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The Role of the Vestibular and Proprioceptive Systems in Processing Dynamic Sound Localization Cues

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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THE ROLE OF THE VESTIBULAR AND PROPRIOCEPTIVE SYSTEMS IN PROCESSING DYNAMIC SOUND LOCALIZATION CUES

(Thesis format: Monograph)

by

Janet Kim

Graduate Program in Health and Rehabilitation Sciences

A thesis submitted in partial fulfillment of the requirements for the degree of Masters of Science

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Abstract

Head movements are known to be beneficial during sound localization because the auditory system can integrate the dynamic cues generated by head movement while maintaining a spatial representation of the position and orientation of the head-in-space. To measure the extent to which vestibular and proprioceptive cues influence processing of dynamic sound localization cues resulting from head rotation, we measured the ability of normally hearing listeners to localize front/back sources of low-frequency sounds while the two modalities were individually or congruently stimulated. Targets were presented over headphones during head rotations using virtual auditory space methods. Dynamic localization cues corresponded to head-in-space and/or head-on-body angle. Discrimination was accurate in passive and active head rotation conditions, but near chance in conditions lacking head-in-space motion, suggesting that among the two sensorimotor cues, vestibular inputs are necessary and sufficient to inform the auditory system about head movement, whereas proprioceptive cues are neither necessary nor sufficient.

Keywords

Binaural sound localization, front back discrimination, head movement, multisensory multimodal sensorimotor integration, efferent copy, vestibular system, auditory system, proprioceptive system, auditory-vestibular integration, auditory-proprioceptive integration
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Chapter 1

1 Introduction

In the throb of a bustling city, we are able to identify and evade possible danger of an oncoming speeding car or recognize our favourite songs across the street in a nearby cafe. These everyday instances exemplify the important role binaural sound localization plays in our ability to make sense of the sounds we hear even in noisy and reverberant environments. As opposed to the controlled conditions of a majority of studies that investigate sound localization, our heads are in continual motion when we try to localize sounds. This raises the question: during such sound localization, how does the auditory system know where the head is and what it is doing in space during head movement?

During sound localization, information about the lateral location of a sound source is provided by interaural level and time differences (ILD and ITD; Section 1.1.1) between the signals reaching the left and right ears. ILD cues tend to be used for higher frequency sounds, whereas ITD cues tend to be utilized for lateral localization of lower frequency sounds and are predominately used by normally hearing listeners when localizing wideband noise in the azimuthal (or horizontal) plane (Macpherson & Middlebrooks, 2002). In the absence of a listener’s head motion, however, these interaural difference cues are insufficient to specify front/back and up/down location of an auditory target. Information about these dimensions can be provided by spectral cues (Section 1.1.2) in regions above approximately 4 kHz (Hebrank & Wright, 1974; Merhgardt & Mellert, 1977; Langendijk & Bronkhorst, 2002; Zhang, 2010). These are created by direction-dependent filtering imposed on incident sound by the pinnae, but errors of localization such as front/back reversals can occur when stimuli are narrowband, which prevents access to the spectral cues (Blauert, 1969/70; Middlebrooks, 1992). In the absence of monaural spectral cues, a listener can take an active role in sound localization to resolve front/back confusions by means of moving the head. Here the relationship between the motion of the head and the resulting changes in the interaural difference cues yield dynamic sound localization cues that can disambiguate a sound source’s location,
whereby, for a given head rotation, the direction of change of ILD and ITD for a sound source in the front hemisphere is opposite to that for a source in the back.

The use of such dynamic localization cues may significantly involve the vestibular and proprioceptive systems, as the auditory system requires an accurate representation of the orientation and motion of the head in space to interpret these dynamic cues. Findings in previous studies in which the vestibular and proprioceptive systems were stimulated through caloric stimulation and neck-muscle vibration respectively (Wallach, 1940; Lewald, 1998, 2000), have been obtained in conditions of static sound localization, where the head and body were kept stationary in space. The biasing effects of stimulation in such studies have been suggested as indirect evidence for their role in dynamic sound localization that requires head movement.

While it has been postulated that visual stimulation (e.g., a rotating visual field) (Wallach, 1940; Otake, 2006) or proprioceptive feedback may play a role in dynamic localization, whether they are sufficient is unknown. Previous dynamic localization experiments carried out in complete darkness have shown that visual stimulation is not necessary for salience of the dynamic cues (Macpherson, 2008).

As there are very few investigations that address auditory-vestibular and/or auditory-proprioceptive integration in the context of dynamic sound localization, the goal of the present study is to determine the contribution of vestibular and proprioceptive (or efference copy) information in spatial hearing and the extent (necessity and sufficiency) to which the sensorimotor integration of vestibular and proprioceptive cues influence the processing of dynamic cues generated during head movement. The following sections present information about the basic principles of binaural sound localization with more specific focus on lateral localization (Section 1.1), benefit of head movement in resolving acoustically ambiguous information in the front or back dimension (Section 1.2), and a review of the existing literature of the influence of vestibular and/or proprioceptive input on the auditory system during binaural sound localization (Section 1.3 and 1.4).
1.1 Static Sound Localization Cues

1.1.1 Interaural Difference Cues (ILD and ITD) for Sound Localization on the Horizontal Plane

Consistent with a part of Lord Rayleigh’s Duplex theory, which provides an explanation for the ability of sound localization in humans by using interaural difference cues between both ears (Strutt, 1907), existing behavioural and physiological evidence suggests that normally hearing human listeners use these interaural differences to estimate the lateral location of a sound stimulus on the azimuth. Two binaural cues play an essential role for localization in the horizontal plane, namely the ILD and the ITD cues.

ILD cues give information about the azimuthal location of a sound source based on the disparities in the amplitude of the acoustic signal arriving at each ear (Yost & Dye, 1988). For instance, a sound source positioned to the right of a listener’s head will be more intense on arrival at the right ear relative to the left ear, as the signal is attenuated on the left due to the head shadow effect, in which the physical presence of the head causes the attenuation of the signal as it travels to the left. This results in the perception of the sound source originating from the right side of the body. ILD cues tend to be used for sounds lacking frequencies below about 1.5 kHz (Macpherson & Middlebrooks, 2002) and are spectrally dependent because the shape of the head reduces the level of high-frequency signals less able to bypass the head. For higher frequency sounds, ILD values exceed about 20 dB, while they tend to be below 10 dB for lower frequencies (Feddersen, 1957).

In contrast, ITD cues provide information about the location of the sound source based on the disparity between the times at which each ear is stimulated by the auditory signal (Middlebrooks & Green, 1991). For instance, a sound source positioned at the left will reach the left ear prior to the right ear, resulting in a perception of the sound coming from the left side of the body. The ITD cues tend to be utilized for lateral localization of sounds containing low frequencies (below about 1.5 kHz; depending on the size of the listener’s head, ITD values tend to range between 600-700 μs for low-frequency sounds),
as the auditory system is unable to track differences in the waveform’s fine structure reliably for mid- to high-frequency (greater than about 1.2 kHz) auditory stimuli (Zwislocki & Feldman, 1956; Newton & Hickson, 1981). ITD cues are also predominantly used by normally hearing listeners when localizing wideband noise in azimuth (Macpherson & Middlebrooks, 2002), and they naturally vary by about 10 μs/° across the midline for an average human head size.

There are three types of ITD cues: 1) onset, 2) offset, and 3) on-going, which refer to the points at which the temporal disparity of the stimulus is compared (i.e., the onset, offset of the stimulus, or continually while the stimulus is being played) (Blauert, 1983). Recent studies demonstrated that on-going cues are dominant compared to the onset and offset cues for determining ITDs. It has been suggested that since the auditory system temporally tracks the waveform of low-frequency stimuli once per cycle, the on-going cues are more important compared to the onset and offset cues, which track the waveform only at the beginning or end of the stimulus, respectively (Macpherson & Middlebrooks, 2002).

A stimulus presented at any location on the median plane (the vertical plane that bisects the body into left and right halves) should produce an ILD of 0 dB and ITD of 0 μs when both the head and ears are symmetric. However, particular values of ILD and ITD cues are not specific to a single lateral angle (on the horizontal plane or azimuth) but to multiple locations in space that are at about the same lateral displacement from the median plane where the overall interaural differences are constant (Strutt, 1907), and it is this area of ambiguity that is now referred to as the “cone of confusion” (Fig. 1). Each cone of confusion represents an infinite number of positions with the same lateral angle, thereby representing an infinite number of possible front/back confusions during sound localization. For instance, if a sound occurs at 45° to the left and to the front, the ITD will be about the same as if it had occurred at 45° to the left and to the back. Similarly, positions at 45° to the left and above or below the horizontal plane will also provide about the same ITD information. A sound produced at any location on the surface of the 45° cone of confusion will produce exactly the same ILD information. Therefore, within a restricted band of frequency, the information provided by interaural difference cues are
spatially ambiguous, especially along the vertical and front/back dimension (Strutt, 1907). Spectral cues (Section 1.1.2) provided by the direction dependent filtering characteristics by the pinnae, head, and torso are used to disambiguate front/back and vertical locations in a cone of confusion.
Figure 1. The Cone of Confusion. The regions in space that have the same ILD values are represented by the magenta outlines (upper right hand corner) and are spaced 3 dB apart. The regions that have the same ITD values are represented by the blue outlines (upper left hand corner) and are spaced 100 μs apart. Each of the outlines represents where a cone of confusion is present. The bottom image is an example of two cones of confusion, one with a moderate ILD favouring the left ear (magenta) and one with a large ITD leading at the right ear (blue). Illustration provided by Ewan Macpherson.
1.1.2 Spectral Cues for Sound Localization in the Vertical Plane

Whereas ILD and ITD cues are used to determine how far left or right of the median plane a sound source is, the spectral (pinnae) cues are specific to vertical directions and are used to determine the elevation and front/back location of a sound source on the vertical plane (Wightman & Kistler, 1989; Middlebrooks, 1992). When a waveform interacts with the pinnae, head, and shoulders, the spectral information in the acoustic signal becomes modified by the resulting sound diffractions and reflections (Shaw, 1997) (see Fig. 2 for example head-related transfer function). The constructive and destructive interference that occurs at the pinnae and external auditory canal are greatest at higher frequencies and can increase or decrease the stimulus amplitude. Such spectral changes are most salient at higher frequencies and are used by listeners as elevation cues to sound localization and used to disambiguate front/back sound sources.

As previously discussed (Section 1.1.1), ILD and ITD cues provide information about the lateral angle only and a single value of an interaural cue can correspond to multiple locations in space. This causes ILD and ITD information to be ambiguous in these areas of the cone of confusion. However, spectral cues in frequency regions above about 4 kHz help distinguish sound sources located in the front from those located in the back of a listener’s head (more specifically bands of approximately 4 – 10 kHz are used to reduce front-to-back confusions and bands of approximately 10 – 12 kHz are used to reduce back-to-front confusions) (Hebrank & Wright, 1974; Langendijk & Bronkhorst, 2002; Zhang, 2010).
Figure 2. Head-related transfer functions (HRTF) for front (blue) and rear (red) sound source locations measured at the right ear of a typical listener.
Localization tends to be inaccurate in the vertical plane if the auditory stimuli lack broadband energy in the high-frequency region (above ~4 kHz) and requires the integration of additional cues derived from changing ILD and/or ITD information during head and/or body movement to resolve front/back confusions (Fig. 3). Without this high-frequency information, stimuli seem to originate from phantom locations that depend on the content of their frequency rather than the actual physical location of the sound source. Depending on the center frequency (Blauert, 1969/70; Butler, 1983), narrowband stimuli appear to originate above, in front, or behind a listener, and this effect differs between subjects (Middlebrooks, 1992; Itoh, 2007), while the position for low-pass sound sources seem to be on or slightly below the horizontal plane in the front (Hebrank, 1974).

1.2 Dynamic Sound Localization Cues

In addition to binaural cues, accurate localization in both the vertical plane and horizontal plane is also dependent on head movement. The auditory system processes the changing information of the interaural difference cues, otherwise known as dynamic localization cues, during head motion in order to better localize sound sources that would otherwise be ambiguous. For instance, if a sound source is located in the front of the listener as their head moves from the left to the right, the intensity of the stimuli and onset time would decrease for the right ear and increase for the left ear, whereas, if the source is located in the back, the intensity and onset of the stimulus would increase for the right ear and decrease for the left ear (Fig. 3). These dynamic cues generated by head movement provide clear information regarding front/back location of the sound source only if it is assumed to be stationary.
Figure 3. Dynamic information is provided by the relationship between the motion of the head and the resulting changes in ILD and ITD cues when localizing auditory targets on the azimuth. Illustration by Devin Kerr (Macpherson & Kerr, 2008).
1.2.1 The Benefit of Head Movement in Reducing Front/Back Localization Error

In 1967, Thurlow et al. conducted an experiment to explore the different types of active/voluntary head movements participants preferred to use during a sound localization task. Fifty blindfolded participants were instructed to localize five loudspeakers emitting low-frequency sounds and five other loudspeakers emitting high-frequency sounds in a free-field anechoic chamber (localization accuracy was not recorded) as their head movements were captured by a motion-picture camera attached to a small head-mounted. This allowed for all different types of head movements to be captured and observed while their torso remained stationary. The results demonstrated that among the three types of head movements (rotational – left/right about the vertical axis, tipping – up/down about the horizontal axis, and pivoting – tilting of head, such that there is an increase in vertical height of one ear and a decrease in the other) (Fig. 4), rotational movement had the greatest amplitude, followed by combinations of rotation with a tipping movement, and a final combination of rotation, tipping, and pivoting. They demonstrated several things with these findings: 1) small head rotations are the most frequent type of head movement during sound localization, 2) head rotations occur either alone or in combination with the other types of head movements, and 3) they suggested that head movement (more specifically suggesting involvement of vestibular and proprioceptive input) is advantageous for sound localization performance, even though accuracy of localization performance was not measured in this experiment.
Figure 4. Rotating, tipping, and pivoting head movements, respectively.
Wallach (1939, 1940) hypothesized and demonstrated that small head motions might be beneficial in disambiguating ILD and ITD to help localize sound sources in the vertical plane. His reasoning was that the auditory system was able to process and use the changes in the ILD and ITD information (dynamic localization cues) from sound sources located in the front or back during horizontal head movement to disambiguate front/back localization confusion, which is referred to as the “Wallach cue” (Perrett & Noble, 1997).

Following Wallach’s behavioural experiment, other psychoacoustical experiments of sound localization in the horizontal plane further supported the notion that head movements cues are advantageous to sound localization (Thurlow, 1967; Perrett & Noble 1997; Wightman & Kistler 1999; Macpherson, 2011; Macpherson, Cumming & Quelch, 2011) and that front/back confusions are reduced as a result, as the motion of the head provides dynamic information from the relationship between the motion of the head and the resulting change in ILD and ITD cues and changes in the sound spectrum (Macpherson & Kerr, 2008).

In Perrett and Noble’s experiment (1997), listeners were instructed to make two types of head movements: 1) oscillatory, by moving their head 30° to the left and right while a stimulus (low-pass, wideband, or high-pass) was presented for a duration of 3 s, or 2) single horizontal rotations over a 45° range on the onset of a 0.5 s or 3 s signal. Listeners were able to use either head movement effectively to accurately localize front/back sources on the azimuth for all the different frequency stimuli. Head movement was also beneficial for low-pass stimuli when localizing source elevations. These results supported the idea that the “Wallach cue” depended on the energy of low-frequency stimuli (below 2 kHz).

Wightman and Kistler (1999) provided more experimental evidence that the changes in ILD and ITD that occur with head movement disambiguated front/back confusions by employing virtual auditory space testing methods, which allowed for more controlled manipulation of interaural and spectral cues. In their experiment, listeners were instructed to keep their head stationary as the experimenters moved the virtual sound source in space, where listeners demonstrated a large number of front/back confusions. When the
listener was allowed to move their head or was in control of the source movement, front/back confusions were resolved, which further supports Wallach’s hypothesis.

Recent experiments done by Macpherson (2011) in free-field and virtual auditory space settings also demonstrated that head movements do not benefit front/back localization accuracy for all frequency stimuli but are most salient for low-frequency stimuli.

1.3 Influence of Vestibular Information in Dynamic Sound Localization

1.3.1 Benefit of Both Passive and Active Head Movement during Sound Localization Suggests Vestibular Involvement

Wallach presented a theory in 1938 related to head movements that discounted pinnae effects on sound localization. In this experiment, Wallach demonstrated that as long as the sound source’s characteristic changes in lateral angle are presented in accordance with head movements, the actual position and perceived location of the sound source are independent of each other. In other words, Wallach showed that it is possible to create front/back confusions using head movements; he hypothesized that the vestibular organ (sensory system located in the labyrinth of the inner ear that provides a sense of balance and movement) provided the motion cues to the auditory system.

