

**A THREE-CHANNEL MODEL OF HUMAN  
BINAURAL SOUND LOCALIZATION**

by

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at

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## ABSTRACT

The most accepted model of mammalian binaural sound localization postulates two neural/perceptual channels with hemifield tuning and overlapping medial borders; the extent to which the two channels are co-activated by the source is the neural "code" for the source's azimuthal location. This model does not take into account physiological data on the existence of a population of cells with spatial receptive fields centered on the azimuthal midline. The following work sought to test the hypothesis that the mammalian binaural sound localization apparatus includes a third, midline-tuned channel. Ten experiments used a selective adaptation paradigm in human listeners to probe for the existence of a midline channel. Psychometric functions were obtained for lateral position based on ITD or ILD both before and after adaptation with high-frequency (2800 and 4200 Hz) or low-frequency (260 and 570 Hz) tones. Listeners experienced highly lateralized adaptor stimuli with different frequencies at each ear (asymmetrical adaptation), highly lateralized adaptor stimuli of the same frequency at each ear (symmetrical adaptation), and single frequency adaptation at the midline (central adaptation). At both high and low frequencies in the domains of both interaural time difference (ITD) and interaural level difference (ILD), location judgements after asymmetrical adaptation shifted away from the fatigued side. These shifts occurred across each adapted hemifield and extended slightly over the midline, as is consistent with the two-channel model. The two-channel model would predict no effect of symmetrical or central adaptation because fatiguing both lateral channels equally would not change their relative activation by a given source. In practice, the result of symmetrical adaptation was a shift in location judgements towards the midline as would be expected if adaptation of the lateral channels resulted in a greater relative contribution of a third, midline channel. Likewise, central adaptation tended to result in shifts in perceived location towards the sides. The evidence for the midline channel was strong for high and low frequencies localized by ILD, and was present for low frequencies, but not for high frequencies, localized by ITD.

## LIST OF ABBREVIATIONS USED

Hz	Hertz
kHz	kilohertz
s	seconds
ms	milliseconds
μs	microseconds
dB	decibels
dB HL	decibels Hearing Level
ITD	Interaural time difference
IPD	Interaural phase difference
ILD	Interaural level difference
SOC	Superior Olivary Complex
MSO	Medial Superior Olive
LSO	Lateral Superior Olive
A1	Primary Auditory Cortex
EE	excitatory-excitatory
EI	excitatory-inhibitory
ICI	Inter-click interval

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## **CHAPTER 1 INTRODUCTION**

### **1.1 INTRODUCTION TO SOUND LOCALIZATION**

Sound localization is important both in identifying a sound's origin and in separating out distinct but co-occurring sounds. Localizing sounds in our world comes so automatically to us that we take the ability for granted. However, while an object's visual location enjoys a direct mapping onto the two-dimensional field of the retina (or its tactile location onto the two-dimensional receptor surface of our skin), sound waves coming into the ear lack this topographical relation between the source location and the sensory receptor cells it activates.

After moving through the external auditory canal, a sound wave vibrates the tympanic membrane and, in turn, the ossicles of the middle ear. The action of the ossicles passes this vibration into the perilymph of the cochlea via the oval window. Compression of the cochlear fluid creates motion in the long, thin basilar membrane. Because the physical properties of the basilar membrane (stiffness, width) are graded along its length, different points along the membrane vibrate maximally at different frequencies; loci of maximum basilar membrane displacement (and thus velocity) occur at the apex of the basilar membrane for the low frequencies and move towards the base as stimulus frequency increases. In man, the range of audible frequencies runs from about 20 Hz to 20 kHz. The effect of this frequency-specific mapping along the basilar membrane is that spectrally-complex sound waves entering the cochlea are decomposed into their sinusoidal elements in a sort of biological Fourier analysis; each frequency causes motion in a different place along the basilar membrane and the timing and amplitude of the

motion at each location reflects the timing and amplitude of the frequency components that exist within the original sound wave.

At each responding point along the basilar membrane, vertical motion causes lateral shearing between the tectorial membrane and the organ of Corti, which in turn causes the stereocilia of the (single row of) inner hair cells running the length of the basilar membrane to deflect at that location. Deflection of the inner hair cell stereocilia drives those cells' receptor potentials—greater deflection results in an increased receptor potential strength, oscillating in sign with the direction of stereocilia deflection. Individual spiral ganglion cells derive information directly from individual inner hair cells (Spoendlin, 1969) and their axons run together as the fibres of the auditory nerve. Because each ganglion cell only synapses on a single hair cell, each fibre in the auditory nerve array inherits its preferred frequency (and other properties, e.g., intensity sensitivity, frequency-tuning bandwidth) from the inner hair cell it innervates. Moreover, at low frequencies the timing of spike initiation in the cochlear nerve is phase-locked to the motion of the hair cell stereocilia, and thus, ultimately to the motion of the tympanic membrane. At high stimulus frequencies, spike rate in the cochlear nerve is proportional to stimulus amplitude, but spike timing has a random relation to the phase of the stimulus (Ruggero, 1992; Phillips, 2007).

Neural signals from the auditory nerves are passed to the cochlear nuclei and then through a series of brainstem nuclei before they reach the auditory cortex. Simply, spiral ganglion cells synapse at the cochlear nuclei and cells of the ventral portions each send projections to both the ipsi- and contralateral superior olivary nuclei, the first site of binaural integration. Projections arising from each superior olive synapse in both the

ipsilateral and the contralateral inferior colliculi, and in the ipsilateral nuclei of the lateral lemnisci which have their own projections to the inferior colliculi. The inferior colliculi send projections to the ipsilateral medial geniculate nucleus in the thalamus, from which projections leave the brainstem and synapse in the auditory cortex (for a review of the basic anatomy of the auditory system, see: Irvine, 1992).

Importantly, the *tonotopic* organization that originates in the basilar membrane is maintained up through the brainstem (e.g. Aitkin *et al.*, 1984) and into the auditory cortex (e.g. Merzenich and Brugge, 1973; Merzenich *et al.*, 1975; Reale and Imig, 1980). Thus, a sound wave entering the cochlea is represented by a rate-place code of activation that carries information about the amplitudes (and timing) of the spectral components in a sound wave. The critical point is that, unlike the mapping of space onto the retina in the visual system, there is no spatial information directly encoded by the cochlea.

How, then, do we manage such precise sound localization? In practice, the human threshold for sound localization around the azimuthal (horizontal) midline is as little as  $1^\circ$  (Mills, 1958). Because there is no direct information about a sound's location encoded by the cochlea, the auditory system has to calculate location from the information that is available. Some information is available within the spectrum of the sound as a result of direction-dependent filtering by the outer ear; the spectral filtering resulting from reflection and absorption of sound energy by the outer ear can be evaluated against a neural template by the auditory system. This information is particularly important for sound localization in the vertical plane, and perhaps at far lateral azimuths. Along the azimuth, the dominant cues for sound location exploit our auditory system's ability to



compare information arriving from two ears: Interaural level differences and interaural time differences.

If a sound source is located to your left, the amplitude of the sound wave that reaches your left ear will be slightly greater than that reaching your right ear. This interaural level difference (ILD; sometimes also called interaural intensity difference) results from two physical properties of sound. First, the intensity of a sound wave decreases as it moves through space. (In an idealized system, the energy of a sound wave moves out spherically from its origin; its intensity is inversely proportional to the square of the distance from the source, resulting in about 6 dB reduction for every doubling of distance [Inverse Square Law].) Because the distance between human ears is so small relative to the distance of most sound sources in nature, this reduction of intensity over distance is negligible for any but very close sound sources. Second and more importantly for sound localization, the head is acoustically opaque for sounds with frequencies whose wavelengths are shorter than the head diameter. Thus, the greater the eccentricity of the sound source, the greater the discrepancy in the sound levels at the two ears (i.e., the ILD). This effect is more robust at high frequencies. At low frequencies the wavelength of a sound approaches and exceeds the width of the head and is thus able to diffract around the head unaffected. The human threshold for ILD has been reported to be about 1-2 dB (Grantham, 1984); in cats, it is about 1 dB (Cranford, 1979).

Interaural time differences (ITDs) occur because the speed of sound is finite (~340 m/s in air). Because it takes slightly longer for a sound to reach the ear opposite the sound source, our auditory system can make use of both the difference in the onset of the sound in each ear as well as the ongoing phase difference imposed on the waveform by

that onset time difference. The smallest detectable ITD reported has been as low as 10  $\mu$ s for broadband noise at 0° elevation (Klumpp and Eady, 1956), which corresponds to a change of about 1°. Such a low threshold is indicative of how precisely the auditory system is able to maintain temporal information. When it is available, the ongoing interaural phase cue is the dominant temporal one in determining perceived source azimuth (Wightman and Kistler, 1992). ITD threshold depends on the precision with which the timing of cochlear neuron action potentials are informative about eardrum position, and on the precision with which that timing information is conveyed to the binaural processor. While a resolution of 10  $\mu$ s seems difficult to imagine for a single neuron, it is possible that the 10  $\mu$ s change in ITD constituting the behavioural ITD threshold actually causes rather little change in the instantaneous firing rate of any given ITD-sensitive neuron. In principle, however, the brain has the opportunity either to sample the response of a given neuron over many cycles of the ITD stimulus, or to sample the activity of many neurons encoding the ITD stimulus simultaneously, or both, and could use that sampling to provide a more salient neural signal for source ITD. In contrast with ILDs, ITDs are more useful for sound localization at low frequencies than they are at high frequencies. At high frequencies, ITD information suffers from phase ambiguity. If the ITD is greater than a half cycle of the waveform, the ongoing phase difference alone becomes insufficient to signal which ear received the leading sound. For an ITD *greater* than a half cycle, a peak in the waveform at the ear facing the sound source will follow quickly *after* one from the ear opposite the source and in the absence of other information the auditory system will locate the sound on the side opposite its actual origin (Hartmann., 1999). The distance between the ears of an adult human allows

for a maximum ITD of about 0.65 ms (distance between the ears / speed of sound). This corresponds well with direct measurements (Middlebrooks and Green, 1990), and translates to increasing ambiguity of large ITDs for frequencies above about 750Hz.

The combined usefulness of ITD information below about 750 Hz and ILD information above about 3000 Hz was named the Duplex Theory of sound localization (Strutt, 1912). The efficacies of each cue leave an odd gap between 750 and 3000 Hz; indeed, at mid-range pure tone frequencies for which neither cue is particularly useful human sound localization suffers in the sense that minimum audible angles become larger (Mills, 1958).

## **1.2 NEUROPHYSIOLOGY OF SOUND LOCALIZATION**

As mentioned above, the inputs from the two ears first converge in the superior olivary complex (SOC) of the brain stem, most importantly for this discussion in two nuclei: the lateral superior olive (LSO) and the medial superior olive (MSO). The main difference between these two nuclei is one of frequency representation (Guinan *et al.*, 1972), wherein the LSO appears to be specialized for high frequencies and the MSO for low frequencies. Early physiological studies in mammals usually avoided recordings from the SOC for technical reasons, and instead assayed the ITD and ILD sensitivity of neurons in higher centers—on the perhaps not unreasonable assumption that stimulus-response associations in the higher centers would accurately reflect those seen at the SOC. Those studies confirmed neural sensitivity to ILDs among high frequency neurons and to ITDs among low frequency cells (see especially Brugge *et al.*, 1969; Brugge *et al.*, 1970; Brugge and Merzenich, 1973).

It should be noted that this research also saw the beginnings of a categorization of binaural cells into those that were excited by neural signals from both the ipsi- and contralateral ears (excitatory-excitatory or EE cells), and those that were excited by the signal from one ear and inhibited by the signal from the other ear (excitatory-inhibitory or EI cells). For the majority of the latter group of cells (especially above the level of the LSO), excitation was caused by signals from the contralateral ear while signals from the ipsilateral ear were inhibitory. EE cells were reported to be found primarily in the low-frequency dominated MSO. Their response properties were consistent with what might form a basis for a coincidence detection model of ITD coding, which will be discussed in more detail below. EI cells, on the other hand, were particularly sensitive to ILDs and were more prevalent in the LSO. While this distinction between EE and EI cells sometimes persists in more recent work, it may not be terribly helpful. When cell responses have been studied with wider intensity and time parameters than in those studies that originally proposed this dichotomy, it is often the case that an individual cell may show EE responding to one set of parameters and EI responding to another regardless of its ITD/ILD sensitivity (see Phillips *et al.*, 2011). Thus, while the division of cells into ITD-sensitive EE cells and ILD-sensitive EI cells is satisfying, it is an oversimplification which might usefully be avoided in discussions of the neural mechanisms underlying sound localization.

As neurophysiological work proceeded, controversy grew as to how the mammalian auditory system encodes sound location. Early in the history of inquiry into sound localization, Jeffress (1948) proposed a model by which the brain might encode ITDs. His model held that signals from each ear were transmitted along axonal ‘delay

lines' of various lengths to an array of neurons such that a particular ITD would result in summative excitation of a particular neuron in the array that would act as a 'coincidence detector'. For example, a coincidence detector sensitive to a 0 ms ITD would receive input from two delay lines of equal length (or equal axonal conduction delay) such that the simultaneous occurrence of a sound at each ear would be maintained as a simultaneous occurrence of signal at that coincidence detector. A coincidence detector sensitive to an ITD favouring the right ear would receive input via a relatively long delay line from the right ear and a short delay line from the left ear such that a sound that reached the right ear before the left would result in binaural signals reaching the coincidence detector sensitive to that ITD simultaneously. Thus, in the Jeffress model, the peak firing of a coincidence detector would correspond to its preferred spatial location for a sound stimulus, and sufficient coincidence detectors would exist to represent all relevant ITDs, and thus all auditory azimuths. One of the consequences of this model was the appealing possibility that a system of coincidence detectors could express its output as a topographical map of auditory azimuth.

By the 80's, the Jeffress model was serving as a guide for neurophysiological research into the mechanisms underlying ITD sensitivity. Because the theorized output of a coincidence detector array, in which the critical issue is the maximal firing of a cell, is a population of cells each tuned to fire maximally for a specific phase delay, research was focussed on finding this sort of cell response specificity. In a number of detailed physiological studies of cell response as a function of ITD in the inferior colliculus (e.g., in the cat, Yin and Kuwada, 1983; in the guinea pig, McAlpine *et al.*, 1998), this specificity was defined as the point at which a cell's sensitivity to interaural phase delays

at different frequencies converged. This point was named the “characteristic delay” and often, but not always, occurred at either the peak (usually for contralateral-leading stimuli) or the trough (usually for ipsilateral-leading stimuli) of the ITD function. The characteristic delay was used to estimate the lengths of Jeffress-like delay lines that were later suggested to have anatomical correlates in the MSO (see Joris *et al.*, 1998). In psychophysical work, the Jeffress model was also being used to guide the interpretation of perceptual data gathered in free-field experiments (Carlile *et al.*, 2001; further discussed in section 2.6).

Around this time, two similar lines of inquiry resulted in two completely different pictures of how the brain codes sound location. First, Knudsen and Konishi (1978) undertook a detailed study of the receptive fields of the barn owl's midbrain medial lateralis dorsalis (MLD), the avian homologue of the mammalian inferior colliculus. Knudsen and Konishi isolated units along the horizontal and transverse planes of the MLD and used a semi-circular, pivoting speaker track to systematically map out the free-field receptive field of each unit. They found that the lateral and anterior margins of the MLD were dominated by “limited-field units” which responded only when an appropriate sound came from a single, well-defined area of space; the borders of these were little affected by intensity changes. The azimuthal and vertical extents of the receptive fields were ultimately shown to be shaped by IPD and ILD sensitivity, respectively<sup>1</sup> (Moiseff *et al.*, 1983; Takahashi *et al.*, 1984). These units were systematically arranged in this

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<sup>1</sup> This is made possible by peripheral and central auditory specializations in barn owls that simply don't exist in mammals. See Phillips (2008) for a review.

midbrain region according to the azimuth and elevation of the neurons' receptive fields. That is, as sounds move from left to right in the barn owl's auditory field, units with narrow spatial tuning for each location are systematically arrayed from the lateral to the medial MLD (along the sagittal plane); as sounds move in elevation from above to below, units responsive to these locations are systematically organized from the dorsal to ventral MLD (along the transverse plane). Thus, the barn owl model, in which the spatial location of a sound is represented by one of many narrowly-tuned units organized topographically, could be consistent with the model theorized by Jeffress thirty years earlier. Indeed, neural delay lines serving ITD (and therefore azimuth) coding have subsequently been found in the owl (Carr and Konishi, 1988; 1990), although evidence for these has been far from compelling in mammals (compare: Smith *et al.*, 1993; Joris *et al.*, 1998; McAlpine and Grothe, 2003).

The second line of inquiry came from Middlebrooks and Pettigrew (1981), who studied the receptive fields of neurons in the cat's primary auditory cortex (A1) in response to free-field stimuli. Rather than finding cells narrowly tuned to stimuli originating in a particular location, as seen in the barn owl, they found that the majority of cells with spatial selectivity in the cat's A1 responded to stimuli broadly located in the acoustic hemifield contralateral to the recording site. A smaller group of cells responded to stimuli located in the ipsilateral acoustic hemifield. In both cases, the medial borders of these cells' receptive fields were usually in the region of the midline. Middlebrooks and Pettigrew named these cells "hemifield cells" on the basis of the disposition of their receptive fields in auditory azimuth. A much smaller group of cells expressed spatial selectivity for sources near the azimuthal midline, especially at low stimulus levels. What

was clear from this report, however, was that the dominance of hemifield units in the cat's cortex was unlikely to be able to support a Jeffress-style mapping. For the cat, the dominance of this type of hemifield-preferring cell has since been confirmed in a number of studies (Imig *et al.*, 1990; Rajan *et al.*, 1990; Brugge *et al.*, 1996; Eggermont and Mossop, 1998). Interestingly, however, all of those studies were restricted to high-frequency neurons; so far as we know, there has never been a study of the free-field spatial selectivity of low-frequency neurons in the cat's primary auditory cortex, nor has there been one of the topography of ITD coding in the mammalian cortex.

While findings in the barn owl spurred a search for a topographic mapping of space in the mammalian auditory system (King and Palmer, 1984; Wise and Irvine, 1985; Carlile and King, 1994), it became increasingly evident that barn owls were unique in their sound localization mechanisms. Even among birds, the barn owl model failed to generalize. While cells with narrow tuning to sound locations along the azimuth were found in other owls (although with no tuning for elevation: Volman and Konishi, 1989), cell receptive fields in other predatory birds were consistent with those found in the cat by Middlebrooks and Pettigrew (Calford *et al.*, 1985).

A second contender for the mechanism of sound localization in mammals was proposed independently by the McAlpine lab in England, the Middlebrooks lab in the United States, and the Phillips lab in Canada. One trouble with research that focussed on characteristic peak or trough delays among low-frequency cells was that many of those delays tended to occur outside of the range that would naturally be experienced by the animal. Rather, it was the steep portion of the function that tended to lie across the midline, i.e., across the physiologically relevant range of ITDs (Phillips and Brugge,



1985; Spitzer and Semple, 1995; McAlpine *et al.*, 2001). In 2002, Brand *et al.* showed that glycine-mediated inhibitory inputs to the MSO critical to ITD coding actually had the effect of shifting the peak response away from the midline ITDs and outside of the physiologically relevant range of ITDs. McAlpine and Grothe (2003) argued that a critical property of Jeffress-like coincidence detection was a full range of cells representing all of auditory space and, as such, all physiologically relevant ITDs. Because most cells, in practice, fired maximally (and minimally) outside of this physiologically relevant range, the data on the mammalian auditory system were inconsistent with a Jeffress model. Rather, McAlpine and Grothe proposed that sound location was represented in the auditory system by two populations of broadly tuned neurons. In this regard, both McAlpine *et al.* (2001, in guinea pigs) and Hancock and Delgutte (2004, in cats) found that "best delays" (as opposed to characteristic delays) were systematically equal to a quarter period of the stimulus cycle, thus positioning the steep portion of the ITD function across zero ITD, and therefore the midline. This model complements the neurophysiological data discussed above from Middlebrooks and Pettigrew (1981) showing that (high frequency) auditory cortex cells are dominated by cells with broad hemifield tuning, likely based on ILD sensitivity. Further recordings in the A1 by Stecker *et al.* (2005) confirmed that preferred locations of cat cortical cells are strongly biased towards contralateral azimuths, whereas the steepest sections of cell response curves are tightly packed around the midline. They suggested an "opponent-channel" theory in which sound localization is dependent upon two channels of broadly-tuned hemifield neurons with subpopulations in each channel of units that respond to ipsilateral tones (fewer) and units that respond to contralateral tones (more). Finally, in 2008, Phillips

reviewed a body of psychophysical data (discussed below) inconsistent with a barn owl type model and used those data to support a two-channel model.

