THE END OF LOCALIZATION DOMINANCE IN HUMANS

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ABSTRACT

Mammals and birds are able to localize sounds coming directly from a source and are less influenced by reflecting sounds, known as echoes. This perceptual feat is accomplished via *the precedence effect*, in which sounds arriving in rapid succession (called "leads" and "lags") are perceived as a single sound coming from the leading source location. Increasing the lead/lag delay causes a recovery in the perception of the lag, called *echo threshold*. In this study, longer noises overlapping in time create a stimulus where the leading or lagging sound is present alone, each flanking a segment when both sounds are present. Previous study in barn owls has shown that the *lag-alone* segment is responsible for perception of the lagging source, and thus echo threshold. Human subjects were asked to localize lead/lag pairs with varying lead/lag-only segment durations. The length of the *lag-alone* segment strongly influenced whether subjects heard two sources, while no such relationship existed for the *lead*-alone segment. The duration of the *lag-only* segment also influenced the ability of subjects to determine the temporal order of the lead/lag pair. The findings from the current study suggest that human behavior mirrors owl behavior in that the duration of the lag-only segment is responsible for echo threshold.

Approved: [redacted]

Dr. Terry Takahashi

Acknowledgements

I'd like to thank Liz Whitchurch, Avinash Bala, and Kip Keller in the Takahashi Lab for all their help with MATLAB programming. I'd especially like to thank Terry Takahashi and Brian Nelson for their time, effort, and support at every step of this project. Also, I'd like to thank Jenna for making me dinner, as well as my other friends for keeping me sane. You know who you are.

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INTRODUCTION

A Complex Auditory Environment

Day-to-day human life requires functional sensory systems that enable us to perceive the surrounding environment. Often, the surrounding environment assessed by our sensory systems can be very complex, so that processes necessary to analyze them can become very sophisticated. The auditory pathway in the human brain is one such sensory system that is able to process very sophisticated stimuli from the environment and transform it into useful information. Echoes present a potentially complex situation for our auditory system to resolve, as multiple sound waves arriving from different locations can arrive in our ears not only directly from the sources themselves, but from nearby surfaces that reflect the direct sound waves. Despite this complexity, humans converse in echoic environments all the time and sort sounds of interest from echoes without difficulty. The current research addresses how the human auditory system accomplishes this feat. As our understanding of the auditory system grows, so too will the ability to treat defective auditory systems (i.e., through the development of more advanced hearing aids). To begin, I will discuss the manner in which the auditory system processes single sounds, and then move on to the processing of sounds in a complex echoic environment. I will then describe the results from my own experiments which will show that when a direct sound and its delayed echo overlap with each other temporally, the perception of the echo is determined by the length of time that the echo is present alone.

Localization of Single Sounds

Humans and other animals compare the auditory inputs from both ears to localize sounds. Interactions between these inputs are known as *binaural cues*. Locating the source of a sound on the horizontal axis requires the information from two such binaural cues, known as *inter-aural time difference* (ITD) and *inter-aural level difference* (ILD), respectively. The ITD of a sound is the difference in arrival-time for a sound between two ears. The greater the ITD, the greater the perception that the sound is coming from a location to the left or right of the listener. ILD represents the difference in "sound pressure level," (SPL) or volume between the two ears. ITD and ILD are processed in separate pathways leading to an area of the midbrain (in avian and mammalian spp.) known as the external nucleus of the inferior colliculus (ICx). The neurons in the ICx respond selectively to specific values of ITDs and ILDs, and are therefore responsive to sounds arriving from a particular location in space. This location in space is called the cell's spatial receptive field (SRF). Adjacent cells have adjacent SRF's, thus forming a map based on these binaural cues. Sounds from specific locations in space will produce binaural cues measured at both ears, which may evoke a response in neurons within this array that is "tuned" for those cues. This array can then be considered a "space-map," on which a sound generates a focus of neural electrical activity, the location of which corresponds to the location of the sound in space. This space map thus functions much like a sonar screen on which sounds in the environment may be displayed.