The participants sat in the center of a circular array of free-field active loudspeakers equidistant from each other on the horizontal plane, all linked to a rotary switch that switched the auditory stimuli to the next loudspeaker in accordance to the rotational movement of the participant’s head. As a result, the auditory stimuli were perceived at the illusory “calculated” location, which did not necessarily concur with the actual location of the loudspeaker. For instance, the sound seemed to originate from the back of the participant’s head when listening to the front speaker if the distance between the loudspeakers were twice the rotational angle of the subject’s head (Fig. 5). It was reported that the participants consistently perceived this illusory stationary source location, from which Wallach developed the ‘principle of least displacement’, which states that spectral cues are subordinated to the preferred stationary-source interpretation of the dynamic interaural difference cues used by the auditory system.
These perceptions were not only demonstrated in active head rotations but also in passive head rotations by passively rotating the participant’s head and body with the use of a swivel chair, which was consistent with his hypothesis of auditory-vestibular integration. Wallach also demonstrated through his experiments that sound localization in humans is highly dependent on dynamic localization cues and that such cues are relatively dominant relative to spectral cues, as the physical direction (perceived by the pinnae) and the direction in which they were perceived differed. Recent studies that similarly replicated Wallach’s study in virtual auditory space demonstrate that this illusion, however, is strongest for low-pass filtered sounds that lack strong pinnae cues, suggesting that it is the low-frequency ITD information that carries the dynamic cues instead of higher frequencies that contain information of the target location, which conflicts with the illusory location (Macpherson, 2011; Brimijoin & Akeroyd, 2012).
Figure 5. Front/back ambiguity for stationary (lower panel) or moving sources (upper panels). Upper panels: Similar interaural cues produced for front- and back-hemisphere source locations at three different head angles. Lower panel: Stationary (filled circle) and moving (shaded circles) – changing interaural difference cues derived from head rotation are compatible with the source trajectories. Adapted from Macpherson (2011).
1.3.2 Effect of Passive/Induced Head Movements on Sound Localization

In order to measure whether passive/induced head movement affected localization performance, Thurlow et al. (1967) attached to the participant’s head a head frame apparatus that was accompanied by a bite bar placed in the mouth and used this to induce the head movements (either a rotational, pivoting, or a combination of a rotational and pivoting movement) about the vertical and/or horizontal axis at a given time instant. In addition to rotation, tipping, and pivoting movement conditions (Section 1.2.1), there was a control condition in which there was no head movement at all. “Click”-sounds were used in addition to low- or high-pass filtered noises and participants were instructed to localize these signals in all four experimental conditions by extending their arm towards the perceived location. The rotation was conducted at about 19.8°/s, but the velocity of the pivot motion was not reported. The results demonstrated that sound lateralization accuracy increased even with induced lateralized head movements, further supporting the importance of head movement in sound localization and suggesting that vestibular cues from the change in head position and proprioceptive cues from the neck (afferent cues, not efference copy) during the induced head movements were used by the auditory system to detect their head location and orientation in space during the sound localization task.

The effect of passive head and body rotation on sound lateralization was investigated by Lewald (2001). Participants were rotated passively at a maximum velocity of 90°/s over a displacement of 194° and made left/right (of their median plane) two-alternative forced-choice judgments of the stimuli as they fixated on a visual target. 1 kHz dichotic stimuli were presented over headphones with varying ITD in order to generate an intracranial image between the ears of the participant’s head. Results demonstrated that the median plane of the intracranial image shifted to the left when they were passively rotated to the right, whereas the image shifted to the right when they were rotated to the left, suggesting that vestibular information is used by the brain to help localize stationary sounds during head (and/or body) movement.
1.3.3 Effect of Vestibular Stimulation by Cold-water Irrigation on Sound Lateralization

Previous neurophysiological findings suggest that vestibular afferent information has a compelling influence on the perception of sound localization. Munsterberg and Pierce (1894) and Clark et al. (1949) employed whole-body passive rotation on blind-folded participants to induce vestibular stimulation. Their findings showed systematic shifts in localization performance that were opposite to the direction of the rotation applied on the subject during the movement or in the same direction as the former rotation immediately following the end of the rotary movement. However, Lewald (2000) reasoned that this could not be taken as a direct influence of vestibular input, as it may have just been a result of kinesthetic illusions (in which the body appears to shift relative to external space or the head shifts relative to the trunk) (Lester & Morant, 1970) that accompany vestibular stimulation induced by the passive body rotation (Munsterberg & Pierce, 1894; Clark & Graybiel, 1949).

Thus, in order to avoid this issue and to directly target the vestibular system alone and investigate its isolated interactions with the auditory system, Lewald (2000) employed the cold-water irrigation method (Barany, 1906) to induce nystagmus evoked by vestibular stimulation in an auditory lateralization task. The process of cold-water irrigation involves applying iced water to one external auditory canal for approximately one minute and subsequently drying before beginning the task at hand, which induces a caloric nystagmus (rapid involuntary movements of the eyes) with a “fast phase to the side opposite of stimulation, a slow phase to the stimulated side, and sensation of rotation” (Lewald, 2000). In addition, to suppress kinesthetic illusions mentioned above, participants were instructed to keep their eyes open and to fixate on a visual target. Participants were presented over headphones with dichotic band-pass-filtered noise (1.5-4 kHz) that were perceived as an intracranial image between the two ears (Blauert, 1997). ILDs were randomly varied trial-by-trial, and the participants were instructed to adjust a potentiometer to “shift” the sound image to the left or right so that the perceived image would lie in the median plane of their head.
Results indicated that the sound image was shifted toward the non-stimulated side, suggesting that vestibular input influences auditory perception of space. The results, however, may have been confounded by the fact that the visual input was not removed and while it is suggested as such, these findings do not directly reflect the influence of vestibular stimulation in the direct context of dynamic sound localization because there was no head movement and no resulting changes in interaural cues generated by such movement.

1.4 Influence of Neck Proprioceptive Information in Sound Localization

Even when localizing a stationary sound source in space during head movement, we generally maintain a stable frame of spatial reference of the auditory target by using the resulting changes in interaural cues that are generated by the head movement. Previous neurophysiological and psychoacoustic studies have investigated the role of vestibular influence in such tasks, as the listener requires a stable representation of the location and orientation of their head for a given movement, which is conceivably supplied by the vestibular system. However, Lewald (1998a) reasoned that the changes in interaural differences and vestibular information from head movement alone do not provide explicitly unambiguous information as to whether the head or body (or both) positions have changed. Investigations exploring the effect head position has on the visual system suggests that the neck-proprioceptive information is also used to provide a stable neural representation of body-centered space visually (Andersen et al., 1993; Brotchie et al., 1995). Therefore, it is conceivable that afferent proprioceptive signals from the neck muscles or efference copy from the head position motor signal may also contribute information to the auditory system in coordinating a connection between a head-centered and body-centered frame of reference to maintain a stable perception of auditory space. This understanding of auditory space is required to facilitate body-centered movements like walking or turning our head and/or bodies. The following sections are a review of the existing literature of the influence proprioceptive input may have on the auditory system during static sound localization.
1.4.1 The Influence of Head-On-Body Position

Lewald (1998a) demonstrated that horizontal head position with respect to the body position in space influences sound lateralization. The participants sat still in the center of a dark sound-proof room without any head or body restraints and were instructed to participate in two experiments pertaining to the influence of neck proprioception on sound lateralization performance. For both experiments, band-pass dichotic stimuli with varying ILDs were presented over headphones to create an intracranial sound image. This was done for two reasons: (1) to ensure that the sound stimuli at both left and right ears remained unaffected even during head movement, (2) to create stimuli that would be perceived from a head-centered frame of reference (contrary to free-field or virtual sound sources that are perceived externally, enabling participants to use a body-centered or a head-centered frame of spatial reference) individually or interchangeably.

In Experiment 1, participants were instructed to shift the intracranial sound image within the head to where they perceived their auditory median plane to be by changing the ILD of the stimulus. This was done by adjusting a knob on a response device while at the same time orienting their head to visual targets (screens) in different pre-determined azimuthal locations via a head-mounted laser beam.

In Experiment 2, participants listened to stimuli with varying ILD cues and had to determine via button press whether they perceived the sound to be to their left or right in a two-alternative forced-choice task. Results in both experiments demonstrated that their subjective auditory median plane shifted as a function of the azimuthal head position, such that it shifted in the opposite direction to their head position (i.e., if the head was directed to the left, their intracranial sound image shifted to the right, and vice versa), demonstrating that head position has an effect on shifting sound lateralization. These results suggest that neck-proprioceptive information plays a role in such a shift during static localization (stationary head position), and are consistent with previous studies (Perrott et al., 1987; Pierce, 1901). However, it is difficult to directly translate these results in a quantitative way for sound sources that are perceived in the external auditory space and as evidence for the influence of the neck proprioceptive input in dynamic sound localization where continual head movement is required.
1.4.2 The Influence of Afferent Neck Proprioception

In Lewald’s subsequent study (1999), he attempted via neck-muscle vibration, to further support his results that suggested that neck-proprioceptive input influences the shift in sound lateralization (as described above in Section 1.4). Transcutaneous vibration of the participant’s posterior neck muscles was applied to create an *illusory* lengthening of the muscles. He hypothesized that the resulting muscle-spindle afferents produced a false signal that the muscles were lengthened as if there was head movement. For instance, if the left posterior muscles were vibrated, the brain interpreted this signal as a rightward head rotation (relative to a stationary body) or a leftward body rotation (relative to a stationary head) (Goodwin et al., 1972a; 1972b). This method of muscle vibration was employed in order to tackle the physiological basis of the head-position effects observed in his previous study. Instead of inducing real head movements, neck muscle afferent proprioceptors were stimulated without stimulating the vestibular system and efference copy.

Participants were presented with dichotic stimuli with varying ILD cues over headphones and were instructed to make left/right judgments in a two-alternative forced-choice judgment task as their neck-muscles were simultaneously being vibrated. The results demonstrated that when the left posterior neck muscles were vibrated, the subjective auditory median plane was perceived as shifting to the left of the median sagittal plane of the head, while the vibration of the right neck posterior muscles had the opposite effect, indicating that the sound shifted in the direction of the vibration. These results were interpreted as suggesting that neck-proprioceptive information is used in transforming auditory spatial coordinates onto a body-centered frame of spatial reference.
1.5 Objective

Findings from previous research outlined above regarding the biasing effects of stimulation of the vestibular and proprioceptive systems on static sound localization have been suggested as evidence for their role in dynamic sound localization (through caloric stimulation, neck-muscle vibration, and head-on-body bias, respectively) but direct evidence is lacking. Therefore, in order to directly explore the effect of these systems in dynamic sound localization, we designed a task that offers an objective measure of multi-modal sensory integration (auditory-vestibular and auditory-proprioception) in the interpretation of dynamic sound localization cues.

In order to assess the necessity and sufficiency of these systems in the interpretation of these cues, participants localized the front/back location of dynamic auditory targets while the two sensorimotor modalities were individually or congruently stimulated.

The following is a basic outline of specific objectives we sought to examine:

1. Whether head movement reduces front/back confusions;
2. How front/back localization accuracy performance differs across conditions that require head-in-space movement compared to conditions that do not;
3. Whether passive (whole-body) and active (head-on-body) rotation conditions demonstrate a significant difference in performance;
4. Whether changes in front/back localization performance due to faster head movement are linked to vestibular input.

1.6 Hypotheses

Evidence from the literature and results from pilot testing allow for several predictions to be made about the accuracy of performance on tests of dynamic sound localization when the two modalities (vestibular and proprioceptive) are individually or congruently stimulated. Whether proprioceptive feedback is sufficient is unknown, however, for the results of studies in which listeners localized while being passively rotated suggests that
voluntary movement (and therefore neck proprioception) is not necessary for effective utilization of dynamic cues while vestibular inputs are necessary and sufficient. The specific hypotheses for the present study are as follows:

1. Head movement will greatly benefit front/back localization accuracy;

2. Passive and active head rotation conditions will demonstrate significantly higher front/back localization accuracy compared to the other conditions lacking head movement. If so, among the two sensorimotor cues, **only the vestibular inputs are necessary and sufficient** for the correct interpretation of dynamic auditory cues generated by head movement (See Section 2 for more detail);

3. Front/back localization performance in the passive and active conditions will not be significantly different from each other as a function of stimulus duration and head rotation velocity. If so, this further suggests auditory-vestibular integration;

4. Changes in front/back localization performance with increasing head rotation velocity are linked to the interaction of the auditory and vestibular systems.
Chapter 2

2 Methods

2.1 Overview

This study consisted of two main experiments. Experiment 1 explored listeners’ front/back localization performance, and Experiment 2 explored their sensitivity to the dynamic binaural difference cues upon which front/back localization is based (Fig. 6 provides a flowchart outlining the sequence of procedures).
Experiment 1

Screening

1. Pure-tone audiometry
2. Hearing/vestibular history taken
3. HRTF measurement
4. Preliminary test of free-field sound localization behaviour (low frequency/wide-band stimuli)

1a. Free-field Front/Back Sound Localization (randomized; low-frequency stimuli)
   - Active (25°/s, 50°/s, 100°/s)

1b. Virtual Front/Back Sound Localization (randomized; low-frequency stimuli)
   - Static
   - Passive (25°/s, 50°/s, 100°/s)
   - Active (25°/s, 50°/s, 100°/s)
   - Counter (50°/s)
   - Dynastatic (25°/s, 50°/s, 100°/s)
Experiment 2

Figure 6. Flowchart of Experiment 1 and 2 describing the overall study design and general procedure.
For Experiment 1 (a - free-field presentation, and b – virtual auditory space presentation), in order to assess the necessity and sufficiency of the vestibular and proprioceptive (or efference copy) information in the interpretation of dynamic localization cues, normally hearing listeners localized the front or back location of dynamic auditory targets presented in the horizontal plane while the two modalities were stimulated individually or congruently. There were five experimental conditions: static, passive, active, “counter”, and “dynastatic”, which are further explained in Section 2.5.3 (conditions represented in quotations are new terms defined by the experimenters for the purposes of the present study). In order to measure localization accuracy as a function of head velocity, stimulus window width, and stimulus duration, the head and/or body of the participant oscillated to the left and right directions in the passive, active, and counter conditions at varying desired velocities (but counter was performed at one velocity).

In the static condition, participants kept their head and body stationary during the front/back localization task, eliminating both vestibular and proprioceptive input. In the passive condition, information about rotation carried by efference copy was minimized and vestibular input maximized by passively oscillating the participant’s body to the left and right at varying desired velocities with no neck movement, whereas in the active condition, the participant actively oscillated their own head-on-body at the same practiced desired velocities in order to measure for vestibular and proprioceptive influence. During the counter condition, the efferent proprioceptive input from the neck was isolated and vestibular influence minimized by the participant by actively using their neck muscles to counter-rotate their heads on their bodies while their bodies were mechanically oscillated, such that their head-in-space motion was minimized. In the dynastatic condition, participants kept both their head and body stationary in space, eliminating vestibular and proprioceptive input. In both the counter and dynastatic conditions (unlike the static condition), the same sound stimuli used in the passive and active conditions were presented as if their head was in motion. In order to eliminate visual input, participants were blind-folded and performed the localization tasks in a darkened sound-proof room. Following each trial in each experimental condition, participants indicated the apparent front or back location of the stimulus via button press.
In addition to the aforementioned dynamic front/back sound localization tests, Experiment 2 consisted of two auditory-only experimental conditions (2a and 2b) of left-to-right/right-to-left (L/R) sound source motion discrimination tests in order to measure auditory sensitivity to the dynamic cues generated in Experiment 1.

In Experiment 2a, participants were presented with the same HRTF-filtered low-frequency bursts as in the dynamic sound localization conditions in Experiment 1, with the same dynamic cues generated during head movement. Participants maintained a stationary head and body position and were instructed to discriminate between leftward and rightward motion of the auditory targets.

In Experiment 2b, in order to determine whether the temporal dynamics of dynamic cue processing are particular to the integration of the auditory and vestibular systems, we measured in an equivalent auditory-only task like Experiment 2a, where the stimuli were presented with only varying ITD.
2.2 Participants

Seven normally hearing listeners (4 females, 3 males, age range = 25-35, mean age = 28) participated in Experiment 1 and six of those listeners (4 females, 2 males, age range = 25-35, mean age = 28) participated in Experiment 2, as one participant withdrew from the latter part of the study. They gave informed consent according to the ethical standards of Western’s Research Ethics Boards. Participants were all graduate students at Western University where this research was conducted. Participants received no feedback regarding their performance in any of the experiments. All participants were compensated $15/hour for their participation.

In order to determine an appropriate participant sample size for the present experiment, data that had previously been collected using similar procedures to determine the Minimum Head Movement Angle (MHMA) required for accurate front/rear localization of low-frequency (0.5-1 kHz) noise stimuli as a function of head velocity (50, 100, 200, or 400 °/s) (Macpherson, 2008) were used. Inter-velocity effect sizes in that study ranged from 1.13 to 1.90 with a mean of 1.56. A power analysis was conducted using G*Power software (Erdfelder, 1996). Input variables were: Type I error, 0.05, Type II error 0.9, Effect size, 1.5, and yielded a required sample size of 6 participants. In the present study we compared MHMAs between passive, voluntary, and conflicting-cue rotation conditions. As the present study uses new test paradigms, we do not have effect-size estimates, but we expect similar inter-velocity effect sizes in this study, and by hypothesis even bigger effect sizes between active/passive and counter. We therefore enrolled 7 participants to preserve statistical power.