In all cases, the critical properties of the two-channel model include each channel having a relatively undifferentiated response rate in the deep lateral hemifields and steep, overlapping medial borders (Figure 1). Rather than the firing of small populations of cells representing discrete ITDs and thus spatial locations, source location is represented by the relative outputs of the two channels. Because the steep portion of the curve straddles the midline, small changes in source location in this area will result in the large changes in relative output as compared to changes in source location in the lateral hemifields. This is consistent with behavioural data that show neural ILD acuity to be best near the azimuthal midline (Phillips and Irvine, 1981a; Phillips and Brugge, 1985; Brugge *et al.*, 1996). Further, while each cortical hemisphere localizes sound in the contralateral acoustical hemisphere, each hemisphere must contain the neural substrate of both channels (contra- and ipsilateral) in order for sound to be localized via a comparison of the two channels. If it were the case, rather, that one channel were located in each cortical hemisphere, unilateral lesions to the auditory cortex should impair this comparison process and result in a total loss of binaural sound localization. Such lesion studies have found that unilateral lesions to A1 ruin an animal's ability to localize sounds in the contralateral hemifield only (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984; Kavanagh and Kelly, 1987). It follows, then, that each cerebral hemisphere must be independently capable of localizing sound in the contralateral acoustic hemifield. Indeed, recall that a minority of hemifield cells have been found to have receptive fields sensitive to sound stimuli located in the ipsilateral hemifield. Each cortical hemisphere thus

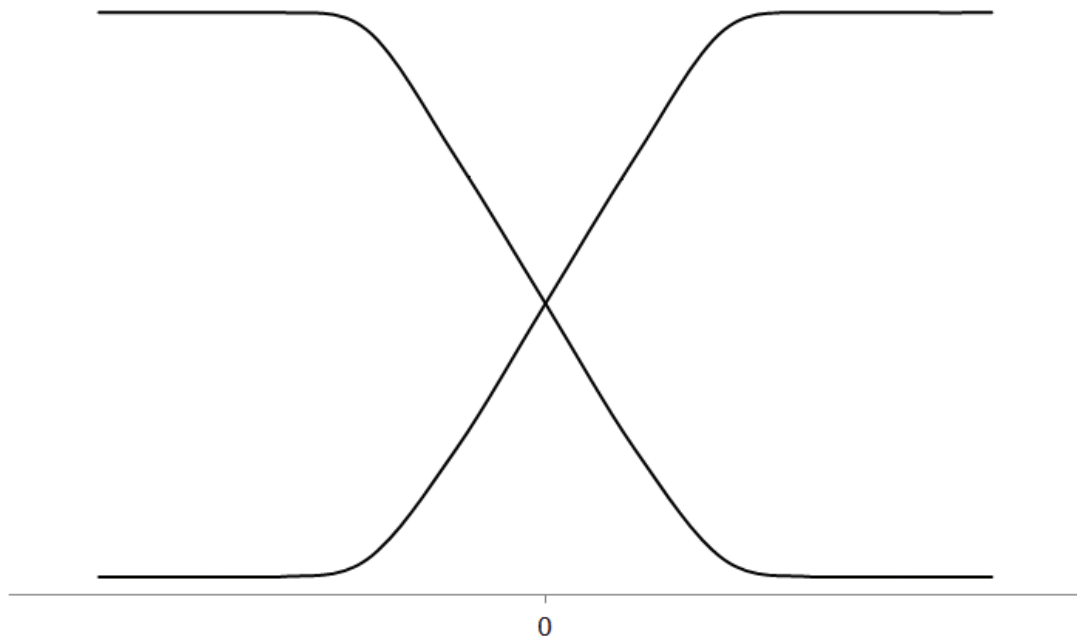


Figure 1. Schematic diagram illustrating the two-channel model. Cells that make up each channel have similar hemifield tuning to interaural disparity or intensity. Sound azimuth is represented by the relative rates of activation of the two channels.

contains its own sets of hemifield-tuned cells, with both acoustic hemifields being represented. Why it is that one auditory hemisphere is only able to localize sound in contralateral auditory space despite having cells sensitive to both contralateral and ipsilateral sides is mysterious. Note that while data from lesion studies in mammals show that each forebrain hemisphere is responsible for localizing sounds in the contralateral acoustic hemifield, they do not speak to the architecture of the mechanisms by which that responsibility is executed. That is, they do not independently offer a way to select between barn owl and mammalian models. The deficits in localizing sounds in contralateral space resulting from unilateral lesions are equally accounted for by postulating that each cortical hemisphere contains narrowly tuned units that code the range of ITDs/ILDs spanning the contralateral hemifield.

### **1.3 PSYCHOPHYSICS AND THE TWO-CHANNEL MODEL**

Psychophysical evidence for a two channel model in humans has come from a number of paradigms including gap-detection (Boehnke and Phillips, 1999), spatial release from masking (Phillips *et al.*, 2003), and selective adaptation (Phillips and Hall, 2005; Phillips *et al.*, 2006; Vigneault-MacLean *et al.*, 2007). The gap detection paradigm measures a listener's ability to detect a brief silent interval in a sound stimulus. When the sounds on either side of the interval are at the same frequency, the minimum detectable gap is only a few ms in length. Using different frequencies on either side of the gap increases minimum detectable gap to tens of ms (Chatterjee, *et al.*, 1998; Formby *et al.*, 1998a; Formby *et al.*, 1998b). This change in detection threshold has been attributed to the two tasks reducing to either discontinuity detection within one perceptual channel or a

relative timing mechanism between two channels (recall that auditory information is organized into different frequency streams or channels). Thus, by using identical-spectrum sound stimuli but moving the trailing (post-gap) sound to different spatial locations, Boehnke and Phillips (1999) used the gap-detection paradigm to map out the azimuthal tuning of human spatial channels. They found that gap detection thresholds were low when both the leading and trailing sound were within one spatial hemifield, and increased as the trailing sound crossed the midline and moved into the contralateral hemifield. This suggested the existence of two perceptual channels with hemifield tuning (left, and right), and that it was the relative outputs of these two channels that specified source azimuth.

Phillips et al. (2003) applied the spatial release from masking paradigm in a similar way and found support for the two-channel model. The Hearing-in-Noise Test (HINT) is a clinical application of spatial release from masking designed to determine how much a patient benefits from having a spatial separation between a sound target (usually a speech stimulus) and a noise masker. Traditionally, normal hearing listeners experience  $\sim 7$  dB decreases in their threshold (release from masking) for detecting the target sound at the midline when the noise masker is separated from the target by  $90^\circ$  (e.g. Soli and Nilsson, 1994). Phillips et al. (2003) hypothesized that rather than absolute separation of the target and the masking noise, the critical factor for improving detection threshold was whether the two stimuli were located in the same perceptual channel. While maintaining an absolute separation of  $90^\circ$ , the traditional task locations ( $-90^\circ$  and  $0^\circ$ ) were compared with the stimuli either in separate channels ( $-45^\circ$  and  $45^\circ$ ) or the same channel ( $-135^\circ$  and  $-45^\circ$ ). When stimuli were located in separate channels, listeners

experienced a greater release from masking ( $\sim 9$  dB) than seen traditionally. When stimuli were located in the same channel no release from masking was seen despite a  $90^\circ$  separation. This result could be explained using a two-channel model.

Selective adaptation is a paradigm used throughout sensory neuroscience in which exposure to a specific stimulus is thought to “fatigue” the neural mechanisms (or channel) responsible for coding that signal and subsequently cause alterations in the perceptions aroused by stimuli in close proximity to the adaptor stimulus along the relevant psychophysical stimulus dimension (in the auditory system e.g., Eimas and Corbit, 1973; Cooper, 1974; Grantham and Wightman, 1979; for a review, see: Phillips, 2008). More recently, this paradigm has been applied to spatial hearing in man (ITD: Kashino and Nishida, 1998; free-field: Carlile *et al.*, 2001; ITD/ILD: Phillips and Hall, 2005; Phillips *et al.*, 2006; Vigneault-MacLean *et al.*, 2007) and it is this paradigm that is used to explore the mechanisms of sound localization in the chapters that follow.

There are two ways that exposure to the adapting stimulus could affect neural response dynamics and therefore perceptual channel output. First, neurons sensitive to the adaptor could become generally less responsive (i.e., “fatigued”) across the channel such that the channel’s total output is reduced in a test situation (see Phillips, 2008: Figure 3). A second possibility is that the neurons responsive to the adaptor could shift their tuning towards the adaptor. In this regard, there is a precedent for neurons adjusting their tuning in the spatial domain (Lee & Middlebrooks, 2010). However, neurons that have been found to shift their receptive fields towards a stimulus are in the minority and, more critically, these receptive field shifts do not occur after passive exposure—they require active attention. In the adaptation experiments presented below, participants were told

that they could ignore the adaptor stimuli and thus it is unlikely that the results seen here are due to a lateral shift in the adapted channel rather than an overall reduction in the channel's response.

Three experiments were direct theoretical predecessors to the work presented here. In the first (Phillips and Hall, 2005), participants were asked to distinguish whether low-frequency (260, 570 Hz) test tones with a range of source locations were to the left or right of the midline (judged against a brief train of midline clicks presented between each trial) both before and after lateral adaptation. Adaptation consisted of 35 s trains of highly lateralized (0.25 cycle ITD) tones at the same frequencies as the test tones, but presented alternately to opposite sides. A refresher adaptor train of 5 s was presented between each trial. As participants were simply asked to make a left-right judgement for each ITD, the effects of adaptation were judged by the shift in the perceived point of centrality between the pre- and post-adaptation ITD functions. For all participants, the perceived point of centrality shifted towards the adaptor matching the particular test frequency. For example, 260 Hz adaptation in the right ear resulted in a bias towards making "left" judgements for test tones of the same frequency, effectively shifting perceived location-vs-ITD function (and thus, the point of perceived centrality) to the right. This experiment was run separately for stimuli localized by ITD and by ILD. In the former, the magnitude of the shift was 60-115  $\mu$ s and in the latter it was  $\sim$ 3 dB. This effect on the midline after highly lateralized adaptation cannot be explained by a model in which cells are narrowly tuned to specific locations, which would instead predict an adaptation that would be restricted to the lateral extremes of auditory space.

A second experiment sought to answer whether adaptation was specific to the adapted stimulus parameter. Phillips *et al.* (2006) repeated the experiment described above, but presented participants with an adaptor tone that used the opposite cue (ITD/ILD) to the test tones. Resulting shifts in the perceived point of centrality were in the expected direction and of a comparable magnitude as those seen in the previous experiment. This constituted evidence of a spatial processor existent beyond a point of neural integration for ITD and ILD cues. Further, it bolstered previous controls for the ILD condition in indicating that ILD adaptation is not a peripheral effect, since use of an ITD adaptor with ILD test tones removes potential peripheral adaptation.

Most recently, Vigneault-MacLean *et al.* (2007) adopted the general procedure of the two prior studies, but rather than asking participants to simply distinguish left from right, they asked them to assign specific locations to each test tone based upon an overhead diagram of auditory space (see Figure 2). The benefit of this procedure was that not only did it again illustrate the shift that occurs around the midline, but it demonstrated that lateral adaptation causes perceived test tone locations to be displaced away from the adapted side across the entire adapted hemifield. This displacement also bleeds over the midline, consistent with a hemifield channel with borders extending across the center auditory field. This third experiment constitutes strong support for a two-channel model in humans consistent with neurophysiological data from mammals (e.g., Stecker *et al.*, 2005).

However, while the two-channel model is consistent with the majority of binaural “hemifield” cells that have broad tuning centered on one of the two lateral auditory hemifields, the existence of neurophysiological data on a much smaller population of



neurons that are more narrowly tuned to the auditory midline (mentioned above) raises the question of whether there exists a third, midline channel in mammalian auditory localization machinery. These “frontal” or midline-preferring cells have been consistently reported, though at a much lower rate than the hemifield cells, in both free-field studies (e.g., Middlebrooks and Pettigrew, 1981; Rajan *et al.*, 1990; Lee and Middlebrooks, 2010) and dichotic ones (e.g., Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Orman and Phillips, 1984). While earlier psychophysical procedures used to study the two-channel model did not provide methodologies suitable to probing the existence of a midline channel, the addition of specific location judgements to the selective adaptation paradigm by Vigneault-MacLean *et al.* (2007) does so.

#### **1.4 PURPOSE OF THE PRESENT STUDIES**

What follows are three manuscripts, comprising of ten experiments, that make up a body of work that explores the existence of a midline channel in human listeners. Chapter 2 begins by first replicating the selective adaptation experiment in which a different low-frequency ITD adaptor at each ear (asymmetrical adaptation) results in shifts in the perceived location of test tones across the adapted hemifield as would be consistent with a two-channel model (Vigneault-MacLean *et al.*, 2007). The successful replication is followed by two experiments using low-frequency adaptors localized by ITD in which the same frequency is adapted on each side (symmetrical adaptation) or at the midline (central adaptation) in order to uncover evidence consistent with the hypothesized third channel tuned to sounds located at the azimuthal midline. These two experiments provide the first data in man that support a three-channel model of binaural

localization. In chapter 3, four experiments explore the sensitivity of this midline channel to ILD at both high and low frequencies, using both symmetrical and central adaptation. As mentioned above, while the ILD cue is thought to be primarily used in natural settings for frequencies above about 3000 Hz, dichotic listening experiments have shown that the auditory system will nevertheless make use of low-frequency ILD cues if they are made available (for a review, see: Phillips *et al.*, 2011). Consistent with this, experiments in chapter 3 present striking evidence of a midline, ILD-based channel present at both high- and low-frequencies. To complete this data set, chapter 4 describes three experiments in which high-frequency transposed stimuli are used to probe for midline channel sensitivity to high-frequency ITDs. Again, the ITD cue for pure tones can only be effective for frequencies below about 750 Hz in humans because for frequencies above this, for which travel distance between the ears results in a time difference greater than a half period of the sound wave, the ongoing phase difference becomes ambiguous (as per the discussion above). The transposed stimuli used in chapter 4 are made by multiplying a high-frequency pure tone carrier by a half-wave-rectified low frequency modulator. The resulting stimuli contain mostly high-frequency energy, but also provide temporal information in the envelope of the amplitude modulation. The first experiment in chapter 4 demonstrates sensitivity to high-frequency ITDs of two lateral azimuthal channels, while the second and third experiments probe for evidence of a high-frequency ITD-sensitive midline channel.

## CHAPTER 2      MIDLINE CHANNEL: LOW FREQUENCY ITD<sup>2</sup>

### 2.1 ABSTRACT

Neurophysiological and psychophysical evidence has driven the formulation of a hemifield model of mammalian sound localization in which the perceived location of a stimulus is based on the relative activity of two hemifield-tuned azimuthal channels that are broadly responsive to contralateral auditory space and have overlapping medial borders. However, neurophysiological work in mammals has consistently found neurons selective for sound sources at the midline, which may indicate the existence of a third, "midline", perceptual channel. In three experiments, the existence of three (left, right, midline) perceptual channels for azimuth in man was examined using auditory selective adaptation paradigms. If no midline channel exists, exposure to highly lateralized, symmetrical adaptor frequencies should not result in a shift in the perceived intracranial location of subsequent test tones away from the adaptors because the relative activation of the two hemifield channels will remain the same. Rather, our results indicate a shift in perceived test tones towards the azimuthal midline. This result can best be explained by a perceptual/neural channel tuned to sounds located along the midline. The present study gives the first psychophysical evidence of a midline channel serving human auditory

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<sup>2</sup> This chapter has previously been published as:

Dingle, RN, Hall, SE, & Phillips, DP (2010) A midline azimuthal channel in human spatial hearing. *Hearing Research*, doi: 10.1016/j.heares.2010.04.017

localization, adding to the earlier evidence on the same point from animal neurophysiological studies.

## 2.2 INTRODUCTION

A priority assignment in hearing neuroscience is to establish the extent to which descriptions of the neural coding of stimulus dimensions account for perceptual behaviour in the same dimensions. In this regard, the most compelling model of mammalian sound localization mechanisms suggests that perceived source azimuth depends upon the relative activity of two hemifield-tuned neural/perceptual channels that are broadly responsive across the left and right acoustic hemifields, and have overlapping medial borders (McAlpine and Grothe, 2003; Phillips, 2008). The fact that mammals have greatest sound lateralization acuity for sources near the midline (e.g., in man: Stevens and Newman, 1936; Mills, 1985) has been ascribed to the fact that the relative activation of these two perceptual channels is most differentiated for near-midline sources (Boehnke and Phillips, 1999; Stecker *et al.*, 2005; Phillips and Hall, 2005). This general model is heavily based on neurophysiological studies in mammals that consistently find that the majority of spatially-sensitive auditory neurons in each cerebral hemisphere discharge maximally to sounds located in the contralateral hemifields, minimally for sources in the ipsilateral acoustic hemifield, and show greatest sensitivity to position change (steepest changes in firing rate with changes in stimulus location) for sources near the midline (Middlebrooks and Pettigrew, 1981; Phillips and Brugge, 1985; Rajan *et al.*, 1990; Brugge *et al.*, 1996; Stecker *et al.*, 2005), or to the cues associated with those locations (Phillips and Irvine, 1981; Orman and Phillips, 1984; Kelly and

Phillips, 1991; McAlpine *et al.*, 2001). Lesion studies show generalized localization deficits in the hemifield contralateral to unilateral forebrain ablations (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984; Kavanagh and Kelly, 1987; Heffner, 1997; for a review see: McAlpine and Grothe, 2003) suggesting that the neural machinery serving each hemifield channel resides largely in the contralateral auditory forebrain. Note, though, that the ablation-induced contralateral hemifield sound localization deficit does not directly speak to the spatial tuning of neural elements serving the affected acoustic hemifield.

Recent psychophysical experiments in humans support the hemifield model of sound localization. A number of paradigms have provided convergent evidence in support of hemifield tuning, including gap detection (Boehnke and Phillips, 1999), spatial release from masking (Phillips *et al.*, 2003), and selective adaptation (Phillips and Hall, 2005; Phillips *et al.*, 2006). In one selective adaptation paradigm, participants are asked to indicate whether they perceive a tone to be left or right of their auditory midline. Participants complete this task for tones ranging in location along the intracranial auditory azimuth (as determined by interaural time difference [ITD] or interaural level difference [ILD]) both before and after exposure to a highly lateralized auditory adaptor stimulus; in this way, experimenters determine the participants' psychometric functions before and after adaptation. Adaptation results in displacement of the psychometric function towards the adapted side. This shift in the perceived point of centrality towards the adapted side (which can also be construed as a shift in a specific tone's location *away* from the adapted side) has been interpreted as the result of a change in the relative

activation of the two hemifield channels resulting from the adaptor's fatiguing of one channel (Phillips, 2008).

As an alternative to studying distortions of midline perception, Vigneault-MacLean *et al.* (2007) asked participants in a selective adaptation experiment to provide a position judgement for tones of various ITD by responding to each tone with a number corresponding to a specific location as presented to them on an overhead schematic of the frontal spatial hemifield. This variation of the selective adaptation paradigm found that perceptual distortions occurred broadly across the hemifield on the adapted side and with a modest bleed of effect across the midline, as would be predicted by the hemifield model. The results of Vigneault-MacLean *et al.* (2007) thus provide strong psychophysical support for the hemifield model in humans.

However, this conceptualization of mammalian sound localization mechanisms may be incomplete. Some animal neurophysiological work suggests that sound localization may be supplemented by a third group of neurons tuned narrowly to sounds with locations near the midline in free-field studies (Middlebrooks and Pettigrew, 1981; Rajan *et al.*, 1990) or to near-zero ITDs or ILDs in dichotic ones (Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Orman and Phillips, 1984). These cells make up only about 10% or less of the neurons in the auditory cortex (Phillips and Irvine, 1981; Orman and Phillips, 1984; Stecker *et al.*, 2005). If similar cells exist in the human auditory system, then they might support a third, "frontal" or "midline" channel. This group of midline-preferring neurons may increase the precision of localization within that region of space by constituting a third group of neurons whose firing rates are a sensitive function of source location (or the cues for it) near the midline.

The aim of the present study was to probe the existence of this "frontal" channel in humans using the position report psychophysical method. Experiment 1 sought to replicate the study by Vigneault-MacLean *et al.* (2007), in which participants experienced adaptor tones of a different frequency on each side (asymmetrical adaptors), causing opposite shifts in the perceived location of subsequent test tones of those frequencies. In Experiment 2, participants experienced an adaptor stimulus at the same frequency on each side (symmetrical adaptors). If there is no midline channel, symmetrical adaptation of both hemifield channels should result in no change in the perceived location of test tones, since the *relative* outputs of the presumptive two hemifield channels would be uninfluenced by the adaptation. On the other hand, in the case that a midline channel exists and contributes to the relative output calculation, fatiguing the lateral channels should result in a shift in the perceived location of test tones towards the midline. The complementary experiment to this involves fatiguing the midline channel with an adaptor located at the midline, which should result in a shift in the perceived location of test tones away from the midline (Experiment 3).

