training measurements was the Word Recognition-in-Noise Test (WINT). This test was done to evaluate participants' SIN perception with words presented in noise. These types of tests have been shown to be effective in the literature in auditory training-based studies and are an efficient way to measure an individual's SIN perception (Burk et al., 2006). Furthermore, these types of tests allow for stimuli to be set at specific SNRs, and therefore, allow for an assessment of an individual's ability to perceive the stimulus with varying levels of noise (Wilson, 2011). The stimulus used for this test was Meaningful Consonant-Vowel-Consonant words (CVC). These words are monosyllabic, arranged in lists and are composed of three phonemes arranged as a consonant-vowel-consonant (Wilson, Arcos, & Jones, 1984). The scoring for this test is based on the components of the word the participant got correct and can be scored either 0, 3, 7 or 10 out of 10 for each word.

The participants were set up with two Dell laptops and a Grason-Stadler Audiostar pro audiometer. One laptop was set to provide the BBN stimulus at 60 dB SPL through ER-3A insert earphones coupled with a 13mm foam tip to the left ear. The other laptop provided a 60 dB SPL BBN stimulus through the second channel of the audiometer, alongside the CVC words to the right ear using the same type of transducer. As the audiometer dial provided intensities in dB HL, these were converted to dB SPL using the IEC 60645-2 1997 standard RSPL for speech to ensure accurate SNR stimuli were being provided. Lists 5-12 of the built-in CVC lists were used at a randomly assigned SNR in a random order. These SNRs were +12, +8, +4, 0, -4, -8, -12, -16 with one practice list at +16 SNR. Before the presentation of the CVC lists, the BBN stimulus was presented for two seconds to ensure activation of the MOCR (Boothalingam, Goodman, MacCrae, & Dhar, 2021). Instructions to the participants were provided, which asked for them to repeat (or guess if needed) the words they heard. The scoring for each word was done with the scores mentioned above. The total WINT score was calculated by taking the sum of the scores of each word in one list (specific SNR). This allowed for the change in WINT score to be calculated by subtracting the pre-training total WINT score from the post-training measurement. This provided an evaluation of how the participant performed following the training programme.

3.1.2. Quick Speech-in-Noise Test (QuickSIN)

Another test done to evaluate participants' SIN perception was the QuickSIN Test. This test has been shown to be effective in evaluating SIN perception in individuals alongside MOC activity. Therefore, it provides a good measurement to assess training effects (Greaves, 2018). The QuickSIN test is a list of sentences, each with five keywords that are embedded in multi-talker babble. Each sentence in the list has a different SNR, starting at 25 and decreasing to 0 (Greaves, 2018; Killion, Niquette, Gudmundsen, Revit, & Banerjee, 2004). This again provides a way to assess participants' ability to perceive SIN for varying levels of noise. Each keyword is scored one mark totalling to a maximum of 30 marks. Each list then provides an SNR loss which indicates how much louder the stimulus must (in dB) be for it to be heard in noise. This is also believed to be quite accurate (within 2.7 dB), as has been shown through research (Killion et al., 2004).

The participants were set up with a Grason-Stadler Audiostar pro audiometer. The built-in QuickSIN lists were used and delivered through ER-3A insert earphones coupled with a 13mm foam tip to the right ear. The audiometer dial was set to 70 dB HL, and each list presented the stimuli in varying SNRs. This was carried out for three lists, each with six sentences. Instructions to the participants were provided, which asked for them to repeat (or guess if needed) the words they heard in each sentence. The scoring for each list was done with the scoring mentioned above. The total score in one list was subtracted from 25.5 to provide the SNR loss. The average SNR loss across the three lists provided the mean SNR loss. This mean SNR loss from the pre-training measurements was subtracted from the post-training measurement to show the change in SNR loss for each participant after training. This provided an evaluation of how the participant performed following the training programme.

3.2. Medial Olivocochlear Activity Measurements

3.2.1. DPOAE Measurements

DPOAE measurements were undertaken on each participant as a measure of MOC activity. Research has shown for there to be MOCR related suppression of DPOAE amplitudes with CAS; therefore, this measurement was undertaken. It has been widely used in literature and has proved effective in various studies (James, Harrison, Pienkowski, Dajani, & Mount, 2005; Konomi, Kanotra, James, & Harrison, 2014). Research suggests that primaries within the range of 55-65 dB SPL provide the greatest accuracy when undertaking these measures. Primary levels that are louder may not, in fact, reflect cochlear amplifier activity, and therefore, may not be accurate (Caroline Abdala & Visser-Dumont, 2001). Furthermore, a frequency separation ratio of 1.2 and a level difference of 10 dB between the two tones are believed to provide the largest amplitudes of DPOAEs. (Caroline Abdala & Visser-Dumont, 2001). As per recommended guidelines, an SNR of 6 dB was required for the responses to be accepted to ensure accuracy of the responses obtained (McCreery, 2013).

The participants were set up with an Interacoustics Titan system coupled to a Dell computer. This computer ran the Titan Suite software, which was used to measure the DPOAEs from the participants. The probe was placed in the right ear of participants, with an ER-3A insert transducer coupled with a 13mm foam tip placed in the left ear. This was connected to a Dell laptop which provided the 60 dB SPL BBN stimulus. This was played for two seconds before the 'with CAS' DPOAE measurements were taken. A ten-second interval was provided between 'with' and 'without' CAS measurements to ensure the MOCR was not actively affecting responses (Boothalingam et al., 2021). The level of the primaries was L1=65 dB SPL and L2= 55 dB SPL. The frequency separation ratio was 1.22. The frequencies tested were between 500 Hz and 8000 Hz, logarithmically arranged to create 24 frequencies for DPOAE testing. Two measurements were taken for each participant: a 'without CAS' and a 'with CAS' measurement. DPOAE suppression was calculated by subtracting the DPOAE response amplitudes with CAS from the DPOAE response amplitudes without CAS for the frequencies tested. This was done for the pre-training and post-training measurements. The change in DPOAE suppression was calculated by subtracting the pre-training suppression values from the post-training suppression values.

3.2.2. ABR Measurements

ABR measurements were undertaken on each participant as a measure of MOC activity. Research has shown for there to be MOCR related suppression of ABR waveform amplitudes with CAS; therefore, this measurement was undertaken. There have been prior studies that have evaluated these effects, showing the effectiveness of ABRs as a measure (Chabert et al., 2002; Folsom & Owsley, 1987; Lichtenhan et al., 2016). In specific, this study focusses on wave I amplitudes as they are believed to be correlated to auditory nerve activity, and research has suggested a reduced firing rate in AN fibers as a result of CAS (Berger & Blum, 2007; de Boer et al., 2012). Therefore, being effective in measuring MOC activity and evaluating the potential mechanism.

The ABR measurements were conducted using the Interacoustics Eclipse EP25 system. The participants were instructed to remain still and quiet during the measurement procedure. The electrode placement sites were cleaned with alcohol wipes, and Nuprep skin preparation gel was applied to these sites. The active electrodes were placed on the high forehead, with the common electrode being placed on the low forehead, ensuring there was sufficient distance between the two electrodes. A reference electrode was placed on the left mastoid. The right ear electrode was a TipTrode which was connected to the insert earphone transducers to deliver the stimulus and recorded through an alligator clip cable which contacted the gold foil of the TipTrode itself. Impedance values were required to be 5 kiloohms or lower to be accepted. For the TipTrodes, research has suggested impedance values below 20 kiloohms to also be acceptable (Interacoustics, 2016). Two measurements were taken for each participant: a 'without CAS' and a 'with CAS' measurement, with each repeated twice to check for the reliability of the results. An ER-3A insert transducer coupled with a 13mm foam tip was placed in the left ear. This was connected to a Dell laptop which provided the 60 dB SPL BBN stimulus. This was played for two seconds before the 'with CAS' ABR measurements were taken. A ten-second interval was provided between 'with' and 'without' CAS measurements to ensure the MOCR was not actively affecting responses (Boothalingam et al., 2021). The testing parameters used are provided in Table 1. ABR suppression was calculated by subtracting the ABR wave I response amplitude with CAS from the ABR wave I response amplitude without CAS. This was done for the pre-training and post-training measurements. The change in ABR suppression was calculated by subtracting the pre-training suppression values from the post-training suppression values.

Table 1: Table showing the parameters used for ABR measurements.

Parameter	Values Used
Stimulus Type	LS CE-Chirp
Stimulus Level	80 dB
Stimulus Rate	11.1/s
High and Low Pass Filters	10 Hz to 3000 Hz
Waveform Sampling	40 kHz over 25.6 ms epoch
Averaging	2000 averages with an option to go to 4000 if needed.
Artifact Reject	20-25 microvolts

Table 1 shows the parameters used for the ABR measurements conducted. These parameters have been selected based on research outlined in Section 6.1.1, as well as experimentation with varying parameters to identify those that provide the most accurate and reliable results.

4. Part Three: Speech-in-Noise Auditory Training Programme

The SIN auditory training programme used in this study has been kept the same as that used in a previous study (Bhattacharya, 2020). This training programme was designed and implemented to elicit auditory-training related changes in SIN perception ability relating to MOC activity. This auditory training programme used monosyllabic words as the stimulus for the training. Previous research in this area has used varying forms of stimuli. However, monosyllabic words are believed to show effective results with auditory training. Furthermore, the effects of the auditory training on MOC related activity and SIN perception are also speculated to be affected by the stimuli chosen (Mertes et al., 2019; Mertes, Wilbanks, & Leek, 2018). The specific stimuli used for this study were Northwestern University Auditory Test No.6 (NU-6) and the Central Institute for the Deaf (CID) W-22-word lists. Each list is comprised of 50 words, totalling to 200 words in total for each of the NU-6 and the CID W-22 words (Thomson, 2002).