2.2.1 General Inclusion Criteria

Participants had to be 18-35 years of age, and to be able to understand instructions for the localization and discrimination tasks involved. All had to agree to pure-tone audiometric testing and to demonstrate normal hearing (defined as thresholds of 20 dB HL or less at standard audiometric octave frequencies between 125 and 8000 Hz) as well as to perform satisfactorily in a preliminary test of sound localization behaviour prior to testing.
2.2.2 General Exclusion Criteria
Participants were ineligible to participate in the study if they demonstrated any of the following issues:

1. History of vestibular/balance disorders or dizziness because the participant might be at risk during sound localization tests that involve head movement;
2. Lack of neck and/or back flexibility that might limit the ability of the participant to orient their head towards a sound source during sound localization tests;
3. Reporting of active external ear canal pathology and/or active middle ear dysfunction;
4. Current use of ototoxic medication;
5. Difficulty standing and/or sitting for extended periods of time because sound localization tests were performed in these positions and were two or more hours in duration.

2.3 Apparatus and Materials
Experiment 1a (free-field stimulus presentation) was performed in the large hemi-anechoic chamber at the National Centre for Audiology (NCA) at Western University. Participants were positioned in the center of a 16 loudspeaker array and had an electromagnetic tracker (Polhemus FASTRAK) mounted on their head to track the position of their head-in-space in real-time. Responses regarding the apparent location of the stimuli were recorded via button press on a hand-held response device (as well as for Experiment 1b, 2a).

Experiment 1b (virtual auditory space presentation) was performed in a darkened sound-proof room at the NCA where participants were positioned in the center of the room (1 m away from walls) and were seated on a motorized oscillatory platform, which oscillated sinusoidally 45° to the left and right about the vertical axis.

The virtual static and dynamic auditory stimuli used were presented by means of occluding ER-2 insert earphones using individualized head-related transfer functions (HRTFs) that were pre-recorded for various positions around the participant. Real-time interpolation between measured HRTF locations was performed by a Tucker-Davis
Devices RX6 processor. Target presentation over insert earphones was necessary to simulate the motion of the sound source relative to the head in the counter and dynastatic conditions as described further below (Section 2.5.3.1). In addition, the insert earphones partially attenuated noise from the motor of the oscillatory platform. Motor noise was further attenuated by wearing earmuffs (Leightning L3), with a noise reduction rating of 30 dB, over the insert earphones. This attenuated the motor noise to a very quiet level that was much lower than that of the target stimuli, which were clearly audible. Head orientation was tracked continuously in real-time and the stimuli were subsequently presented to the listener as a function of the angle of head orientation tracked by the electromagnetic tracker in both passive and active (and dynastatic) conditions. Similarly in the counter condition, head-on-body angle was calculated as the head moved in the opposite direction in response to the body orientation.

Experiment 2 took place in the same darkened sound-proof room at the NCA. Stimuli were presented by means insert or circumaural headphones (ER-2 or Sennheiser HD 280 PRO, respectively) and a button response device or computer keyboard was used to indicate the apparent direction of motion of the stimuli that moved either left-to-right or right-to-left.

2.4 Stimuli

Sound stimuli for all experimental conditions in the study were bursts of low-frequency noises (0.5-1 kHz) with 5-ms raised cosine onset and offset ramps and were generated using MATLAB 7.10.0 (R2010a, MathWorks Inc., C.A.). Low-frequency stimuli were used because it has been demonstrated that dynamic cues appear to be more salient for low-frequency stimuli and that such stimuli typically cannot be localized accurately without head motion, which forces participants to use the dynamic cues during localization (Macpherson, 2011). Basic screening tests of free-field localization for localization ability (Experiment 1a) used wideband stimuli (0.5-16 kHz), however. Bursts were presented over occluding insert earphones (ER-2) using individualized, head-tracked (Polhemus FASTRAK) HRTF-filtering to reflect head motion in Experiment 1b, whereas bursts were presented over headphones (Sennheiser HD 280 PRO) in Experiment 2 (See Section 2.6 for more detail). In Experiment 1 and 2a, levels were
roved trial-by-trial (± 5 dB) at a mean level of 70 dB SPL. Stimuli were presented from 6 total positions located at azimuths of 0° and ±22.5° (front) and 180° and ±157.5° (back). The bursts were gated by listener head-in-space and/or head-on-body position.

### 2.4.1 Individualized Head-Related Transfer Functions (HRTFs)

HRTF measurements (Fig. 7) were made inside a large hemi-anechoic chamber. For each listener, miniature omni-directional electret microphones (Knowles FG3629) were inserted facing outwards in foam earplugs (ER1-14B) and were inserted flush with the ear canal entrances (in-ear measurement). During the measurement, the listener stood in the middle of an adjustable platform that positioned his or her head within the center at a height equivalent to an array of 16 loudspeakers (1.45 m radius, Tannoy i5 AW) spaced in 22.5° intervals around the listener’s head. Foam was placed on the floor around the platform to attenuate any reflections. Impulse responses were measured using a 2047-point maximum-length sequence signal (Rife & Vanderkooy, 1989) presented around the listener’s head by each speaker one after another starting at 0° at a sampling rate of 48828 Hz by a Tucker Davis Technologies RX6 real time processor and QSC CX168 power amplifiers and were measured by the left and right microphones each ear canal entrance. Listeners were equipped with a head-mounted LED and electromagnetic tracker (Polhemus FASTRAK) and were instructed to aim the light at a target position at 0° azimuth in order to minimize head motion during the measurement, while the tracker served to monitor head position. Each individual HRTF measurements was divided by its respective loudspeaker transfer function that was previously measured with a reference microphone that was placed in the center of the array of loudspeakers to equalize the frequency domain in order to correct for individual loudspeaker characteristics (Bruel & Kjaer 4189). In order to remove any residual reflections, the impulse responses were windowed in post-processing.

Headphone-to-microphone transfer functions were measured immediately after the in-ear measurement using the same 2047-point maximum-length sequence signal over a pair of Beyerdynamic 990-Pro circumaural headphones that were placed over the pinnae of both left and right ears without removing the electret microphones. This equalization calibration method of the in-ear measurements (Moller, Hammershoi, & Sorensen, 1995)
was conducted to ensure that the appropriate HRTFs were present at the tympanic membrane during the presentation of stimuli over headphones even though the HRTFs were measured with blocked ear canals. An average of three measurements was taken with repositioned placement of the headphones over the pinnae in order to account for varying positions of headphone placement. Measured HRTFs were divided by this headphone transfer function.

Figure 7. Example of a head-related transfer function measured for the left (blue) and right (red) ears for a sound source 90° to the right of a typical listener.
2.5 Sound Localization Experimental Conditions

2.5.1 General Outline

A flowchart describing the sequences of test procedures is outlined earlier in Figure 6. Participants made multiple visits to the NCA, where a portion of the testing took place in the large-hemi anechoic chamber while the remainder of the testing took place in a smaller sound-proof booth. The participants were assessed over approximately 10 visits lasting approximately 1.5-2 hours each and progressed through the required tests at their own pace, whereby testing did not follow a strict session-by-session schedule and those progressing quickly completed testing in fewer sessions.

During the first visit, the tasks involved in the study were explained to the participant and any questions pertaining to the study were answered by the experimenter. In order to assess the eligibility of the participant, pure-tone audiometry was administered, information about age, sex, handedness, and any history of hearing, vision, balance, or flexibility problems were obtained, and a preliminary test of free-field static sound localization behavior using wideband and low-frequency auditory targets was conducted. In the next session or two, eligible participants performed the active sound localization test (see Section 2.5.3.1) at head-turn velocities of 25°/s, 50°/s, and 100°/s in free-field conditions with low-frequency stimuli.

Participants performed all conditions of Experiment 1b (static, passive, active, and dynastatic sound localization conditions) all at 25°/s, 50°/s, and 100°/s, as well as the counter condition at 50°/s in the darkened sound-proof booth (see Section 2.5.3.1) for the following four to six sessions. All conditions were administered in a randomized order to avoid sequence and learning effects. Randomization was done by listing all the conditions and using the Excel spreadsheet randomization function for each participant.

Participants were later invited back to participate in Experiment 2, which was divided into two experimental conditions, in each of which they were instructed to perform a lateral source motion discrimination task. The order of conditions was randomized in order to avoid sequence effects.
2.5.2 Experiment 1a: Free-field Sound Localization Tests

Participants were familiarized with each of the sound localization tasks prior to data collection. Sound localization tests were performed by all participants under two head movement conditions in free-field in the anechoic chamber: i) static (no head movement, wideband [0.5-16 kHz] and low-frequency [0.5-1 kHz] stimuli, 250 ms in duration); and ii) active (active head rotation, low-frequency stimuli). Localization screening tests were performed in free-field for two reasons: 1) to conduct initial testing in a more natural listening condition, and 2) to provide a means to verify the virtual auditory space presentation method (Experiment 1b) to ensure that the HRTF’s representing head motion were behaving accurately.

Static: In the static condition, which was a part of the participant screening tasks, participants were instructed to fixate their head and body at 0° azimuth during stimulus presentation, then to orient their head to the apparent sound source and press two buttons to register the response, in which this final reading of head orientation constituted the participant’s response. All stimuli in the static condition were presented from speakers in the circular array (Section 2.4.1) at positions ± 22.5°, 67.5°, 112.5°, 157.5°, 0°, and 180°. This was performed only as a basic screening for localization ability that determined if potential participants were eligible to participate in the study. Eligible participants were expected to localize accurately for wideband stimuli, while producing many back-to-front reversals for the low-frequency stimuli to continue their participation in the study, as it has previously been demonstrated that dynamic cues appear to be more salient for low-frequency stimuli and that such stimuli typically cannot be localized accurately without head motion (Macpherson, 2008). Three test blocks were performed for each of the static conditions, each consisting of 48 trials.

Active: In the active condition, stimuli were presented while the listeners continuously oscillated his or her own head from side to side at a practiced velocity (Fig. 14). The condition was performed once in the free-field setting and another time in the virtual setting to directly compare localization performance in order to account for potential discrepancies between the two settings.
In order to initiate a trial, the participant oriented his or her head at 0° azimuth, which was recorded as the reference position by the head-tracker. The participant then actively oscillated his or her own head-on-body via neck motion to the left and right (±45°) at three specified range of desired velocities of 25±10°/s, 50±15°/s, 100±25°/s (the ± values represent the acceptable deviation from the desired velocity). The velocity was computed as an average value recorded by the head tracker over the central 50° portion of each head rotation during which a stimulus was presented. Movement by the oscillatory platform and/or participant in both Experiments 1a and 1b were required to stay within this velocity range for the trial to be retained for analysis (Fig. 13, 16, 19); trials in which the listener’s head and body deviated from the desired velocity were repeated at the end of the block. In order to produce average velocities of 25°/s, 50°/s, and 100°/s over the 50° recorded portion, oscillation frequencies of 0.0938 Hz, 0.1875 Hz, and 0.375 Hz were required (Fig. 8). The participant’s body faced 0° azimuth as the head rotated in order to measure for combined vestibular (head movement) and proprioceptive (neck movement) influence during the active head movement.

When the head passed through a specified stimulus spatial window of width 2.6°, 5°, 10°, 20°, or 40° (as represented by the pink slopes in Fig. 8) that was centered at 0° azimuth (increasing window width provided access to larger interaural cues), the stimulus was gated on and off by such listener head-in-space position. Wider windows allowed for more onset-to-offset cue change and longer stimulus durations, and were therefore expected to lead to more accurate localization. Faster head movement velocities necessarily reduced stimulus duration for a given spatial window width. Participants then indicated the perceived front or back location of the stimulus via button press following each trial. After a front/back response was made, the head and/or body had to oscillate fully to the left or right, (as represented by R-to-L/L-to-R in Fig. 8) in order for the next trial to commence. Participants then made their front/back response.

The stimuli were presented from six of sixteen speakers at positions ±22.5, ±157.5°, 0°, and 180°. These speakers were selected in pairs, as they can be ambiguous in the front and back dimension. Six sound source locations, five window widths, two oscillatory directions, and two blocks of three repetitions for each velocity accounted for 360 trials.
that the participants completed. Participants had to complete 7 out of 10 accurate head rotation practice trials before the main experimental session in order to familiarize them with the task and ensure they were actively rotating their head at the desired velocities. Auditory feedback was provided if the head velocity over the central 50° portion of the sweep was outside the specified acceptable range in both practice trials and test trials. The entire room was kept completely dark in order to eliminate visual input.
Figure 8. Schematic diagram of head and/or body oscillatory behaviour as a function of time. The y-axis plots the left and right oscillatory movement continuously being tracked over a $90^\circ$ range ($\pm 45^\circ$). The two dashed horizontal lines represent the range during the oscillation in which the movement was actually being recorded, which was a range of $50^\circ$. In order to produce average velocities of $25^\circ/s$, $50^\circ/s$, and $100^\circ/s$ over the $50^\circ$ recorded portion, oscillation frequencies of 0.0938 Hz, 0.1875 Hz, and 0.375 Hz were required.
2.5.3 Experiment 1b: Virtual Auditory Space Dynamic Sound Localization Tests

In the virtual setting in the darkened sound-proof booth, there were five experimental conditions that all used low-frequency stimuli: i) static (no head or body movement); ii) passive (involuntary head and body rotation); iii) active (voluntary head rotation); iv) counter (head-on-body rotation, but no head-in-space rotation); and v) dynastic (no head or body movement but listeners listened to sound stimuli as if there were head movement, as with the counter condition) (See Table 1 for general overview of conditions). After each trial in each condition, participants indicated the apparent front or back location of the sound stimulus by pressing one button for any sound presented in the anterior hemisphere (“front” response) or another button for sounds in the posterior hemisphere (“back” response). Each participant completed 6 testing blocks for a total of 360 trials in each condition. After each block of trials, the participant was then cued to return to the starting position by three brief noise bursts. Breaks were taken as needed during testing. All head movement conditions were presented in a random order to avoid sequence effects. Participants were blindfolded in all conditions in order to eliminate visual input during the tasks.

The stimuli in all experimental conditions (Section 2.4) were 0.5-1 kHz bands of low-frequency, head-tracked HRTF-filtered noise (Section 2.4.1) and their duration were dependent on the head movement condition (Section 2.5.3.1).
<table>
<thead>
<tr>
<th>Condition</th>
<th>Procedural Details</th>
<th>Head-Motion Cues</th>
<th>Stimulus Gating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Static</td>
<td>Head and body orientation maintained at 0° azimuth</td>
<td>None</td>
<td>250-ms temporal window</td>
</tr>
<tr>
<td>Passive</td>
<td>Head held straight relative to body.</td>
<td>Vestibular</td>
<td>Head-in-space orientation window.</td>
</tr>
<tr>
<td></td>
<td>Head and body immobilized with foam packing inside enclosure to minimize neck movement.</td>
<td></td>
<td>Stimuli were gated on and off the head orientation entered and exited a selected spatial window [2.6 - 40° wide] centered at 0° azimuth.</td>
</tr>
<tr>
<td></td>
<td>Head and body oscillated together passively by the motorized platform.</td>
<td></td>
<td>Spatial window is represented by the pink area in Figure 17.</td>
</tr>
<tr>
<td>Active</td>
<td>Head actively oscillated via neck motion while body faced 0° azimuth.</td>
<td>Vestibular and Proprioceptive</td>
<td>Head-in-space orientation window, as for passive.</td>
</tr>
<tr>
<td>Counter</td>
<td>Active counter of head via neck motion while body was oscillated by the motorized platform.</td>
<td>Proprioceptive</td>
<td>Head-on-body orientation window.</td>
</tr>
<tr>
<td></td>
<td>A tactile reference point on the back of the head allowed minimization of head-in-space motion (and therefore vestibular information).</td>
<td></td>
<td>Stimuli were the same as those that would have occurred if the head had rotated and the body remained stationary as in the active head movement condition.</td>
</tr>
<tr>
<td></td>
<td>Neck motion provided proprioceptive input correlated with the dynamic auditory cues.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dynastatic</td>
<td>Head and body orientation maintained at 0° azimuth</td>
<td>None</td>
<td>Head-in-space orientation window, as for passive and active.</td>
</tr>
</tbody>
</table>

**Table 1.** Summary of the dynamic sound localization conditions (Experiment 1b).
2.5.3.1 Conditions (Static, passive, active, counter, dynastatic)

Static: The participant fixated his/her head and body at 0° azimuth to initiate a block of trials, and his/her head position was recorded by the head-tracker (Fig. 9). Deviation from this starting position did not allow the participant to progress onto the next trial. In each trial, a 250-ms burst of low-frequency noise was played at one of the 6 azimuthal positions (0°/180°, ±22.5°, and ±157.5°) (Fig. 10). Participants then indicated the apparent front or back location of the stimulus via button press. The button press was used instead of the noise-pointing technique used in Experiment 1a because 1) it was difficult for the participants to move their head and/or body while seated on the rotary platform throughout all of the tasks, and therefore 2) the participants could only feasibly perform a front/back discrimination task, not an absolute location judgment task. Vestibular and proprioceptive motion information was eliminated by keeping the head and body stationary in one position centered at 0° azimuth during the entire localization task.