### **2.3 EXPERIMENT 1**

The purpose of Experiment 1 was to replicate the findings of Vigneault-MacLean *et al.* (2007). Participants were asked to localize tones at each of eleven ITDs before and after adaptation with strongly lateralized sequences of 260 and 570 Hz tone pulses. Two adaptor conditions counterbalanced the side of the adaptor frequency. It was expected that after adaptation the perceived location of the test tones would shift away from the

adaptor tone of the same frequency within the adapted hemifield, as was found previously.

### 2.3.1 Methods

*a) Participants.* Participants were 10 normal hearing adults between the ages of 23 and 45. All participants had tone detection thresholds better than 20 dB HL at octave frequencies from 0.25 to 4.0 kHz, and thresholds for the two ears did not differ by more than 10 dB at any tested frequency within this range. Procedures used in this and subsequent experiments received ethics approval from the Dalhousie University Social Sciences & Humanities Human Ethics Board under protocol # 2004-860.

*b) Stimuli.* The stimuli used were 70 dB (A-weighted sound pressure level) tones at 260 Hz and 66 dB tones at 570 Hz, roughly 4.5 critical bands apart (Phillips and Hall, 2005) and judged of equal loudness in pilot work. Each test tone was 200 ms in duration, including 10 ms linear rise and fall ramps. For each frequency, eleven test tones ranged in ITD from +454  $\mu$ s (right leading) to -454  $\mu$ s (left leading) in steps of  $\sim$ 90  $\mu$ s resulting in one test tone at 0 ITD (midline) and five test tones on either side. 500 ms before each test tone, three 0-ITD high-pass (2 kHz cut-off) dichotic clicks were presented to orient listeners to the midline. Adaptor stimuli were trains of 200 ms tone pulses (including 10 ms rise and fall ramps) with inter-tone intervals of 20 ms. Pulses alternated between  $\pm$  one quarter period ITD (961  $\mu$ sec for the 260 Hz tone and 439  $\mu$ sec for the 570 Hz tone) such that the participants perceived a highly lateralized 260 Hz tone on one side alternating with a 570 Hz tone lateralized to the other side. Two adaptor conditions were used in Experiment 1, identical to those used in Vigneault-MacLean *et al.* (2007). In one



condition, the 260 Hz tone was on the left and a 570 Hz tone was on the right, and in the other condition the tones were reversed.

Tones were digitally synthesized on an Apple Powermac G4 computer with MatLab at a sampling frequency of 44100 Hz, and were presented on Sennheiser HD25-1 headphones. Participants sat in a sound-attenuating booth with the monitor and keyboard; the CPU was located outside of the booth. Tone levels were measured with an Extech sound level meter (model 407750). Participant responses were made via the number pad of the keyboard.

*c) Procedure.* Listeners were first familiarized with the response scale and the test-tone ITD range to which they would be exposed. They were instructed that in the experiment, they were to use as much of the response scale as they deemed appropriate. The task completed by the participants has been previously described in (Vigneault-MacLean *et al.*, 2007). Briefly, participants were presented with a test tone and asked to respond with a number corresponding to the perceived location of that tone as described by a schematic showing an overhead view of the frontal hemisphere with numbers from 0-32 marking locations in 6° intervals (Figure 2). As in Vigneault-MacLean *et al.*'s (2007) study, subjects in the present experiment found it easy and intuitive to make the translation from perceived intracranial location to the externalized position report. Each test tone was preceded by three midline clicks (ICI = 60 ms) which were presented to help participants orient to the midline. Participants made five judgements for each tone at each of eleven ITDs, for a total of 110 trials per block in random order. One session consisted of one block of trials without the adaptors (baseline; Figure 3, upper) and one block with the adaptors, and took 20-30 minutes to complete. During adaptation blocks

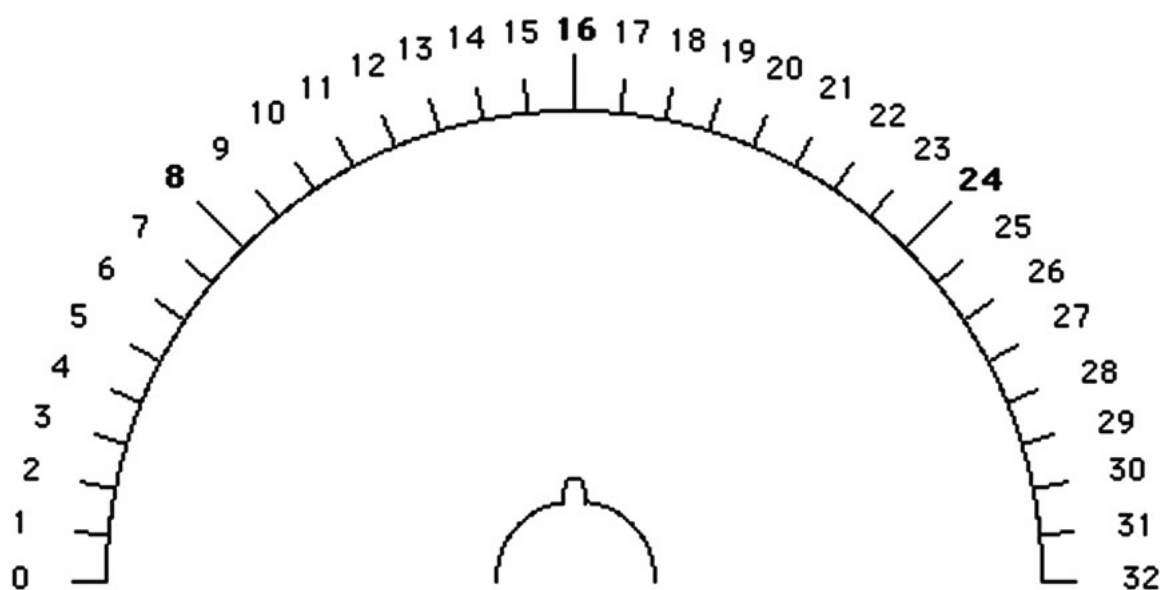


Figure 2. The schematic used by participants to localize tones both in this paper and in Vigneault-MacLean *et al.* (2007).<sup>3</sup>

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<sup>3</sup> Reprinted from: Hearing Research, vol. 224, Vigneault-MacLean, B. K., Hall, S. E., and Phillips, D. P. "The effects of lateralized adaptors on lateral position judgements of tones within and across frequency channels," pp. 93-100, Copyright (2007), with permission from Elsevier.

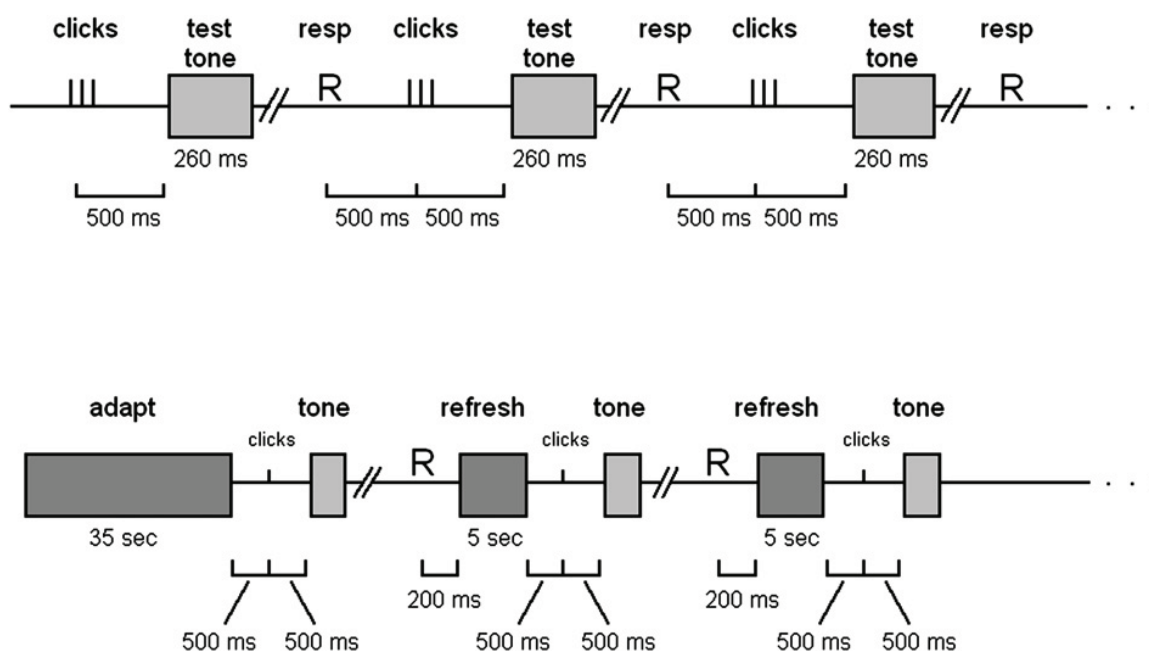


Figure 3. Stimulus timing for baseline trials (upper) and adaptation trials (lower). (From: Phillips and Hall, 2005).<sup>4</sup>

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<sup>4</sup> Reprinted from: Hearing Research, vol. 202, Phillips, D. P., and Hall, S. E.

"Psychophysical evidence for adaptation of central auditory processors for interaural differences in time and level," pp. 188-199, Copyright (2005), with permission from Elsevier.

(Figure 3, lower), participants were presented with 35 s of an adaptor stimulus before beginning the task, as well as 5 s of the adaptor between each trial (after Kashino and Nishida, 1998; Phillips and Hall, 2005). Two sessions, one with each of the two adaptors, were carried out, separated by at least 24 hrs. (See Figure 3 for pictorial representation of the experimental design.)

### 2.3.2 Results & Discussion

Figure 4 shows the mean position report for each test tone ITD before and after adaptation. The top panels present the data for the 260 Hz test tones for each adaptor condition, while the bottom panels present the data for the 570 Hz test tones. In this, and following data illustrations, the ribbons overlaying the lines represent the Fisher's least significant difference calculated for the data sets. Conservatively, pre- and post-adaptation ITDs at which these ribbons do not overlap can be considered significantly different. All panels show an orderly progression of perceived intracranial location as stimulus ITDs progress from left-leading to right leading, confirming the participants' ability to discriminate reliably between the test tones. Further, all the pre-adaptation curves cross the perceived midline (16) at or very near 0 ITD.

As seen previously (Vigneault-MacLean *et al.*, 2007), an adaptor tone presented on one side caused a shift in the perceived location of subsequent test tones in that hemifield away from the adapted side (toward the midline). Specifically, when the adaptor was presented at 260 Hz on the left and at 570 Hz on the right, the perceived location of the 260 Hz test tones within the left hemifield shifted rightwards, while the perceived locations of the 570 Hz test tones in the right hemifield shifted leftwards, and

vice versa when adaptor tones were reversed. This use of these two adaptor types was the first repetition of this paradigm, and provided a replication of the earlier results. The perceived location post-adaptation often showed the greatest shift for middle values of test-tone ITD, rather than for the largest test ITDs which were those closest in size to the ITDs of the adaptor tones. This was clearest in the case for responses to 570 Hz tones, for which the range of test tone ITDs extended to equal almost a quarter period (the size of the adaptor ITD). For responses to the 260 Hz tones, the range of test ITDs was only half of the adaptor quarter period, and it is perhaps for this reason that the pre- and post-adaptation curves do not merge at extreme test tone ITDs. What is more evident here than in the previous study, however, is a difference in effect size between the lower and higher tones; there is clearly a greater shift in the perceived location of tones after the 260 Hz adaptor than the 570 Hz adaptor.

These conclusions were supported by four 11 (ITD) x 2 (Condition) repeated measures ANOVAs, each performed for a specific adaptor pair and test-tone frequency. Each of the four ANOVAs resulted in main effects of ITD (260 Hz tones with 260 Hz adaptor on the left,  $F(10,90)=37.451$ ; 570 Hz tones with 260 Hz adaptor on the left,  $F(10,90)=58.898$ ; 260 Hz tones with 570 Hz adaptor on the left,  $F(10,90)=32.607$ ; 570 Hz tones with 570 Hz adaptor on the left,  $F(10,90)=46.764$ ; for all  $p < 0.0001$ ) reflecting the orderly psychometric functions. There were main effects of condition (i.e., adaptation, 260 Hz tones with 260 Hz adaptor on the left,  $F(1,9)=24.589$ ; 570 Hz tones with 260 Hz adaptor on the left,  $F(1,9)=30.453$ ; 260 Hz tones with 570 Hz adaptor on the left,  $F(1,9)=13.136$ ; 570 Hz tones with 570 Hz adaptor on the left,  $F(1,9)=21.383$ ; for all  $p < 0.006$ ). All but one ANOVA (the 570 Hz tone with the right ear 570 Hz adaptor,

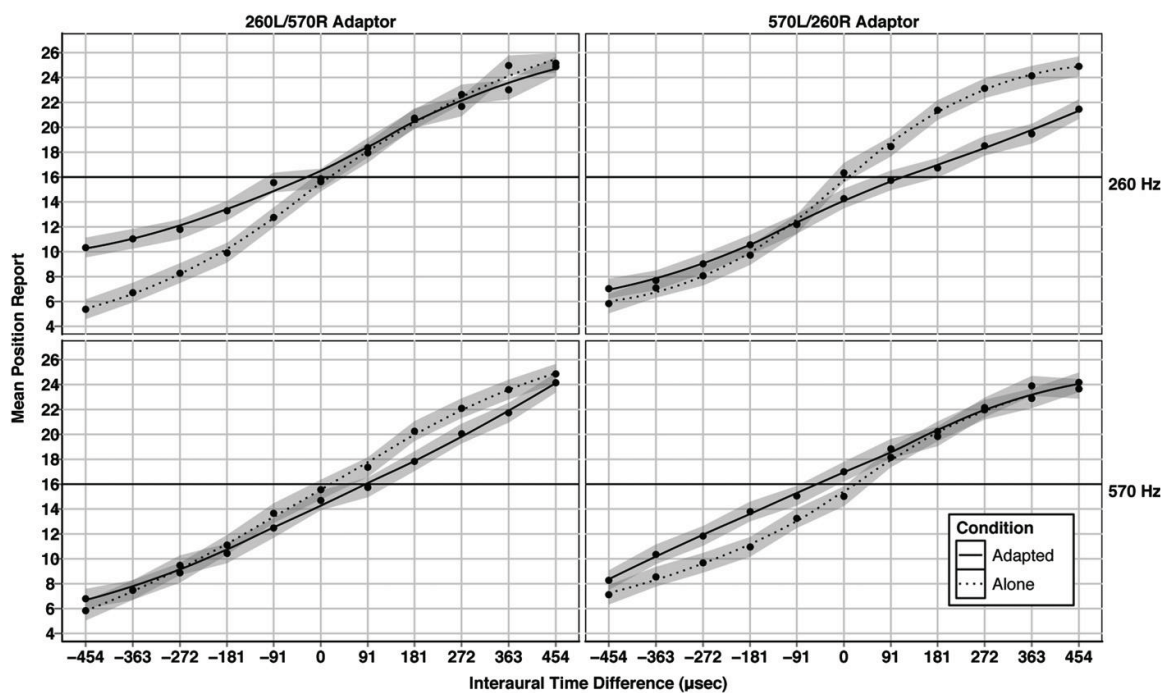


Figure 4. Data from Experiment 1. The mean perceived location of test tones as a function of ITD before and after adaptation (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptors and each row represents one of two test tones. Numbers on the ordinate are positions reported by the subjects using the response schematic shown in Figure 2. The ribbons overlaying the lines represent the Fisher's least significant difference calculated for the data set. Conservatively, pre- and post-adaptation ITDs at which these ribbons do not overlap can be considered significantly different.

$F(10,90)=1.294$ ,  $p=0.245$ ) resulted in significant ITD x condition interactions (260 Hz tones with 260 Hz adaptor on the left,  $F(10,90)=4.385$ ; 260 Hz tones with 570 Hz adaptor on the left,  $F(10,90)=6.890$ ; 570 Hz tones with 570 Hz adaptor on the left,  $F(10,90)=2.948$ ; for all  $p < 0.004$ ), reflecting the change in the slope of the psychometric functions between the adapted and non-adapted states.

## 2.4 EXPERIMENT 2

The purpose of Experiment 2 was to explore the existence of a possible third perceptual channel tuned specifically to the auditory midline. This was done by adapting both lateral channels with the same tone frequency. Symmetrical adaptation of both lateral hemifields should result in a shift in the perceived location of test tones towards the midline if a frontal channel exists. If there is no frontal channel, symmetrical adaptation should result in no change of perceived location since the relative activation across the two channels will remain the same.

### 2.4.1 Methods

All listeners from Experiment 1 participated in Experiment 2, which consisted of two more sessions structured identically to those in Experiment 1 but with new symmetrical adaptors. Thus, participants reported the perceived location of test tones (260 and 570 Hz) five times at each of 11 ITDs in random order for baseline and adapted blocks as in experiment 1, but adaptors were dichotic tones, of either 260 Hz on first one side and then the other, or of 570 Hz on both sides, again first on one side and then the other. All adaptor tones contained a quarter period ITD. All sessions occurred at least 24

hours apart and the order of the four adaptation conditions from Experiments 1 and 2 was counterbalanced pseudo-randomly.

#### *2.4.2 Results & Discussion*

Figure 5 presents the results of the symmetrical adaptation in Experiment 2. Rather than resulting in no shift, adapting the same frequency on both sides caused the perceived location of all test tones at that frequency to shift towards the centre, as represented by the shallower adapted curves in the upper left and bottom right panels. Note that there was little or no “bleeding” of the adaptation effect to the responses to the non-adapted frequency (upper right and lower left panels). Once again, the effect of the 260 Hz adaptor appears much stronger than that of the 570 Hz adaptor.

Each of the four ANOVAs for the symmetrical adaptors resulted in main effects of ITD (all  $p < 0.0001$ ) confirming that different test-tone ITDs led to different lateral position judgements. Symmetrical adaptors resulted in no main effect of condition, which would be expected in light of the equal but opposite shifts on either side of the midline. Both the 260 Hz test tones after 260 Hz adaptation (upper left panel) and the 570 Hz test tones after 570 Hz adaptation (lower right panel) resulted in significant ITD x Condition interactions ( $F(10,90)=11.596$ ,  $p < .0001$  and  $F(10,90)=5.630$ ,  $p < 0.0001$ , respectively).



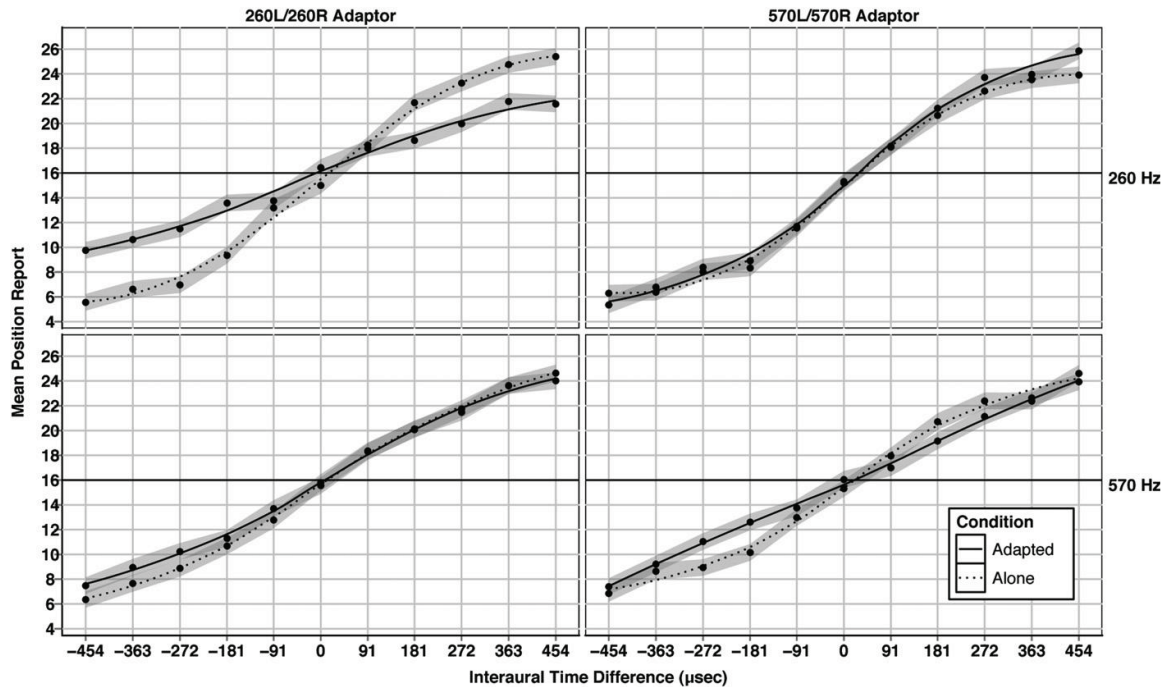


Figure 5. Data from Experiment 2. The mean perceived location of test tones as a function of ITD before and after adaptation (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptors and each row represents one of two tones. The ribbons overlaying the lines represent the Fisher's least significant difference calculated for the data set.