The auditory space map was discovered in owls (Knudsen & Konishi, 1978) and subsequently in the cat (Middlebrooks and Knudsen 1984). Whether or not humans have one is not known, but it is commonly accepted that they do.

Localization Amid Echoes

In the auditory space-map of the ICx, the identity and locations of sounds respectively determine the temporal pattern and location of neuronal activity. When the environment contains echoes that overlap with the sound arriving directly from the source, the mixing of these soundwaves at the eardrums alter the binaural cues and may degrade the neural signal that represents the two sound sources (Keller and Takahashi, 2005) (Fig. 1). Despite these degraded cues, humans often carry on conversations in echoic rooms and hallways without difficulty. How does the auditory system distinguish these direct sounds from the reflected sounds in order to extract pertinent information about them?

The collection of phenomena thought to assist the auditory system in preferentially selecting direct sounds over echoes is known as "the precedence effect" (Wallach et al., 1949). Auditory perception under the precedence effect depends on the time delay separating the sound coming directly from the source of interest, i.e., the "leading" sound, from the echo or "lagging" sound (Fig. 2). This should not be confused with ITD, which is a time-of-arrival difference of a *single sound* between both ears.

When two sounds are presented simultaneously from different locations in space, the perception of the event depends on the specific time delay between the two sounds. When the delay between lead and lag is in the range of 1-5ms, the listener will perceive only one sound coming from the direction of the leading source. This is a component of the precedence effect known as "localization dominance", or "the law of the first wavefront." (Wallach et al., 1949; Litovski et al., 1999) As the delay is gradually increased to about 6ms, humans begin to hear the lagging sound (i.e., the echo). The delay between leading and lagging sounds at which the lag sound is perceived is called the "echo threshold."

When a single sound is presented to a barn owl or cat from a particular location in space, a corresponding location in the ICx (or analogous structure) fires a neural response. When a single sound is presented from a different location, a different location in the ICx responds (Keller and Takahashi, 1996). Neurophysiological studies as to why the perception of a lagging sound is dependent on the lead-lag delay have determined that a neuron's response in the ICx to a lag source is much weaker than the neurons response to a lead source, and that as the delay is increased, this response recovers, leading to echo threshold (Yin, 1994; Keller and Takahashi, 1996; Tollin et al., 1994, Tollin and Yin, 2003; Tollin 2004). In other words, when two sounds are played from different locations at a short delay, there will be a burst of neural activity in the ICx at the position corresponding to the leading sound, while the lag sound will elicit a weaker response at its corresponding location. As the delay increases, the neural response to the lag will increase, until the response is large enough for the lagging sound to be perceived by the animal.

Studies of the precedence effect are typically done with clicks, which offer the advantage of being so short that there is typically no superposition of the lead with the lag. Therefore, the echo threshold has been thought to be related to time-of-arrival separation (the inter-click interval) between these two short noises. Although clicks are useful for neurophysiological experimentation in order to simplify neural responses to each sound, they are not very realistic. In nature, sounds typically last longer than the delay between a sound and its echo so that the directly-arriving sound and its echo overlap in time. Therefore, there is a period of time when both the leading and the lagging sounds are superposed, flanked on each side by *lead-only* and *lag-only* segments during which only the lead or lag sounds are present alone (respectively) (Fig. 2).

However, when sounds overlap in time, what is responsible for the echo threshold? Since the recovery of lag perception at longer delays has classically been thought of as the inter-stimulus interval between lead and lag clicks, there has been a hypothesized "inhibition-like" process across the ICx in which the response to the lead inhibits the response to the lag at short delays. At longer delays this hypothesized inhibition weakens, allowing for perception of the lag. Applying this classical situation to longer, more realistic stimuli, the inter-stimulus interval could be considered analogous to the *lead-only* segment of the superposed stimuli. Thus, lengthening the lead-alone segment, which is equivalent to increasing the inter-stimulus interval, would presumably weaken this hypothetical inhibition process and allow for the response to, and the perception of the lagging sound. On the other hand, because the lead/lag delay also determines the length of the *lag-alone* segment, this lag-alone segment may be responsible for eliciting the neural response that produces echo threshold. Recovery of responses to the lag in the case of superposed sounds could thus potentially be attributed to two different events: *1.) The neural response during the superposed segment, e.g., at the onset of the lag sound* (the "classical" view) and *2.) The neural response at the offset of the lead sound* (Fig.2, Fig. 3).