![Figure 9](image)

**Figure 9.** Static: Illustration demonstrating the procedural paradigm. Participant was instructed to maintain their head and body fixated towards 0° throughout the entire task. Black box #1 represents the electromagnetic transmitter that emits a magnetic field. The red sensor on top of the participant’s ear muff uses the transmitter to record the head position of the participant in space.
**Figure 10.** Static: An aerial view of the participant during the static condition. 250-ms bursts of low-frequency noise were played at one of the 6 virtual target locations over headphones as the participant fixated their head and body centered at $0^\circ$. 
Passive: For this condition, the velocity of the head (as well as for the active condition) and body movement was required to stay within a specified range of desired velocities (25±10°/s, 50±15°/s, 100±25°/s). Both head and body were immobilized with foam inside a wooden enclosure to minimize neck movement, while the legs were strapped together to prevent further potential body movement (Fig. 11). An ideal difference of 0° between head-in-space and body-in-space position was aimed for.

In order to begin a block of trials, the participant had to orient their head and body at 0° azimuth, and this was recorded as the reference position by the head-tracker. The motorized platform was then turned on by the experimenter, which allowed the head and body of the participant to oscillate together passively to the left and right over a 90° range (±45°) at one of the three specified average velocities. Thus, setting the oscillatory platform to the correct desired velocity in order to obtain the desired average velocity of both the head and body movement was the responsibility of the experimenter, not of the participant.

Following each stimulus presentation, participants indicated the apparent front or back location of the stimulus via button press. The duration of the stimulus was dependent on the velocity of the movement and the spatial window width selected on that trial. In both the passive and active conditions, head motion was tracked in real-time to reflect head motion. The appropriate HRTF filter was applied to the stimulus at the corresponding head position of the participant in order to preserve the spatial information of the respective stimulus location. By moving the head straight relative to the body with no neck movement during stimulus presentation, information about rotation carried by efference copy was minimized and vestibular input maximized.
**Figure 11.** Passive: Illustration demonstrating the procedural paradigm. Participant held head straight relative to body immobilized by foam packaging within a wooden enclosure, while their head and body oscillated passively together. Dynamic stimuli were presented over headphones in real-time using individualized HRTF’s that were pre-recorded for various positions around the subject, as a function of the angle of head orientation tracked by an electromagnetic tracker. Black box #1 represents the electromagnetic transmitter that emitted a magnetic field used by the black box #2 and the red box (on the participant’s head), which represent the body-in-space sensor and head-in-space sensor, respectively. The difference between head and body position was calculated to determine how accurately they were aligned throughout the task.
Figure 12. Passive: An aerial view of the participant during the passive condition. The sound stimuli were gated on and off as the participant’s head and body oscillated through the specified stimulus window widths in the passive condition (as represented by the pink area; 2.6 – 40°).

Figure 13. Passive: Head tracker signals, and velocity and error computation. The image above illustrates an example of what the head trackers were measuring in more detail (See Section 3.2.2 for actual average movement and error values). Head-in-space position was measured, as represented by the blue line, while the magenta line represents the measured position of the body in space. These positions were recorded over a 50° range. The green line represents the “error”, which is the difference between the head and body position, as an ideal difference of 0° was aimed for.
**Active:** In order to initiate a block of trials, the participant oriented his/her head at 0° azimuth, which was recorded as the reference position by the head-tracker. The participant then actively oscillated their own head on body via neck motion to the left and right (±45°) at the three specified average velocities while the body faced 0° azimuth (Fig. 14) in order to measure for combined vestibular and proprioceptive influence. Participants had to complete seven accurate practice trials accurately before moving onto the actual experimental condition in order to familiarize them with the desired velocities. Auditory feedback was provided if the velocity was not acceptable, and in such cases the trial was repeated at the end of the block, similarly to Experiment 1a.

Similarly to the passive condition, head motion was tracked continuously and the stimuli was gated on and off by listener head-in-space position as the head passed through a specified stimulus spatial window width of 2.6°-40° that was centered at 0°. Participants indicated the perceived front or back location of the stimulus via button press following each trial.
Figure 14. Active: Illustration demonstrating the procedural paradigm. The participant actively oscillated their own head on body via neck motion to the left and right. The head-tracker (red box) measured the head position and velocity of the head movement in space.
Figure 15. Active: An aerial view of the participant during the active condition. The sound stimuli were gated on and off as the participant’s head oscillated through the specified stimulus window widths (as represented by the pink area; 2.6 – 40°).

Figure 16. Active: Head tracker signal and velocity computation. Illustration of a head sweep done by the participant’s head-in-space over a 50° range, as represented by the blue line.
Counter: The reference position of the head was registered again at 0° azimuth by the head-tracker. Participants were then instructed to actively counter-rotate their head via neck motion to keep it centered at 0° azimuth while the body was oscillated by the motorized oscillatory platform (Fig. 17) in order to provide head-motion information only via efferent neck proprioceptive input. The oscillation was conducted at only one desired velocity of 50°/s, as we hypothesized that this would be sufficient to demonstrate a difference in performance compared to the conditions that generated vestibular input and that faster velocities would be too difficult for the participants to perform.

Two tactile reference points on the back of the head allowed the listener to minimize head-in-space motion (and therefore vestibular information) while providing proprioceptive input from the neck motion that correlated with the dynamic auditory cues.

The sound stimuli were those that would have occurred if the head had rotated like in the passive and active head movement conditions described above. Source motion was driven by head-on-body angle, where the difference between the two head tracker signals were obtained (Fig. 17, 18).
Figure 17. Counter: Illustration demonstrating the procedural paradigm. Participants actively counter-rotated their head-on-body via neck motion centered at 0° azimuth while their body was oscillated by the motorized oscillatory platform. Two tactile reference points were provided on the back of the head to help the participant to minimize movement of their head-in-space. Black box #1 (electromagnetic transmitter) set up the reference field and the red box and black box #2 measured the head-on-body angle.
**Figure 18.** Counter: An aerial view of the participant during the counter condition. The sound stimuli were gated on and off as the participant’s body oscillated through the specified stimulus window widths (as represented by the pink area; 2.6 – 40°).

**Figure 19.** Counter: Head tracker signals, and velocity and error computation. Illustration of the measured head and body position in space. The magenta line represents the position of the body in space, as the oscillatory platform moved their body. The green line represents the head-on-body angle as the body moved in the opposite direction in response to the head orientation that was used to generate dynamic localization stimuli. The blue line represents the “error”, which is the position of the head in space and how much it deviated from 0° azimuth, as it was required to be fixated.
**Dynastatic:** In this condition, the procedure for the task was similar to the static condition; the participant oriented both their head and body centered at 0° azimuth for the entire duration of the task as they responded with the apparent perceived front or back location of the stimuli. However, instead of static bursts of 250-ms low-frequency noise, the stimuli were the same as those generated in the passive, active, and counter conditions (Fig. 21), in order explore sensitivity to dynamic binaural difference cues upon which the front/back localization was based with no vestibular or proprioceptive influence. The position of the oscillating platform was measured, which represented head movement, just in order to generate the dynamic stimuli (Fig. 20). This condition was intended to see whether participants could extract spatial information from the dynamic auditory signal in the absence of head-motion cues that would aid in their interpretation.
Figure 20. Dynastatic: Illustration demonstrating the procedural paradigm. The participant was instructed to fixate their head and body position centered at 0°. In order to generate the same dynamic stimuli as in the head and/or body rotation conditions, the oscillatory platform oscillated to the left and right and the position of the platform was measured as a function of the angle of platform (equivalent to head angle in passive/active conditions) orientation.
Figure 21. Dynastatic: An aerial view of the participant during the dynastatic condition. The sound stimuli were gated on and off as the oscillatory platform oscillated through the specified stimulus window widths in the passive condition (as represented by the pink area; 2.6 – 40°) while the participant remained stationary centered at 0°.
2.6 Left-to-right/Right-to-left Sound Source Motion Discrimination Tasks

Experiment 2 consisted of two auditory-only experiments (2a: L/R-Dynastatic and 2b: L/R-ITD). Participants were instructed to discriminate the left-to-right/right-to-left direction of source motion as they kept their head and body stationary in space in order to assess whether the temporal dynamics of dynamic sound localization cue processing are particular to head movement or auditory processing of acoustic cues.

Stimuli were low-frequency noise bursts of 0.5-1 kHz with 5-ms raised cosine onset and offset ramps, which were presented over headphones (Sennheiser HD 280 PRO) in the L/R-ITD condition and ER-2 insert earphones during the L/R-Dynastatic condition. Participants were blind-folded to eliminate visual input. Testing took place in a darkened sound-proof room. There were two blocks of 60 trials in each condition and velocity. Conditions were randomized for each participant to avoid sequence effects, using the Excel randomization function.

2.6.1 Experimental Conditions (L/R-Dynastatic and L/R-ITD)

L/R-Dynastatic: This auditory-only task required the participants to discriminate the left or right direction of motion of the same low-frequency noise that was presented in the head rotation conditions (passive, active, counter, and dynastatic) in the dynamic sound localization experiment (Section 2.5.3.1), where the low-frequency sound stimuli were those that would have occurred if the head had rotated in space. Participants responded on the same button-press response device as used in the dynamic sound localization experiments.

L/R-ITD: This discrimination task required the participants to discriminate the left or right direction of motion of low-frequency noise (applied to both left and right channels) that monotonically increased or decreased in ITD, where the magnitude of ITD change over the duration of each stimulus was 25 μs, 50 μs, 100 μs, 200 μs, or 400 μs and the rate of ITD change was ±250, ±500, ±1000, or ±2000 μs/s (equivalent to 25, 50, 100, or 200°/s). For all the trials, a rove of 250-μs was applied to the starting ITD in order to prevent the participant from using the start or end point being used as a direction cue for
the perceived motion, and was intended to require the participant to pay attention to the
direction of motion. These ITD-change values approximate those that would be produced
by head rotation in the aforementioned head rotation dynamic localization tasks, as ITD
naturally varies by about 10 μs/deg across the midline for an average human head size.
Participants reported the perceived left or right directions on a computer keyboard.
Chapter 3

3 Results

The data collected in Experiments 1 and 2 consisted of absolute judgments of front/back target location in the static free-field localization screening task (Experiment 1a), front/back responses during dynamic sound localization (Experiment 1b), head movement tracks (Experiment 1b), and left-to-right/right-to-left sound source motion discrimination responses (Experiment 2). Using these data, we sought to answer the following questions:

**Experiment 1a:** Could participants localize accurately in the static free-field condition using wideband and low-frequency stimuli?

**Experiment 1b:**

1. What were the participants’ head and/or body movement behaviour during the dynamic localization tasks? In other words, were they accurately doing the tasks as instructed?
2. How similar is front/back localization performance in free-field vs. virtual auditory space settings?
3. How did front/back localization performance differ between the dynamic localization conditions?
4. How did performance compare between the passive and active conditions?
5. Does velocity of head and/or body movement affect front/back localization accuracy? If so, is this suggestive of auditory-vestibular interactions?

**Experiment 2a/b:**

1. Are the temporal dynamics of dynamic cue processing particular to auditory-vestibular integration? Or can front/back localization performance be explained just based on sensitivity to acoustic cues?
2. Can front/back localization performance be explained based on the sensitivity to a single acoustic cue, namely ITD?

In the following sections, front/back localization and L/R discrimination performance data for each individual participant are presented first as a function of stimulus window
width, followed by the mean performance data as a function of stimulus window width and stimulus duration, and subsequent analyses are presented to examine the outlined questions above for both Experiments 1 and 2.

### 3.1 Screening for Basic Sound Localization Ability

In order to assess the basic sound localization ability of each listener in the free-field static condition, response azimuth was plotted versus target azimuth for low frequency and wideband sound stimuli. In such a plot, veridical responses lie on the positive diagonal and front/back reversals lie near the negative diagonal axis. Data analysis (only for screening purposes) involved computing “small-error” responses, which were defined as those falling within 30° of the true auditory target location (shaded region, Fig. 22). The proportion of responses yielding “small” errors was computed as a simple measure of performance. The majority of larger (>30 degrees) errors were front-to-back (upper left quadrant) or back-to-front (lower right quadrant) reversals. Fig. 22 is an example of a typical error rate analysis showing front/back localization errors used only for localization screening purposes in Experiment 1a. Eligible participants were expected to localize accurately for wideband stimuli and to produce many front/back reversals for the low-frequency stimuli to progress through the study.
Figure 22. Example error rate analysis. Target azimuth is plotted on the x-axis while the response azimuth lies on the y-axis. The filled red circles plotted on the positive diagonal line represent the correct responses, whereas the unfilled circles presented on the negative diagonal line represent front/back confusions.
Target-response plots for one typical listener (L092) in the static condition presented with low frequency and wideband stimuli are shown below (Fig 23). Wideband stimuli were localized accurately but all of the responses for the low-frequency stimuli fell in the front hemisphere, producing many front/back reversals.

Figure 23. Target-response plot for one typical listener (L092) in the static condition of Experiment 1a (freefield) for low and wideband sound stimuli.

The table below shows localization performance for each individual participant during static localization when wideband and low-frequency were presented. As expected, participants performed well for wideband noise and poorly for low-frequency noise in the absence of head movement. All participants that were screened were kept in the study although L093 performed less well than the others for wideband stimuli, scoring just above 75% correct, which may reflect a generally poor localization ability and may explain why their performance in the remainder of the study (Experiment 1b, 2) was markedly inferior to other subjects’.
<table>
<thead>
<tr>
<th>Subject ID</th>
<th>L061</th>
<th>L065</th>
<th>L087</th>
<th>L089</th>
<th>L090</th>
<th>L092</th>
<th>L093</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small Error (&lt;30°)</td>
<td>Wideband</td>
<td>99.31%</td>
<td>100%</td>
<td>96.06%</td>
<td>100%</td>
<td>97.22%</td>
<td>95.14%</td>
</tr>
<tr>
<td>Low-frequency</td>
<td>65.97%</td>
<td>68.75%</td>
<td>67.36%</td>
<td>68.06%</td>
<td>62.50%</td>
<td>56.25%</td>
<td>54.86%</td>
</tr>
</tbody>
</table>

**Table 2.** The percentage of responses yielding “small” errors (azimuth error <30 degrees) in static free-field localization conditions.

### 3.2 Experiment 1a and 1b: Dynamic Front/Back Sound Localization

#### 3.2.1 Analysis Methods

All analyses of variance (ANOVA) were performed using the Statistical Package for the Social Sciences (SPSS version 19; IBM Corporation) and used the Greenhouse-Geisser correction for all repeated measures designs to protect against violations of sphericity (Max & Onghena, 1999). The Bonferroni correction was applied to control Type 1 errors for multiple comparisons (Bland, 1995). Additional analyses used linear regression and curve-fitting functions from the MATLAB Statistics Toolbox.

#### 3.2.2 Head Movement Behaviour during Dynamic Localization Tasks

The tables found below (Tables 3-12) demonstrate the accuracy of the head and/or body movement by the participant or the oscillatory platform in the dynamic localization conditions (passive, active, counter, and dynastatic) for Experiment 1b. Head and/or body movement was continuously tracked and was recorded over the central 50° portion of each head rotation during which a stimulus was presented in order to determine whether the participants and/or oscillatory platform were performing the tasks accurately as instructed (Section 2.5.2; Fig. 8). Overall, participants’ performances were relatively accurate and any movements that deviated from a previously set range of permitted movement were discarded and the participant was required to repeat the same trial at the end of the block (as mentioned in Section 2.5.2).
Passive: In the passive condition, participants were instructed to try to maintain their head and body as still as possible while the oscillatory platform rotated them to the left and right in order to maintain a theoretical difference of 0° between the head and body position during the rotation to prevent proprioceptive input from the neck. The values below demonstrate, across trials, the participant’s mean head velocity with standard deviation (SD), difference between their head and body position (“error” because these values represent deviations from the 0° difference in head and body position that was aimed for) with SD that was recorded during the entire 50° rotation averaged across stimulus spatial window widths, as well as the “error” as a function of varying spatial window width (2.6°, 5°, 10°, 20°, 40°) with SD (Fig. 13).

When the participants were being rotated passively at 25°/s, their head on body moved at an average of 23.51±0.88°/s, with a mean head-to-body position deviation of 5.19±0.94° averaged over the 50° rotation and across stimulus window widths. However, it is important to also observe the behavior during the window widths in which the stimulus is actually being presented for the participant to localize since it is of interest to determine the head/body behavior during the period in which localization was required. The deviation of head on body position was almost negligible, where the average difference in angle was about 0.07±0.18°, 0.12±0.3°, 0.23±0.49°, 0.43±0.89°, and 0.86±1.74° for each individual window width of 2.6°, 5°, 10°, 20°, and 40°, respectively.

During the 50°/s passive rotation of the head and body, participants were being rotated at an average of 48.77±1.92°/s by the oscillatory platform. The average head-to-body deviation (or “error”) averaged across window widths was about 5.16±1.07°, while they deviated at 0.10±0.3°, 0.16±0.37°, 0.24±0.55°, 0.44±0.9°, and 0.85±1.69°, respectively for each window width.