## 2.5 EXPERIMENT 3

Experiment 2 provided evidence for the existence of a midline perceptual channel for source azimuth by revealing shifts in perceived location towards the midline following exposure to highly lateralized adaptors. Experiment 3 offers the converse paradigm: a study of the effects on perceived test tone location following exposure to midline adaptor tones.

### 2.5.1 *Methods*

Twelve participants were used in Experiment 3, seven of whom had already participated in Experiment 1 and 2. Again, participants were all normal hearing adults between the ages of 23 and 45 with tone detection thresholds better than 20 dB HL and not differing more than 10 dB at any tested frequency. The design of the experiment was the same as Experiment 2 with the exception that each adaptor condition presented pulse trains at the midline rather than alternating from side to side: A 260 Hz 0-ITD adaptor, or a 570 Hz 0-ITD adaptor, presented in different blocks of trials.

Notably, because the adaptor tones in this experiment used one ITD rather than two but the duration of the adaptation was held constant from Experiment 1, the amount of adaptation at the single location was twice that in the earlier experiments (i.e., twice the number of adaptor tones targeting the channel of interest).

### 2.5.2 *Results & Discussion*

Figure 6 shows the mean position reports for each test tone ITD before and after adaptation for Experiment 3. A shift in the perception of test tones away from the midline

(in this case, a steeper curve) is evident at the 570 Hz test tones after central adaptation of the same tone, although it is only obvious in the right hemifield. After 260 Hz adaptation, no shift is evident for responses to the 260 Hz test tones. This is in contrast to the previous experiment in which a greater effect was seen for the lower-frequency tone. As expected, there is no effect on test tones at 570 Hz after 260 Hz adaptation but, interestingly, there appears to be a small effect of the 570 Hz adaptor on responses to the 260 Hz test tones (upper right panel). When the data were divided into listeners who had participated in the first experiment and those who had not, the effect at 260 Hz was present for the former group and not the latter. Similar effects were seen in Vigneault-MacLean *et al.* (2007), and may be the result of a learned connection between the tones after repeated experience with them in conjunction, or may be a simple "bleed" effect across frequency.

Again, four ANOVAs were done, one for each combination of test tones and adaptor frequencies. All ANOVAs showed a significant main effect of ITD ( $p < 0.0001$ ), again demonstrating the orderly ITD psychometric function. Only the 570 Hz tones tested after 570 Hz adaptation showed a significant ITD x condition interaction ( $F(10,110)=4.7778$ ,  $p < 0.0001$ ). When broken down into experienced participants versus naive participants, the significant ITD x condition interaction for the 260 Hz test tones after 570 Hz adaptation was maintained for the experienced participants ( $F(10,60)=2.175$ ,  $p = 0.0317$ ) but not for the naive participants.

Interestingly, one participant in Experiment 3 experienced a strongly opposite effect to the others. Adaptation at the midline resulted in a clear shallowing of her psychometric function, rather than a steepening, and she verbally reported a shift in

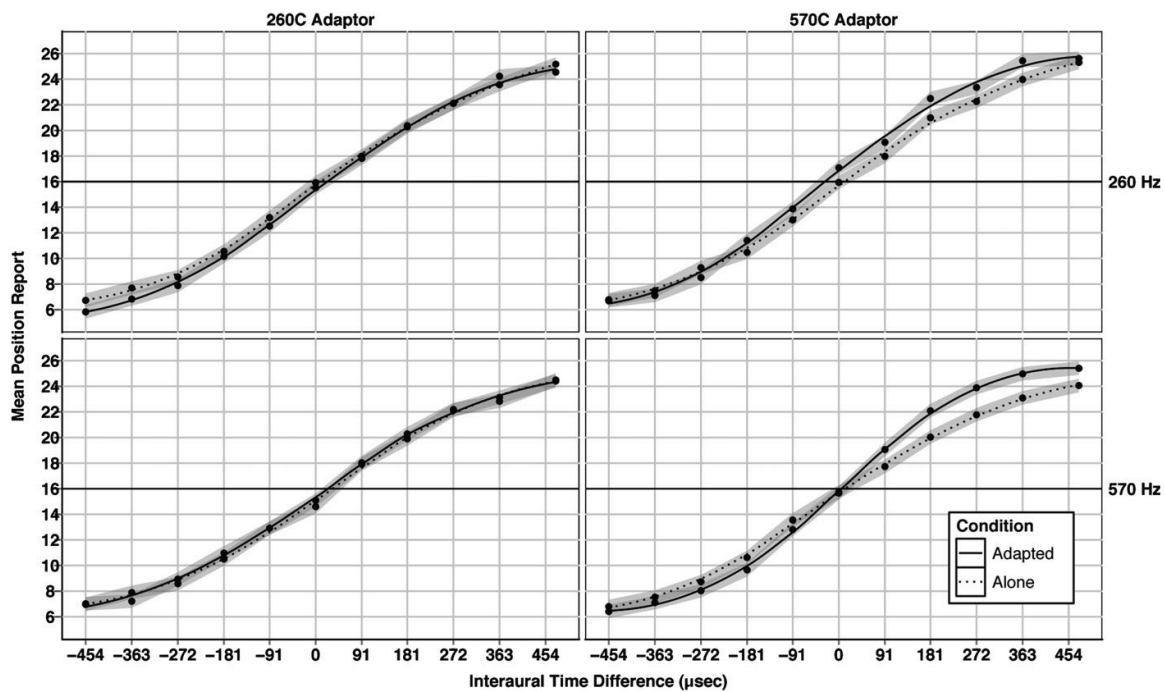


Figure 6. Data from Experiment 3. The mean perceived location of test tones as a function of ITD before and after adaptation (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptors and each row represents one of two tones. The ribbons overlaying the lines represent the Fisher's least significant difference calculated for the data set.

perception *towards* the midline. In all other cases for both this and previous experiments, the individual participant's results showed either no shift or a shift in the expected direction. However, removal of this subject from statistical analysis did not result in any significant changes, nor was there any obvious reason for this individual difference.

## 2.6 GENERAL DISCUSSION

Data from psychophysical studies using selective adaptation paradigms have supported the hemifield model of sound localization in humans (Phillips and Hall, 2005; Phillips *et al.*, 2006). Neurophysiological evidence for the existence of a midline-tuned channel has existed for 30 years (Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Rajan *et al.*, 1990), but to date, there has been no definitive psychophysical evidence for its existence in man. Here we extend the psychophysical selective adaptation paradigm to probe for the existence of this midline perceptual channel.

Experiment 1 replicates the effect seen in the study by Vigneault-MacLean *et al.* (2007). Lateral adaptation resulted in a frequency-specific shift in position reports away from the side of the adaptor tone. Adaptation tended to be strongest for the middle values of ITD in the hemifield of the adapted side, with some bleeding of effect into the contralateral hemifield. This is consistent with the hemifield model, which proposes two populations of neurons tuned to stimuli in the contralateral auditory field with overlapping medial borders (McAlpine and Grothe, 2003; Phillips, 2008).

The novel findings of this study were the shifts in the perceived location of test tones towards the midline after adaptation in Experiment 2. This is clear evidence of a third channel serving auditory azimuth and tuned specifically to locations at or near the

midline. The direction of the position report shifts is consistent with our hypothesis, namely that perceived location depends on the relative outputs of the three perceptual channels. With both of the lateral hemifield channels selectively adapted, the midline channel contributes disproportionately and thus draws the perceived location towards the midline. This perceptual channel may have its neural basis in the small percentage of neurons which fire preferentially to midline stimuli in free-field studies (Rajan *et al.*, 1990; Stecker *et al.*, 2005), or the cues for them, as seen in dichotic neurophysiological studies (Phillips and Irvine, 1981; Orman and Phillips, 1984; Rajan *et al.*, 1990; Stecker *et al.*, 2005).

Two features of the effect warrant special mention. The first concerns the size of the effect. At 260 Hz, adaptation caused a shift in perceived location of about 4 steps ( $24^\circ$ ) while at 570 Hz the maximum shift was closer to 2 steps ( $12^\circ$ ), consistent with the data from Vigneault-MacLean *et al.* (2007). The fact that the effect was about twice as strong at 260 Hz as at 570 Hz may suggest that the midline channel is not uniform across frequencies. However, this difference may also be explained by the difference in absolute ITDs used for the adaptor stimuli. A quarter period ITD at 260 Hz is a difference of about 961  $\mu\text{sec}$  as compared to about 439  $\mu\text{sec}$  for a 570 Hz tone. It may simply be that the larger absolute ITD for the 260 Hz tone resulted in a stronger adaptation, although it would be hard to imagine a stronger 570 Hz ITD adaptor than a quarter cycle one. The second feature is the range of test tone ITDs over which the effect occurred. Although the effect was often strongest for test tones with middle ITD values, the effect sometimes spanned the full range of test tone ITDs on the adapted side (e.g., Figure 5A). At first glance, this might be taken as an indication of the tuning of the midline channel being

quite broad, which is in contrast to the narrow tuning of the midline cells identified neurophysiologically. However, the neurophysiological descriptions of "midline cells" have all come from high-frequency cells (outside the range encoding interaural phase differences of simple tones), so it is not clear that the tuning seen in the present psychophysical study should match that seen in the neurophysiology. In this regard, psychophysical evidence for the existence of left and right hemifield channels based on interaural level differences for frequencies as high as 3 kHz has been presented previously (Phillips and Hall, 2005). It would be helpful to the evaluating of the 3-channel model to know if the ITD and ILD channels of the kind described to date extend to even higher frequencies. A second way of interpreting the breadth of test tone ITDs affected by unmasking of the midline channel through adaptation of the lateral ones depends on two factors. One is the breadth of tuning of the midline channel itself. The second is the extent to which the lateral channels may work independently for sounds located at azimuthal extremes. This will be discussed in more depth below. There is, parenthetically, the further complication of the unknown fashion in which listeners might have scaled their responses to test tones to exploit the response range available.

Experiment 3 did not reveal as strong a complementary effect as that seen in Experiment 2, although the directions of the perceptual disturbances seen were those hypothesized. The lack of a statistically significant shift, despite twice as much adaptation at the midline as was given laterally in Experiment 1 and 2, is perhaps unsurprising. As discussed earlier, the majority of location-sensitive neurons in neurophysiological studies (~60%) have been found to fire preferentially to stimuli in the contralateral hemifields (Middlebrooks and Pettigrew, 1981; Phillips and Brugge, 1985;

Rajan *et al.*, 1990; Brugge *et al.*, 1996). In contrast, only about 10% of neurons respond preferentially to stimuli at the midline. Thus, the degree to which the midline channel contributes disproportionately little to perceived location after adaptation is far less than the degree to which it is over-represented after adaptation of the lateral hemifield channels.

One could argue that if the results of Experiment 2 are considered in isolation, then it is not necessary to posit the existence of a third channel to explain those data. If it were the case that each of the lateral channels were independently capable of supporting localization within its own hemifield, then it could be argued that adapting each channel would fatigue neural firing strengths within those channels such that the perceived location of test tones would move away from the side of the adaptors and that the combination of two independent shifts would give identical results to those seen here. However, normal sound localization must depend on the *relative* activation of the neural channels in order to account for the shifts in perceived midline seen in Experiment 1. That is, adapting a single hemifield channel results in perceived position shifts, despite the presumably intact functioning of the non-adapted channel whose tuning encompasses the midline azimuths (after Boehnke and Phillips, 1999; Phillips, 2008). Further, if the lateral channels worked entirely independently and without input from a third, midline channel, then adaptation at the midline, as used in Experiment 3, should be expected to have same effect as two symmetrical lateral adaptors since both types should fatigue the lateral channels equally. The effect seen in Experiment 3 was, if anything, opposite to that in Experiment 2, which is consistent with the existence of a channel tuned to midline azimuths.



The introduction of a frontal channel to the mammalian model of sound localization is not a huge overhaul. It does, however, offer an additional basis for the superior accuracy of sound localization for sources near the midline (Mills, 1985). Historically, this superiority has been explained by the fact that the stimulus information used for sound azimuth judgements (rate of change of interaural disparity size as a function of source eccentricity) is most precise for near-midline sources, as is the neural code for disparity magnitude (for a review see: Phillips and Brugge, 1985). That is, the brain's firing rate code for the size of interaural disparities is most specific for disparity sizes that themselves most precisely specify source azimuth. Stecker *et al.* (2005) find a more recent expression of the same general hypothesis in their free-field studies. The present study now adds psychophysical evidence of a midline channel to the earlier evidence on the same point from animal neurophysiological studies.

There is some previous psychophysical evidence compatible with the present model. Carlile *et al.* (2001) had human participants sit in the dark with an electromagnetic positioning system on their head. Sounds were delivered via a speaker on a robotic arm that could move the source anywhere on a sphere of constant radius around the participant, and participants were asked simply to orient their heads towards the sound. Adaptor tones at 0 or 30° azimuth were presented in a similar manner to those in this experiment—an initial 4 minutes of adaptation was followed by 15 sec maintenance adaptation between each trial. When Carlile *et al.* compared the mean perceived location of sounds pre- and post-adaptation, they found a radial shift in the participants' judgement away from the location of the adaptor. Carlile *et al.* interpreted these results as supporting a “population” model of human spatial hearing, in which a population of

topographically organized auditory neural units are each narrowly tuned to respond to a sound at a discrete location. Thus, fatiguing those units whose receptive fields contain the adaptor tone causes the perceptual shift away from the adaptor. This interpretation is a direct corollary to the neural model of spatial hearing developed by Knudsen and Konishi's work in the barn owl (Knudsen and Konishi, 1978; Knudsen, 1981; Konishi, 2003). But while the population model of spatial hearing is demonstrably true for barn owls, it has failed to generalize fully to other owls (Volman and Konishi, 1989), and has not at all successfully explained data from other predatory birds (Calford *et al.*, 1985) or mammals (Stecker *et al.*, 2005; Phillips, 2008). Further, Carlile *et al.*'s model of neural units with narrowly-tuned, overlapping receptive fields would suggest that any perceived shift after adaptation would be fairly localized around the adaptor, as a relatively small number of neural units will be fatigued. This is inconsistent with the results seen here and in Vigneault-Maclean *et al.* (2007), which show adaptation effects across the entire lateral hemifields. In this regard, while Carlile *et al.* (2001) interpret both the 0 and 30° adaptation effects as being radial shifts away from the location of the adaptor, a close inspection of their figures shows that the azimuthal shift seen after 30° adaptation appears to be an entirely lateral shift towards the midline, consistent with our proposed model.

A remaining question concerns the location of the neural machinery supporting the three perceptual channels. Behavior-lesion studies have consistently shown that unilateral forebrain lesions result in free-field sound localization deficits only for the contralateral acoustic hemifield (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984; Kavanagh and Kelly, 1987; Heffner, 1997). This suggests that each cerebral hemisphere is independently capable of supporting localization of sounds in the

contralateral hemifield, including those near the midline. Because accurate localization, perhaps especially of sources near the midline, receives contributions from all three perceptual channels, it follows that the neural machinery supporting those channels must also reside in each cerebral hemisphere. In this regard, neurophysiological studies of free-field sound location coding (Rajan *et al.*, 1990; Stecker *et al.*, 2005) and studies of binaural interactions and/or interaural disparity coding in dichotic experiments (Imig and Adrian, 1977; Middlebrooks *et al.*, 1980; Phillips and Irvine, 1981; 1983; Brugge *et al.*, 1996; Zhang *et al.*, 2004) indicate the presence of contralateral-hemifield, ipsilateral-hemifield and "frontal" (midline) preferring neurons in the auditory cortex of a given side. Thus, while the three-channel model has each cerebral hemisphere serving localization exclusively in the contralateral auditory hemifield, it does so by having each cerebral hemisphere equipped with neural apparatus serving all three perceptual channels.

## **2.7 ACKNOWLEDGEMENTS**

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## CHAPTER 3      MIDLINE CHANNEL: ILD<sup>5</sup>

### 3.1 ABSTRACT

The current understanding of mammalian sound localization is that azimuthal (horizontal) position assignments are dependent upon the relative activation of two populations of broadly-tuned hemifield neurons with overlapping medial borders. Recent psychophysical work has provided evidence for a third channel of low-frequency interaural time difference (ITD)-sensitive neurons tuned to the azimuthal midline. However, the neurophysiological data on the free-field azimuth receptive fields, especially of cortical neurons, has primarily studied high-frequency cells whose receptive fields are more likely to have been shaped by interaural level differences (ILDs) than ITDs. In four experiments, a selective adaptation paradigm was used to probe for the existence of a midline channel in the domain of ILD. If no midline channel exists, symmetrical adaptation of the lateral channels should not result in a shift in the perceived intracranial location of subsequent test tones away from the adaptors because the relative activation of the two channels will remain unchanged. Instead, results indicate a shift in perceived test tone location away from the adaptors that supports the existence of a midline channel in the domain of ILD at both low and high frequencies.

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<sup>5</sup> This chapter has been submitted for consideration to be published as:

Dingle, RN, Hall, SE, & Phillips, DP. (in review) “The three-channel model of sound localization: Interaural level differences.” JASA.

### 3.2 INTRODUCTION

The current most popular model of the neural mechanisms underlying mammalian sound localization states that the perceived location of a sound depends upon the relative activity of two channels of neurons, both of which are broadly responsive across one acoustic hemifield (left or right) with overlapping medial borders (e.g. Boehnke and Phillips, 1999; McAlpine *et al.*, 2001; Grothe, 2003; Stecker *et al.*, 2005; Phillips, 2008). This is in contrast to a “place code” model in which sound location is represented by the activation of one of many channels with narrow spatial tuning that are organized topographically within the midbrain or higher central auditory structures, as is seen in the barn owl (Knudsen and Konishi, 1978). The two-channel model has been informed heavily by neurophysiological studies in mammals (most commonly, the cat) showing that the majority of spatially-selective neurons in the primary auditory cortex are broadly responsive to stimuli located in one auditory hemifield. These “hemifield” neurons respond maximally to sound stimuli located either ipsi- or contralaterally, and their response rate drops steeply as stimuli cross the azimuthal midline. Neurons in the primary auditory cortex that do not show this hemifield tuning include “omnidirectional” cells, which are not selective for location in their responding, and a small minority of “frontal” cells that have narrow receptive fields centered on the midline (e.g. Brugge *et al.*, 1996). These patterns of spatial selectivity have been visualized directly in free-field studies (e.g. Middlebrooks and Pettigrew, 1981; Rajan *et al.*, 1990; Stecker *et al.*, 2005) and can be inferred from dichotic ones (Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Orman and Phillips, 1984; Kelly and Phillips, 1991; Brugge *et al.*, 1996; McAlpine *et al.*, 2001).

Evidence supporting the two-channel model in humans came first from psychophysical work, including studies of gap detection (Boehnke and Phillips, 1999), spatial release from masking (Phillips *et al.*, 2003), and selective adaptation (Phillips and Hall, 2005; Phillips *et al.*, 2006; Vigneault-MacLean *et al.*, 2007). In the selective adaptation paradigm, listeners were asked to localize sound stimuli ranging in intracranial azimuth both before and after they were exposed to highly lateralized adaptor tones of the same frequency. Exposure to the adaptor tone is thought to temporarily fatigue the neural channel(s) that respond to stimuli at the adaptor tone's location and frequency, reducing the relative contribution of those channels to subsequent azimuthal position assignments of subsequent test stimuli. After adaptation, listeners indeed exhibited a shift in the perceived locations of test tones away from the side of the adaptor tone of matching frequency. Support specifically for the two-channel model comes from the demonstration that this shift in the perceived location of test tones occurs across the adaptor's entire auditory hemifield (Vigneault-MacLean *et al.*, 2007; Dingle *et al.*, 2010), as opposed to a more localized shift for test tones with intracranial locations close to the adaptor's. The hemifield-wide effect has been demonstrated for low-frequency tones lateralized on the basis of both interaural time difference (ITD) and interaural level difference (ILD) (Phillips and Hall, 2005). Further, adaptation in one of these domains will result in a shift in perception of tones localized by the other, indicating that adaptation is functioning beyond some point of neural integration for these two binaural cues (Phillips *et al.*, 2006). More recently, human data supporting the two-channel model has also come from magnetoencephalography studies (Salminen *et al.*, 2010).

However, the two-channel model as presented may not be a sufficient explanation for the data collected thus far. As mentioned above, neurophysiological work in mammals has consistently found a small subset of neurons that respond maximally to sound stimuli located at the azimuthal midline (e.g., Rajan *et al.*, 1990; Stecker *et al.*, 2005; Lee and Middlebrooks, 2010), in addition to those neurons broadly responsive to the contra- or ipsilateral hemifields. Taking these data into account, our lab has lately extended the selective adaptation paradigm to unmask a third, midline channel contributing to the localization of low-frequency tones in humans (Dingle *et al.*, 2010). This experiment employed "symmetrical" adaptor tones; the adaptor tone alternated between an ITD of +/- one quarter period such that listeners perceived a highly lateralized adaptor tone alternating from side to side. In this way, both hemifield channels were adapted simultaneously such that their relative contribution to sound localization would remain equal. Following the traditional two-channel model, this sort of adaptation should result in no change in subsequent location assignments of test tones. Rather, results were a shift in the perceived location of test tones towards the midline, as would be expected if adaptation of both hemifield channels led to an exaggerated contribution of a midline channel. In a companion experiment, adaptation of the midline channel revealed a modestly greater contribution of the hemifield channels to post-adaptation test tone lateralization (i.e., test tones shifted towards the lateral hemifields).