This auditory training programme was conducted over five days using a staircase method. This staircase method is suggested to provide an SNR of which intensities higher result in correct responses 50% of the time (Cornsweet, 1962). The participants were set up with two Dell laptops and a Grason-Stadler Audiostar pro audiometer. One laptop was set to provide the BBN stimulus at 60 dB SPL through ER-3A insert earphones coupled with a 13mm foam tip to the left ear. The other laptop provided a 60 dB SPL BBN stimulus through the second channel of the audiometer, alongside the NU-6 and/or CID W-22 words (built-in) to the right ear using the same type of transducer. As the audiometer dial provided intensities in dB HL, these were converted to dB SPL using the IEC 60645-2 1997 standard RSPL for speech to ensure accurate SNR stimuli were being provided. Before the presentation of the word lists, the BBN stimulus was presented for two seconds to ensure activation of the MOCR (Boothalingam et al., 2021). Instructions to the participants were provided, which asked for them to repeat (or guess if needed) the words they heard. The initial presentation was at 65 dB SPL, which correlated to a +5 SNR. If the participant repeated an incorrect word, the intensity was increased by 1 dB and alternatively was reduced by 1 dB if they got the word correct (Cornsweet, 1962). After each word, the participant was shown the correct word on a separate laptop. In addition to this, the word was also repeated for the participant if they had repeated it incorrectly. This has been shown to be effective in auditory training and learning (Olson, 2015). This staircase method was conducted for 25 words in each staircase. The first and fifth days of training saw eight staircases be completed, whereas ten staircases were completed for the days in between. This was scored by calculating the mean of the intensities during the last four reversals of each staircase, which provided the word recognition threshold (WRT) presented in the form of an SNR (Cornsweet, 1962). Averaging all the WRTs across the staircases for one day provided the mean WRT. The change in WRT was calculated by subtracting the mean WRT of the fifth day of training from the first day of training to show changes in SIN perception.

5. Part Four: Post-Training Measurements

The post-training measurements were undertaken on the fifth day of the study. These included: WINT, QuickSIN testing as well as DPOAE and ABR measurements. These were conducted in the same manner as outlined in the previous sections of these methods.

6. Statistical Analysis

The data obtained through the study was statistically analyzed and presented in the results section below. The analysis conducted included a variation of inferential and descriptive statistical methods. The statistical analysis methods used included repeated-measures ANOVA as well as Pearson correlation analysis. Furthermore, some forms of descriptive statistical methods have also been used. The statistical analysis was conducted using the SPSS software.

Results

1. Hearing Assessment

Table 2: Table showing the ipsilateral and contralateral acoustic reflex thresholds for participants in both treatment and control groups.

Group	**Participant**	**Right Ipsilateral (dB HL)**	**Right Contralateral (dB HL)**	**Left Ipsilateral (dB HL)**	**Left Contralateral (dB HL)**
Treatment	1	80	80	70	85
	2	70	75	70	75
	3	85	85	80	85
	4	70	70	70	70
	5	75	75	75	70
	6	75	75	70	85
Control	1	70	75	70	75
	2	70	75	70	70
	3	75	80	75	80
	4	70	70	70	75

2. Speech-in-Noise Perception and the Auditory Training Programme

2.1. Word Recognition Thresholds (WRTs)

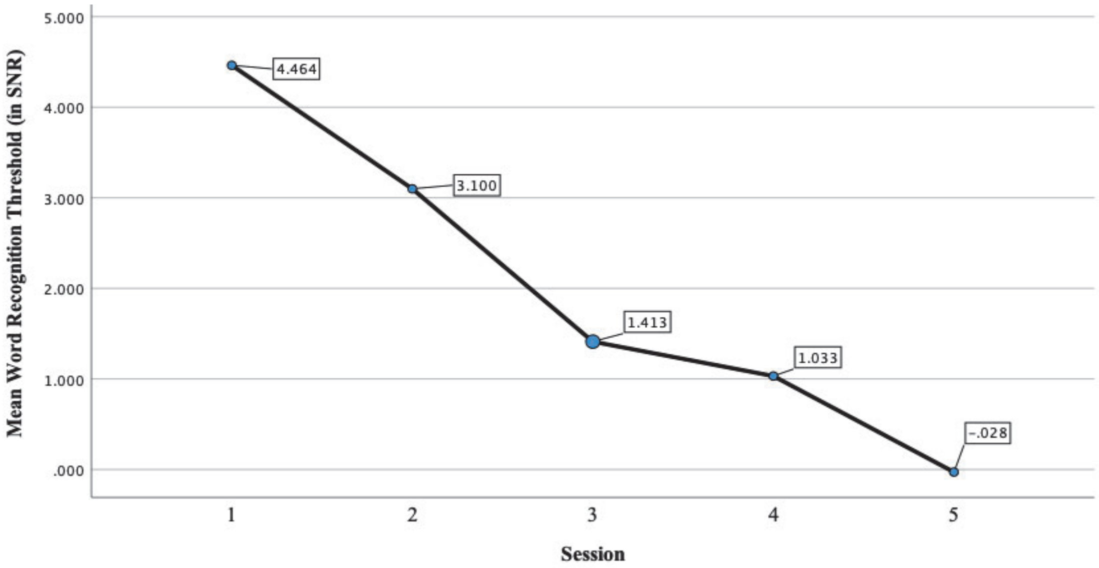


Figure 2: Figure showing the mean WRTs (in SNR) in each session for the participants having undergone the auditory training programme.

Figure 2 shows that, on average, the WRTs improved over the five-day auditory training programme. This is shown through a mean WRT of 4.46 SNR (SD = 1.48) on the first day, decreasing to -0.03 SNR (SD = 1.12) on the fifth day of training. This shows that the participants, on average, were able to perform better on the task (lower SNR). There was also an improvement seen throughout the training programme each day. These results were deemed statistically significant using a repeated measures ANOVA with a Greenhouse-Geisser correction, F(1.854, 9.272) = 25.545, p = <0.001.

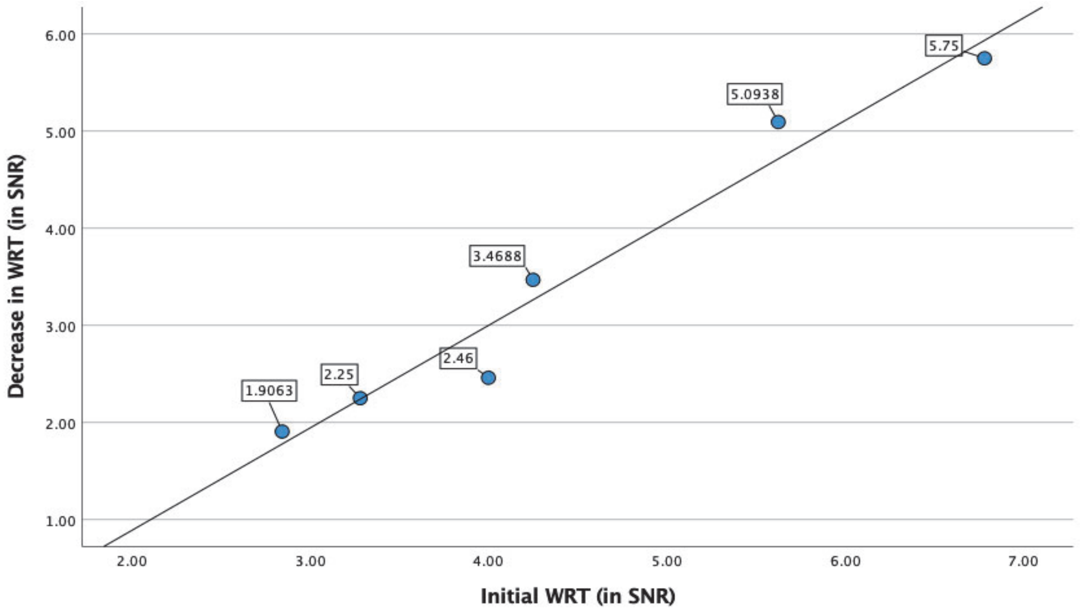
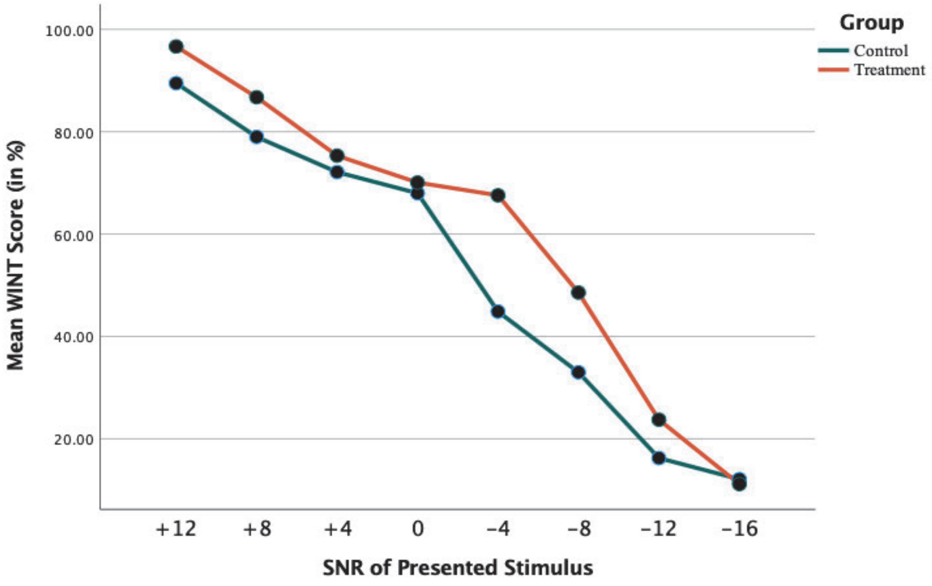