Participants on average rotated at about 102.63±6.19°/s during the 100°/s condition with a mean head-to-body deviation of about 4.50 ±1.6°. Again, the deviations as a function of window width were almost negligible with differences of 0.27±0.66°, 0.30±0.68°, 0.31±0.78°, 0.46±1.12°, 0.79±1.73°, respectively. As these deviations were almost
negligible during stimulus presentation, it is conceivable that proprioceptive input was also insignificant.
<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°/s)</th>
<th>Error ± SD (°)</th>
<th>Error (Window widths) ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passive 25 °/s</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>21.38±1.15</td>
<td>9.92±2.22</td>
<td>0.11 ±0.28</td>
</tr>
<tr>
<td>L065</td>
<td>22.21±1.65</td>
<td>6.13±0.90</td>
<td>0.09 ±0.22</td>
</tr>
<tr>
<td>L087</td>
<td>23.62±0.46</td>
<td>6.15±0.78</td>
<td>0.075 ±0.18</td>
</tr>
<tr>
<td>L089</td>
<td>25.18±0.35</td>
<td>1.80±0.34</td>
<td>0.055 ±0.13</td>
</tr>
<tr>
<td>L090</td>
<td>24.17±0.78</td>
<td>3.13±1.06</td>
<td>0.056 ±0.14</td>
</tr>
<tr>
<td>L092</td>
<td>22.52±1.33</td>
<td>7.18±0.73</td>
<td>0.07 ±0.17</td>
</tr>
<tr>
<td>L093</td>
<td>25.46±0.45</td>
<td>2.04±0.53</td>
<td>0.05 ±0.13</td>
</tr>
<tr>
<td>Mean</td>
<td>23.51±0.88</td>
<td>5.19±0.94</td>
<td>0.07±0.18</td>
</tr>
</tbody>
</table>

**Table 3.** Head/body behaviour for the passive condition at 25°/s.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°/s)</th>
<th>Error ± SD (°)</th>
<th>Error (Window widths) ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passive 50 °/s</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>44.84±2.12</td>
<td>9.18±1.46</td>
<td>0.14 ±0.34</td>
</tr>
<tr>
<td>L065</td>
<td>47.77±1.93</td>
<td>5.69±1.63</td>
<td>0.08 ±0.18</td>
</tr>
<tr>
<td>L087</td>
<td>46.80±1.77</td>
<td>6.59±0.91</td>
<td>0.09 ±0.26</td>
</tr>
<tr>
<td>L089</td>
<td>53.43±1.96</td>
<td>1.85±0.75</td>
<td>0.15 ±0.35</td>
</tr>
<tr>
<td>L090</td>
<td>49.82±1.82</td>
<td>3.80±0.87</td>
<td>0.084 ±0.25</td>
</tr>
<tr>
<td>L092</td>
<td>47.37±1.54</td>
<td>7.32±1.171</td>
<td>0.10 ±0.23</td>
</tr>
<tr>
<td>L093</td>
<td>51.39±2.32</td>
<td>1.67±0.67</td>
<td>0.07 ±0.21</td>
</tr>
<tr>
<td>Mean</td>
<td>48.77±1.92</td>
<td>5.16±1.07</td>
<td>0.10 ±0.3</td>
</tr>
</tbody>
</table>

**Table 4.** Head/body behaviour for the passive condition at 50°/s.
<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°/s)</th>
<th>Error ± SD (°)</th>
<th>Error (Window widths) ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Passive 100°/s</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>97.04±7.55</td>
<td>7.47±2.86</td>
<td>0.32±0.74, 0.33±0.75, 0.44±1.06, 0.77±1.78, 1.37±2.92</td>
</tr>
<tr>
<td>L065</td>
<td>102.17±6.06</td>
<td>3.91±1.52</td>
<td>0.26±0.62, 0.32±0.71, 0.38±0.87, 0.40±1.05, 0.71±1.53</td>
</tr>
<tr>
<td>L087</td>
<td>99.33±5.35</td>
<td>5.72±1.40</td>
<td>0.30±0.67, 0.25±0.59, 0.28±0.68, 0.51±1.16, 0.94±1.94</td>
</tr>
<tr>
<td>L089</td>
<td>110.38±6.61</td>
<td>2.09±1.14</td>
<td>0.24±0.63, 0.38±0.81, 0.18±0.49, 0.29±0.75, 0.38±0.93</td>
</tr>
<tr>
<td>L090</td>
<td>102.99±5.24</td>
<td>3.40±1.53</td>
<td>0.25±0.63, 0.27±0.63, 0.28±0.71, 0.41±0.99, 0.65±1.42</td>
</tr>
<tr>
<td>L092</td>
<td>100.43±5.98</td>
<td>5.81±1.34</td>
<td>0.27±0.64, 0.30±0.69, 0.32±0.80, 0.40±1.00, 0.94±1.96</td>
</tr>
<tr>
<td>L093</td>
<td>106.04±6.55</td>
<td>3.10±1.53</td>
<td>0.29±0.68, 0.24±0.59, 0.33±0.82, 0.45±1.11, 0.57±1.38</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>102.63±6.19</td>
<td>4.50±1.61</td>
<td>0.27±0.66, 0.30±0.68, 0.31±0.78, 0.46±1.12, 0.79±1.73</td>
</tr>
</tbody>
</table>

**Table 5.** Head/body behaviour for the passive condition at 100°/s.

**Active:** For the active condition, each participant’s head movement was continuously tracked and was recorded over the central 50° portion of head motion on each trial. The average velocity of the movement was measured and computed as found in the tables below. Mean velocity with SD of head rotation were 25.62±6.12°/s, 55.78±14.63°/s, and 98.67±16.12°/s for conditions where they were instructed to rotate their head at 25°/s, 50°/s, and 100°/s respectively (Fig. 16).

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Active 25°/s</strong></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>24.19±6.19</td>
</tr>
<tr>
<td>L065</td>
<td>27.35±3.02</td>
</tr>
<tr>
<td>L087</td>
<td>25.57±4.96</td>
</tr>
<tr>
<td>L089</td>
<td>22.40±5.74</td>
</tr>
<tr>
<td>L090</td>
<td>29.92±6.84</td>
</tr>
<tr>
<td>L092</td>
<td>28.94±11.22</td>
</tr>
<tr>
<td>L093</td>
<td>20.97±4.85</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>25.62±6.12</td>
</tr>
</tbody>
</table>

**Table 6.** Head behaviour for the active condition at 25°/s.
Table 7. Head behaviour for the active condition at 50°/s.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active 50°/s</td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>50.84±9.46</td>
</tr>
<tr>
<td>L065</td>
<td>50.43±7.51</td>
</tr>
<tr>
<td>L087</td>
<td>46.43±12.23</td>
</tr>
<tr>
<td>L089</td>
<td>52.12±11.73</td>
</tr>
<tr>
<td>L090</td>
<td>67.59±22.66</td>
</tr>
<tr>
<td>L092</td>
<td>58.71±18.87</td>
</tr>
<tr>
<td>L093</td>
<td>64.33±19.96</td>
</tr>
<tr>
<td>Mean</td>
<td>55.78±14.63</td>
</tr>
</tbody>
</table>

Table 8. Head behaviour for the active condition at 100°/s.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Head Velocity ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active 100°/s</td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>100.23±13.88</td>
</tr>
<tr>
<td>L065</td>
<td>101.60±12.39</td>
</tr>
<tr>
<td>L087</td>
<td>99.73±24.64</td>
</tr>
<tr>
<td>L089</td>
<td>97.76±15.04</td>
</tr>
<tr>
<td>L090</td>
<td>102.87±19.01</td>
</tr>
<tr>
<td>L092</td>
<td>88.78±10.83</td>
</tr>
<tr>
<td>L093</td>
<td>99.75±17.07</td>
</tr>
<tr>
<td>Mean</td>
<td>98.67±16.12</td>
</tr>
</tbody>
</table>

Counter: In the counter condition, participants were instructed to try and maintain their head centered at 0° in space while their body was oscillated left and right at 50°/s by the oscillatory platform. The table below demonstrates the mean velocity of the body of each participant with SD that was measured over the central portion of the rotation (50° range), mean angle in which the head deviated from the center of 0° with SD, and the head’s deviation from the center as a function of stimulus spatial window width with SD. Across all participants, the body oscillated at a mean velocity of 49.54±5.10°/s while the head deviated at a mean of 3.39±3.64° from the center and 0.05±0.14°, 0.08±0.30°, 0.15±0.45°, 0.29±0.85°, and 0.55±1.37° at each stimulus window width, respectively (Fig. 19). It is conceivable then that vestibular input was negligible, as head movement in space was significantly minimized and controlled for. Even if there was slight head movement, however, the results below (Section 3.2.5) suggest that it did not aid with the localization task.
<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Body Velocity ± SD (°)</th>
<th>Mean Error ± SD (°)</th>
<th>Mean Error (Window widths) ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.5</td>
</tr>
<tr>
<td><strong>Counter 50°/s</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>54.73±2.44</td>
<td>0.98±1.074</td>
<td>0.02 ±0.05</td>
</tr>
<tr>
<td>L065</td>
<td>52.51±1.75</td>
<td>0.94±0.53</td>
<td>0.02 ±0.05</td>
</tr>
<tr>
<td>L087</td>
<td>49.66±2.46</td>
<td>3.22±1.68</td>
<td>0.04 ±0.11</td>
</tr>
<tr>
<td>L089</td>
<td>49.93±7.54</td>
<td>3.39±3.64</td>
<td>0.065±0.29</td>
</tr>
<tr>
<td>L090</td>
<td>48.94±4.75</td>
<td>3.58±2.48</td>
<td>0.035±0.10</td>
</tr>
<tr>
<td>L092</td>
<td>47.44±5.32</td>
<td>5.99±2.71</td>
<td>0.079±0.21</td>
</tr>
<tr>
<td>L093</td>
<td>43.60±11.43</td>
<td>8.16±5.77</td>
<td>0.07±0.19</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>49.54±5.10</td>
<td>3.75±2.56</td>
<td>0.05±0.14</td>
</tr>
</tbody>
</table>

**Table 9.** Head/body behaviour for the counter condition at 50°/s.

**Dynastatic:** For the dynastatic condition, the movement of the oscillatory platform was continuously tracked and recorded as it rotated to the left and right, as the participant sat and maintained their head and body still in space at 0°. This was done in order to generate the same stimuli as in the passive/active conditions as if the head was moving through space and also in order to demonstrate that the velocities of the rotation in this condition is comparable to the other conditions. Mean velocity with SD of platform rotation were 24.20±1.12°/s, 48.64±2.15°/s, and 102.61±6.50±16.12°/s at conditions of 25°/s, 50°/s, and 100°/s respectively.
<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Velocity ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dynastatic 25°/s</strong></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>23.34±0.88</td>
</tr>
<tr>
<td>L065</td>
<td>25.02±1.40</td>
</tr>
<tr>
<td>L087</td>
<td>24.67±1.13</td>
</tr>
<tr>
<td>L089</td>
<td>23.23±1.21</td>
</tr>
<tr>
<td>L090</td>
<td>23.23±0.73</td>
</tr>
<tr>
<td>L092</td>
<td>25.56±1.70</td>
</tr>
<tr>
<td>L093</td>
<td>24.36±0.81</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>24.20±1.12</td>
</tr>
</tbody>
</table>

**Table 10.** Oscillatory platform behaviour for the dynastatic condition at 25°/s.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Velocity ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dynastatic 50°/s</strong></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>48.57±2.75</td>
</tr>
<tr>
<td>L065</td>
<td>48.00±1.86</td>
</tr>
<tr>
<td>L087</td>
<td>47.67±3.23</td>
</tr>
<tr>
<td>L089</td>
<td>49.01±1.66</td>
</tr>
<tr>
<td>L090</td>
<td>49.00±2.27</td>
</tr>
<tr>
<td>L092</td>
<td>47.77±1.53</td>
</tr>
<tr>
<td>L093</td>
<td>50.44±1.74</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>48.64±2.15</td>
</tr>
</tbody>
</table>

**Table 11.** Oscillatory platform behaviour for the dynastatic condition at 50°/s.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>Mean Velocity ± SD (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dynastatic 100°/s</strong></td>
<td></td>
</tr>
<tr>
<td>L061</td>
<td>101.94±5.87</td>
</tr>
<tr>
<td>L065</td>
<td>104.48±7.01</td>
</tr>
<tr>
<td>L087</td>
<td>104.98±6.01</td>
</tr>
<tr>
<td>L089</td>
<td>100.78±8.26</td>
</tr>
<tr>
<td>L090</td>
<td>97.86±5.31</td>
</tr>
<tr>
<td>L092</td>
<td>101.28±6.24</td>
</tr>
<tr>
<td>L093</td>
<td>106.97±6.82</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>102.61±6.50</td>
</tr>
</tbody>
</table>

**Table 12.** Oscillatory platform behaviour for the dynastatic condition at 100°/s.
3.2.3 Front/back Localization Performance Comparison between Free-field and Virtual Auditory Space Parameters

Front/back sound localization performance was measured at all three velocities (25°/s, 50°/s, and 100°/s) in the active condition for both free-field and virtual auditory space (Section 3.2.5 for individual performance) presentation methods in order to directly compare performance between the two presentation methods, as the main part of the experiment was conducted in the latter (Fig. 24). In other words, this analysis was performed to ensure that the dynamic HRTF filtering was working and accurately representing external acoustical space over headphones. Analyses demonstrated that there were no significant differences in performance between the two presentation methods as described in further detail below.

**Figure 24.** Across-listener mean correct performance of front/back sound localization as a function of stimulus window width in the active condition at 25°/s, 50°/s, and 100°/s for free-field and virtual auditory space presentation methods.

In order to examine whether there was a difference in performance between the presentation methods, a 2-way repeated measures ANOVA was applied for assessment of front/back sound localization mean correct performance separately for all three velocities (25°/s, 50°/s, and 100°/s). The presentation method in which the tasks were performed was the first factor of interest, which had two levels (free-field and virtual auditory space). The second factor was the sound stimulus window width, which had five levels (2.6°, 5°, 10°, 20°, and 40°). There was no significant main effect of presentation method observed at any of the three velocities as hypothesized a-priori, which confirms that participants behaved similarly in both conditions:
A significant main effect of stimulus window width was observed, which was consistent with our hypothesis that front/back performance would improve with increasing stimulus window width, $F_{1.025, 5.127} = 11.355, p < 0.05; \eta^2_{\text{partial}} = 11.644$.

As expected, a significant interaction between head movement condition and stimulus window width was not observed, which further confirms that participants were behaving similarly in both conditions:

$$\text{i) } 25^\circ/s: F_{0.003, 5} = 79.889, p < 0.0005; \eta^2_{\text{partial}} = 0.941$$
$$\text{ii) } 50^\circ/s: F_{2.530, 12.651} = 133.722, p < 0.0005; \eta^2_{\text{partial}} = 0.964$$
$$\text{iii) } 100^\circ/s: F_{2.970, 14.851} = 109.334, p < 0.0005; \eta^2_{\text{partial}} = 0.956$$

### 3.2.4 Individual and Mean Front/back Sound Localization Performance Data for all Dynamic Sound Localization Tests

In order to assess the front/back localization accuracy in each dynamic localization condition (static, passive, active, counter, and dynastatic), performance was quantified as a percent of correct responses, where correct “front” responses indicated by the participant originated in the front hemi-field ($0^\circ$ and $\pm22.5^\circ$) and correct “back” responses originated from the back hemi-field ($180^\circ$ and $\pm157.5^\circ$) for all three velocities ($25^\circ/s$, $50^\circ/s$, $100^\circ/s$). The data of participant L093 was retained in graphs showing individual data (Fig. 25-29) but was removed as an outlier from mean analyses (Fig. 30), as their data markedly deviated compared to the other participants.
Figure 25. Free-field Active (Experiment 1a): Individual listeners’ mean performance of front/back sound localization as a function of stimulus spatial window width in the free-field active condition at each velocity.

Figure 26. Passive: Individual listeners’ mean performance of front/back sound localization as a function of stimulus spatial window width in the passive condition at each velocity.
**Figure 27.** Active: Individual listeners’ mean correct performance of front/back sound localization as a function of stimulus spatial window width in the (virtual auditory space) active condition at each velocity.

**Figure 28.** Counter: Individual listeners’ mean performance of front/back sound localization as a function of spatial window width in the counter condition.
Figure 29. Dynastic: Individual listeners’ mean performance of front/back sound localization as a function of spatial window width in the dynastic condition at each velocity.