The congruence between these results and the neurophysiological data is encouraging, but incomplete. In order to probe ITD coding mechanisms, Dingle *et al.* (2010) used low frequency tones, whereas the vast majority of neurophysiological data on the spatial receptive fields of central neurons has come from studies of cells with best

frequencies that are higher than those normally thought useful for ITDs. In an effort to seek a more satisfying behavioural corollary with the neurophysiological data, we now present psychophysical evidence for a midline channel in the domain of ILD at both high and low frequencies.

### **3.3 EXPERIMENT 1**

#### *3.3.1 Experiment 1a*

The general design of these experiments was to obtain intracranial location reports for test tones over a range of ILDs, spanning the frontal hemifield, before and after exposure to adaptor tones of the same frequency. Experiment 1a used symmetrical lateralized adaptors (ILD  $\pm$ 12 dB) to probe for the existence of a midline channel at high frequencies (2800 and 4200 Hz). If human sound lateralization in the ILD domain is explained by a two channel model, equal adaptation of these two channels will cause no shift in the perceived location of test tones since the relative activity of the two channels will remain the same. On the other hand, if there is indeed a channel of cells tuned to sounds at the azimuthal midline, adapting the lateral channels should result in a stronger relative contribution of this center channel to the lateralization of test tones, resulting in a post-adaptation shift in perceived test-tone azimuth toward the midline.

#### *Methods*

*a) Participants.* Nine normal hearing adults between the ages of 22 and 45 each participated in two sessions. Five of the listeners had prior experience participating in a similar paradigm using ITDs (Dingle *et al.*, 2010). All participants had tone detection



thresholds better than 20 dB HL (hearing level, as measured with a Grason-Stadler GSI 16 audiometer) at octave frequencies from 250 to 4000 Hz. Thresholds for each ear at each tested frequency did not differ by more than 10 dB. All procedures in this and later experiments received ethical approval from the Dalhousie University Social Sciences & Humanities Human Ethics Board under protocol # 2010-2243.

*b) Stimuli.* The high-frequency stimuli used in Experiment 1 were 2800 Hz and 4200 Hz tones of 56 and 54 dB, respectively (A-weighted sound pressure level, as measured by an Extech sound level meter, model 407750), judged of equal loudness in pilot work and roughly 4.5 critical bands apart (after Phillips and Hall, 2005). Test tones were each 200 ms in duration, including 10 ms linear rise and fall ramps. ILDs were introduced by raising the stimulus level by half the intended ILD at one ear and lowering it by the same amount at the other ear. Nine test tones at each frequency ranged in ILD from -12 dB (left favoring) to +12 dB (right-favoring) in steps of 3 dB, resulting in one test tone at 0 ITD (midline) and four test tones on either side ( $\pm 3, 6, 9, 12$  dB). Three 0-ILD high-pass (2000 Hz) dichotic clicks (ICI=60ms; amplitude of 48 dB SPL A-weighted) were presented 500 ms before each test tone to orient participants to the midline. Adaptor stimuli were trains of 200 ms tone pulses (including 10 ms rise and fall ramps) at one of the two frequencies with inter-tone intervals of 20 ms. Pulses alternated at  $\pm 12$  dB ILD such that listeners perceived the adaptor as a highly lateralized tone alternating from one side to the other. All stimuli were digitally synthesized on an Apple Powermac G4 computer with MatLab at a sampling frequency of 44100 Hz. Participants sat in a sound-attenuating booth with headphones (Sennheiser HD590), monitor and keyboard; the CPU was located outside of the booth.

*c) Procedure.* All participants completed two sessions, one with each frequency as the adaptor stimuli. Sessions were separated by at least 24 hours and the order of the sessions was randomized.

The procedures used in this experiment were described previously in Vigneault-MacLean *et al.* (2007) and Dingle *et al.* (2010). During each session, a schematic of an overhead view of the frontal hemisphere was displayed on the monitor; numbers from 0-32 marked locations around the hemisphere in 6° intervals. The task of the participants was to respond to each test-tone presentation with a number from the schematic corresponding to the perceived intracranial location of that tone. Participants find this task fairly intuitive and translate the perceived intracranial location of the tone to the externalized location with little effort. Each session included a block of test tones presented without the adaptor stimuli (alone condition) followed by a block of test tones presented with the adaptor stimuli (adapt condition). Participants made 90 judgements per block; test tones at each frequency were presented five times at each of the nine ITDs, in random order. During the adaptation blocks, participants heard 35 s of the adaptor stimulus before beginning the task, as well as 5 s of the adaptor between each trial (after Phillips and Hall, 2005). Sessions took 20-30 minutes to complete.

### *Results & Discussion*

Figure 7 shows the mean perceived location of the test tones before and after adaptation at each frequency. The figure columns present data from each session (2800 or 4200 Hz adaptors) while the rows specify test-tone frequencies. As can be seen from the dotted pre-adaptation curves in all panels, participants were able to reliably assign discrete intracranial azimuths to the test tones. This is indicated by the ordered

progression of intracranial position reports from left to right (negative to positive ILDs), though the perceived azimuth functions seem to flatten in the lateral hemifields.

Most importantly, the top left and bottom right panels of Figure 7 show the mean pre- and post-adaptation responses to test tones at the adaptation frequencies.

Symmetrical adaptation resulted a shift in the perceived location of test tones at the adapted frequency towards the midline (indicated by the darker line at abscissa location 16), resulting in shallower post-adaptation curves. This shift in the perceived location of tones was robust across each hemifield rather than largest at ILDs closest to that of the lateralized adaptors; in fact, the effect appears to lessen at the lateral edges of each hemifield, a result we've seen previously (Vigneault-MacLean *et al.*, 2007; Dingle *et al.*, 2010). This pattern of results is incompatible with a place code model of localization which would predict localized adaptation of test tones with ILDs similar to that of the adaptor tone. Moreover, that there is a shift at all indicates the existence of a channel of neurons tuned to the azimuthal midline. This is congruent with past results using low frequency ITDs (Dingle *et al.*, 2010). Test tones of the non-adapted frequency show no shift in perceived location after adaptation (top right and bottom left panels in Figure 7).

These conclusions were supported by four 9 (ILD) x 2 (Condition) repeated measures ANOVAs, performed for each test-tone frequency at each adaptor frequency (corresponding to each of the four panels in Figure 7). All ANOVAs showed a main effect of ILD (all  $p < 0.001$ ) as expected, confirming the orderly effect of ILD on the perceived location of the test tones. None of the ANOVAs resulted in a significant main effect of Condition (alone vs. adapted curves), which was also expected given the symmetrical nature of the adaptation. The two ANOVAs for which the test tones matched

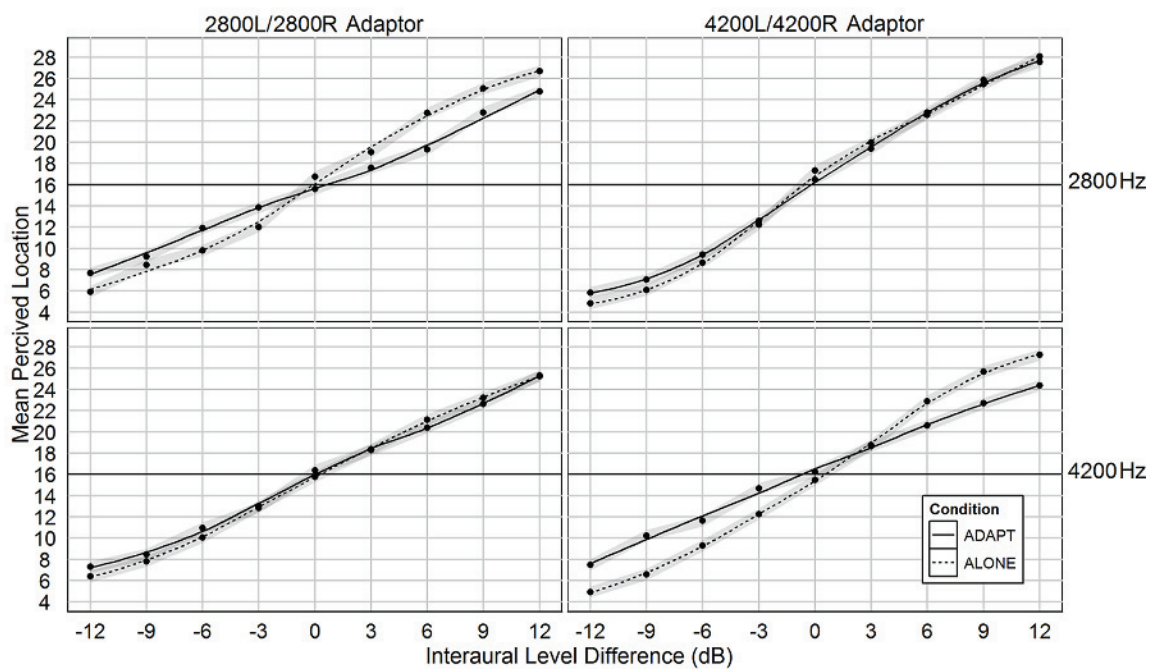


Figure 7. Data from Experiment 1a. Mean position reports as a function of test tone ILD before and after adaptation (dotted and solid lines, respectively). Columns are arranged such that each row contains data from one of the two test tones and each row contains data from one of the two adaptors. The ribbons overlaying the lines represent Fisher's Least Significant difference calculated for that data set; conservatively, pre- and post-adaptation data points at which the ribbons do not overlap can be considered to be significantly different. (N=9)

the frequency of the adaptors resulted in significant ILD x Condition interactions (2800 Hz tone with symmetrical 2800 Hz adaptor,  $F(8,64)=13.258$ ,  $p=0.000$ ; 4200 Hz tone with symmetrical 4200 Hz adaptor,  $F(8,64)=22.680$ ,  $p=0.000$ ) while the ANOVAs for the non-adapted tones in each session yielded ILD x Condition interactions that were not statistically significant (4200 Hz tone with symmetrical 2800 Hz adaptor,  $F(8,64)= 1.731$ ,  $p=0.108$ ; 2800 Hz tone with symmetrical 4200 Hz adaptor,  $F(8,64)= 0.856$ ,  $p=0.558$ ).

### *3.3.2 Experiment 1b*

In complement to Experiment 1a, Experiment 1b uses a central adaptor (ILD 0 dB) to probe for the existence of a midline channel at high frequencies. If sound localization in the ILD domain is dependent on the relative firing of not only the two lateral hemifield channels, but also a midline channel, then fatiguing the midline channel should result in a shift in the perceived location of test tones at the adapted frequency away from the midline.

#### *Methods*

Experiment 1b was structured identically to Experiment 1a but with central adaptors rather than symmetrical adaptors. As in Experiment 1a, participants reported the perceived location of test tones (2800 and 4200 Hz) five times at each of nine ILDs both before and after adaptation. However, in this experiment adaptors were pulse trains presented at the midline (0 ILD) rather than alternating from side to side. Note that the absolute duration of adaptation was the same as in Experiment 1a, but that there is only one adapted location in this experiment in contrast to the two locations in the previous experiment. This resulted in twice the number of adaptor tones targeting the channel of

interest. Again, the two sessions were completed at least 24 hours apart and the order of frequency conditions tested was randomized. The same participants completed both experiments.

### *Results & Discussion*

Data from Experiment 1b are presented in Figure 8. For both adaptors, test tones at the adapted frequency shifted away from the midline. This can be seen as a steepening of the curves in the upper left and lower right panels. Test tones at the unadapted frequencies did not show a shift in perceived location after adaptation (upper right and lower left panels). These findings were supported by four repeated-measures ANOVAs, one associated with each panel of the figure. In all cases, there was a significant main effect of ILD (all  $p < 0.001$ ). As expected from the symmetrical nature of the shift in reported location, there were no significant main effects of Condition (unadapted vs adapted curves). Test tones at both of the adapted frequencies showed significant ILD x Condition interactions (for 2800 Hz tones with the 2800 Hz adaptor  $F(8,64) = 3.879$ ,  $p = 0.001$ ; for 4200 Hz tones with the 4200 Hz adaptor,  $F(8,64) = 8.765$ ,  $p = 0.000$ ). There were no significant ILD x Condition interactions for test tones of the non-adapted frequency (4200 Hz tones with the 2800 Hz adaptor,  $F(8,64) = 0.763$ ,  $p = 0.764$ ; 2800 Hz with the 4200 Hz adaptor, ILD x Condition  $F(8,64) = 1.647$ ,  $p = 0.129$ ).

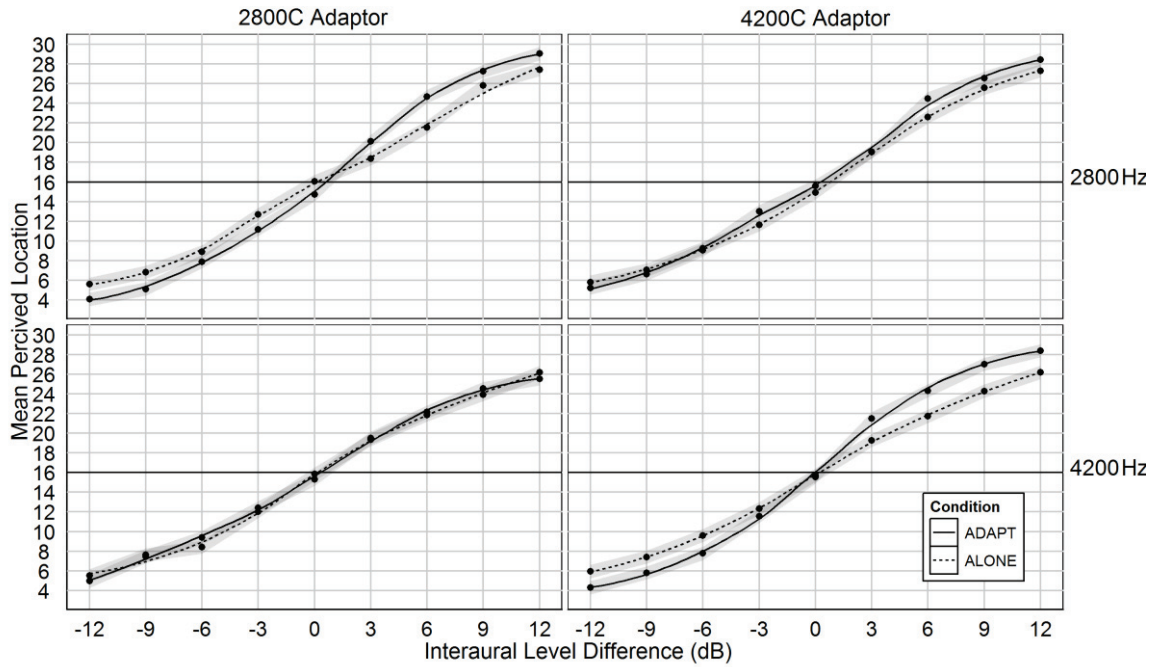


Figure 8. Data from Experiment 1b. Mean position reports as a function of test tone ILD before and after adaptation (dotted and solid lines, respectively). Columns contain data from one of the two test tones and rows contain data from one of the two adaptors. The ribbons overlaying the lines represent Fisher's Least Significant difference calculated for that data set. (N=9)

### 3.4 EXPERIMENT 2

The second experiment was an attempt to replicate the findings obtained with high-frequency stimuli in Experiment 1 at lower frequencies. Low frequency sounds are more commonly associated with ITDs than ILDs, principally because low-frequency sounds in nature do not generate a significant ILD cue for azimuth. Nevertheless there is both psychophysical (Yost, 1981) and electrophysiological evidence (Massoud *et al.*, 2010) in man for sensitivity to ILDs at low frequencies. This raises the possibility that the architecture of the mechanisms mediating azimuthal position assignments on the basis of ILD is the same at high and low frequencies, despite the absence of a natural ILD cue at low frequencies. In Experiment 2a, symmetrical adaptors were once again used, but at new frequencies of 260 and 570 Hz, while Experiment 2b employed central adaptors at these frequencies.

#### *Methods*

Each of 10 participants completed four sessions, two with symmetrical adaptors (Experiment 2a) and two with central adaptors (Experiment 2b). Nine of the ten participants in Experiment 2 had also participated in Experiment 1. All participants had tone detection thresholds better than 20 dB HL at octave frequencies from 250 to 4000 Hz, and participants' thresholds for each ear at each tested frequency did not differ by more than 10 dB. The low-frequency stimuli used were 260 Hz and 570 Hz tones at 64 and 62 dB, respectively (A-weighted sound pressure level, as measured by an Extech sound level meter, model 407750), judged of equal loudness in pilot work and roughly



4.5 critical bands apart (Phillips and Hall, 2005). The structure and timing of the stimuli and the procedures were all identical to those in Experiment 1.

### *3.4.1 Experiment 2a*

#### *Results & Discussion*

Symmetrical adaptation with low frequencies resulted in similar patterns to those seen above at high frequencies. The top left and bottom right panels of Figure 9 show the shift in the mean perceived location of the test tones away from the adaptors, towards the midline. Once again, this shift was robust across each adapted hemifield and appeared to lessen towards the lateral extremes. This pattern of results is consistent with the existence of a midline channel existing for low frequency ILDs, in addition to that for high frequency ILDs (Experiment 1, above) and for low frequency ITDs reported earlier (Dingle *et al.*, 2010). It is interesting, but not unprecedented, that in this experiment there appears to have been a significant, though smaller, shift in perceived test tone locations at the unadapted frequencies. This will be discussed in more detail below.

Again, four 9 (ILD) x 2 (Condition) repeated measures ANOVAs were performed, one for each test-tone frequency at each adaptor frequency. All ANOVAs showed a main effect of ILD (all  $p < 0.001$ ) as would be expected, confirming the orderly effect of ILD on test-tone perceived azimuth. There were no significant main effects of Condition, which is unsurprising given the expected equal but opposite shifts in perceived locations around the midline. The two ANOVAs for which the test tones matched the frequency of the adaptors resulted in significant ILD x Condition interactions (260 Hz tone with symmetrical 260 Hz adaptor,  $F(8,72)=8.198$ ,  $p=0.000$ ;

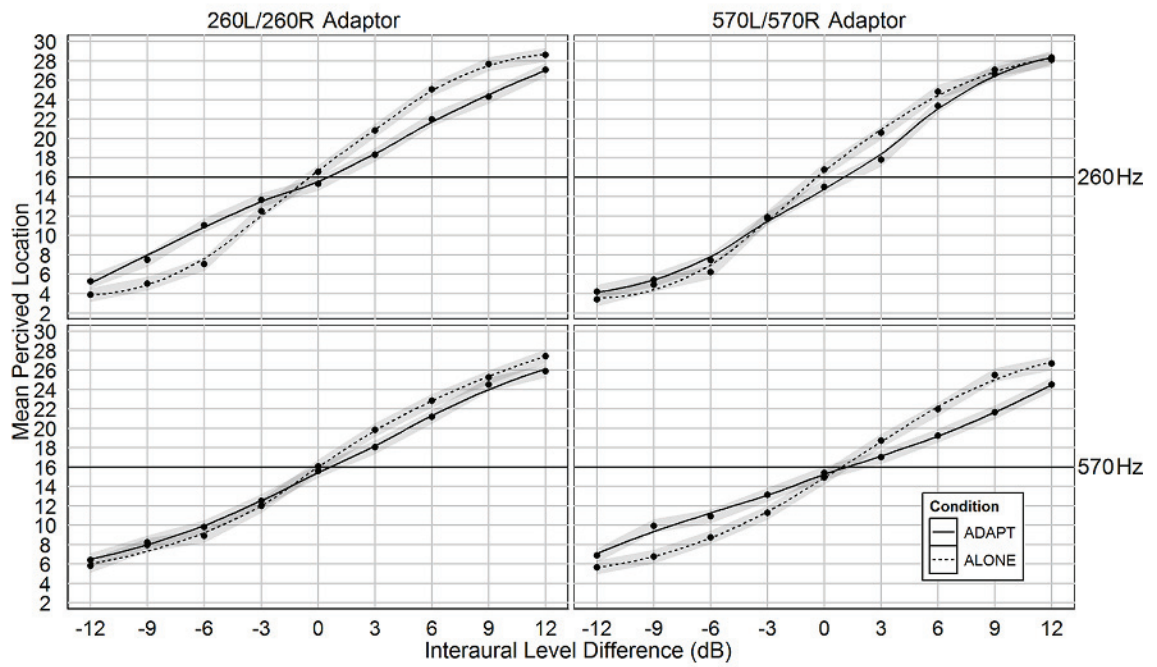


Figure 9. Data from Experiment 2a. Mean position reports as a function of test tone ILD before and after adaptation (dotted and solid lines, respectively). Columns show data from one of the two test tones and rows contain data from one of the two adaptors. The ribbons overlaying the lines represent Fisher's Least Significant difference calculated for that data set. (N=10)

570 Hz tone with symmetrical 570 Hz adaptor,  $F(8,72)=13.778$ ,  $p=0.000$ ). Unexpectedly, the ANOVAs for the non-adapted tones in each session were also significant (570 Hz tone with symmetrical 260 Hz adaptor,  $F(8,72)=13.258$ ,  $p=0.014$ ; 260 Hz tone with symmetrical 570 Hz adaptor,  $F(8,72)=2.639$ ,  $p=0.040$ ).