Recent studies in barn owls (*Tyto alba*), which, like humans and other species, seem to experience the precedence effect, have begun to address the alternative hypotheses proposed above. Barn owls are an established model for spatial hearing, and their behavioral responses to echoic stimuli often mirror those observed in human subjects (Nelson and Takahashi, 2008; Keller and Takahashi, 1996; Spitzer and Takahashi, 2006; Spitzer, Bala, and Takahashi, 2004). When barn owls are presented with an auditory stimulus from a particular location in space, they perform a rapid head-turn to the source of the sound. Similarly, when a specific location of the barn owl ICx is stimulated electrically, the barn owl performs a head-turn to the spatial position represented by that ICx location (Keller and Takahashi, 1996).

Firing rates of single neurons in the ICx of the barn owl were recorded in response to leading and lagging sounds. These firing rates were compared to the proportion of barn owl head-turns to leading and lagging sources, and the results suggest that the neural response to the *offset of the lead sound*, or to the lag-only segment, is the signal that allows the owl to perceive and localize the lag (Fig. 2, Fig. 3). Correspondingly, the authors found that the neural response to the lag increases with a longer lag-only segment, when the initial lead/lag delay is kept constant. If the duration of the lag-only segment is kept constant while the duration of the lead-only segment varies, there is no observed relationship of head-turns towards the lag (Nelson and Takahashi, in prep.). In other words, if the duration of the lag-only segment is increased, barn owls are more likely to perceive the lagging sound. Increasing the duration of the lead-only segment does change how the barn owls perceive the lagging sound.

*The purpose of this study is to behaviorally examine whether this phenomenon generalizes to the **human** auditory system.*

METHODS

Studies were carried out under a protocol (X309-08) approved by the Institutional Review Board for the Protection of Human Subjects.

Lead and Lag Pairs

Stimuli were similar to those used by Nelson and Takahashi (in prep.). Broadband noise-bursts (0.25-3 kHz; ± 1.5dB; with linear, 2.5 ms onset and offset ramps) were used. Lead and lag noises were produced using a single, unique, noise token on each trial. Lag sounds were delayed 3, 6, 12, or 24 ms and both stimuli were converted to analog at 48.8-kHz, amplified (RP2.1, HB6, Tucker-Davis Technologies), and presented over headphones (Sennheiser HD 280 Pro). Lead and lag sounds were correlated, meaning that they were the same waveform, just delayed. In all cases, a 30ms lead noise was presented, followed by a correlated lagging noise of varying duration and delay. Altering lead/lag pairs in this manner allowed for 16 distinct auditory events between 27-54ms of total duration, with lead-only and lag-only segment durations of 3, 6, 12, and 24ms, respectively (Fig. 4).

Procedure

Six human subjects between the ages of 22 and 24 from the University of Oregon with no self-reported hearing deficits participated in this study. All subjects were presented with the aforementioned 16 lead/lag pairs through the computer user-interface system generated in MATLAB (The MathWorks), via circumaural headphones (Sennheiser 280 Pro) and inside a double-walled anechoic chamber (Industrial Acoustics Co. IAC; 4.5 m × 3.9 m × 2.7 m). The intensity of the stimuli was adjusted at the beginning of each session according to the comfort level of each subject.

At the beginning of each trial, a reference noise with an ITD of 0 μs was presented to a subject one second before a lead/lag pair was presented. Each subject judged the lateral position of a lead/lag pair using the reference sound to facilitate localization of the lead/lag pair (see Dizon & Colburn, 2006). In other words, the subjects used the perceived position of the reference sound as marker for the position directly in front of them, so they could more easily localize the lead/lag pair. A single session consisted of a subject being presented with all 16 lead/lag pairs ten times and in random order for a total of 160 presentations. The ITD of each lead/lag presentation switched randomly between either 250μs or -250μs, so that in any given trial, the lead and lag were always presented from opposite locations. Five sessions were conducted with each subject, totaling 30 sessions.