Figure 30. All conditions: Across-listeners mean performance and standard error of front/back sound localization as a function of stimulus spatial window width in all conditions at each velocity.
Passive: In the passive (and active) conditions, front/back localization performance appears to have improved monotonically with increasing spatial window width (which provided access to larger changes in interaural cues) (Fig. 26, Table 13). Furthermore, it appears that as the head rotation velocity increased, which reduced the duration of the stimuli, performance decreased in both conditions (Fig 26, Table 13). That is, small head rotations improved accuracy at slow head rotation velocities, whereas larger head rotations were necessary at faster head rotation velocities.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Sound Stimuli Window Width (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.6</td>
</tr>
<tr>
<td>25</td>
<td>61.97%</td>
</tr>
<tr>
<td>50</td>
<td>61.13%</td>
</tr>
<tr>
<td>100</td>
<td>60.71%</td>
</tr>
</tbody>
</table>

Table 13. Individual listeners’ mean correct performance in the passive condition as a function of stimulus spatial window width.

Active: Similarly to the passive conditions, front/back localization performance monotonically improved as spatial window width increased, while performance decreased with increased head rotation velocity (Fig 27, Table 14).

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Sound Stimuli Window Width (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.6</td>
</tr>
<tr>
<td>25</td>
<td>70.13%</td>
</tr>
<tr>
<td>50</td>
<td>58.35%</td>
</tr>
<tr>
<td>100</td>
<td>59.87%</td>
</tr>
</tbody>
</table>

Table 14. Individual listeners’ mean correct performance in the active condition as a function of stimulus spatial window width.
Counter: Conversely to the passive and active conditions, most participants performed close to chance level in the counter condition (Fig. 28, Table 15), and performance did not significantly improve with increasing window width or with the velocity of their head movement. However, for participant L092, performance appears to have worsened with increasing stimulus window width, whereas for participant L087, they performed above 75% correct.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Sound Stimuli Window Width (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.6</td>
</tr>
<tr>
<td>50</td>
<td>59.12%</td>
</tr>
</tbody>
</table>

Table 15. Individual listeners’ mean correct performance in the counter condition as a function of stimulus spatial window width.

Dynastatic: Similarly to the counter condition and conversely to the passive/active conditions, participants performed just above chance level and their performance did not significantly improve with increasing stimulus window width or vary with sound source velocity (Fig 29, Table 16), even though they were presented with the same HRTF-filtered sounds that would occur during head movement.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Sound Stimuli Window Width (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.6</td>
</tr>
<tr>
<td>25</td>
<td>54.22%</td>
</tr>
<tr>
<td>50</td>
<td>51.39%</td>
</tr>
<tr>
<td>100</td>
<td>54.08%</td>
</tr>
</tbody>
</table>

Table 16. Individual listeners’ mean correct performance in dynastatic conditions as a function of stimulus spatial window width.
3.2.5 Comparison between Static and Head Movement Conditions

In order to assess whether head movement is beneficial for front/back localization accuracy, performance in the static condition was compared with performance in the passive and active conditions. Mean correct performance for both head movement conditions was only taken for the largest stimulus window width of 40° and at the fastest velocity of 100°/s for each participant for analysis. Since performance seems worst at the fastest velocity (Fig. 30), any significant difference observed between conditions in the repeated measures ANOVA would conceivably be even larger at the slower velocities.

Participants could not accurately identify the front/back location of the auditory targets in the static condition (mean correct performance of 53.47%), while participants performed accurately in the passive and active conditions (mean correct performance of 93.57% and 93.66%, respectively). The tables below show mean performance correct values for each individual participant in the static, passive, and active conditions (Table 17-19).

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>L061</th>
<th>L065</th>
<th>L087</th>
<th>L089</th>
<th>L090</th>
<th>L092</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correct Performance</td>
<td>59.72%</td>
<td>50.35%</td>
<td>68.06%</td>
<td>54.86%</td>
<td>57.99%</td>
<td>29.86%</td>
</tr>
<tr>
<td>Across-listeners Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>53.47%</td>
<td></td>
</tr>
</tbody>
</table>

Table 17. Mean front/back localization performance in the static condition.

<table>
<thead>
<tr>
<th>Subject ID</th>
<th>L061</th>
<th>L065</th>
<th>L087</th>
<th>L089</th>
<th>L090</th>
<th>L092</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correct Performance</td>
<td>85.71%</td>
<td>95.92%</td>
<td>100%</td>
<td>92.00%</td>
<td>89.80%</td>
<td>97.96%</td>
</tr>
<tr>
<td>Across-listeners Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>93.57%</td>
<td></td>
</tr>
</tbody>
</table>

Table 18. Mean front/back localization performance in the passive condition.
Table 19. Mean front/back localization performance in the active condition.

In order to assess whether head movement improved front/back localization accuracy when compared to no head movement, a 1-way repeated measures ANOVA was conducted, in which the listening condition (static; passive and active) was the factor of interest. Significant differences between front/back accuracy across listening conditions were observed, $F_{1,474, 7.372} = 36.899, p < 0.0005; \eta^2_{\text{partial}} = 0.881$. The lower rate of front/back errors in the passive and active head movement conditions compared to the static condition suggests that head movement is beneficial in front/back sound localization.

When a post hoc t-test was applied, the results demonstrated that there was a significant difference between the static condition ($M = 53.47, SD = 12.97$) and passive condition ($M = 93.57, SD = 5.38$), $t(5) = -6.456, p < 0.05$, which is consistent with the hypothesis that head movement is beneficial to resolving front/back confusions. In addition, a significant difference was found between the static condition ($M = 53.47, SD = 12.97$) and active condition, ($M = 93.66, SD = 3.83$), $t(5) = -6.606, p < 0.05$, which is also in agreement with the hypothesis.

3.2.6 Analysis of Performance as a Function of Head Movement Condition and Stimulus Window Width

All Conditions: In order to measure the extent to which vestibular and proprioceptive cues influence processing of dynamic sound localization cues, performance of mean front/back localization accuracy and standard error in the static, passive, active, counter, and dynastatic conditions across all participants are presented in Figure 30 above as a function of sound stimulus window width (separated into three different graphs by increasing head and/or body velocity). Comparison of mean performance across head
movement conditions (Fig. 30) suggests that front/back localization in the passive and active performance was accurate, whereas performance was just above chance in the static, dynastatic, and counter conditions.

In order to determine if there was a significant interaction between the head movement conditions and sound stimulus window width, a 2-way repeated measures ANOVA was applied for assessment of front/back sound localization mean correct performance for all three velocities. These assessments were run separately at each velocity because the counter condition was only run at 50°/s and the effect of velocity on performance is addressed later in Section 3.2.7. In addition, as it was hypothesized a-priori that a comparison between the passive/active conditions and the dynastatic/counter condition would result in better front/back localization accuracy in the prior conditions, the following post hoc paired t-tests (mean correct performance as a function of sound stimulus window width) were subsequently run at each velocity:

i) Passive vs. active
ii) Passive vs. counter
iii) Passive vs. dynastatic
iv) Active vs. counter
v) Active vs. dynastatic
vi) Dynastatic vs. counter

For 25°/s, the head movement condition had three levels (passive, active, and dynastatic conditions), while the stimulus window width had five levels (2.6°, 5°, 10°, 20°, and 40°). A significant interaction between head movement condition and stimulus window width was observed, $F_{2.383, 11.914} = 8.117, p < 0.005; \eta^2_{\text{partial}} = 0.619$, which is explored further in using a regression analysis in Section 3.2.7. Significant main effects of head movement condition, $F_{1.610, 8.048} = 51.599, p < 0.0005; \eta^2_{\text{partial}} = 0.912$, and stimulus window width, $F_{0.413, 0.032} = 65.223, p < 0.0005; \eta^2_{\text{partial}} = 0.929$, were also observed. Post hoc paired t-tests demonstrated that there was a significant difference between the passive condition ($M = 80.29, SD = 11.65$) and the active condition ($M = 86.20, SD = 9.99$), $t(4) = -6.526, p < 0.05$, which is inconsistent with the hypothesis that passive and active would demonstrate similar front/back localization performance. On the other hand, the
following comparisons between the passive/active conditions with the dynastatic condition are also statistically significant, which is consistent with the hypothesis that performance would be better in the passive/active conditions than the dynastatic condition:

i) Passive ($M = 80.29, SD = 11.65$) and dynastatic ($M = 54.62, SD = 1.98$), $t(4) = 5.364, p < 0.05$

ii) Active ($M = 86.20, SD = 9.99$) and dynastatic ($M = 54.62, SD = 1.98$), $t(4) = 7.753, p < 0.05$

For $50^\circ/s$, the head movement condition had four levels (passive, active, counter, and dynastatic conditions), while the stimulus window width had five levels ($2.6^\circ$, $5^\circ$, $10^\circ$, $20^\circ$, and $40^\circ$). A significant interaction between head movement condition and stimulus window width was observed, $F_{3.439, 17.197} = 10.691, p < 0.0005; \eta^2_{\text{partial}} = 0.681$. Significant main effects of head movement condition, $F_{1.215, 6.075} = 17.149, p < 0.005; \eta^2_{\text{partial}} = 0.774$, and stimulus window width, $F_{0.533, 0.069} = 38.780, p < 0.0005; \eta^2_{\text{partial}} = 0.886$, were also observed. A post hoc paired t-test comparing the mean correct performance as a function of stimulus window width between the passive condition ($M = 82.05, SD = 13.42$) and active condition ($M = 80.27, SD = 15.24$), $t(4) = 1.065, p > 0.05$, demonstrated that there was no statistically significant difference in performance, which is consistent with the hypothesis that participants would perform similarly in passive and active conditions. In addition, there was no significant difference between dynastatic ($M = 55.88, SD = 3.80$) and counter ($M = 57.60, SD = 1.08$), $t(4) = -0.888, p > 0.05$. However, there was a statistically significant difference between:

i) Passive ($M = 82.05, SD = 13.42$) and counter ($M = 57.60, SD = 1.08$), $t(4) = 3.779, p < 0.05$

ii) Passive ($M = 82.05, SD = 13.42$) and dynastatic ($M = 55.88, SD = 3.80$), $t(4) = 5.011, p < 0.05$

iii) Active ($M = 80.27, SD = 15.24$) and counter ($M = 57.60, SD = 1.08$), $t(4) = 3.116, p < 0.05$

iv) Active ($M = 80.27, SD = 15.24$) and dynastatic ($M = 55.88, SD = 3.80$), $t(4) = 4.069, p < 0.05$
These findings are consistent with the hypothesis that there would be significant differences in front/back accuracy between passive/active conditions and the counter/dynastatic conditions, demonstrating higher front/back percent correct in the latter conditions, whereas there would be no statistically significant difference between the passive and active comparisons.

For 100°/s, the head movement condition had three levels (passive, active, and dynastatic), while the stimulus window width had five levels (2.6°, 5°, 10°, 20°, and 40°). A significant interaction between head movement condition and stimulus window width was observed, $F_{3.140, 15.699} = 15.268, p < 0.0005; \eta^2_{partial} = 0.753$. Significant main effects of head movement condition, $F_{1.965, 9.825} = 25.565, p < 0.0005; \eta^2_{partial} = 0.836$, and stimulus window width, $F_{3.052, 15.258} = 56.651, p < 0.0005; \eta^2_{partial} = 0.919$, were also observed. Similarly to the 50°/s condition, a post hoc paired t-test comparing the passive condition ($M = 76.43, SD = 15.57$) and active condition ($M = 78.70, SD = 15.46$), $t(4) = -1.609, p > 0.05$ showed no statistically significant difference. Conversely, there was a significant difference between the passive condition ($M = 76.43, SD = 15.57$) and the dynastatic condition ($M = 55.10, SD = 1.85$), $t(4) = 3.330, p < 0.05$. Moreover, a comparison between the active condition ($M = 78.70, SD = 15.46$) and the dynastatic condition ($M = 55.10, SD = 1.85$), $t(4) = 3.711, p < 0.05$, demonstrated a significant difference in performance. All of these statistical tests are consistent with the hypothesis that performance in the passive and active performance would be similar and be superior to performance in the counter and dynastatic conditions.

Finally, in order to explore the interaction between conditions and spatial window widths that we observed in the repeated measures ANOVA, a linear regression model was fitted to each plot for each velocity using the MATLAB `regress` function to obtain and test their respective slopes (Fig. 32). The independent variable used in the regression was the base-2 logarithm of the window width, and therefore the slopes are in units of proportion correct per doubling of window width. Significant positive slopes ($s$) were observed for only passive and active conditions, further suggesting that front/back localization performance improved monotonically with increasing spatial window width in the passive and active conditions at all three velocities, whereas there was no significant
improvement with increasing stimulus window width in the counter and dynastic conditions:

i) Passive 25°/s (s = 0.070, SD = 0.0066), F = 96.34, p < 0.05
ii) Passive 50°/s (s = 0.081, SD = 0.0082), F = 97.15, p < 0.05
iii) Passive 100°/s (s = 0.096, SD = 0.0081), F = 144.63, p < 0.05
iv) Active 25°/s (s = 0.061, SD = 0.0066), F = 84.67, p < 0.05
v) Active 50°/s (s = 0.098, SD = 0.0083), F = 138.54, p < 0.05
vi) Active 100°/s (s = 0.107, SD = 0.0072), F = 217.75, p < 0.05
vii) Counter 50°/s (s = 0.008, SD = 0.0080), F = 0.91, p > 0.05
viii) Dynastic 25°/s (s = 0.008, SD = 0.0061), F = 1.71, p > 0.05
ix) Dynastic 50°/s (s = 0.008, SD = 0.0083), F = 1.01, p > 0.05
x) Dynastic 100°/s (s = 0.006, SD = 0.0074), F = 0.56, p > 0.05

Since only passive and active conditions demonstrated slopes with a significance level less than 0.05, a two-tailed test was run at each velocity in order to test the statistical difference between the slopes for these two conditions, the results of which demonstrated that there was no significant difference in the rate of increase of performance with increasing window width, as hypothesized:

i) 25°/s: t(116) = -0.7957, p > 0.05
ii) 50°/s: t(116) = 1.4286, p > 0.05
iii) 100°/s: t(116) = 0.8322, p > 0.05
3.2.7 Analysis of Velocity Effect in the Passive and Active Conditions

Figure 31. A side-by-side overview of across-listeners mean performance of front/back sound localization as a function of 1) stimulus spatial window width and 2) stimulus duration in passive and active conditions.

The figure above (Fig. 31) demonstrates in both passive and active conditions a velocity penalty in front/back localization performance as a function of window width, such that performance is worse with increasing head rotation velocity. This can be seen in in the left panels as a rightward shift in the psychometric functions as velocity increases. Performance was also plotted as a function of stimulus duration to analyze the results, as duration, window width, and velocity are confounded factors (results described below).

In order to assess the effect of velocity of head/body rotation on the accuracy of front/back sound localization, threshold spatial window width values required to reach a
75% correct performance were computed at each velocity for each listener in passive and active sound localization conditions. After linearly interpolating between observed values to improve fitting stability, a sigmoid function (4-parameter hyperbolic tangent) was fit to each set of performance versus window-width data using the MATLAB \texttt{nlinfit} function. The 75%-correct threshold was then determined, as shown in Fig. 31.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure32.png}
\caption{A hyperbolic tangent sigmoid curve fitting was interpolated onto the participants' data in order to extract their sound stimulus window width threshold values at 75% mean correct performance.}
\end{figure}

Values were only obtained from the passive and active conditions (Fig 30, Table 20, 21), as mean correct performance never reached 75% in the counter and dynastatic conditions.

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|c|}
\hline
\textbf{Velocity} (°/s) & \textbf{Stimulus Window Width Threshold (°)} & \\
& \textbf{L061} & \textbf{L065} & \textbf{L087} & \textbf{L089} & \textbf{L090} & \textbf{L092} \\
\hline
25 & 5.09 & 2.60 & 5.22 & 6.06 & 3.61 & 5.15 \\
50 & 8.37 & 3.50 & 4.59 & 5.49 & 4.75 & 3.36 \\
100 & 25.58 & 6.00 & 5.76 & 10.78 & 12.20 & 6.71 \\
\hline
\end{tabular}
\caption{Individual listeners’ stimulus window width thresholds at 75% mean correct performance at each velocity in the passive condition.}
\end{table}
Velocity \((^\circ/s)\) | Stimulus Window Width Threshold \((^\circ)\)  
<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L061</td>
<td>L065</td>
<td>L087</td>
<td>L089</td>
<td>L090</td>
<td>L092</td>
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<td>2.60</td>
<td>4.84</td>
<td>2.60</td>
</tr>
<tr>
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<td>6.09</td>
<td>4.14</td>
<td>6.20</td>
<td>4.34</td>
<td>6.17</td>
<td>4.94</td>
</tr>
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<td>9.73</td>
<td>6.23</td>
<td>6.44</td>
<td>6.03</td>
<td>7.35</td>
<td>8.37</td>
</tr>
</tbody>
</table>

Table 21. Individual listeners’ stimulus window width thresholds at 75% mean correct performance at each velocity in the active condition.