### *3.4.2 Experiment 2b*

#### *Results & Discussion*

Results of Experiment 2b are shown in Figure 10, and were similar to those seen previously in Experiment 1b. At each adapted frequency (Figure 10, upper left and lower right panels) test tones shifted away from the midline resulting in a significant ILD x Condition interaction (for 260 Hz with the 260 Hz adaptor,  $F(8,64)= 4.703$ ,  $p=0.000$ ; for 570 Hz with the 570 Hz adaptor,  $F(8,64)= 5.315$ ,  $p=0.000$ ). Test tones at the non-adapted frequencies did not show a significant change in perceived location (for 260 Hz with a 570 Hz adaptor,  $F(8,64)= 2.037$ ,  $p=0.058$ ; for 570 Hz with a 260 Hz adaptor,  $F(8,64)= 1.922$ ,  $p=0.072$ ). Interestingly, after midline adaptation with the 570 Hz adaptor, the 570 Hz test tones also showed a main effect of Condition which was not seen in any of the previous experiments (Figure 10, lower right panel,  $F(1,8)= 8.071$ ,  $p=0.022$ ). This is perhaps reflective of a slightly stronger adaptation effect in the right hemifield. For all test tones there was a significant main effect of ILD (all  $p < 0.000$ ).

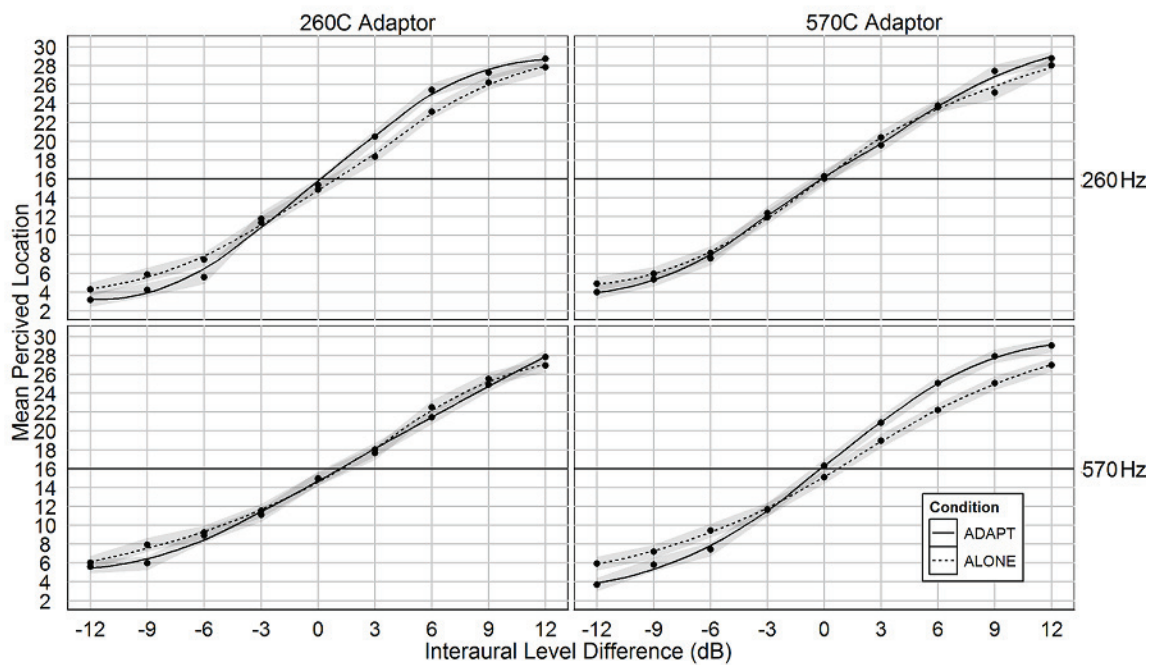


Figure 10. Data from Experiment 2b. Mean position reports as a function of test tone ILD before and after adaptation (dotted and solid lines, respectively). Columns contain data from one of the two test tones and rows contain data from one of the two adaptors. The ribbons overlaying the lines represent Fisher's Least Significant difference calculated for that data set. (N=9)

### 3.5 GENERAL DISCUSSION

The results of these experiments extend the evidence that sound localization in humans is dependent upon the contribution of a third channel with spatial tuning around the midline, in addition to the two lateral channels already included in the two-channel model. In all four experiments reported here, adaptation resulted in a shift in the mean position report for test tones in a manner consistent with the existence of a midline channel. In the two symmetrical adaptor conditions (Exps 1a and 2a), fatiguing the lateral channels revealed a shift in the perceived location of test tones towards the midline whereas, in the two central adaptor conditions (Exps 1b and 2b), adaptation of the midline channel resulted in a shift in the perceived location of test tones away from the midline.

Many of the azimuth-vs-ILD functions in these experiments seem to become shallower in the lateral hemifields (see also Yost, 1981). This likely reflects the differential abilities in localizing tones close to the midline versus those in the periphery: ILD-vs-azimuth functions themselves tend to be steeper for sources near the midline than for those in the periphery and neurophysiological data indicate that the neural code for ILD size is most unambiguous for small ILDs (Phillips and Brugge, 1985). This means that both the stimulus information available to localize on the basis of ILDs and the neural code for that information are superior for near-midline position judgements.

Interestingly, there was a small but significant shift in the test tones at the non-adapted frequency in Experiment 2a. This was also seen at one non-adapted frequency during the final experiment in the ITD study (Dingle *et al.*, 2010), but when participants

were divided into those who had completed the previous experiments and so experienced the two tones (260 and 570 Hz) being paired together and those that hadn't, the effect disappeared for the inexperienced listeners. Because this study used many of the same participants, almost all of them now have experience with the low frequency tone pair; there may well be an element of perceptual learning that caused this "bleed" across frequencies.

For test tones at the adapted frequencies, the maximum shift caused by adaptation in each condition runs about 3 to 4 steps, which translates to approximately 18 to 24 degrees. Despite that in the central adaptor conditions the midline channel received twice the adaptation that each lateral channel received in the symmetrical adaptation conditions, the shifts seen after central adaptation seem to be slightly smaller than those seen after symmetrical adaptation. The stronger effect of symmetrical adaptation seems plausible given the much larger population of cells devoted to encoding the lateral channels versus the midline channel (In free-field cortical studies, of total cell types recorded, hemifield vs. central cells are reported at about 63% and 11%, Rajan *et al.* 1990; 69% and 7%, Brugge *et al.* 1996; 45% and 16%, Eggermont and Mossop, 1998; when excluding low directionality cells, 83% and 17%, Imig *et al.* 1990; In dichotic ILD studies, 69% and 12%, Phillips and Irvine, 1981). However, any difference in the magnitude of the adaptation in the symmetrical and central conditions seen here was not nearly as obvious as that seen in previous ITD experiments (Dingle *et al.*, 2010), in which the lowest frequency test tones shifted up to 24 degrees after symmetrical adaptation and sometimes not at all after central adaptation. It may be, therefore, that there are even fewer ITD-

sensitive cells that are tuned to the midline than there are ILD sensitive-cells; there are currently no physiological data to either confirm or deny this hypothesis.

There is a difficulty in arguing that a smaller population of cells may imply a “weaker” neural channel. Because deficits in sound localization acuity following unilateral forebrain lesions are restricted to sources in the contralesional auditory hemifield (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984), it follows that the machinery for localizing in that hemifield must reside wholly within the lesioned cerebral hemisphere. This is possible, because each side of the auditory forebrain contains both cells with spatial tuning for the ipsilateral auditory hemifield and cells with spatial tuning for the contralateral auditory hemifield, though cells with spatial tuning for the ipsilateral auditory hemifield are in the minority (eg. 17% ipsilateral vs 46% contralateral, Rajan *et al.*, 1990; 16% ipsilateral vs. 30% contralateral, Eggermont and Mossop, 1998). Nevertheless, ipsilateral-preferring cells appear to contribute equally with the contralateral-preferring cells in the two-channel (Boehnke and Phillips, 1999; Phillips and Hall, 2005; Stecker *et al.*, 2005) and three-channel accounts (Dingle *et al.*, 2010). This suggests that the relative numbers of neurons whose activity contributes to a neural "channel" is insufficient to account for the weighting of their input to the comparison process.

While the main goal of these experiments was to extend the data on the existence of a midline channel contributing to mammalian sound localization, the present data also bear on another issue. Experiment 2 revealed that the perceptual architecture for ILD seen at high frequencies extends to low frequencies. This is not surprising given pre-existing psychophysical (Yost, 1981) and electrophysiological (Massoud *et al.*, 2010) evidence of

human sensitivity to ILD at low frequencies. What is interesting is the existence of neural/perceptual machinery for the processing of ILDs at low frequencies, when low frequency stimuli do not generate significant ILDs in man. This suggests an evolutionary constancy of ILD coding mechanisms across the frequency domain (see Phillips *et al.*, 2011). It remains to be determined whether the same is true for ITD coding mechanisms, although there is some neurophysiological (Griffin *et al.*, 2005) and psychophysical evidence (Bernstein and Trahiotis, 2002) that this may be the case. The available data on this point, however, do not yet extend to confirming a three-channel model for ITDs at low and high frequencies. This is the topic of a companion paper.

### **3.6 ACKNOWLEDGEMENTS**

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## **CHAPTER 4      MIDLINE CHANNEL: HIGH FREQUENCY ITD<sup>6</sup>**

### **4.1 ABSTRACT**

Previous psychophysical work on sound localization in humans has proposed that a third, midline channel be added to the current two-channel model of mammalian sound localization. Evidence for this third channel has been found in interaural time difference (ITD) studies with low-frequency tones, and interaural level difference (ILD) studies with both high- and low-frequency tones. The latter is interesting because it suggests that, despite the fact that low frequencies do not generate significant ILDs for humans in natural settings, there is a constancy of ILD coding mechanisms across the frequency domain. To complement this finding, the present study sought to determine whether the three-channel model holds for ITDs at high frequencies. In three experiments, a selective adaptation paradigm was used in combination with transposed tones to probe for the existence of three (left, right, center) perceptual channels for sound source azimuth. The experiments provided strong evidence for lateral hemifield ITD channels, but little evidence for a midline ITD channel at high frequencies.

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<sup>6</sup> This chapter has been submitted for consideration to be published as:

Dingle, RN, Hall, SE, & Phillips, DP. (in review) Perceptual channels for interaural time differences at high tonal frequencies. JASA.

## 4.2 INTRODUCTION

In 2005, two independent studies provided data that led to a clarification of the architecture of the perceptual mechanisms used by mammals to localize sounds in azimuth. Stecker *et al.* (2005) described the azimuth receptive fields of cat cortical neurons. They found that the majority of neurons in the primary auditory cortex had hemifield-wide receptive fields centered on the contralateral or ipsilateral sides, with medial borders close to, or straddling, the midline. A small minority of neurons had receptive fields centered on the midline. Stecker *et al.* (2005) proposed that sound azimuth judgments were based on the relative outputs of the left- and right-tuned neural populations, in what they termed an “opponent-process” model. In the same year, Phillips and Hall (2005) described the results of human psychophysical studies that used a selective adaptation methodology in the interaural time (ITD) and interaural level (ILD) dimensions. They showed that the point of perceived centrality (intracranial midline) behaved as if position judgements were based on the relative outputs of two (left, right) perceptual channels. Those channels were subsequently shown to have hemifield tuning (Vigneault-MacLean *et al.*, 2007), and the model (Phillips, 2008) has since been extended to include a midline channel (Dingle *et al.*, 2010). The neural substrate of the midline channel likely resides in the minority of central neurons possessing midline-centered receptive fields as seen in free-field studies (e.g., Rajan *et al.*, 1990; Stecker *et al.*, 2005) or neurons “tuned” to zero ITD or ILD as seen in dichotic neurophysiological studies (Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Orman and Phillips, 1984).

The vast majority of neurophysiological data on the spatial receptive fields of central neurons has come from studies of cells with best frequencies that are high—certainly above frequencies at which sensitivity to the ITD of simple tones would be expected. Psychophysical evidence on a midline perceptual channel for sound azimuth, however, has so far come only from ITD experiments using low-frequency tones (Dingle *et al.*, 2010).

Behavioral sensitivity to ITDs of high frequency signals is typically studied by using a high-frequency carrier tone that is amplitude modulated by a low-frequency tone; the resulting stimulus contains only high-frequencies, and an ITD can be imposed on the modulated waveform (e.g., Henning, 1974). Bernstein and Trahiotis (2002) devised “transposed stimuli” to study ITD perception at high frequencies. In transposed stimuli, a high-frequency carrier is multiplied by a half-wave rectified low-frequency modulator to produce high-frequency pulses separated by equal-duration silent periods. The advantage of transposed stimuli over sinusoidally amplitude-modulated ones is that the temporal distribution of auditory nerve fiber action potentials evoked by the former is more likely to resemble that driven by a simple low-frequency tone than does the response evoked by the latter (see Figure 2 in Phillips *et al.*, 2011). Bernstein and Trahiotis (2002) reported that sensitivity to ITDs of transposed tones was better than that supported by sinusoidally amplitude-modulated tones, and at least as good as that supported by low-frequency tones at the modulator frequency. More recently, Griffin *et al.* (2005) studied the neural coding of ITDs of transposed tones in the guinea pig midbrain, and concluded that “the neural mechanisms that mediate sensitivity to ITDs at high and low frequencies are functionally equivalent.”

The purpose of the present study was to question whether the three-channel psychophysical model evinced by ITD studies with low-frequency tones also holds at high-frequencies when listeners are studied with transposed tones.

### **4.3 EXPERIMENT 1**

Previous ITD work using low-frequency tones has found that exposure to a strongly lateralized adaptor tone will result in a subsequent shift in the perceived location of test tones of the same frequency away from the adapted side (Vigneault-MacLean *et al.*, 2007; Dingle *et al.*, 2010). This shift in perceived location is effected throughout the auditory hemifield of the adaptor and extends slightly beyond the midline, as would be predicted by the two-channel model (after Boehnke and Phillips, 1999). The aim of the first experiment was to extend these findings to higher frequencies normally reserved for ILD work. Participants localized 2800 and 4200 Hz transposed stimuli at each of nine ITDs before and after adaptation with strongly lateralized sequences of the same tone. The adaptor stimuli were trains of transposed stimuli alternated between ear and frequency such that the listener received, for example, the 2800 Hz transposed stimuli on the right alternating with the 4200 Hz transposed stimuli on the left. It was expected that adaptation would result in a shift in the perceived location of same-frequency test tones within the adapted hemifield, as found in similar studies using lower frequency stimuli.

#### **4.3.1 Methods**

*a) Participants.* Twelve normal hearing adults between the ages of 22 and 45 each participated in two sessions, five of whom has previous experience participating in a

similar paradigm using low-frequency tones of varying ITDs (Dingle *et al.*, 2010). All participants had tone detection thresholds better than 20 dB HL (hearing level, as measured with a Grason-Stadler GSI 16 audiometer) at octave frequencies between 250 and 4000 Hz. Thresholds for each ear did not differ by more than 10 dB at any tested frequency within this range. The procedures used in all experiments presented here received ethics approval from the Dalhousie University Social Sciences & Humanities Human Ethics Board under protocol # 2010-2243.

*b) Stimuli.* Stimuli were digitally synthesized on an Apple Powermac G4 computer with MatLab at a sampling frequency of 44100 Hz. Following Bernstein and Trahiotis (2002), we multiplied a half-wave rectified, low-passed (<2000Hz) 128 Hz modulating tone with a high-frequency carrier tone (2800 or 4200 Hz). We then imposed a delay on the stimulus to one or other ear, resulting in dichotic stimuli whose envelopes contained an ITD. The two high-frequency carriers were 2800 and 4200 Hz (approximately 4.5 critical bands apart). We thus produced two “transposed” stimuli with the spectral energy dominated by the carriers and the amplitude envelopes dominated by the modulator. The transposed 2800 Hz and 4200 Hz stimuli were presented at 65 and 66 dB, respectively (resultant from 71 and 72 dB carriers, A-weighted sound pressure level); these levels were judged to be of equal loudness in pilot work. Test and adaptor stimuli were created as described previously (Dingle *et al.*, 2010). The adaptors were trains of 200 ms transposed stimuli (including 10 ms linear rise and fall ramps, inter-train interval = 20 ms) which alternated both in frequency and  $\pm 0.8$  ms ITD such that listeners perceived the adaptor as alternating highly lateralized stimuli, one frequency per side.

The use of an adaptor ITD of  $\pm 0.8$  ms is a departure from our usual practice of using  $\pm$  one quarter-period ITD (Phillips and Hall, 2005; Dingle *et al.*, 2010). In the present study, a quarter period of the modulator waveform would be about 1.8 ms, which is far outside the behaviourally-relevant range in man. Instead, we employed an ITD of 0.8 ms, which is perhaps the largest ITD that the human head could generate (after Middlebrooks and Green, 1990). Test stimuli were 200 ms (including 10 ms linear rise and fall ramps) and for each frequency ranged in ITD from 0.8 ms (right leading) to -0.8 ms (left leading) in steps of 0.2 ms, resulting in one test stimulus at 0 ITD (midline) and four test stimuli ITD conditions on either side. Three 0-ITD high-pass (2000 Hz) dichotic clicks (ICI=60ms; amplitude of 60 dB SPL A-weighted) were presented 500 ms before each test stimulus to orient participants to the midline.

Participants sat in a sound-attenuating booth with headphones (Sennheiser HD590), monitor and keyboard, and made their responses using the keyboard's number pad. The CPU was located outside of the booth. Tone levels were measured with an Extech sound level meter (model 407750).

*c) Procedure.* Two adaptor conditions were used to counterbalance the side of the adaptor frequencies. In one condition, the 2800 Hz stimulus was on the left and a 4200 Hz stimulus was on the right, and in the other condition the stimulus lateralities were reversed. All participants performed one session with each condition (> 24 hours between sessions). The order of the conditions tested was randomized.

The procedures used in this experiment were the same as those described previously in Dingle *et al.* (2010). A schematic of an overhead view of the frontal

hemisphere with numbers from 0-32 (from left to right) marking locations in  $6^\circ$  intervals was displayed on the monitor. Participants were asked to respond to stimulus presentations with a number from the schematic corresponding to the perceived location of that stimulus; participants translate the perceived intracranial location of the stimulus to the externalized location easily. One session included one block of trials with no adaptor stimulus (baseline) and one block with adaptors. Participants made 90 judgements per block, in which each of the two test stimuli was presented at each of the nine ITDs five times, in random order. During the adaptation blocks, participants heard 35 s of the adaptor stimulus before beginning the task, as well as 5 s of the adaptor between each test trial (after Phillips and Hall, 2005). Sessions took 20-30 minutes to complete.

#### *4.3.2 Results & Discussion*

Figure 11 presents the mean position reports for each test stimulus before and after adaptation. The top row of panels presents data for 2800 Hz test stimuli, while the bottom row presents data for 4200 Hz test stimuli. Columns divide the data by adaptor condition; in the left column, the adaptor was presented with 2800 Hz on the left side and 4200 Hz on the right side; in the right column vice versa. In all conditions, adaptation resulted in a shift in the perceived location of test stimuli away from the side of the adaptor of matching frequency. This shift extends broadly across the adaptor's hemifield and some way over the azimuthal midline, consistent with results seen previously at lower frequencies (Vigneault-MacLean *et al.*, 2007; Dingle *et al.*, 2010). Further, the

greatest shift in perceived location occurred at the middle values of ITD as opposed to at the largest test-tone ITDs, which were closer in magnitude to the adaptor stimuli.