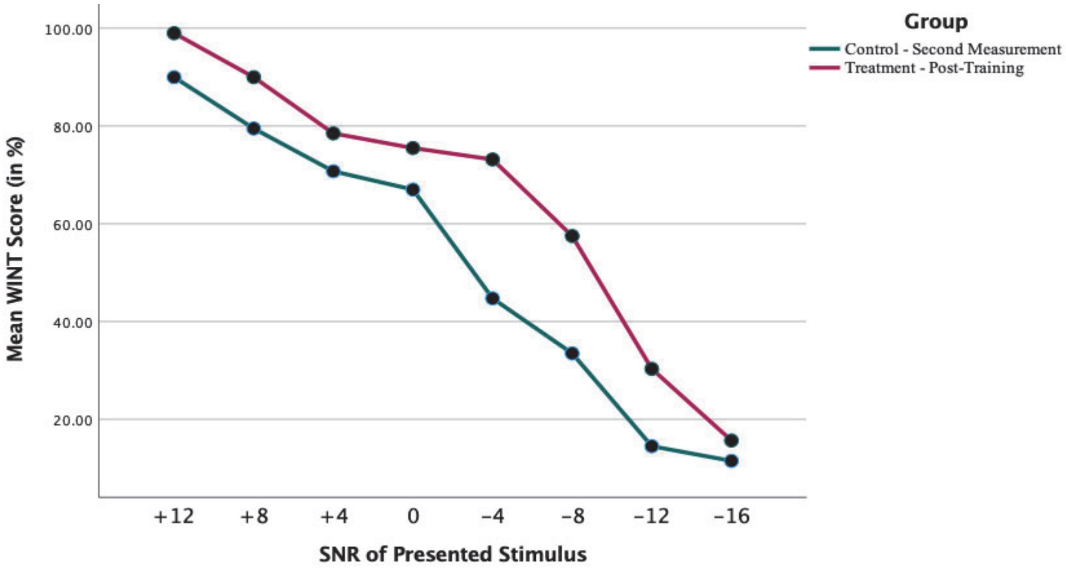
Figure 3: Figure showing the initial mean WRTs (in SNR) for each participant and the corresponding decrease in mean WRTs (in SNR) observed when comparing the last day of auditory training to the first.

Figure 3 shows that there is a strong positive association between the initial mean WRT and the mean reduction in WRT when comparing the fifth day of auditory training to the first. This shows that participants who performed relatively poorer on the first day saw a greater reduction in mean WRTs on the last day of auditory training, indicating greater improvement. These results were analyzed using Pearson's Correlation and are statistically significant, $r(4) = 0.98$, $p = <0.001$.

2.2. <u>Word Recognition-in-Noise Test (WINT)</u>



<u>Figure 4:</u> Figure showing the presented stimulus (in SNR) and the corresponding mean WINT scores (in %) observed when comparing the control group to the treatment group.



<u>Figure 5:</u> Figure showing the presented stimulus (in SNR) and the corresponding mean WINT scores (in %) observed when comparing the second measurement of the control group to the post-training scores of the treatment group.

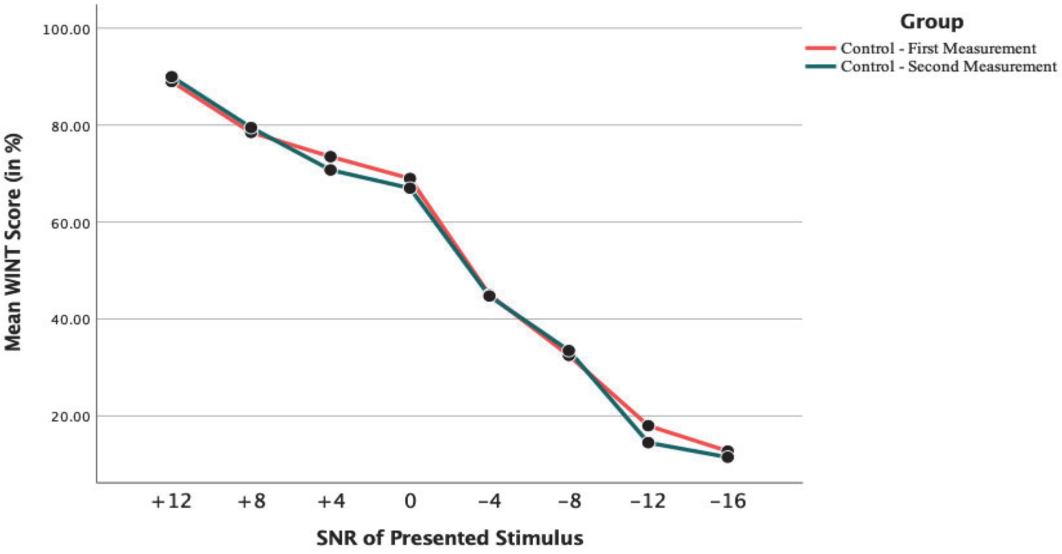


Figure 6: Figure showing the presented stimulus (in SNR) and the corresponding mean WINT scores (in %) observed when comparing the first and second measurements of the control group.

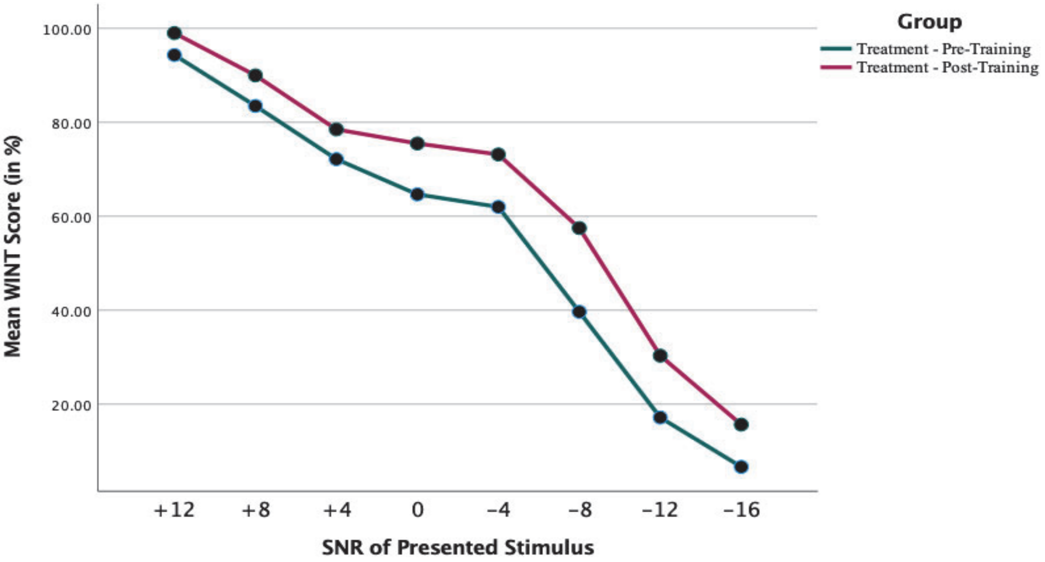


Figure 7: Figure showing the presented stimulus (in SNR) and the corresponding mean WINT scores (in %) observed when comparing the pre- and post-training measurements of the treatment group.

The WINT results were analyzed to assess participants' SIN perception when taking into consideration the auditory training programme. Repeated measure ANOVAs were used to analyze these results. Figure 4 showed a significant interaction (F(7, 126) = 5.88, p = <0.001) which indicated that the mean WINT scores varied by group (control and treatment). Further analysis indicated no significant interaction between the first measurement of the control group and pre-training measurements in the treatment group (F(14, 119) = 1.46, p = 0.135), indicating no significant difference in mean WINT scores between the two groups prior to training (first measurement). Figure 5 showed a further analysis where a significant interaction was shown between the second measurement of the control group and post-training measurements in the treatment group (F(14, 119) = 1.90, p = 0.033). This showed that there was a difference in mean WINT scores for the participants who underwent the training programme compared to those who did not. Furthermore, figure 6 showing no significant interaction (F(2, 17) = 2.15, p = 0.147) and figure 7 showing a significant interaction (F(14, 119) = 3.54, p = <0.001) indicate for there to be improvements in mean WINT scores for those who underwent training, compared to those who did not. These improvements can be seen in figure 7, across all the SNRs measured, where it can be seen that participants who underwent auditory training saw improvements following the auditory training programme.