A 2-way repeated measures ANOVA was applied to examine the interaction between both head movement conditions and the velocity of movement during front/back sound localization using stimulus window width thresholds as the dependent variable. The head movement condition factor had two levels (passive and active) and the velocity factor had three levels \((25^\circ/s, 50^\circ/s, \text{and} 100^\circ/s)\). Significant interactions between head movement condition and velocity was not observed, \(F_{1,031,5.155} = 1.603, p > 0.05; \eta^2_{\text{partial}} = 0.243\) and a significant main effect of condition was not observed either, \(F_{1,5} = 2.352, p > 0.05; \eta^2_{\text{partial}} = 0.320\). However, a significant main effect of velocity was observed, as we hypothesized a-priori that the window width required to accurately localize front/back sound sources would increase with velocity, \(F_{1,025,5.127} = 11.355, p < 0.05; \eta^2_{\text{partial}} = 0.694\). The linear contrast of velocity was significant, \(F_{1,5} = 13.194, p < 0.05; \eta^2_{\text{partial}} = 0.725\), further suggesting that the stimulus window width threshold significantly increased with velocity.

Since a significant interaction between condition and velocity or a main effect of condition were not found, follow-up tests were conducted to evaluate pairwise differences among the mean values of stimulus window width versus velocities \((25^\circ/s \text{ vs.} 50^\circ/s \text{ and} 50^\circ/s \text{ vs.} 100^\circ/s)\) collapsed across conditions. There was a significant difference observed between means of \(25^\circ/s \text{ vs.} 50^\circ/s\) \((p = 0.009)\) but not between \(50^\circ/s \text{ vs.} 100^\circ/s\) \((p = 0.089)\). The 95% confidence intervals for the pairwise differences as well as the means and standard deviations for the three velocities are reported in Table 22.
Table 22. 95% Confidence intervals of pairwise differences in mean stimulus window width versus velocity collapsed across passive and active conditions.

As we observed above, stimulus window width thresholds increased with increasing velocity. However, head rotation velocity, stimuli duration, and stimulus spatial window width are confounded variables. Minimum head movement angles required are larger at faster velocities, however, a given head movement takes less time at higher velocities. Since the decline in performance with increasing velocity may be due to the durations getting shorter with increasing velocity, here we examine what the threshold performance looks like as a function of stimulus duration, which we obtained by dividing the window width threshold value by the respective velocity (Fig. 31, Table 23, 24).

Table 23. Individual listeners’ stimulus duration thresholds at 75% mean correct performance at each velocity in the passive condition.

Table 24. Individual listeners’ stimulus duration thresholds at 75% mean correct performance at each velocity in the active condition.
Figure 33. Across-listener stimulus window width thresholds (ms) and standard error at 75% mean correct performance as a function of velocity in both passive and active conditions. It appears that the stimulus window width thresholds increase with velocity.
Figure 34. Sound stimulus duration and standard error at 75% mean correct performance as a function of velocity in both passive and active conditions.
When the passive and active conditions are plotted as a function of stimulus duration (Fig. 34), the performance seems to be duration-limited, such that about 100 ms is required for accurate front/back localization during rotation at 50°/s and 100°/s, whereas 150 – 170 ms is required at 25°/s rotation. In addition, an increase in minimum head movement angle required is observed with increasing velocity, in which approximately 2.6-5°, 5-10°, and 10-20° are required at 25°/s, 50°/s, and 100°/s, respectively for both conditions.

A 2-way repeated measures ANOVA was applied for assessment of stimulus duration at 75% mean correct performance as the dependent variable for all three velocities. Head movement condition was one factor and consisted of two levels (passive and active) and velocity was the second factor, which had three levels (25°/s, 50°/s, and 100°/s). There was no significant interaction between the head movement condition and velocity, $F_{1.047, 5.233} = 1.889, p > 0.05; \eta^2_{\text{partial}} = 0.274$, as well as no main effect for condition, $F_{1, 5} = 0.935, p > 0.05; \eta^2_{\text{partial}} = 0.158$. However, there was a main effect of velocity, $F_{1.701, 8.504} = 25.796, p < 0.05; \eta^2_{\text{partial}} = 0.838$. The linear contrast of velocity was also significant, $F_{1, 5} = 84.132, p < 0.05; \eta^2_{\text{partial}} = 0.944$.

Since a significant interaction between condition and velocity or a main effect of condition were not found, follow-up tests were conducted to evaluate pairwise differences among the mean values of stimulus duration thresholds for velocities collapsed across conditions. There was a significant difference observed between means of 25°/s vs. 50°/s ($p = 0.002$) but not between 50°/s vs. 100°/s ($p = 1.000$). The 95% confidence intervals for the pairwise differences as well as the means and standard deviations for the three velocities are reported in Table 25.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Mean (ms)</th>
<th>Std. Error (ms)</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lower Bound</td>
</tr>
<tr>
<td>25</td>
<td>166.872</td>
<td>17.171</td>
<td>122.732</td>
</tr>
<tr>
<td>50</td>
<td>103.255</td>
<td>9.879</td>
<td>77.861</td>
</tr>
<tr>
<td>100</td>
<td>92.664</td>
<td>17.725</td>
<td>47.099</td>
</tr>
</tbody>
</table>

Table 25. 95% Confidence intervals of pairwise differences in mean stimulus duration versus velocity collapsed across passive and active conditions.
3.3 Experiment 2: Left-to-right/Right-to-left Discrimination of Source Motion without Head Movement

3.3.1 Individual and Mean Performance Data

Performance in discrimination of left-to-right and right-to-left source motion in Experiment 2 was quantified as a percent of correct responses similarly to Experiment 1. This was done in order to assess whether the duration-limited (~100 ms) temporal dynamics of dynamic sound localization cue processing for higher velocities (50°/s and 100°/s) observed in the passive/active conditions are particular to head movement (the integration of the auditory and vestibular systems) or whether it is due to just auditory processing of acoustic cues.

Psychometric functions are shown below in Fig. 35/36 for the individual listeners as well the across-listeners means for the L/R-Dynastatic and L/R-ITD discrimination tasks. For the L/R-Dynastatic condition, when performance is plotted as a function of stimulus window width, results also show improved performance with increasing window width with slightly worsening performance with increasing sound source velocity (Fig. 35), similarly to the passive/active conditions above. When plotted as a function of stimulus duration, the psychometric functions appear to be aligned particularly for the higher velocities of 50°/s and 100°/s.

When performance is plotted as a function of ΔITD in the L/R –ITD condition, the results demonstrate that performance improved with greater cue change (higher ΔITD), while little to no velocity penalty was observed (Fig. 36). When plotted as a function of stimulus duration, it appears that the velocity penalty is too small to align the psychometric functions contrary to the L/R-Dynastatic condition.
Figure 35. Individual listeners’ psychometric functions for discrimination of left-to-right/right-to-left sound source motion in the L/R-Dynastatic condition at each velocity.

Figure 36. Individual listeners’ psychometric functions for left-to-right/right-to-left discrimination of ITD sweep direction in the L/R-ITD condition at each velocity (analogous to the velocities in the L/R-Dynastatic condition).
Figure 37. Across-listener psychometric functions for discrimination of left-to-right/right-to-left sound source motion in the L/R-Dynastatic condition at each velocity. Proportion correct responses are plotted as a function of 1) sound stimulus window width and 2) sound stimulus duration.

Figure 38. Across-listener psychometric functions for left-to-right/right-to-left discrimination of ITD sweep direction with a roving of 250 µs. Proportion correct responses are plotted as a function of 1) sweep ΔITD and 2) sweep duration.

3.3.2 Analysis of Effects of Listening Condition on Sensitivity to Cue Change (ΔITD/Stimulus Window Width)

In order to determine whether or not L/R discrimination performance in the L/R-Dynastatic condition could be attributed to ITD being a sufficient cue to discriminate direction of source motion, a 2-way repeated measures ANOVA was applied to compare L/R motion discrimination performance in both conditions (L/R-Dynastatic and L/R-ITD) for all three velocities. Lateral motion condition was one factor, consisting of two
levels (L/R-Dynastatic and L/R-ITD), while the stimulus window width had five levels (2.6°, 5°, 10°, 20°, and 40°). For the L/R-ITD task, the ΔITD (μs) values were converted to units of degrees by dividing them by 10 μs/°, which yielded values analogous to L/R-Dynastatic stimulus window width values.

For 25°/s, a significant interaction between the conditions and stimulus window width was not observed, $F_{2.231, 8.924} = 2.036, p > 0.05; \eta^2_{\text{partial}} = 0.337$, and a significant main effects of condition was also not observed, $F_{1.4} = 1.156, p > 0.05; \eta^2_{\text{partial}} = 0.224$. However, a significant main effect of stimulus window width was observed, $F_{1.390, 5.560} = 40.464, p < 0.001; \eta^2_{\text{partial}} = 0.910$, which is consistent with the hypothesis that a larger stimulus window width is required for higher velocities.

For 50°/s, a significant interaction between the conditions and stimulus window width was not observed, $F_{1.985, 7.941} = 2.244, p > 0.05; \eta^2_{\text{partial}} = 0.359$. A significant main effect of condition was observed, however, which was unexpected, $F_{1.4} = 9.842, p < 0.05; \eta^2_{\text{partial}} = 0.711$, a significant main effects of stimulus window width was observed, $F_{2.385, 9.542} = 330.305, p < 0.0005; \eta^2_{\text{partial}} = 0.988$, which is consistent with the hypothesis that higher velocities require larger stimulus window widths.

For 100°/s, a significant interaction between the conditions and stimulus window width was not observed, $F_{2.302, 9.209} = 0.458, p > 0.05; \eta^2_{\text{partial}} = 0.103$. A significant main effect of condition was also not observed, $F_{1.4} = 3.546, p > 0.05; \eta^2_{\text{partial}} = 0.470$, but consistent with the hypothesis, a significant main effect of stimulus window width was observed, $F_{1.638, 6.551} = 91.233, p < 0.0005; \eta^2_{\text{partial}} = 0.958$, suggesting that window width required increases with velocity.

3.3.2.1 Velocity Effect on Accuracy of L/R Discrimination Performance

A hyperbolic tangent using the MATLAB `nlinfit` function (Section 3.2.7) was used to determine the stimulus window width threshold values required to reach a 75% sensitivity threshold at each velocity in both L/R-Dynastatic and L/R-ITD conditions (Table 26, 27) in order to assess the effect of source motion velocity on L/R
discrimination performance. As aforementioned, only five participants were included for the mean analyses, as L092 withdrew from the study and L093 was an outlier.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Stimulus Window Width Threshold (°)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>L061</td>
</tr>
<tr>
<td>25</td>
<td>9.10</td>
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<tr>
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<td>7.64</td>
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<tr>
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</table>

**Table 26.** Individual listeners’ stimulus window width threshold at 75% correct performance at each velocity in the L/R-Dynastatic condition.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Stimulus Window Width Threshold (°)</th>
</tr>
</thead>
<tbody>
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<td>50</td>
<td>9.03</td>
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<tr>
<td>100</td>
<td>10.60</td>
</tr>
</tbody>
</table>

**Table 27.** Individual listeners’ stimulus window width threshold at 75% correct performance at each velocity in the L/R-ITD condition.

In order to examine the interaction between the velocity penalties that occurred in the two L/R discrimination tasks, a 2-way repeated measures ANOVA was applied between the two conditions for each velocity of the sound source/ITD sweep using stimulus window width thresholds as the dependent variable. The condition was one factor and consisted of two levels (L/R-ITD and L/R-Dynastatic) and the velocity was the second factor with three levels (25°/s, 50°/s, and 100°/s). There were no significant interaction observed between the discrimination condition and velocity, $F_{1,435}, 5.740 = 3.520, p > 0.05; \eta^2_{\text{partial}} = 0.0468$. However, a significant main effect of condition was observed as observed in Section 3.3.2, which was unexpected because it was hypothesized a-priori that the ITD cue used by the participants only in the L/R-ITD condition would be sufficient since ITD cues tend to be used at low frequencies, $F_{1,4} = 264.798, p < 0.05; \eta^2_{\text{partial}} = 0.985$. In
addition, a significant main effect of velocity was observed, as expected, F_{1.598, 6.391} = 6.289, p < 0.05; \eta^2_{\text{partial}} = 0.611.

When post hoc paired t-tests were run to compare the thresholds window widths at different velocities within each condition, a significant difference was observed except for i) L/R-ITD at 50°/s (M = 8.10, SD = 1.05) and L/R-ITD at 100°/s (M = 9.17, SD = 1.95), t(4) = -0.957, p > 0.05 and ii) L/R-Dynastatic at 25°/s (M = 5.18, SD = 2.51) and L/R-Dynastatic at 50°/s (M = 6.15, SD = 1.02), t(4) = -1.413, p > 0.05:

i) L/R-ITD at 25°/s (M = 6.29, SD = 1.81) and L/R-ITD at 50°/s (M = 8.10, SD = 1.05), t(4) = -2.814, p < 0.05

ii) L/R-ITD at 25°/s (M = 6.29, SD = 1.81) and L/R-ITD at 100°/s (M = 9.17, SD = 1.95), t(4) = -2.927, p < 0.05

iii) L/R-Dynastatic at 50°/s (M = 6.15, SD = 1.02) and L/R-Dynastatic at 100°/s (M = 10.56, SD = 1.75), t(4) = -9.980, p < 0.05

iv) L/R-Dynastatic at 25°/s (M = 5.18, SD = 2.51) and L/R-Dynastatic at 100°/s (M = 10.56, SD = 1.75), t(4) = -8.988, p < 0.05

The velocity effect was also examined by determining the relationship between the duration of the sound stimulus at the threshold window width value at 75% mean correct performance as a function of velocity in each condition (Table 28/29), which we obtained by dividing the window width threshold value by the respective velocity (Table 26/27).

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Stimulus Duration Threshold (ms)</th>
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</thead>
<tbody>
<tr>
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Table 28. Individual listeners’ stimulus duration thresholds at 75% mean correct performance at each velocity in the L/R-Dynastatic conditions.
<table>
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<th>Velocity (°/s)</th>
<th>Stimulus Duration Threshold (ms)</th>
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</table>

**Table 29.** Individual listeners’ stimulus duration thresholds at 75% mean correct performance at each velocity in the L/R-ITD conditions.

A 2-way repeated measures ANOVA was applied between the two conditions and the velocity of the sound source/ITD sweep using stimulus duration thresholds as the dependent variable in order to examine the velocity penalty between the two conditions. The first factor was the condition that had two levels (L/R-Dynastatic and L/R-ITD) and the second factor was the velocity with three levels (25°/s, 50°/s, and 100°/s). A significant interaction was observed between the conditions and velocity, $F_{1.427.5.709} = 6.024, p < 0.05; \eta^2_{\text{partial}} = 0.601$ and velocity, $F_{1.100, 4.401} = 12.626, p < 0.05; \eta^2_{\text{partial}} = 0.759$, whereas a significant main effect was not found for condition, $F_{1.4} = 5.004, p > 0.05; \eta^2_{\text{partial}} = 0.556$. The linear contrast of condition demonstrated a significant main effect of velocity as expected, $F_{1,4} = 15.988, p < 0.05; \eta^2_{\text{partial}} = 0.800$.

Post hoc paired t-tests were run to compare the different velocities within each condition and a significant difference was observed except for i) L/R-Dynastatic at 25°/s ($M = 207.01, SD = 100.47$) and L/R-Dynastatic at 50°/s ($M = 122.98, SD = 20.32$), $t(4) = 2.324, p > 0.05$ and ii) L/R-Dynastatic at 25°/s ($M = 207.01, SD = 100.47$) and L/R-Dynastatic at 100°/s ($M = 105.60, SD = 17.56$), $t(4) = 2.624, p > 0.05$:

i) L/R-ITD at 25°/s ($M = 251.71, SD = 75.46$) and L/R-ITD at 50°/s ($M = 161.91, SD = 20.91$), $t(4) = 3.245, p < 0.05$

ii) L/R-ITD at 50°/s ($M = 161.91, SD = 20.91$) and L/R-ITD at 100°/s ($M = 91.67, SD = 19.52$), $t(4) = 4.753, p < 0.05$

iii) L/R-ITD at 25°/s ($M = 251.71, SD = 75.46$) and L/R-ITD at 100°/s ($M = 91.67, SD = 19.52$), $t(4) = 5.207, p < 0.05$

iv) L/R-Dynastatic at 50°/s ($M = 122.98, SD = 20.32$) and L/R-Dynastatic at 100°/s ($M = 105.60, SD = 17.56$), $t(4) = 4.012, p < 0.05$
Figure 39. Stimulus window width threshold at 75% mean correct performance as a function of velocity in both L/R-ITD and L/R-Dynastatic discrimination conditions.
Figure 40. Sound stimulus duration at 75% mean correct performance as a function of velocity in both L/R-ITD and L/R-Dynastic discrimination conditions.
In the passive and active head movement conditions in Experiment 1, it appeared that localization performance decreased with velocity such that performance was stimulus duration-limited, such that about 100 ms was required for accurate front/back localization for the higher velocities of 50°/s and 100°/s. In order to determine whether that duration threshold only applies in dynamic localization tasks or whether it applies as well to auditory-only tasks, namely the L/R-Dynastatic task (since they use the same stimuli), a 2-way repeated measures ANOVA was applied between the two conditions and the velocity of the sound source/ITD sweep using stimulus window width thresholds as the dependent variable. A mean performance value across all participants was computed for the mean analyses of the L/R tasks to compare against the passive condition because one less participant was included for the L/R conditions (Section 2.2). The first factor was the condition that had two levels (Passive and L/R-Dynastatic) and the second factor was the velocity with three levels (25°/s, 50°/s, and 100°/s). A significant interaction was not observed between the conditions and velocity, F(4.600, 14.733) = 0.312, p > 0.05; η² partial = 0.059 and condition, F(1.5) = 0.162, p > 0.05; η² partial = 0.031, whereas a significant main effect was found for velocity, F(1.058, 5.290) = 15.340, p < 0.05; η² partial = 0.754. It appears that the front/back localization performance can be explained just based on sensitivity to the acoustic cue information participants were receiving.