These conclusions were supported by four 9 (ITD) x 2 (Condition) repeated measures ANOVAs, each performed for a specific adaptor pair and test-stimulus frequency. Each of the four ANOVAs resulted in main effects of ITD (2800 Hz test stimuli with 2800 Hz adaptor on the left,  $F(8,88)=43.110$ ; 4200 Hz test stimuli with 2800 Hz adaptor on the left,  $F(8,88)=54.162$ ; 2800 Hz test stimuli with 4200 Hz adaptor on the left,  $F(8,88)=55.013$ ; 4200 Hz test stimuli with 4200 Hz adaptor on the left,  $F(8,88)=54.162$ ; for all  $p<0.001$ ) reflecting the orderly psychometric functions, confirming the participants' orderly ability to assign discrete locations to test stimuli differing in ITD. There were main effects of condition (i.e., adaptation) in all cases (2800 Hz test stimuli with 2800 Hz adaptor on the left,  $F(1,11)=11.877$ ; 4200 Hz test stimuli with 2800 Hz adaptor on the left,  $F(1,11)=8.322$ ; 2800 Hz test stimuli with 4200 Hz adaptor on the left,  $F(1,11)=21.676$ ; 4200 Hz test stimuli with 4200 Hz adaptor on the left,  $F(1,11)=7.667$ ; for all  $p<0.019$ ). All but one ANOVA (the 4200 Hz test stimuli with the right ear 4200 Hz adaptor,  $F(8,88)=1.905$ ,  $p=0.069$ ) resulted in significant ITD x condition interactions (2800 Hz test stimuli with 2800 Hz adaptor on the left,  $F(8,88)=3.461$ ; 2800 Hz test stimuli with 4200 Hz adaptor on the left,  $F(8,88)=5.535$ ; 4200 Hz test stimuli with 4200 Hz adaptor on the left,  $F(8,88)=4.56$ ; for all  $p<0.003$ ), reflecting the change in the slope of the psychometric functions between the adapted and non-adapted states.

Experiment 1 provided convincing evidence for the existence of lateral, hemifield channels for azimuth based on the ITDs of transposed tone envelopes. The adaptation



incurred by a 0.8-ms ITD adaptor was on the side of the adaptor, spanned the entire hemifield, and bled slightly across the midline (Figure 11). These are the same properties that characterize the consequences of exposure to highly lateralized low-frequency tone adaptors (Vigneault-MacLean *et al.*, 2007). The present data suggest, therefore, that both low- and high-frequency portions of the audible frequency range possess hemifield-tuned ITD coding mechanisms. This suggestion from the present psychophysical study is thus in keeping with prior neurophysiological studies of the coding of the ITDs of transposed tones in the guinea pig (Griffin *et al.*, 2005). The present data also have an important bearing on a methodological issue. Recall that this experiment used adaptor stimuli with an ITD of 0.8 ms, rather than our usual practice of using ITDs equal to a quarter period of the delayed waveform. Despite this change in methodology, adaptation effects in Experiment 1 were at least as robust as any of those seen in previous studies using the same general paradigm. This suggests that the change in strategy for selection of the adaptor ITD did not weaken the strength of the adaptation effect.

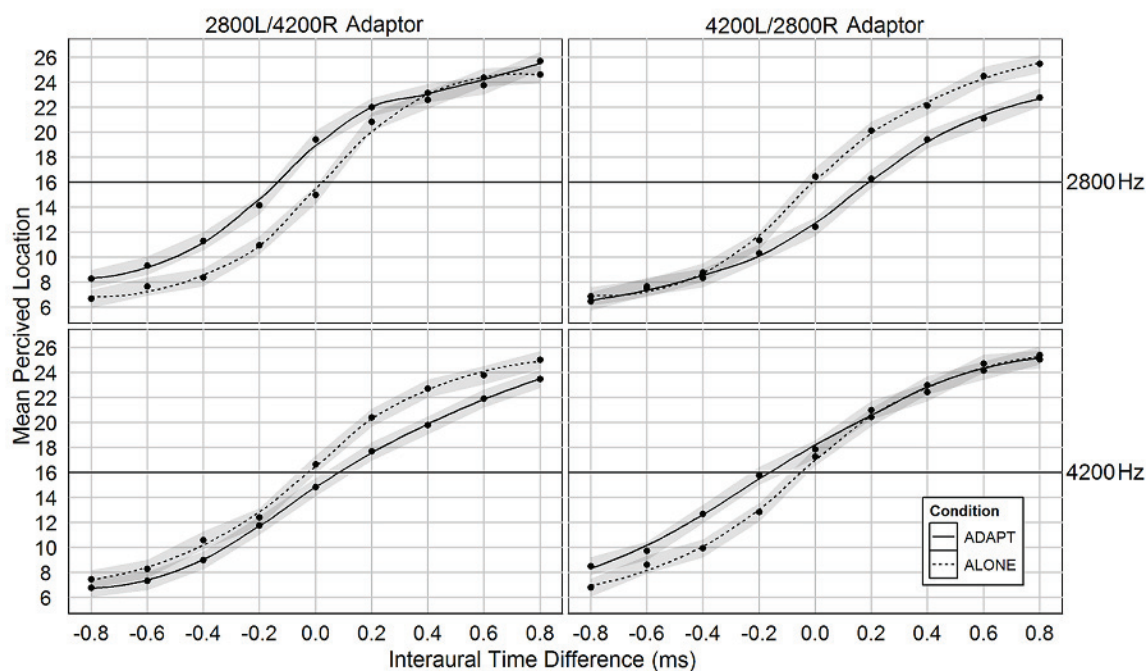


Figure 11. Data from Experiment 1. The mean perceived location of test tones as a function of ITD before and after adaptation (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptor conditions and each row represents test-tone frequency. The ribbons overlaying the lines represent Fisher's least significant difference calculated for the data set. Conservatively, pre- and post-adaptation ITDs at which these ribbons do not overlap can be considered significantly different.

## 4.4 EXPERIMENT 2

Experiment 2 explored the existence of a third channel tuned to the auditory midline by adapting both lateral channels at the same stimulus frequency. If a frontal channel exists for high frequency ITD processing, then symmetrical adaptation should result in a shift in the perceived location of test stimuli towards the midline. If there is no frontal channel, symmetrical adaptation should result in no change in the relative firing of the two lateral channels and, therefore, no change in the perceived location of the test stimuli.

### 4.4.1 Methods

Experiment 2 employed two sessions structured identically to those in Experiment 1 but with symmetrical rather than asymmetrical adaptors. Again, participants were asked to report the perceived location of test stimuli (2800 and 4200 Hz) five times at each of nine ITDs both before and after adaptation. Test stimuli were presented in random order. Adaptors were either trains of 2800 Hz transposed stimuli alternating from side to side, or similarly alternating trains of 4200 Hz transposed tones. The modulating frequency of all adaptor tones was 128 Hz, and the adaptor stimulus ITD was set at 0.8 ms. All listeners from Experiment 1 participated in Experiment 2.

### 4.4.2 Results & Discussion

Shifts in perceived location toward the midline (i.e., shallower post-adaptation curves) are apparent in Figure 12 (upper left and lower right panels), but they were substantially smaller than those seen using low frequency tones localized by ITD (Dingle *et al.*, 2010). A shift towards the midline is more evident for adapted 2800 Hz test stimuli

than adapted 4200 Hz test stimuli; however, after 2800 Hz adaptation, unadapted 4200 Hz test stimuli also showed a small shift in mean position reports. After 4200 Hz adaptation, the apparent shift in 4200 Hz test stimuli appeared more strongly in the right auditory hemifield rather than the symmetrical effect that was expected. The unadapted 2800 Hz test stimuli showed no shift, as expected.

Repeated Measures ANOVAs for each panel resulted in significant ITD x Condition interactions for responses to both the adapted and unadapted test stimulus frequencies after 2800 Hz adaptation ( $F(8,88)=4.011$ ,  $p=0.000$  and  $F(8,88)=2.690$ ,  $p=0.011$ , respectively), confirming the existence of a post-adaptation shift in perceived test-stimulus location. However, neither the 2800 Hz test stimuli nor the 4200 Hz test stimuli showed significant ITD x Condition interactions following adaptation with 4200 Hz stimuli ( $F(8,88)=0.925$ ,  $p=0.500$  and  $F(8,88)=1.805$ ,  $p=0.087$ , respectively). All four ANOVAs resulted in significant main effects of ITD ( $p<0.001$  for all) but no significant main effect of condition. The latter was expected because of the symmetrical nature of the adaptation.

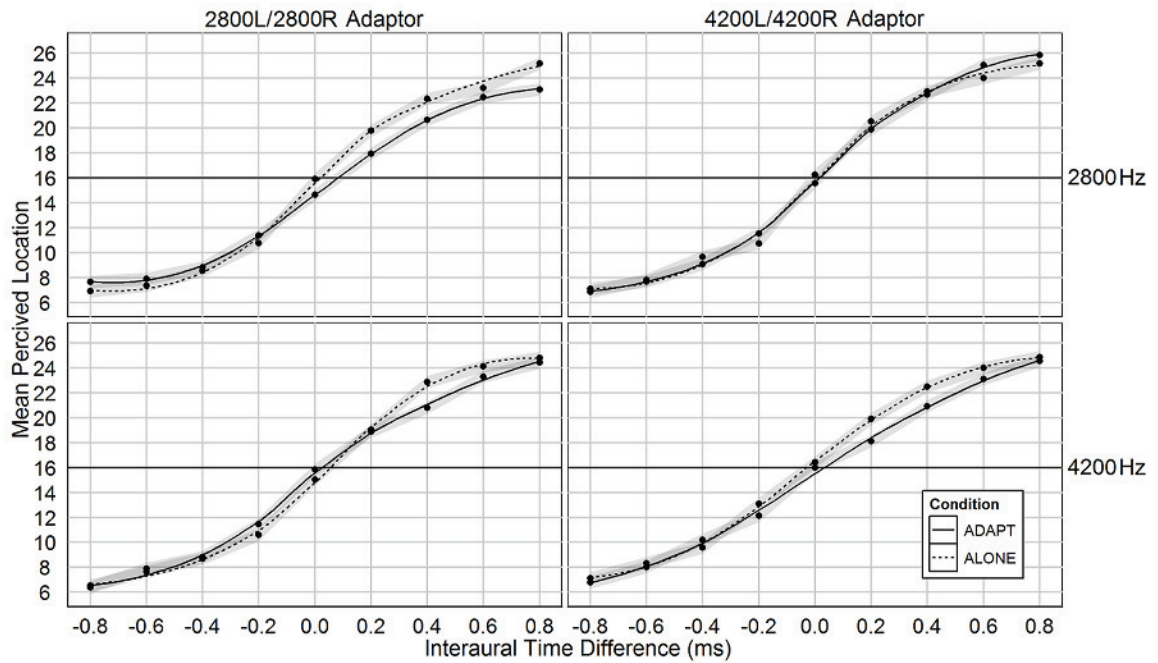


Figure 12. Data from Experiment 2. The mean perceived location of test tones as a function of ITD before and after symmetrical adaptation (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptors and each row represents one of two test-tone frequencies. The ribbons overlaying the lines represent Fisher's least significant difference calculated for the data set.

## 4.5 EXPERIMENT 3

While Experiment 2 probed for the existence of a midline channel by adapting the lateral channels, Experiment 3 seeks to adapt the midline channel by using adaptor stimuli with 0-ms ITD. In this design, the existence of a midline channel would be revealed by post-adaptation shifts in the perceived locations of test tones away from the midline.

### 4.5.1 Methods

Experiment 3 was also structured identically to Experiment 1 and 2 but with a central adaptor rather than asymmetrical adaptors. Participants reported the perceived locations of 2800 and 4200 Hz test stimuli. Test stimuli were presented five times at one of nine ITDs in random order both before and after adaptation. The adaptor stimuli were trains of 2800 or 4200 Hz transposed tones with an ITD of 0 ms, presented in different blocks of trials. The duration of the adaptor stimuli was held constant from the previous experiments but because this adaptor only used one ITD, the amount of adaptation at a single location was double that of the earlier experiments.

### 4.5.2 Results & Discussion

It was expected that central adaptation would result in a shift in the listener's mean position reports away from the midline (i.e., a steeper post-adaptation curve) as this result was seen previously, although more weakly, for low-frequency tones (260 and 570 Hz) lateralized by ITD (Dingle *et al.*, 2010). As can be seen in Figure 13, no shift in the perceived location of either the adapted or unadapted test stimuli is

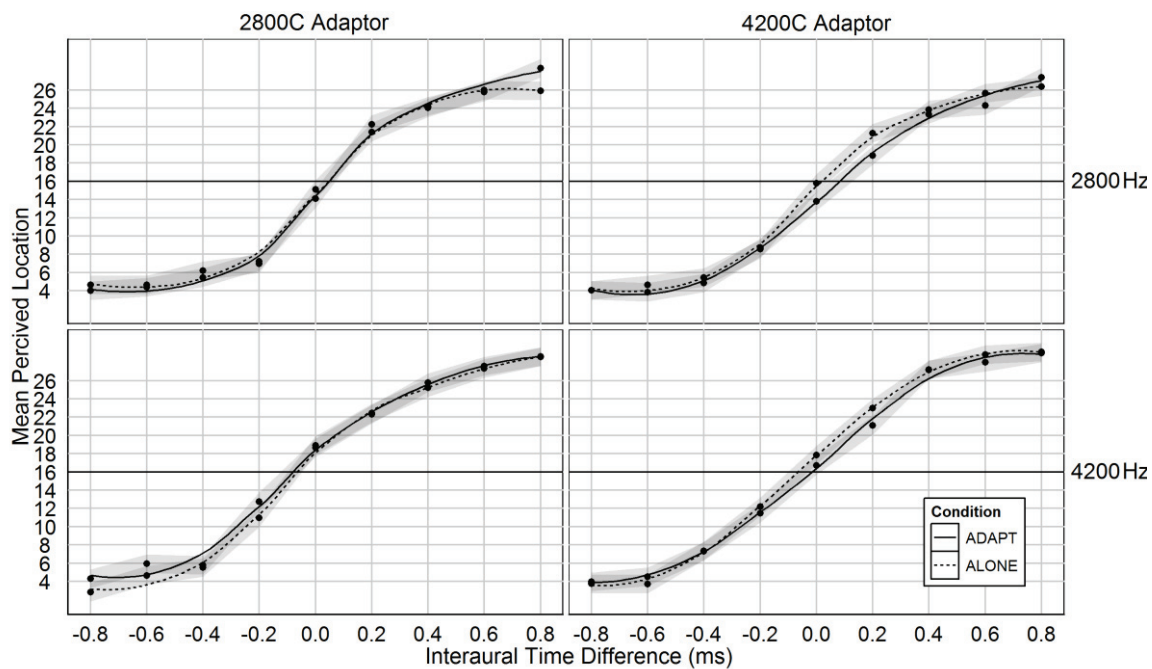


Figure 13. Data from Experiment 3. The mean perceived location of test tones as a function of ITD before and after adaptation with a 0 ITD stimulus (dotted and solid lines, respectively). Panels are arranged such that each column represents one of two adaptors and each row represents one of two test-tone frequencies. The ribbons overlaying the lines represent Fisher's least significant difference calculated for the data set.

apparent in either adaptor condition with the exception, perhaps, of the adapted 2800 Hz test stimuli, which show a very slight shift at the lateral edges. As expected, each of the four ANOVAs (one for each frequency of test tones at each adaptor frequency) resulted in significant main effects of ITD (all  $p < 0.001$ ) and no main effects of condition. After central adaptation with the 2800 Hz adaptor, test stimuli at 2800 Hz did indeed show a significant ITD x Condition interaction ( $F(8,88) = 2.112$ ,  $p = 0.043$ ) confirming the very small shift visible in Figure 13. There were no other significant interactions.

#### 4.6 GENERAL DISCUSSION

This is the first study to use transposed stimuli in a selective adaptation paradigm probing the perceptual architecture of the mechanisms supporting ITD processing at high frequencies. The study is important for two related reasons. First, it provides new psychophysical data on the processing of ITDs at high frequencies, following Bernstein and Trahiotis's (2002) initial demonstration that humans are as sensitive to the ITDs of transposed tones as they are to ITDs of simple, low-frequency tones. Second, the study addresses the question of whether the mechanisms of ITD coding are functionally equivalent at low and high frequencies (Griffin *et al.*, 2005).

On the first point, Experiment 1 showed powerful effects of asymmetric adaptors (Figure 11). Post-adaptation position reports for test tones were shifted away from the adaptor, and were so for ITDs throughout the hemifield of the adaptor's side, with a modest bleed across the midline. This pattern of behaviour is highly consistent with our previous studies using low-frequency tones (Vigneault-MacLean *et al.*, 2007, Dingle *et al.*, 2010). These data constitute strong evidence for the existence of left and right



hemifield-tuned perceptual channels exploiting the ITD, but this time at high frequencies. The psychophysical data on the hemifield channels are thus both highly consistent, and highly compatible with recent neurophysiological studies in the guinea pig that also indicate striking similarity of the coding mechanisms for the ITDs of low-frequency tones (McAlpine *et al.*, 2001) and transposed tones (Griffin *et al.*, 2005).

The second point concerns a more general comparison of the perceptual architecture supporting ITD coding, especially the issue of a channel with a spatial selectivity near the midline (i.e., small ITDs). The evidence for the existence of this channel is quite compelling for ITDs of simple low-frequency tones (Dingle *et al.*, 2010). Using symmetrical adaptors, the present study provided modest evidence for a central channel (Experiment 2). These adaptors produced small shifts of position reports towards the midline, but only in the case of the 2800 Hz adaptor (Figure 12, left side). The 4200 Hz adaptor produced no significant shifts in position reports for test tones (Figure 12, right side). Experiment 3 used the central (0 ms ITD) adaptors, and the existence of a central channel for high-frequency ITDs would have been expressed as post-adaptation position reports shifted away from the midline. Experiment 3, however, offered only modest evidence for a shift in position reports following exposure to the central ITD adaptors (Figure 13). The present study thus offers little support for the existence of a high-frequency ITD central channel in man. This is in contrast to the case for ITDs of low-frequency tones (Dingle *et al.*, 2010). This contrast suggests that at a psychophysical level, the mechanisms available for the processing of ITDs at high and low frequencies may not be as "functionally equivalent" as one might have expected.

#### 4.6.1 Neural Underpinnings of the Midline Channel

Psychophysical studies offer clear evidence of a midline azimuthal channel based on ITD processing at low tone frequencies (Dingle *et al.*, 2010). In that case, evidence for the existence of the midline channel was more compelling in experiments using symmetrical adaptors than central ones. This difference was attributed to the possibility that neurons tuned to near-zero ILDs or ITDs were relatively small in number, so that the decrease in the weighting of their contribution to position judgements following central adaptors should be expected to be modest. It is also possible that, given that the borders of the lateral channels both cross the midline, central adaptation has some effect on all three channels such that the relative difference in activation of the three channels post-adaptation is less than that resultant from symmetrical adaptation. Confronted with symmetrical adaptors, however, the contribution of midline-preferring neurons may become more heavily weighted, particularly given the strength of the adaptor tone effects on the lateral hemifield channels. We shall return to the "numbers of neurons" question below. For now, why should the psychophysical data be less strongly supportive of a midline channel for ITDs (especially those imposed on high-frequency sounds) than for ILDs?

The most direct evidence on the potential neural substrate of the midline channel comes from free-field studies of cat cortical neurons (e.g., Rajan *et al.*, 1990; Imig *et al.*, 1994; Eggermont and Mossop, 1998; Stecker *et al.*, 2005). These studies have in common that at least a small proportion of the neurons studied had restricted azimuthal receptive fields centered on or near the midline. Because the studies were free-field ones, it is difficult to know exactly the contribution of ITDs and ILDs to the formation of the

receptive fields. What all of these studies have in common, however, is that only high-frequency neurons were studied, so perhaps ILD was the major stimulus parameter shaping the receptive fields. Dichotic studies of cortical neurons have shown the existence of cells tuned to zero or near-zero ILD (Kitzes *et al.*, 1980; Phillips and Irvine, 1981; Orman and Phillips, 1984) and interaural onset time disparity (Kitzes *et al.*, 1980). Once again, almost all neurons studied in those reports were high-frequency ones. It is indeed striking that in over four decades of studies on cat auditory cortical neurons, there has been no systematic study of the spatial properties of low-frequency cells, and no studies at all of cortical responses to ITDs of transposed tones. The cortical data thus provide little or no evidence bearing on the question of a midline channel for ITDs in either low- or high-frequency neurons.

There have been a number of recent systematic studies of low-frequency brainstem cells for their sensitivity to ITDs (McAlpine *et al.*, 2001; Brand *et al.*, 2002; Hancock and Delgutte, 2004). These studies report that the preferred ITDs of cells are best-frequency related, such that most cells have preferred ITDs favouring the contralateral ear in a fashion that maintains the preferred interaural phase near 45 degrees. It is difficult to imagine how this physiology could support a midline perceptual channel for ITDs at low frequencies. These recent neurophysiological data are, however, somewhat at variance with those from earlier studies which made no mention of the best-frequency dependence of preferred ITD, and which reported the existence of cells with peak characteristic delays near zero ITD, though not as a discrete class but simply as members of a population of cells with a relatively broad distribution of characteristic delays (e.g., Yin and Kuwada, 1983).