2.3. Quick Speech-in-Noise Test (QuickSIN)

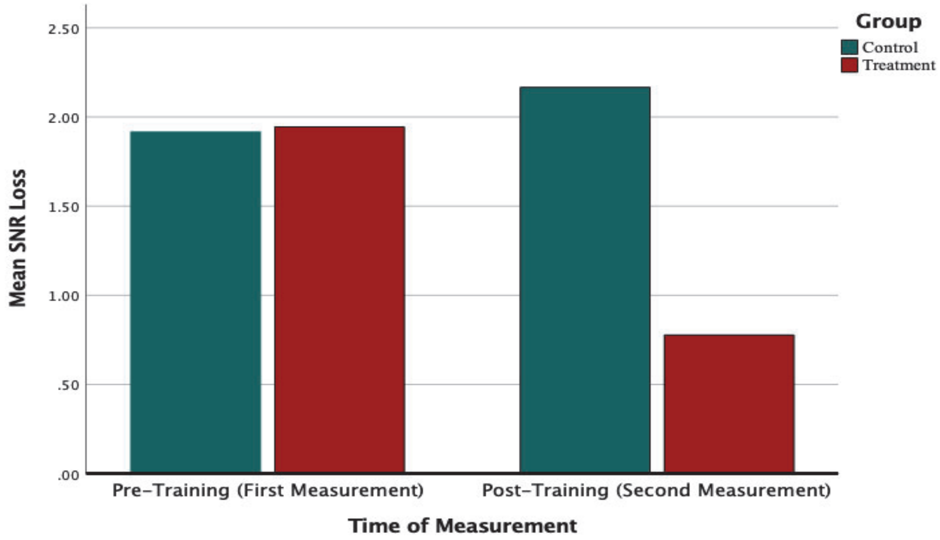


Figure 8: Figure showing the mean SNR loss for participants in the control and training groups as measured before and after the auditory training programme (first and second measurement for the control group).

Figure 8 shows the results of the QuickSIN tests. These results were analyzed using a repeated measures ANOVA and showed a significant interaction (F(1, 8) = 13.21, p = 0.007). This indicates a difference in mean SNR loss shown through the QuickSIN test between the control and treatment groups. Further analysis showed a significant difference in the mean SNR loss for the treatment group when comparing the pre-training measurement to the post-training measurement (F(1,5) =

15.64, p = 0.011). The mean SNR loss decreased from 1.94 (SD = 1.39) to 0.78 (SD = 1.02), indicating improvement following the auditory training programme. Comparatively, no significant difference in mean SNR loss was identified for the control group through the statistical analysis (F(1, 3) = 2.45, p = 0.215).

3. DPOAEs and the Auditory Training Programme

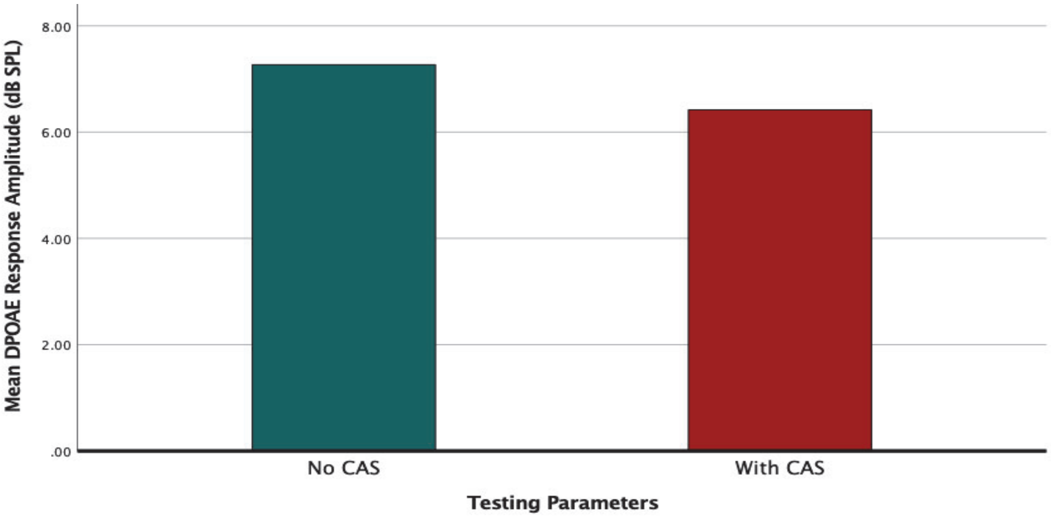


Figure 9: Figure showing the mean DPOAE response amplitudes (in dB SPL) for all participants with and without contralateral acoustic stimulation (CAS).

Statistical analyses on DPOAE results indicated no significant effects of group (control or treatment) or when the measurements were taken (pre- or post-training) (F(3, 16) = 1.07, p = 0.389). This indicated that average DPOAE response amplitudes did not significantly change with the auditory training programme. Further analysis (shown in figure 9) reflected a significant change in mean DPOAE response amplitudes when comparing measurements taken without CAS and with CAS (F(1, 19) = 25, p = <0.001). This showed for there to be a suppression of mean DPOAE response amplitudes from 7.27 dB SPL (SD = 3.22) without CAS to 6.42 dB SPL (SD = 3.11) with CAS.

4. ABR Wave I Responses and the Auditory Training Programme

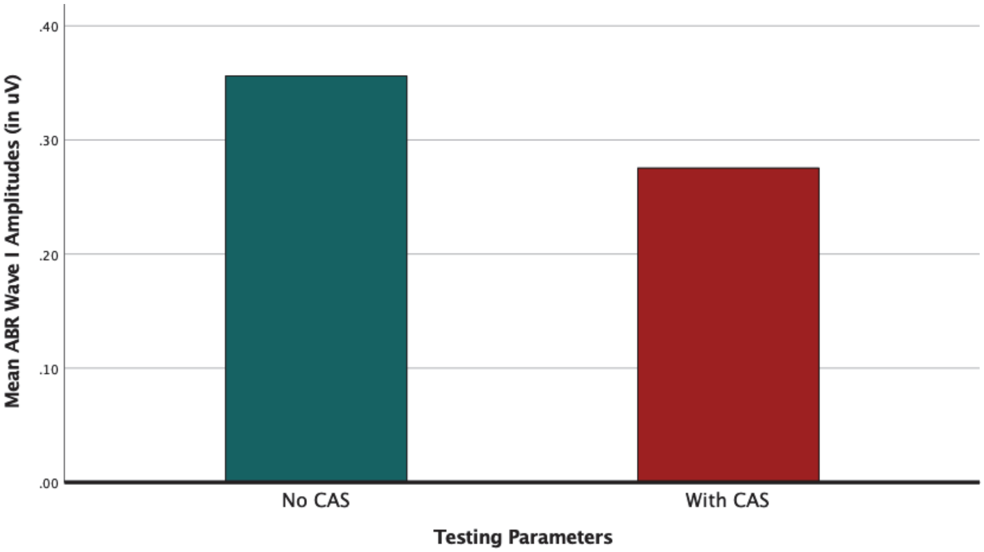


Figure 10: Figure showing the mean ABR Wave I response amplitudes (in uV) for all participants with and without contralateral acoustic stimulation (CAS).

Statistical analyses on ABR results indicated no significant effects of group (control or treatment) or when the measurements were taken (pre- or post-training). These analyses were also conducted within each group; however, no significant results were obtained. This indicated that average ABR wave I response amplitudes did not significantly change with the auditory training programme. Further analysis (shown in figure 10) reflected a significant change in mean ABR wave I response amplitudes when comparing measurements taken without CAS and with CAS (F(1, 19) = 14.87, p = <0.001). This showed for there to be a suppression of mean ABR wave I response amplitudes from 0.36 uV (SD = 0.10) without CAS to 0.28 uV (SD = 0.08) with CAS.

5. Change in Physiological Suppression and SIN Perception

5.1. *Word Recognition-in-Noise Test (WINT)*

A statistical analysis was carried out to evaluate any potential correlation between changes in total WINT scores (in %) and changes in DPOAE suppression for each participant. These findings showed no significant results for either treatment (r(4) = 0.12, p = 0.88) or control group (r(2) = 0.25, p = 0.63). This indicates that changes in WINT scores were not correlated to changes in DPOAE suppression. Similar findings were obtained for ABR results (r(4) = -0.67, p = 0.15) and r(2) = -0.86, p = 0.14, respectively), indicating that changes in WINT scores were not correlated to changes in ABR wave I suppression.

5.2. *Quick Speech-in-Noise Test (QuickSIN)*

A statistical analysis was also carried out to evaluate any potential correlation between changes in SNR loss (in SNR) as measured through the QuickSIN Test and change in DPOAE response amplitude suppression for each participant. These findings showed no significant results for either treatment (r(4) = 0.58, p = 0.23) or control group (r(2) = -0.88, p = 0.12). This indicates that changes in WINT scores were not correlated to changes in DPOAE suppression. Similar findings were obtained for ABR results (r(4) = 0.05, p = 0.92) and r(2) = 0.40, p = 0.60, respectively), indicating that changes in WINT scores were not correlated to changes in ABR wave I suppression.

6. Additional Analyses

6.1. *Absolute Physiological Suppression and SIN Perception*

Additionally, analyses were also conducted on absolute suppression of DPOAE response amplitudes and ABR wave I amplitudes and any related correlation to SIN perception as measured through WINT and QuickSIN tests. Analysis of total WINT scores and absolute suppression of DPOAE response amplitudes for each participant showed no significant results. This was true for pre-training (first measurement) conditions for both treatment (r(4) = 0.37, p = 0.48) and control groups (r(2) = -0.12, p = 0.88). Similarly, post-training results for both groups showed no significant results (r(4) = -0.07, p = 0.88) and r(2) = -0.08, p = 0.90, respectively). Similar results were obtained when analyzing absolute suppression of ABR wave I response amplitudes and total WINT scores, for both pre-training (r(4) = 0.44, p = 0.38) and r(2) = 0.34, p = 0.66, respectively) and post-training measurements (r(4) = 0.13, p = 0.81) and r(2) = 0.57, p = 0.43, respectively).