Since a significant main effect of velocity was observed, follow-up tests were conducted in order to evaluate pairwise differences among the mean values of stimulus window width thresholds with velocities collapsed across the two conditions. A significant difference was not observed between means of 25°/s vs. 50°/s (p = 0.254) but was found between 50°/s vs. 100°/s (p = 0.034). The 95% confidence intervals for the pairwise differences as well as the means and standard deviations for the three velocities are reported in Table 30.
Table 30. 95% Confidence intervals of pairwise differences in mean stimulus window widths versus velocity collapsed across passive and LR-Dynastatic conditions.

<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Mean (°)</th>
<th>Std. Error (°)</th>
<th>95% Confidence Interval Lower Bound</th>
<th>95% Confidence Interval Upper Bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>4.899</td>
<td>.597</td>
<td>3.363</td>
<td>6.434</td>
</tr>
<tr>
<td>50</td>
<td>5.580</td>
<td>.529</td>
<td>4.219</td>
<td>6.940</td>
</tr>
<tr>
<td>100</td>
<td>10.867</td>
<td>1.829</td>
<td>6.166</td>
<td>15.568</td>
</tr>
</tbody>
</table>

A 2-way repeated measures ANOVA was applied between the two conditions (Passive and L/R-Dynastatic) and the velocity of the sound source/ITD sweep using stimulus duration thresholds as the dependent variable in order to examine the temporal dynamics between the two conditions. The first factor was the condition that had two levels (Passive and L/R-Dynastatic) and the second factor was the velocity with three levels (25°/s, 50°/s, and 100°/s). A significant interaction was not observed between the conditions and velocity, $F_{1,041, 5,204} = 0.312, p > 0.05; \eta^2_{\text{partial}} = 0.065$ and a significant main effect of condition was also not found, $F_{1, 5} = 1.136, p > 0.05; \eta^2_{\text{partial}} = 0.185$, whereas a significant main effect was observed for velocity, $F_{1,430, 7,149} = 22.179, p < 0.05; \eta^2_{\text{partial}} = 0.816$.

Since a significant main effect of velocity was found, follow-up tests were conducted to evaluate pairwise differences among the mean threshold duration values for velocities 25°/s vs. 50°/s and 50°/s vs. 100°/s collapsed across conditions. There was a significant difference observed between means of 25°/s vs. 50°/s ($p = 0.010$) but not between 50°/s vs. 100°/s ($p = 1.000$). The 95% confidence intervals for the pairwise differences as well as the means and standard deviations for the three velocities are reported in Table 31.
<table>
<thead>
<tr>
<th>Velocity (°/s)</th>
<th>Mean (ms)</th>
<th>Std. Error (ms)</th>
<th>95% Confidence Interval</th>
<th>Lower Bound</th>
<th>Upper Bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
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<td>23.897</td>
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<tr>
<td>50</td>
<td>111.596</td>
<td>10.585</td>
<td>84.386</td>
<td>138.806</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>108.670</td>
<td>18.286</td>
<td>61.664</td>
<td>155.676</td>
<td></td>
</tr>
</tbody>
</table>

**Table 31.** 95% Confidence intervals of pairwise differences in mean stimulus duration versus velocity collapsed across passive and LR-Dynastic conditions.
Chapter 4

4 Discussion

The present study addressed the importance of head movement in normally hearing listeners in localizing front/back sources of sound and the extent to which vestibular and proprioceptive cues influence the processing and interpretation of dynamic sound localization cues that result from head movement. This was measured by stimulating these systems individually or congruently while participants localized dynamic auditory targets. Performance correct was assessed based on front/back accuracy. It was hypothesized that participants would perform the most accurately in the passive and active conditions because they had the most vestibular stimulation and that they would perform the worst in the counter and dynastatic conditions because we hypothesized that proprioceptive information is neither necessary nor sufficient in informing the auditory system of head position and movement in space. It was also hypothesized that in the passive and active conditions, performance would improve with increasing stimulus window width and based on pilot data, that performance would be duration-limited at 75% correct performance such that a duration of about 100 ms stimuli would be required regardless of head-turn velocity. Results were consistent with that hypothesis at higher velocities but inconsistent at 25%.

In order to determine whether the temporal dynamics observed in the dynamic localization tasks are specific to auditory-vestibular integration, discrimination of left-to-right/right-to-left source motion in an equivalent auditory-only task was performed by the participants. Performance was assessed based on left-to-right or right-to-left discrimination accuracy. It was hypothesized that the duration-limit would not apply in this task since we hypothesized that it was likely due to the contribution of vestibular input required during dynamic sound localization. The following sections discuss these findings in more detail.
4.1 Dynamic Front/Back Sound Localization Performance

4.1.1 Benefit of Head Movement in Resolving Front/back Reversals

When front/back sound localization performance was compared between the static condition and the two head movement conditions (passive/active), results demonstrated a significant benefit of both active and passive head movement. An increase in minimum head movement angle was required with increase velocity for low-frequency stimuli, in which spatial window widths of approximately 2.6-5°, 5-10°, and 10-20° were required at 25°/s, 50°/s, and 100°/s, respectively for both passive and active head movement conditions to reduce front/back reversals. The required increase in minimum head movement with increasing head velocity is consistent with findings that demonstrate a decreased sensitivity to source motion at high velocities (Chandler and Grantham, 1992).

The finding of head movement benefit is consistent with other studies that investigated the role of head movement in normally hearing listeners. Thurlow and Runge (1967) demonstrated that azimuthal localization error was significantly reduced for both high-pass, low-pass, and click-stimuli when head rotation of 19.8°/s (similar to our 25°/s velocity condition) was used by blindfolded participants. Perrett and Noble (1997) showed that even if the listener is not facing a sound source, a (passively or actively) moving auditory system is able to produce information that can help localize the auditory target in space.

Such findings have been seen to translate into animal localization studies where head movement was the factor of interest. Tollin et al. (2005) performed a study in which cats were trained to localize sound sources by using eye position under conditions of free head movements or restrained head movement. Stimuli were broadband noises of a short (15 ms), intermediate (164 ms), and long (1000 ms) durations. Results demonstrated significantly improved localization performance in the unrestrained head movement condition for all three durations of stimuli presentation. Populin et al. (2006) also demonstrated better localization performance of 500-1000 ms broadband noises in monkeys for unrestrained head movement conditions during stimuli presentation.
compared to when their head was limited by a restraint. These findings support findings that the auditory system processes changing ILD and ITD information that is generated by head movement in space.

4.1.2 The Influence of Sensorimotor Integration of Vestibular and Proprioceptive Cues in Processing Dynamic Sound Localization Cues

Based on our results, we know that head movement is beneficial to dynamic sound localization but how does the auditory system know where the head is and what it is doing during the movement? In a recent study, Aytekin, Moss, and Simon (2008) pointed out that accurate sound localization is not limited to an acoustic phenomenon but rather that it is a complex one, involving a multi-modal processing of information to create an auditory space.

From the present study, several conclusions related to the multi-modal integration of auditory-vestibular and/or auditory-proprioceptive systems during head movement in dynamic sound localization can be drawn. To measure the extent to which vestibular and proprioceptive cues influence processing of dynamic sound localization cues resulting from head rotation, we measured in static, passive, active, counter, and dynastatic conditions, the ability of normally hearing listeners to localize front/back sources of low-frequency sounds.

Since the low-frequency stimuli could not have been accurately localized via spectral cues, better overall performance in the active condition (that had both vestibular and proprioceptive/afferent input) suggests that the head-movement-related changes in interaural cues were appropriately combined and integrated with available vestibular and/or proprioceptive information about head movement. Similar performance in the passive condition, where participants conceivably only had vestibular input suggests that active head movement is not required for correct integration of dynamic localization cues with the head movement in space, which suggests that only vestibular input is necessary and that proprioceptive input is not necessary. On the other hand, poor performance in the counter condition (where the participant had only information from proprioception and
efference copy) suggests that proprioceptive feedback is neither sufficient nor necessary, but rather that only vestibular inputs are necessary and sufficient for correct interpretation of dynamic auditory cues generated by head movement. Finally, poor performance in the dynastatic condition (no vestibular or proprioceptive input) demonstrated that although participants were being presented with dynamic localization cues that one would get from head movement (without actually moving the head, and thus, eliminating both sensorimotor cues), they still could not accurately localize the front/back sound sources, suggesting that the auditory system requires the necessary vestibular input in order to correctly interpret the dynamic localization cues. These findings are consistent with, in the direct context of dynamic sound localization, previous perceptual research done by Lewald (2000), which demonstrated that information generated by the vestibular system is taken into account by the auditory system during sound localization when illusions of head movement were created by tricking the system in its perception of space and/or movement by cold-caloric stimulation (Section 1.2.3).

It is not precisely known where the auditory and vestibular information is being integrated in the nervous system, although there are many polymodal components of projections that originate from the brainstem and travel to the cortex and that may potentially interact directly or indirectly at a number of levels, both subcortically (Oertel & Young, 2004) and cortically (Phillips-Silver & Trainor, 2007). Existing literature suggests that ITD cues are encoded by cells in the medial superior olive (MSO) (Goldberg and Brown, 1969; Yin and Chan, 1990), while spectral cues are encoded in the dorsal cochlear nucleus (DCN) that are thought to show sensitivity to sharp notches in the spectra (Young and Davis, 2002). Along these lines, it is conceivable then that the processing of spectral information used in the static front/back localization task may stem from the DCN. However, for the dynamic localization tasks, the processing of changing ITD information generated from head movement done by the MSO needs to be integrated with vestibular information about head movement suggests that such processing of dynamic cues may take place elsewhere in the nervous system. Moreover, the finding that dynamic cues do not seem to dominate spectral cues also argues for separate loci of processing. While visual-vestibular, and auditory-proprioceptive (or somatosensory) integration has been well studied both at the perceptual and physiological level (256 and
175 Pubmed results for search terms “visual vestibular integration” and “auditory somatosensory integration”, respectively), evidence for auditory-vestibular integration at the physiological level remains an area to be further explored and examined (only 70 Pubmed results for search terms “auditory vestibular integration”).

4.1.3 Temporal Integration

In the passive and active conditions, we were able to observe that the effects of increasing velocity and increasing spatial window width were almost exactly reciprocal, such that performance was stimulus duration-limited at the higher velocities of 50°/s and 100°/s. To reach 75% correct front/back discrimination (regardless of cue-change), about 100 ms duration was required. This temporal integration is seen in both passive and active conditions at 50°/s and 100°/s, whereas at 25°/s the stimulus duration required was about 150 - 170 ms. It is unknown why this increase in duration is required at the slowest velocity, especially because the temporal integration of 100 ms duration trend is also seen at faster velocities of 200°/s and 400°/s in previous head movement studies (Macpherson & Kerr, 2008; Macpherson, 2013) (Fig. 41). Results in those experiments were derived from proportion of responses yielding “small” azimuthal errors that was computed as a measure of performance, in the same way the basic localization screening measure was computed in the present study (Section 3.1.1).

The increase in stimulus duration threshold during the 25°/s condition may possibly be due to a loss of vestibular sensitivity to slower horizontal rotations of the head. Previous findings (Grabherr et al., 2008; Valko et al., 2012) demonstrate that horizontal motion thresholds in the vestibulo-ocular reflex began to increase at 0.2 Hz, which is equivalent to approximately the oscillation frequency (0.1875 Hz; Fig. 8) required for rotation in the present study for a velocity of 50°/s during the passive and active conditions. This suggests that the poor sensitivity to dynamic localization cues at 25°/s in the present study might be a consequence of the declining sensitivity of the vestibular system at lower oscillation frequencies required at this velocity. Furthermore, it is also possible that the results at the slower velocity of 25°/s may be an aberration, as it was commonly noted by the participants that they felt fatigued during the task due to the slower nature of the head and/or movement and were subsequently unable to focus as well compared to the faster
velocities. This may also explain why post hoc analyses of the two conditions at 25°/s showed significant differences, which was inconsistent with the hypothesis that no significant would be observed between the passive and active conditions.

**Figure 41.** Effect of stimulus duration and head velocity on localization performance. Illustration provided by Ewan Macpherson.

During a head rotation (passive or active), a listener must determine whether the sound source moves to the left or to the right and whether it moves in the same direction as the head rotation during dynamic front/back sound location. In order to examine whether these temporal dynamics observed at the higher velocities are specific to auditory-vestibular integration, the L/R-ITD task was performed in which participants were instructed to discriminate the direction of motion of low-frequency stimuli that monotonically increased or decreased in ITD. Results demonstrated that performance improved with greater cue change, while little to no velocity penalty was observed for higher rates of ITD change.

When the same task was run (L/R-Dynastatic task) but with the same HRTF-filtered stimuli used for the dynamic localization tasks in order to simulate a more realistic acoustical representation, it appeared that performance improved with greater cue change. Unlike the LR-ITD task however, where only ITD was manipulated, there was a greater velocity penalty, which suggests that the difference in stimuli (perhaps more ILD cue
changes from the HRTF-filtered stimuli) might account for this difference in observed velocity penalty. The difference in stimuli may also account for why we unexpectedly observed a difference in left-to-right/right-to-left discrimination performance between the two tasks, as the participants may have used the extra ILD cues derived from the LR-Dynastatic task to assist them.

The finding of a velocity penalty without a vestibular signal suggests that front/back localization performance can be explained based on sensitivity to the changing acoustic cue information and that the temporal dynamics observed in the passive and active conditions are not a signature of auditory-vestibular integration.

4.1.4 Clinical Relevance

A study that examined the role of the vestibular system in a whole-body motion discrimination task demonstrated that patients with complete bilateral vestibular ablation had a significantly higher average threshold measurement than those without vestibular ablation (Valko et al., 2012). As demonstrated in this present study, when the vestibular system is not influencing the auditory system with information about head movement, sound localization in the front and back dimension is inaccurate for normally hearing listeners. Thus, it is likely that in clinical populations that demonstrate vestibular difficulty, they will not demonstrate accurate sound localization performance since the auditory system is not receiving information about head movement from the vestibular system.

4.2 Limitations

A possible limitation of this study is that the participants’ knowledge of the experimental setup in the counter condition could have informed the participants that their head was not moving in space, which may have reduced the influence of proprioceptive input they were generating. Future work might involve using a robotic apparatus that would allow for the relationship between head-on-body and head-in-space motion to be manipulated without the participant’s knowledge in order to provide less contextual information about what their heads were doing in space.
Another limitation was that participants felt fatigued particularly in the slowest head/body rotation conditions at 25°/s. Future work may incorporate more break times and/or modify the number of testing sessions.

4.3 Future Work

Recent findings have demonstrated that optokinetic stimulation alters sound lateralization sensitivity during interaural time difference discrimination (Otake, 2006). While it has been postulated that visual stimulation may play a role in dynamic localization, whether they are sufficient are unknown. Future research might incorporate the use of a head-mounted display to create an optokinetic field for a listener whose head will be stationary. If the visual input is sufficient for the auditory system to accurately interpret dynamic localization cues, the perception of the front/back location of a sound stimulus should change if the optical rotation created by the display is reversed in direction.

Future research might also attempt to determine the relative dominance between the vestibular and proprioceptive cues in the interpretation of dynamic localization cues by counter-rotating a listener’s body at twice the speed to that of their head rotation as to produce conflicting vestibular motion cues and proprioceptive input from the neck.

The addition of participants with vestibular impairment in future studies might provide additional information about the influence of cues from the vestibular system during localization during head movement. It has been hypothesized above that vestibular impaired populations will not be able to accurately localize front and back sound sources, particularly in the passive condition where only the vestibular system is involved because the auditory system would not know where the head is and what it is doing in space during movement. If so, this would reflect the necessity of the vestibular system for accurate sound localization during head movement. However, if such participants demonstrate accurate performance in the active and/or counter condition, this may further indicate plasticity in the relative weighting between the two sensory cues, which may reflect that the proprioceptive system may compensate for the lack of vestibular input. Such results may be helpful in advising vestibular impaired populations on the
importance of manipulating *active* head movements to aid with accurate sound localization.

### 4.4 Significance

Dynamic binaural sound localization plays an important role in our ability to make sense of the sounds that occur around us even in noisy or reverberant environments. It is a complex phenomenon, requiring normally hearing listeners to acquire a sense of auditory space by combining multi-modal information from their surroundings to accurately localize a sound source even during head movement. As opposed to previous studies that examined the biasing effects of the vestibular and proprioceptive systems during static sound localization, the present study is the first to successfully demonstrate the roles of these systems in the direct context of dynamic sound localization and may offer more reliable conclusions.
References


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