The attempt to relate psychophysical and neurophysiological data on a midline channel for ITDs is confronted with an evidence of absence (present study, for high frequencies) from the psychophysics, and an absence of evidence (cortical) or evidence of absence (brainstem) from neurophysiology. The underpinnings of the midline ITD channel seen psychophysically for low-frequency tones (Dingle *et al.*, 2010) are a mystery.

Above, we mentioned that psychophysical efforts to reveal a midline channel using central adaptors have been less compelling than those using symmetric adaptors. We reasoned that this may be linked to the fact that midline preferring neurons are relatively few in number compared to hemifield ones. Adaptation of the hemifield channels might thus easily reveal a more heavily-weighted contribution of the midline one, while the reverse may be less obvious in its effect. An argument based on the relative numbers of neurons is not without a significant problem. Recall that unilateral auditory forebrain lesion studies show that sound localization deficits resulting from the ablations are restricted to the sound hemifield contralateral to the lesion. This means that all of the neural machinery for localizing in that hemifield must lie within a single auditory cortex. Even the original two-channel model thus requires that cells with contralateral hemifield receptive fields and cells with ipsilateral receptive fields must exist within the auditory cortex of each side. This is indeed the case (Rajan *et al.*, 1990; Stecker *et al.*, 2005; Lee and Middlebrooks, 2010). The ipsilateral-preferring cells are, however, in the significant minority, yet appear to contribute on an equally-weighted basis with the contralateral-preferring cells. The numbers of neurons available to contribute to the perceptual decision-making process, i.e., to the relative outputs of left,

right and midline channels, then cannot in itself be a deciding factor in the weighting process.

#### *4.6.2 Adaptation or Response Bias?*

There is a potential criticism of the selective adaptation paradigm used in this and in our previous studies. It is that exposure of the listeners to the adaptor stimulus does not so much induce a “fatigue” in the target neural/perceptual channel, but introduces some kind of response bias or criterion shift in the responses to the test tones. The present data suggest that this more cognitive explanation of the data can be rejected. This is because a cognitive account that would have predicted the outcome of Experiment 1 (highly significant shifts in the perceived location of the test tones) must also predict highly significant effects in Experiments 2 and 3, and this did not happen. That is, highly lateralized adaptors capable of inducing a response (or other cognitive) bias in one experiment should also do so in the others, especially given that the same listeners participated in all three experiments. The very small (or absent) effects of the adaptors revealed in Experiments 2 and 3 thus appear genuinely to suggest that human listeners have a poorly-developed or no midline channel for ITDs at high frequencies.

### **4.7 ACKNOWLEDGEMENTS**

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## CHAPTER 5 CONCLUSION

### 5.1 OVERVIEW OF RESULTS

The purpose of this research was to investigate the presence of a midline azimuthal channel in human spatial perception. This channel was proposed to exist in complement with the two lateral, hemifield-tuned channels that comprise one currently well-accepted model of mammalian spatial hearing. Ten experiments used a selective adaptation paradigm to fatigue one or more of these three channels (two lateral, one midline) in an effort to reduce their relative contribution to sound localization and so uncover evidence of the midline channel in subsequent changes in the reported location of test stimuli. Four of the ten experiments used symmetrical adaptation to fatigue the two lateral channels. The hypothesized consequence of this was an increased contribution of the midline channel relative to reduced activation in the lateral channels. In all four of these experiments, it was expected that the influence of the midline channel would be seen as a post-adaptation shift in the perceived locations of test stimuli *towards* the azimuthal midline. This effect was seen clearly at both high and low frequencies when the cue for sound location was ILD, and at low frequencies when sound was localized with ITD. Testing high frequencies in the domain of ITD yielded only weak evidence of a post-adaptation shift. Four experiments examined the complementary condition in which the midline channel was adapted (its relative contribution reduced) with the expectation that post-adaptation position reports would shift *away* from the azimuthal midline. This effect, too, was clearly seen in conditions localized with ILDs. When the cue for location was ITD, the shift away from the midline for low-frequency conditions was weaker than

the shift towards the midline after lateral adaptation and for high-frequency conditions it was mostly absent. Finally, two ITD experiments, one using low-frequency stimuli and one using high-frequency stimuli, used asymmetrical adaptation (presented a different frequency to each ear). Both low- and high-frequency conditions saw robust shifts in post-adaptation location reports away from the adapted side. While these two experiments do not speak to the existence of a midline channel, the first was undertaken before all other experiments as a replication of previous work using this paradigm (Vigneault-MacLean *et al.*, 2007), while the second offers the first data on adaptation of ITD channels at high frequencies.

## **5.2 THE TWO- (NOW THREE-) CHANNEL MODEL**

The data presented here bear on a number of important issues. First, the two asymmetrical conditions offer further confirmation that human sound localization is mediated by two hemifield channels (Boehnke and Phillips, 1999; McAlpine *et al.*, 2001; Stecker *et al.*, 2005; Phillips, 2008). An alternative could have been that the neural foundation of human sound localization involved a barn owl-like mechanism in which small groups of neurons are narrowly tuned to discrete spatial locations. In that case, the asymmetrical adaptation used here should have resulted in shifts in post-adaptation position reports that were confined to the lateral extremes of the test-tone ITD/ILD ranges, close to the perceived locations of the adaptor tones. Empirically, asymmetrical adaptation resulted in a perceptual shift that extended across the entire adapted hemifield and bled over the midline. This pattern of adaptation is consistent with the fatiguing of a channel that is broadly tuned to one acoustic hemifield with a border that extends across

the midline. This finding fits with data from electrophysiological work on the mammalian cortex which shows that the primary auditory cortex is dominated by neurons that respond broadly to sound stimuli located in one hemifield (most commonly the contralateral field) and whose medial borders result in the steepest functions, or most salient change in firing rate, crossing the azimuthal midline (e.g. Middlebrooks and Pettigrew, 1981; Rajan *et al.* 1990; Eggermont and Mossop, 1998).

These electrophysiological studies were of the receptive fields of high-frequency neurons in the auditory cortex that used primarily pure tone stimuli at the characteristic frequency of the neuron (the frequency that will elicit a response at the lowest intensity). Because neurons respond to a range of frequencies, another approach to classifying cell responses in dichotic experiments is to examine a low-frequency cell's "characteristic delay", and studies using this paradigm offer further support for a two-channel, hemifield model. The characteristic delay has been defined as the point at which a cell's response rates to interaural phase delays (IPD) at different frequencies coincide (Rose *et al.*, 1966). If sound location were represented by the maximal firing of cells, one would expect to see cells with characteristic delays always located at the peak (or possibly trough) of their spike rate vs. IPD function. Yin and Kuwada (1983) recorded from cells in the cat inferior colliculus and found that the characteristic delay could occur at any point along the spike rate-IPD function. Of those cells with characteristic delays that did occur at a peak, the majority favoured stimuli leading at the contralateral ear, often for delays beyond the cat's physiologically relevant range. Likewise, trough characteristic delays tended to favour strongly ipsilateral-leading stimuli. The implication of these data is that the slopes of the spike rate-IPD function consistently straddle 0 IPD. Similarly, studies



looking at the “best” interaural delays of neurons (the delay for which the cells fire maximally) have also demonstrated that the peak firing of cells in the inferior colliculus occurs in response to large ITDs. This results in the maximum slope of the rate vs ITD function crossing the range of naturally occurring ITDs, centered on the midline (in the guinea pig, McAlpine *et al.*, 2001; in the gerbil, Brand *et al.*, 2002; in the cat, Hancock and Delgutte, 2004: in particular, see figure 5). All of this is consistent with the two-channel model. While the congruence between the results of asymmetrical selective adaptation of sound location perception and data from electrophysiology has been pointed out before (Vigneault-MacLean *et al.*, 2007), the addition here of the high-frequency ITD condition strengthens this relationship, since all of the electrophysiological data on the free-field receptive fields of cells in the auditory cortex has been drawn from high-frequency preferring neurons.

Secondly, and more central to the purpose of this work, both the symmetrical and central adaptation conditions provide the first evidence in humans for a perceptual midline channel contributing to sound localization, in addition to the two lateral channels. If there were no midline channel, both of these types of adaptation would have resulted in equivalent fatiguing of the two lateral channels and thus no change in their relative contribution to position judgements of test tones; no shift would be expected in the post-adaptation test-tone position reports. Empirically, the robust shifts of test-tone position reports towards the midline seen after symmetrical adaptation of ILD conditions and the low-frequency ITD condition, and the shifts away from the midline after central adaptation seen in the ILD conditions, fit with what would be expected if these sorts of adaptation affected the relative contribution of a third channel centered on the midline.

This, too, is consistent with neurophysiological work. Neurons that have narrow spatial receptive fields centered on the midline have been found in both free-field (Rajan *et al.* 1990; Brugge *et al.* 1996; Eggermont and Mossop, 1998; Imig *et al.* 1990) and dichotic studies (Phillips and Irvine, 1981). Despite neurophysiological evidence for midline-preferring cells being consistently reported in recording studies, the potential contribution of a midline channel has been largely ignored in formulations of the two-channel model (McAlpine *et al.*, 2001; Stecker *et al.*, 2005).

It is possible that the inclusion of a midline channel into the model of mammalian sound localization may also help to reconcile some of the work that has argued for a barn owl-like model in mammals. It could be argued that while mammals lack a complete population of sharply-tuned neural units spanning the physiological relevant ranges of preferred ITDs or ILDs, the group of midline cells represents *one* of these sorts of units. However, one of the critical features of a barn owl-like model is that what codes a sound's location is the maximal firing of independent cells narrowly tuned to different points along the ITD, ILD and/or azimuth dimensions. Proponents of the two-channel model have pointed out that because the maximal firing of the lateral channels most commonly occurs to ITDs outside of the range that would be experienced in nature, the critical information for a sound's location must be contained within the steep slopes of the firing rate functions of each channel rather than their peak firing (Phillips and Brugge, 1985; McAlpine *et al.* 2001). This idea drove the suggestion that sound location is coded by the *relative activation* of these two channels (Boehnke and Phillips, 1999; McAlpine *et al.*, 2001; Phillips, 2008). Likewise, when it comes to the midline channel it is easy to take the perspective that maximal firing rate codes sound location and thus

refer to it differentially as “narrowly-tuned” in comparison to the “broadly-tuned” lateral channels. If one focuses instead upon the slopes of the midline-preferring cells, their action across the physiological range of binaural sound cues is really very similar to that of the hemifield cells (see Figure 14). It may be the case that, just as with the lateral channels, the midline channel cannot represent sound location independently. Of course, with no way to selectively silence hemifield cells, this can only be speculation.

“How wide is the midline channel” is an interesting question. Figure 14 offers a schematic illustration of the three-channel model. It draws upon data from Orman and Phillips (1984), in which the frontal cells have ITD functions whose skirts extend 20 dB ILD on either side of zero ILD, to place the midline channel relative to the hemifield channels. In this case, the midline channel spans the entire behaviourally relevant range (compare to the range of ILDs spanning the frontal perceptual hemifield in Chapter 3, which is only about  $\pm 12$  dB). However, Rajan *et al.* (1990) reports a much narrower range of  $\pm 20^\circ$  azimuth on either side of the midline using free-field stimuli (in humans at least, this is equivalent to about  $\pm 3$  dB ILD based on the pre-adaptation curves in figures 7-10 or to about  $\pm 200$   $\mu$ s ITD based on the pre-adaptation curve in figure 5; the range of relevant binaural cues in cats should be quite a bit smaller, considering the smaller size of their head). Notably, some of the midline unit responses reported by Rajan *et al.* (1990) are expansive with increasing intensity such that their range comes closer to that reported by Orman and Phillips (1984) at comparable intensity levels. It is perhaps unsurprising that midline receptive fields for free-field stimuli are narrower than those predicted from dichotic studies. Because increasing stimulus intensity reduces the latency of neural responding, the neural coding of ILDs enjoys not only a comparison between intensities

but also a sort of ‘neural’ ITD caused by this intensity-latency co-variation. The addition of the physical ITD available in free-field stimuli to the ‘neural’ ITD would predict a much narrower tuning of the midline cells. Indeed, Kitzes *et al.* (1980) used dichotic stimuli to examine the response patterns of cells in the A1 of cats, but co-varied ITD and ILD. The addition of a 10 dB ILD halved the width of the ITD response curve of midline cells. Nevertheless, even with the inclusion of this large ILD, the ITD tuning of the midline cells was broad, with skirts of about  $\pm 5$  ms (recall that the distance between the ears of an adult human allows for a maximum ITD of about 0.65 ms). Beyond these three papers, data on the breadth of response of midline cells are lacking. The data presented here from the central adaptor conditions in the domain of ILD (chapter 3) suggest a broader tuning of the midline channel, since the post adaptation shift was evident across the entire frontal acoustic hemifield. If the breadth of the midline channel were limited to  $20^\circ$  around the midline, one might have expected the effects of central adaptation to be similarly limited.

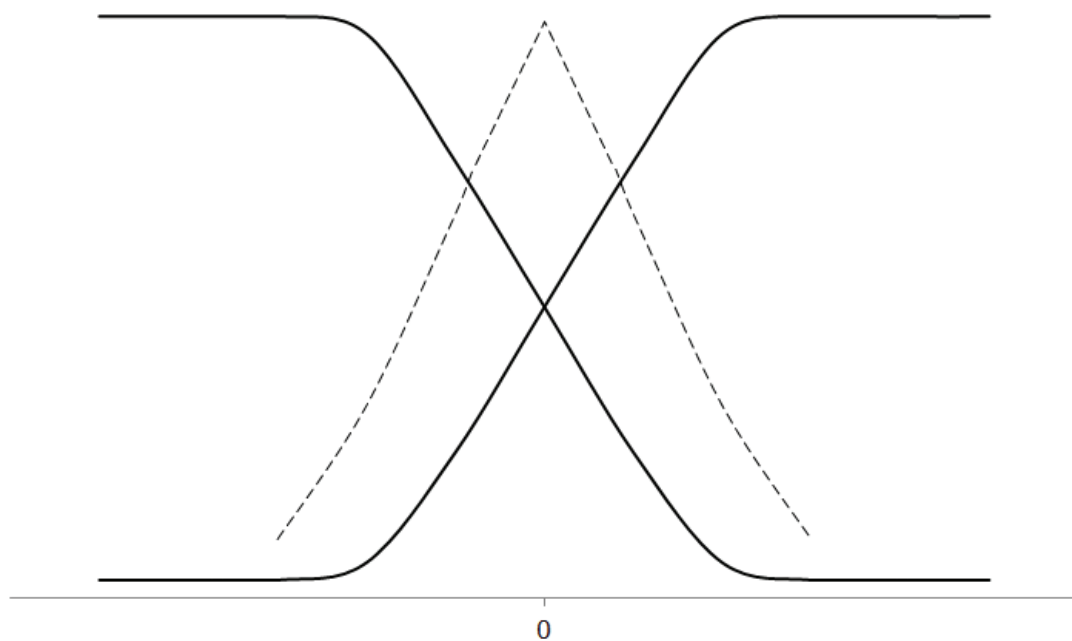


Figure 14. Schematic diagram illustrating the three-channel model. Cells that make up each lateral channel have hemifield tuning to interaural disparity or intensity with overlapping medial borders. Cells that make up the midline channel respond maximally to sounds at the midline.

### 5.3 CODING CONSTANCY

It has been suggested that the neural machinery underlying sound localization is functionally equivalent for high and low frequencies (Griffin *et al.*, 2005; Phillips *et al.*, 2011). This does appear to be the case for the lateral channels. Recall that, in natural settings, ITD is the dominant cue for localizing low frequency tones while at high frequencies, for which the travel time of the sound from one ear to the other can be longer than a half period of the sound wave, ITD becomes an ambiguous cue. In contrast, ILD is more effective at higher frequencies; low frequency sounds diffract around the head with little loss of intensity at the ear further from the source. Regardless, the data here indicate that participants are readily able to localize high frequency stimuli using ITD and low frequency stimuli using ILD when the relevant information is available, i.e., when the stimulus design permits the nervous system to encode the cues unambiguously. In the former case, the use of transposed stimuli allows for ITD information to be present in the low-frequency amplitude envelope of the waveform despite there being predominantly high-frequency energy in the stimulus. In the latter case, conditions of dichotic listening simply allow for the presentation of ILDs that wouldn't occur in nature. In both cases, stimulus presentations resulted in orderly psychometric functions reflective of the participants' ability to assign locations to the stimuli (see also Yost, 1981). Further, adaptation of the lateral channels resulted in robust post-adaptation shifts in position reports away from the adapted side for both high- and low-frequency ITDs, and both high- and low-frequency ILDs.

On the other hand, for the midline channel this constancy of coding across frequencies was only evident in the domain of ILD. Symmetrical adaptation using low-frequency stimuli in the ITD condition resulted in a post-adaptation shift, but did not likewise result in much of a shift at high frequencies. Why this is so is a bit of a mystery. It may be the case that there are simply no midline-preferring high-frequency cells that are sensitive to ITD. While this work presents evidence of a midline channel at both low and high frequencies, the most direct neurophysiological evidence of midline preferring cells has come from studies recording from only high-frequency neurons. Further, these studies have used either free-field stimuli, or dichotic ILD stimuli. It is easy, therefore, to draw a link between the psychophysical evidence here of the high-frequency ILD condition and high-frequency ILD electrophysiology data. The lack of consistency between our high-frequency ITD condition and recording studies may indicate that in recording studies using free-field stimuli, the dominant cue for midline-preferring neurons is ILD. Little can be said about neurophysiological underpinnings of the low frequency midline channel data presented here because, rather shockingly, there are as of yet no direct data on the free-field spatial tuning of low frequency cortical cells in mammals.

#### **5.4 METHODOLOGICAL ISSUES AND PATTERNS IN THE DATA**

An early concern was that the shifts in test tone position reports seen after exposure to trains of lateralized (or central) stimuli was not strictly an adaptation response, but instead some form of response bias. While the lack of a post-adaptation shift for high-frequency stimuli in the domain of ITD was unexpected, it does offer a

panacea for this worry (see Chapter 4). Any response bias induced by the adaptor tones should reasonably have been equally present in all conditions. Thus, the very failure to find evidence of a midline channel sensitive to high-frequency ITDs allows the rejection of the idea that results in other domains were simply due to some kind of a criterion shift.

One inconsistent finding seen in these experiments was that adaptation affected the perception of test tones with smaller ITD/ILDs more than it did tone tones with ITD/ILDs closer to those of the adaptors. This pattern is most notable in the convergence of the pre- and post-adaptation functions in figures 4, 5, 9 and 11. The argument was made earlier that this may reflect the superior performance of humans in localizing sounds closer to the midline than in the periphery. This fits well with the idea that neural coding for positions near the midline is most unambiguous because it corresponds to the steep portion of the ILD-vs-azimuth function (Phillips and Brugge, 1985). However, it is also a possibility that the convergence of pre- and post-adaptation functions for strongly lateralized stimuli may reflect something more methodological. For example, the very fact that stimulus location may be more ambiguous in the periphery might lead to a strategy whereby participants assign the most extreme numbers (see Figure 2) to the tones that they identify as “furthest out” in the face of a reduced ability to assign discrete locations. Even without acuity differences in localization ability, the most extreme numbers may act as perceptual anchors. In any case, it is unclear why this pattern was inconsistent across conditions.

A third methodological point concerns the high-frequency ITD study (Chapter 4). It could well be argued that the spectra of transposed tones extend to low frequencies, or that even if they didn't, the harmonics introduced by the transposition permit the



development of low-frequency distortion products at the level of the cochlea. By this line of reasoning, the effects seen with high-frequency ITD adaptors may be due as much to those distortion products as to the intended properties of the stimuli. The contribution of any such low-frequency distortion products could have been eliminated by the use of low-pass noise to mask them. Note, however, that this argument carries the implication that high-frequency ITD stimuli would have enjoyed the joint benefits of the low-frequency modulator *and* the low-frequency distortion products to induce an adaptation effect. In practice, this simply didn't happen. Psychophysical evidence for the existence of a midline channel was in fact weakest (or nearly absent) for the transposed tones experiment. Extraordinary special pleading would be required to explain why the asymmetrical high-frequency ITD adaptors resulted in the expected hemifield-wide adaptation response, while the midline and symmetrical adaptors did not, despite their being synthesized in the same way. It is thus unlikely that any low-frequency distortion products contributed to the outcome of the high-frequency ITD experiments.

## 5.5 SUMMARY

The results of this work are accountable in terms of a three-channel model of azimuthal sound localization. Further, these are the first studies that clearly hypothesize the existence of, and directly pursue evidence supporting a midline channel. The existence of a midline channel received strong support at both low and high frequencies when the cue for sound location was ILD. The evidence for a midline channel was weaker in the ITD domain for low-frequency tones, and virtually absent for high-frequency ones. Hopefully, future work in both auditory psychophysics and

neurophysiology will increase its emphasis on (or simply include reference to) the existence of the midline channel. Most obviously, there is a gap in neurophysiological work in regards to spatial tuning of cells that make use of ITD. Further inquiry along this line may contribute to our understanding of the neural substrate that mediates the midline channel.

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