Similar results were found for QuickSIN measurements, indicating no significant correlation between absolute ABR and DPOAE suppression and SNR loss. This was seen for pre-training (first measurement) conditions for both treatment (r(4) = 0.09, p = 0.86) and control groups (r(2) = 0.02, p = 0.98). Similarly, post-training results for both groups showed no significant results (r(4) = -0.32, p = 0.53) and r(2) = 0.15, p = 0.85, respectively). Similar results were obtained when analyzing absolute suppression of ABR wave I response amplitudes and SNR loss, for both pre-training (r(4) =

0.20, p = 0.70) and r(2) = 0.19, p = 0.81, respectively) and post-training measurements (r(4) = 0.43, p = 0.85) and r(2) = 0.73, p = 0.28, respectively).

Analyzing both treatment and control groups together for pre-training and post-training measurements also showed no significant relationships for DPOAE and ABR suppression measurements in relation to the WINT and QuickSIN test. These results show no significant correlation or relationship between absolute ABR and DPOAE suppression and SIN perception as measured through the WINT and QuickSIN test.

6.2. Physiological Suppression and SIN Perception: First Measurement

An additional analysis was carried out to evaluate if there was a correlation between the DPOAE and ABR wave I response amplitude suppression observed on the first day with changes seen in SIN perception as measured through the WINT and QuickSIN test for the treatment group. This analysis showed no significant results for a correlation between DPOAE suppression and change in total WINT score (in %) (r(4) = -0.001, p = 0.99) or for changes in SNR loss (r(4) = 0.44, p = 0.38). Similarly, the correlation between ABR wave I suppression and change in total WINT score (in %) (r(4) = 0.08, p = 0.89) and changes in SNR loss (r(4) = -0.14, p = 0.79), showed no significant results. These results indicate for there to be no significant relationship between DPOAE and ABR wave I response suppression measured on the first day and the improvements seen in SIN perception following the auditory training programme.

Discussion

1. Summary of Results

The findings of this study reflected improvements in SIN perception for individuals that underwent the auditory training programme. There were improvements seen on each day of training, further reflecting the effectiveness of the auditory training programme. This was seen through improvements in participants' WRTs that used monosyllabic words masked with a BBN stimulus. Furthermore, the WINT and QuickSIN results showed a similar improvement in SIN perception for those participants that underwent auditory training compared to those who did not.

DPOAE measurements reflected suppression of response amplitudes across both groups when measurements were taken with the presence of CAS compared to without. However, the results did not indicate changes in DPOAE response amplitude suppression with the auditory training programme. Similar results were found for ABR measurements. Although there was an observed suppression in ABR wave I amplitudes when measured with the presence of CAS compared to without, there were no significant changes in suppression with the auditory training programme.

The findings also do not reflect any significant correlation between DPOAE and/or ABR suppression and the changes seen in SIN perception, as measured through the WINT and QuickSIN test. This was evaluated for both changes in suppression and absolute suppression values. Both analyses found no significant correlation. Additionally, the results did not indicate a significant correlation between the initial suppression observed in DPOAE and ABR measurements and the improvements seen in SIN perception, as measured through the WINT and QuickSIN test.

2. Auditory Training-Induced Improvements in SIN Perception

Improvements were seen in participants' ability to perceive SIN. This was shown through both WINT and QuickSIN tests that measured performance before and after training and reflected improvements in the group that underwent auditory training. The control group did not reflect any significant changes in SIN perception between their two measurements. These findings were consistent with those hypothesized in this study. Furthermore, these findings are also generally consistent with those obtained in the previous study conducted on this topic. Although, there were contrasting results obtained for the QuickSIN test, which will be discussed further in section 3.2 (Bhattacharya, 2020). Additionally, the WRTs obtained across the five days of auditory training also reflect similar results. Improvements were seen on each day of the training programme. These findings are also consistent with those hypothesized in this study and those found in the previous study (Bhattacharya, 2020). These findings are also supported by the literature, which shows improvements in SIN perception following a period of auditory training (de Boer & Thornton, 2008; Mertes et al., 2019; Song et al., 2012). However, these findings are shown to be, in some cases, dependent on the stimuli and the perceptual tasks used (Amitay, Hawkey, & Moore, 2005; de Boer & Thornton, 2008; Mertes et al., 2019; Song et al., 2012). Furthermore, although improvements were seen in SIN perception following the auditory training programme, some studies show that these improvements are restricted to the stimuli used for the training programme. Therefore, extrapolating this information to more naturalistic environments can be difficult to assume (Burk et al., 2006; Karawani et al., 2016; Song et al., 2012).

Additionally, an improvement in WRTs was seen on each day of the training programme in this study, similar to the previous study on this topic (Bhattacharya, 2020). This leads to an assumption that longer periods of auditory training could result in proportional improvements in SIN perception. Although this could be seen, other studies have shown that shorter periods of auditory training result in more effective improvements in perceptual learning (Barlow, Purdy, Sharma, Giles, & Narne, 2016; Henshaw & Ferguson, 2013). These studies show that extended periods of auditory training have similar outcomes to those conducted for shorter periods of time. Therefore, providing uncertainty to any expected changes with longer periods of auditory training (Barlow et al., 2016; Henshaw & Ferguson, 2013).

Furthermore, an additional analysis evaluating initial mean WRTs for participants and the improvement seen across the training programme reflected a positive correlation. This meant that individuals who performed relatively poorer on the first day saw a greater reduction in mean WRTs on the last day of auditory training, indicating greater improvement. This was also consistent with the earlier study (Bhattacharya, 2020). This finding has also been shown through the literature (Amitay et al., 2005; de Boer & Thornton, 2008). The mechanisms underlying these results are difficult to interpret as these findings could be a result of multiple interconnecting factors. However, a speculated mechanism that could explain these results relates to brain plasticity (Feng et al., 2018). Individuals who initially performed worse on the WRT task could see a greater range for them to improve with training compared to those who performed relatively better. This could be due to plasticity-related effects that allow for greater neurophysiological changes with training that underlie greater levels of relative improvement (Feng et al., 2018).

An important consideration in this study is the stimuli used for the WRT measurements during the training programme. As described above, 400 words were used as the stimuli for the WRT measurements. Due to the nature of this testing and the limited number of words available, some measurements were taken with a repeating set of words. However, it is unlikely that this played a role in the results that were obtained. Research has shown that the auditory information an individual can retain is restricted in instances where the stimuli is presented continually, with the duration between the stimuli being short. Furthermore, multiple lists of words and the absence of knowing when the list will end have also been shown to make the remembrance of words difficult for individuals (N. Cowan, 2001; Nelson Cowan, 2010; Tehan & Turcotte, 2002). For this study, as the words were presented with short duration intervals and were separated into lists of 25 words, which were presented randomly on any given day. Memory-related effects on the results obtained are unlikely. Furthermore, improvements in other measurements, such as the WINT and QuickSIN test which would be less affected by these memory affects, further provide evidence for the auditory-training related improvements in SIN perception.

3. WINT and QuickSIN Test

3.1. Word Recognition-in-Noise Test (WINT)

This study shows that were improvements in participants' SIN perception following the auditory training programme. This was seen through an improvement in WINT scores, as hypothesized. These findings are also consistent with the previous study on this topic (Bhattacharya, 2020). When considering the performance of participants across the range of SNRs measured during the WINT test, the findings from this study reflect slight differences from that of other studies. Some studies have shown greater improvement in SIN perception at intermediate SNRs, whereas others have shown greater improvements at the most challenging SNRs tested (Giraud et al., 1997; Kumar & Vanaja, 2004). Additionally, the study conducted by Bhattacharya (2020) showed minimal improvements for the least challenging SNRs. However, the results from this study show an improvement in WINT scores across all SNRs following the period of auditory training. This contradicts the explanation surrounding 'ceiling effects' provided in the previous study, as both studies show a similar measure for pre-training scores at those least challenging SNRs. This therefore, shows that the amount of improvement was not, in this case, restricted by the test (Bhattacharya, 2020). However, the findings of this study do show slightly greater improvement in more challenging SNRs, which could be explained by the potential effects of the MOCR and greater effectiveness at these SNRs compared to higher SNRs (Kumar & Vanaja, 2004; Mertes et al., 2019).

3.2. Quick Speech-in-Noise Test (QuickSIN)

The findings of this study also showed an improvement in SIN perception following the auditory training programme when measured through the QuickSIN test. These results were consistent with those hypothesized. Previous studies have shown for the QuickSIN test to be an effective measure of SIN perception and is able to provide accurate results (Killion et al., 2004; Sharma, Tripathy, & Saxena, 2017; Song et al., 2012; Yund & Woods, 2010). The accuracy is believed to be within 1.6 dB of the true thresholds, further reflecting its effectiveness (Killion et al., 2004). Furthermore, the QuickSIN test has also been shown to be more effective when compared to tests that provide percentage scores. These tests are believed to be limited by floor and ceiling effects, which is a limitation that is overcome with a test such as the QuickSIN test (Duncan & Aarts, 2006; Sultan, Mahallawi, Kolkaila, & Lasheen, 2020). The findings of this study are consistent with other studies that have shown improvements in QuickSIN results following a period of auditory training (de Boer & Thornton, 2008; Song et al., 2012). However, these findings are inconsistent with the previous study on this topic. The previous study found no significant improvement in QuickSIN performance following the auditory training programme. These results were especially inconsistent as the other measurements indicated improvements in SIN perception following the auditory training period (Bhattacharya, 2020). These results could be attributed to a couple of factors. Research shows that the QuickSIN test can be affected by factors such as memory, cognition and other linguistic factors due to the stimulus involving longer sentences compared to single word tests (Le Prell, 2018). Therefore, there is a possibility that the results obtained in the previous study could have been impacted by these factors, which did not allow for an accurate depiction of participants' SIN performance. Furthermore, the small sample size could have also contributed to the results obtained by not showing a significant improvement across the small sample. Therefore, this potentially indicates why there could be inconsistencies with the previous study (Bhattacharya, 2020).

These WINT and QuickSIN results indicate that there were significant improvements in SIN perception following the auditory training programme.

4. Physiological Mechanisms

4.1. Study Findings

This study hypothesized that changes seen in SIN perception with the auditory training programme could be correlated to and explained by changes seen with MOC system activity. Namely, changes in DPOAE response amplitude and ABR wave I amplitude suppression were theorized to show an increase in MOC system activity following the auditory training programme. This is due to the design of the auditory training programme, which was, in ways, stimulating the MOC system throughout the training period. Additionally, studies have shown plasticity in the MOC system, indicating an ability for change to occur (Brown et al., 1998; Illing et al., 2000; Romero & Trussell, 2021). However, the findings of this study were contradictory to those theorized. The findings reflected no significant relationship between changes in MOC activity, as measured through DPOAE and ABR amplitude suppression following the auditory training programme, and improvements seen in SIN perception. This indicates a potential for other underlying physiological mechanisms that could have mediated the improvements seen in SIN perception following the auditory training programme. These findings are consistent with the previous study on this topic (Bhattacharya, 2020).

Contrastingly, the findings of this study are inconsistent with some other studies in the literature. These studies show a relationship between MOC activity and SIN perception following a period of auditory training (de Boer & Thornton, 2008; de Boer et al., 2012). These findings were attributed to potential antimasking effects, which aided SIN perception mediated by MOC system activity. This was further shown through animal studies which showed that lesions in the MOC system impaired vowel discrimination (Dewson, 1968; Mertes et al., 2019). However, research also shows inconsistencies with these findings (Mertes et al., 2019). Studies conducted in human models have shown there to be no significant differences in SIN perception between control groups and groups of individuals who have undergone unilateral vestibular neurectomy. This resulted in a loss of MOC activity, which did not seem to affect SIN perception (Mertes et al., 2019; Scharf et al., 1997). Furthermore, studies conducted in animals have also shown the effects of morphological elimination of the MOC efferent fibers (Igarashi, Alford, Nakai, & Gordon, 2009; Mertes et al., 2019; Trahiotis & Elliott, 1970). One study in cats showed no changes in varying tasks, such as those involving varying SNRs as well as behavioral auditory thresholds (Igarashi et al., 2009). These findings, therefore, show that alternative mechanisms could be underlying the changes seen in SIN perception with auditory training, as seen in this study.

4.2. <u>Central Mechanisms: Cortical, Subcortical and Corticofugal Connections</u>

An important consideration underlying the plasticity of the MOC system is the involvement of central mechanisms. As an alternative mechanism for the changes seen in SIN perception with auditory training, central mechanisms are believed to be the most important. Studies have shown there to be changes in corticofugal activity following periods of auditory training. Multiple aspects of central processing have been shown to change following varying periods of stimulation (Perrot & Collet, 2014; Song et al., 2012; Suga, 2012). Furthermore, the demand on higher cognitive processes during tasks such as those carried out during periods of auditory training is also believed to be an important mediator. This cognitive demand ensures that subcortical processing is similarly strengthened, which works to improve hearing speech in noisy background situations (Song et al., 2012). This works as a loop where strengthened processing is further relayed to cortical structures, which aids in the processing of information. Furthermore, this research also showed that auditory training could improve the coding of pitch-related information (Song et al., 2012). As discussed in earlier sections, pitch and frequency coding are important when perceiving SIN. Therefore, these improvements could underlie the training-induced changes seen (Song et al., 2012). Additionally, it is also important to consider the ascending and descending innervation and the multiple interconnections that are important in mediating MOC efferent activity (Perrot & Collet, 2014; Romero & Trussell, 2021; Song et al., 2012; Suga, 2012). This, therefore, provides an alternative mechanism by which auditory training-related improvements in SIN perception could have occurred. This could have been through auditory training-related changes in central mechanisms such as brainstem processing and/ or corticofugal regulation of MOC activity (Song et al., 2012). Therefore, speculating that greater changes in central mechanisms with auditory training potentially saw greater improvements in SIN perception for the participants. Through this, the improvements that were seen in the participants' SIN perception ability could have been mediated by these central mechanisms.

4.2.1. <u>MOC System and Learning-Associated Memory</u>

Interestingly, research has also shown for a concept surrounding a 'long-term' memory, which is associated with learning and is found in higher brain areas (de Boer & Thornton, 2008; Suga, Xiao, Ma, & Ji, 2002; Weinberger, 2007). This learning can potentially, therefore, become active in situations where there is SIN and act on the MOC system to exert its effects in improving SIN perception (de Boer & Thornton, 2008). However, the changes in MOC system activity could potentially be limited in duration, and therefore, not show longer-term changes with auditory training, as seen in this study. However, MOC activity could potentially play a role in establishing these 'learning' and short-term effects (de Boer & Thornton, 2008). An important idea to further investigate, therefore, could be to investigate long-term changes in SIN perception following a period of auditory training. Although this theory could also explain the underlying changes in SIN perception, it is important to consider other studies that have shown changes in MOC activity relating to changes in SIN perception (de Boer & Thornton, 2008). Therefore, this theory could potentially be an important aspect of a larger, more complicated mechanism that mediates these changes.

4.3. Auditory Nerve Adaptation

A key concept discussed in other studies is auditory nerve adaptation. This is where the auditory nerve is able to adapt its characteristics based on the incoming stimulus (Marrufo-Pérez, del Pilar Sturla-Carreto, Eustaquio-Martín, & Lopez-Poveda, 2020). Studies have shown for there to be changes in the dynamic range of auditory neurons in the presence of background noise. This is believed to aid in the coding of other relevant stimuli, such as speech (Marrufo-Pérez et al., 2020). This dynamic nerve adaptation is believed to underlie more accurate coding of the speech envelope, and therefore, result in better SIN perception (Marrufo-Pérez et al., 2020; Marrufo-Pérez, Eustaquio-Martín, & Lopez-Poveda, 2018). Research has suggested for this adaptation to potentially play a role in the improvements seen in SIN perception in other studies (Mertes et al., 2019). A study conducted by Marrufo-Pérez et al., (2018) investigated the differences in SIN perception for normal hearing individuals and cochlear implant users in the presence of ipsilateral noise. The findings reflected no significant differences between either group in SIN perception ability. These findings, therefore, reflected that alternative mechanisms might contribute to the improvements seen in SIN perception, aside from MOC activity (Marrufo-Pérez et al., 2018; Mertes et al., 2019). This is because the cochlear implant users would not typically have working MOCR effects, yet still saw similar improvements in SIN perception as the control group. This led to an alternative mechanism of auditory nerve adaptation to be speculated in mediating these improvements in SIN perception with noise (Marrufo-Pérez et al., 2018; Mertes et al., 2019).

In relation to this study, this mechanism could potentially explain the improvements seen in SIN perception following the period of auditory training. The period of auditory training could have led to an adaptation in the auditory neurons that resulted in improved SIN perception ability post-training. This could have been mediated by longer-term plasticity-related changes that came as a result of the auditory training period. Therefore, this mechanism could explain the changes seen in SIN perception with auditory training. This theory is consistent with that speculated in the previous study due to a similarity in the results obtained (Bhattacharya, 2020).

4.3.1. Critique

Importantly, the literature has shown for the MOCR to be involved in improving the responses of AN fibers in noisy situations as well as improving the dynamic range and altering the discharge rate of firing (Marrufo-Pérez et al., 2020). This works to provide a basis for improved SIN perception, which has been discussed as the antimasking effect. This is also theorized to underlie the changes that are seen with MOCR activity and ABRs (Chintanpalli, Jennings, Heinz, & Strickland, 2012; de

Boer et al., 2012; Lichtenhan et al., 2016). This information contradicts some of the speculations in the previous study (Bhattacharya, 2020). Due to the MOCR being involved in exerting similar effects as to those seen with auditory nerve adaptation, it is difficult to assume that this mechanism operates independently of the MOC system, as speculated in the previous study (Bhattacharya, 2020; de Boer et al., 2012; Winslow & Sachs, 1987). However, the findings of this current study support the idea that there may be some components of auditory nerve adaptation that operate independently of the MOC system. This is because the findings of this study did not show any significant changes in ABR wave I suppression after the auditory training programme, as theorized. Changes in ABR wave I amplitudes were theorized as these responses typically correlate to auditory nerve activity (de Boer et al., 2012; Lichtenhan et al., 2016). These changes were also believed to be mediated by MOCR-related effects on auditory nerve activity, which did not show a relationship with the improvements seen in SIN perception (de Boer et al., 2012; Lichtenhan et al., 2016). Although a suppression in ABR wave I amplitudes was observed when using CAS in both pre-training and post-training measurements (potentially indicating the effects of the MOCR on auditory nerve activity), no significant changes in suppression were identified post-training. This indicated that there was no significant difference in MOC system activity following the auditory training programme. Therefore, leading to the assumption that there were alternative mechanisms that underlie these improvements seen in SIN perception after auditory training. One such speculated mechanism is auditory nerve adaptation, which may have components independent of the MOC system, as discussed in section 3.3 (Marrufo-Pérez et al., 2018; Mertes et al., 2019). Having said so, although the findings of this study contradict other studies that have shown potential antimasking effects, these biological mechanisms could still be important in mediating the changes seen in SIN perception alongside other important mechanisms. Additionally, there could be undetected changes in MOC activity that could be present. This would be consistent with the speculations in the previous study (Bhattacharya, 2020).

4.4. Undetected Changes in MOC System Activity

An idea that was discussed in the previous study on this topic was of undetected changes in MOC activity (Bhattacharya, 2020). Based on the findings of this study, as well as information presented in the literature, this idea could also be of significance. Therefore, this study supports the speculation made in the previous study (Bhattacharya, 2020). Multiple studies have shown a relationship between MOC activity and SIN perception, which provides evidence supporting the involvement of the MOCR in training-related changes in SIN perception. This indicates for the results obtained in this study to be inconsistent with some other studies (de Boer & Thornton, 2008; de Boer et al., 2012). A careful analysis of methodological factors indicates slight differences from those used in other studies. These methodological factors have been shown to be very important in influencing the results obtained. This has been shown through a variety of studies (Bhatt & Sokolowski, 2017; Guinan, Backus, Lilaonitkul, & Aharonson, 2003; Rao, Koerner, Madsen, & Zhang, 2020). Therefore, there is a possibility that the changes seen in SIN perception following the auditory training programme could have a significant relationship with changes in MOC activity, as has been shown in other studies (de Boer & Thornton, 2008; de Boer et al., 2012). However, due to methodological and other factors, this study was unable to detect changes in MOC plasticity (Bhattacharya, 2020).

An important characteristic that was different in this study compared to another study which shows a relationship between MOC activity and SIN perception is attention (de Boer & Thornton, 2008). The study conducted by de Boer and Thornton (2008) tried to ensure that their participants were focusing and paying attention to the measurements and training being undertaken. This was ensured by the participants being seated in a blacked-out room facing a monitor (de Boer & Thornton, 2008). Controlling for attention was not carried out in this current study, which could explain the differences in results. Studies have shown that attention is an important factor in the measurement of MOC activity (de Boer & Thornton, 2007; de Boer et al., 2012; Kalaiah, Theruvan, Kumar, & Bhat, 2017; Perrot & Collet, 2014; D. W. Smith & Keil, 2015). It has been shown that there is a decrease in MOC activity when the subject attends to the ear in which the OAE measurement is being undertaken. Contrastingly, when the same subject focusses on the ear with the CAS stimulus, there is an increase in MOC activity (de Boer et al., 2012; Kalaiah et al., 2017). This shows how attention can affect the responses obtained, and therefore, could potentially have led to undetected changes in MOC activity following the training period. This could have occurred depending on the participant's attention at the time of OAE and ABR measurement, as well as potential differences in attention between the auditory training tasks and the suppression measurements being undertaken. This could provide an inaccurate picture of underlying MOC activity. Furthermore, although there could have been changes in MOC activity post-training, these may not have been detected.

The stimulation pattern of the MOC system using the BBN stimulus also varied throughout the research. During the training programme, BBN was being provided binaurally to the participants. In contrast, during the ABR and OAE measurements, the stimulation was only provided contralaterally. This could have affected the measurement of these responses, whereby they did not reflect accurate MOC system activity that could be underlying the changes seen in SIN perception due to the training occurring with binaural stimulation. Signs of this specificity have been speculated through research, where MOC activity measures may only show changes in activation depending on the stimulus eliciting the MOCR (de Boer & Thornton, 2008).

Additionally, studies have indicated for MOCR effects to be short-lasting in some cases. This has been indicated to be approximately a few minutes, after which the level of activity can be seen to decrease (Brown et al., 1998). Therefore, it is possible that there were changes in MOC activity following the auditory training programme. However, these were not detected due to the interval between the end of the training period and the post-training measurements. This interval was shorter in this study (approximately 15 minutes) compared to the previous study, yet the results are consistent (Bhattacharya, 2020).

This information, therefore, shows that there is a possibility that changes in MOC activity were not detected following the training programme and could have potentially shown a significant relationship between the improvements seen in SIN perception and changes in MOC activity relating to auditory training. Additionally, the alternative mechanisms discussed above could have played a role in mediating these changes, and an interplay between cortical and subcortical structures could be an important mediator. Further research is required to understand these mechanisms.

5. DPOAE Measurements

This study hypothesized that there would be an increase in MOC activity as measured through DPOAE suppression after the auditory training programme. The findings of this study did not support this hypothesis. Additionally, the findings of this study were consistent with the previous study, showing that DPOAE suppression did not significantly increase following the auditory training programme, indicating that there was no significant change in MOC activity (Bhattacharya, 2020). However, these findings are inconsistent with other studies that have shown changes in MOC activity and the corresponding DPOAE amplitudes following a period of auditory training (de Boer & Thornton, 2008). Various factors could have resulted in these results, some of which have been discussed in earlier sections. Another possible explanation involves consideration of the DPOAE fine-structure. Research shows that evaluation of the fine-structure maxima and fine-structure minima are important as they are composed of in-phase and out-of-phase DPOAE components, respectively (Henin, Thompson, Abdelrazeq, & Long, 2011). As the DPOAEs are composed of two components, which are believed to be affected differently by varying stimulus and recording parameters, this can result in the fine-structure minima and maxima reflecting different effects on DPOAE suppression (Henin et al., 2011; Sun, 2008; Williams & Brown, 1997). Therefore, as this study did not evaluate the fine-structure of the recorded DPOAEs, there could have been changes in DPOAE suppression following the auditory training programme that were potentially undetected, which could potentially explain the results obtained (Carolina Abdala, Mishra, & Williams, 2009; Henin et al., 2011).

This study did, however, show a reduction in DPOAE amplitudes when a contralateral BBN stimulus was presented to elicit the MOCR. This finding is consistent with the previous study on this topic and various studies in the literature that have found similar results (Bhattacharya, 2020; de Boer & Thornton, 2008; de Boer et al., 2012; Rao et al., 2020). The mechanisms underlying this suppression in DPOAE amplitudes have been covered in earlier sections. Interestingly, this study showed for this suppression to generally occur across the frequencies measured. This differed from the previous study, which showed the suppression to typically occur at the lower frequencies (Bhattacharya, 2020). The findings of this study are consistent with other studies that reflect suppression across the frequency range tested (Bulut et al., 2019). Having said so, the literature also suggests for there to be differences that can exist from one study to another and can be due to varying factors such as the stimulus parameters used (Palmietto, 2017).

6. ABR Measurements

This study aimed to evaluate whether ABR wave I amplitudes could show an increase in MOC activity following auditory training. This was especially important as it was building on previous research, which could not identify a significant relationship between MOC activity and SIN perception through changes in DPOAE suppression (Bhattacharya, 2020). Therefore, this research implemented ABR wave I amplitudes as a measure to identify a significant relationship between these factors. This was attempted as research showed that MOC effects alter AN activity and reduce wave I amplitudes (Lichtenhan et al., 2016). Furthermore, changes in AN activity that are mediated by MOC effects are also shown to be a mechanism by which the effects of the MOCR are elicited, which was thought to hold importance in potentially showing a significant relationship between MOC activity and SIN perception, as has been shown through other studies (de Boer & Thornton, 2008; de Boer et al., 2012; Winslow & Sachs, 1987). Additionally, other studies have shown that there is plasticity in the AN, where changes in neural activity can be seen (Anderson & Jenkins, 2015; Gold & Bajo, 2014; Rumschlag et al., 2022). This further contributes to the idea that there could be changes seen in ABR wave I amplitudes following a period of auditory training. Therefore, this study hypothesized that there would be an increase in MOC activity as measured through ABR wave I suppression after the auditory training programme. The findings of this study, however, did not support this hypothesis, indicating that there was no significant change in MOC activity. It is possible that, similar to the DPOAE measurements, there were undetected changes in ABR wave I amplitudes following the auditory training programme. This could underlie the results obtained. Moreover, when considering the relationship between SIN perception and MOC activity, the alternative mechanisms discussed in section 4 could underlie the results obtained, with there being no significant changes in ABR wave I amplitudes, following training. Additionally, a combination of mechanisms could underlie the changes seen in SIN perception with auditory training, as discussed.

It is also difficult to compare these results with other studies, as to my knowledge, other studies have not yet been conducted that evaluated changes in ABR wave I amplitudes relating to MOC activity following a period of auditory training. Having said so, comparisons can tentatively be made to studies that evaluate neural activity in musicians who undergo a form of auditory training. These studies reflect longer-term changes in neural activity, which can indicate some inconsistencies with this study (Anderson & Kraus, 2013). However, a direct comparison is difficult to make due to a multitude of differences between these studies, as well as these other studies not evaluating the effect of the MOCR as in this study.

This study did, however, show a reduction in ABR wave I amplitudes when a contralateral BBN stimulus was presented to elicit the MOCR. This was similar to the DPOAE measurements obtained. These findings are consistent with those hypothesized and with studies in the literature that have found similar results (Lichtenhan et al., 2016; Mertes & Potocki, 2022; Schochat, Matas, Samelli, & Mamede Carvallo, 2012). A study conducted by Lichtenhan et al., (2016) showed a 16% reduction in amplitudes with activation of the MOCR. The findings of this study show a 23% reduction in ABR wave I amplitudes. This, therefore, shows how the findings of this study are relatively consistent with other studies. The mechanisms underlying this suppression in ABR wave I amplitudes have been covered in earlier sections.

7. Additional Considerations

7.1. *Initial Physiological Suppression and Improvements in SIN Perception*

An additional analysis conducted in this study showed no correlation between the level of initial suppression as measured through DPOAE and ABR responses with the presence of CAS and the overall improvements seen in SIN perception. These findings were inconsistent with another study that evaluated these effects (de Boer & Thornton, 2008). A study conducted by de Boer and Thornton (2008) showed that participants who had relatively lower levels of suppression during the first measurement showed the greatest improvements in SIN perception. This suggested a mechanism in which the participants' initial MOC activity (reflected through the level of suppression) indicated the range available for improvement in the MOC system with auditory training. Those individuals who showed lower levels of initial MOC activity had more room for improvement and saw greater improvements in SIN perception following auditory training (de Boer & Thornton, 2008). The opposite applied to those who had greater levels of initial MOC activity. This explanation fits this other study as they were able to show changes in MOC activity and SIN perception with auditory training (de Boer & Thornton, 2008). However, this current study did not show these effects, which could explain the results obtained. Furthermore, the results obtained could be a result of some of the factors discussed in earlier sections. Additionally, the small sample size in this study could have impacted the results, where a significant relationship was difficult to obtain.

7.2. *Acoustic Stapedial Reflex (ASR)*

Another important consideration that needs to be addressed involves the ASR or the MEMR. A common limitation shown in the literature is the potential effects of the MEMR on DPOAE and ABR suppression. The CAS used to elicit the MOCR can also activate the MEMR, which can have a confounding effect on the results (Jedrzejczak, Milner, Ganc, Pilka, & Skarzynski, 2020). However, all participants in this study had ASR thresholds at or above 70 dB. This meant that the reflexes were activated at higher intensities than the CAS used at 60 dB. Furthermore, studies have shown that the effects of the MEMR are negligible when measured with ABR parameters similar to this current study (Lichtenhan et al., 2016). This further indicates that the results obtained in this study were most likely not affected by the MEMR. To obtain certainty, it would be important to carry out measurements in future research that are able to identify the effects of the MEMR, separate from the MOCR (Jedrzejczak, Milner, Ganc, Pilka, & Skarzynski, 2020).

8. Clinical Implications

The findings of this study make it difficult to identify clinical implications that can potentially be observed. However, it is important to allude to potential clinical implications that can come as a result of further research in this area. Identifying potential connections between the MOC system and auditory training-related changes in SIN perception can be an important factor. Furthermore, understanding the underlying physiological mechanisms that potentially underlie these connections is also important. This information can provide further areas to address and target when considering individuals who have difficulties with SIN perception. This is particularly true for those individuals who have clinically normal hearing, as their MOC systems and efferent targets tend to be better intact compared to individuals with hearing loss (Hernandez-Perez et al., 2021). Moreover, MOC measures could potentially be used clinically to better understand varying characteristics, such as an individual's SIN perception ability, when considering the amount of improvement they could potentially see with auditory training (de Boer & Thornton, 2008). Therefore, further showing the importance of further research in this area.

9. Strengths and Limitations

9.1. *Strengths*

This study generally showed consistency with the previous study on this topic. This is valuable information as it indicates that the results obtained in the previous study may not have been completely study-specific and could indicate a trend in this topic (Bhattacharya, 2020). This is important as it provides more evidence concerning this topic in the research field, which is significantly important as there is contradicting and varying evidence present in the literature.

Furthermore, this study also investigated some of the future directions outlined in the previous study. This is valuable information as the previous study was not able to identify the physiological mechanisms underlying the improvements seen in SIN perception with auditory training and the MOCR (Bhattacharya, 2020). Therefore, this study evaluated whether additional measures could be used to show a relationship between MOC system activity and the improvements seen in SIN perception. Although this study did not find a significant relationship, it added valuable evidence to this research field by showing how ABR measures reflect this relationship. Moreover, this study measured multiple measures of MOC activity to evaluate this relationship. This worked to ensure that an accurate depiction of MOC activity could be obtained in the case where it may differ between measurements.

This study was also developed with careful consideration of the methodological approach. This was important and ensured that the parameters and other methods used resulted in accurate measurements, aiding in obtaining information to address the aims and hypotheses of this study.

Additionally, this study showed improvements in participants' SIN perception with a period of auditory training. This provided valuable information, alongside more evidence supporting research that identifies auditory training as an important tool for perceptual improvements (Besser & Launer, 2020). Further showing the clinical uses of such training programmes. The use of multiple measures such as the WINT and QuickSIN test reflected improvements in participants' SIN perception ability following the training period. This further showed the validity and usefulness of these measurements in clinical practice and in other research studies.

9.2. *Limitations*

A potential limitation of this study included factors associated with the methodological approach. The results obtained could potentially include undetected changes in MOC system activity, which could come as a result of varying aspects of the methods. Factors such as attention and the stimulation pattern of the MOCR elicitor could have potentially impacted the results, as discussed in section 4.4.

This study was also limited in terms of the sample size. This restriction was caused due to funding availability as well as COVID-19 related disruptions. Ten participants were recruited, which meant that the control and treatment groups had a very small number of participants in each. This could have potentially impacted the results, whereby significant trends in the data were not seen. This could mean that the study was not able to reflect relationships that may have existed otherwise. However, the consistency of the findings to the previous study indicates that the results may not have been impacted to a large extent by the small sample size (Bhattacharya, 2020).

Although this study reflects findings that may be beneficial in clinical settings, it is difficult to directly apply this information to 'real-life' situations. This is due to factors such as the nature of the training programme and measurements conducted being in a controlled environment. The findings, therefore, may be different in 'real-life' situations. This also indicates potential future research directions.

10. Future Research

The findings of this study resulted in speculations surrounding possible undetected changes in MOC system activity. Therefore, further research could be conducted by controlling the factors discussed in section 4.4 to evaluate whether the results were affected by these factors. An important parameter to potentially consider could be forward masking. This could potentially be used to provide binaural stimulation to elicit the MOCR when measurements assessing MOC activity are undertaken. This could potentially overcome the limitations of providing the MOCR elicitor to the testing ear with the DPOAE and ABR measurements.

Similarly to the previous study, this study was not able to identify the physiological mechanisms underlying the improvements seen in SIN perception with auditory training and the MOCR (Bhattacharya, 2020). Therefore, future research could investigate other mechanisms that could underlie these improvements. Potential analysis of responses such as a frequency following response (FFR) could be explored. The FFR is a non-invasive measurement which indicates both a transient response (for stimulus onset) and a sustained response for periodic features of speech when elicited using speech stimuli. These features include both the spectral and temporal characteristics of the eliciting stimulus. This could potentially indicate alternative mechanisms underlying these improvements as have been outlined in other studies (Kumar et al., 2013; Ribas-Prats et al., 2019). Furthermore, investigations could also be conducted to assess late responses of AEPs, which could provide information regarding higher processing centers and their potential involvement in this relationship.

Future research could also carry out studies that evaluate MOC activity and SIN perception with auditory training over a longer period of time. This may reflect findings that have not been reported yet. Furthermore, assessing long-term outcomes for participants having undergone these training periods could also be useful as it may provide information regarding the usefulness of the training programme as well as potential information surrounding the underlying mechanisms.

Lastly, a useful future study could combine datasets from this study and the previous study on this topic. This may reflect information that was not found in these individual studies, mainly due to relatively small sample sizes in both studies (Bhattacharya, 2020).

Summary and Conclusions

Important information regarding the human auditory system was covered in this study. This included a range of information providing a background for the study conducted. Important areas covered in this research included the MOC system as well as auditory training and SIN perception. Moreover, a greater focus was put on ABR measurements as these were evaluated to attempt to identify potential changes in MOC activity with auditory training.

This study was designed to further investigate the effects of an auditory training programme on SIN perception and MOC system activity. To do so, this study built on previous research and aimed to identify a potential relationship between MOC activity and SIN perception by conducting additional measurements. The findings of this study were primarily similar to the previous study on this topic (Bhattacharya, 2020).

The findings of this study showed an improvement in SIN perception for participants who underwent the auditory training programme. Furthermore, physiological suppression of DPOAE and ABR wave I responses were observed when the MOCR was elicited. However, this study did not identify a change in DPOAE and ABR suppression following the auditory training programme. This showed that there was no significant change in MOC activity. Additionally, no significant relationship between MOC activity and SIN perception was identified.

The absence of an underlying connection between MOC activity and SIN perception meant that alternative mechanisms were speculated to have mediated the improvements seen in SIN perception. These mechanisms included central mechanisms, which could potentially include cortical, subcortical and corticofugal connections. Furthermore, consistent with the previous study, the potential for an undetected change in MOC system activity was also theorized (Bhattacharya, 2020). Therefore, this means that the improvements seen in SIN perception with auditory training could have been mediated by alternative mechanisms, or there could be an involvement of the MOC system. Importantly, this study identifies that perceptual improvements seen with auditory training and MOC activity are a result of complex interconnections between multiple structures, and therefore, require further research to develop certainty regarding these mechanisms.

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