Computer Interface

The computer interface (Fig. 5) consisted of two arcs, representing the horizontal plane immediately in front of the subjects' head. The subjects placed colored bars to represent where they localized a sound source, if it was perceived. One such arc represented the leading sound. The second arc represented the lagging sound. When a lead/lag pair was perceived by the subject to have come from two different sources, the subject used a computer mouse to plot the perceived location of the leading source on the lead arc, and the perceived location of the lagging source on the lag arc. If no lagging source was detected, the listener was instructed to leave the lag arc blank. (Fig. 5)

Subjects were also asked to indicate their level of certainty in their localization decision, and did so by varying the width of the colored bars plotted on the lead and lag arcs. A large bar-width indicated that the subjects felt that their localization was more ambiguous, while a small bar-width indicated that the subjects were confident in their localization.

RESULTS

Perception of the Lag as a Function of Lag-Only Segment Duration

To quantify the behavioral response of each subject towards the lagging source, the proportion of instances that the subject perceived one sound versus two sounds was calculated for each lead/lag pair and averaged across all sessions (Fig. 6). A strong relationship exists between the probability of hearing two sources and the duration of the lag-only segment, whereby increasing the duration of the lag-only segment increased the chances of that the listener detected the lag. Also, notice that this relationship is nearly identical for all lead-only segment durations (Fig. 6). Remember that if echo threshold were dependent on the lead/lag delay, as suggested by classical studies (Wallach et. al 1949, Yost and Soderquist, 1984, Yang and Grantham, 1997; Keller and Takahashi, 1996, Yin, 1994), lengthening the lead-alone segment should increase the likelihood of perceiving the lagging sound (Fig. 6). The data suggest that the lead-alone segment, and thus lead/lag delay (in the classical sense), do not have a significant effect on echo threshold.

The relationship between the duration of the lag-only segment and the probability of hearing two sounds is displayed in Figure 6. The top four plots represent individual subjects to lead/lag pairs, and the four plots immediately below refer to the average responses across subjects and sessions. In all plots, the Y-axes represents the proportion of instances the subjects heard two sources, given from 0 (i.e., subjects perceive one source) to 1 (i.e., subjects perceive two sources). The x-axes in all plots refer to the lead-only and lag-only segment durations of the stimuli. The lead-only segment durations are displayed above the lag-only segment durations, each given in milliseconds.

The upper two rows of plots in Figure 6 show that when the lead-only segment is held constant (value given by the top number on the x-axes), and the lag-only segment is lengthened (value given by the lower number on the x-axes), the probability of hearing two sounds increases in a similar manner, regardless of the lead-only segment duration. The colored lines in the upper-most plot refer to individual subject responses across all sessions. When the lead-only segment was held constant at 3ms, the cross-subject average typically indicated that two sources were detected 10-20% of the time, and in all cases, the probability of hearing two sounds increased in a linear fashion until it reached around 100% with a lag-only segment of 24ms.

The bottom plot displays the behavioral responses of barn owls to similar lead/lag combinations (Fig. 6). The results observed in the human subjects closely mirrors that observed in the barn owl behavioral data. This suggests that the current data is consistent with the trends observed in Nelson and Takahashi (in prep.). Again, colored lines indicate individual owl subjects, while the dashed line indicates the average (Fig.6).

The human inter-subject variability in these data is very apparent, and is especially interesting considering the relative absence of variability in the responses of the barn owls. For example, subjects 3 and 6 were much more likely than the rest of the subjects to perceive two sources, regardless of the specific lead/lag pair presented.

Perception of the Lag as a Function of Lead-Only Segment Duration

The data suggest that the duration of the lead-only segment does not influence the probability of detecting two sources as strongly as the duration of the lag-only segment. Plots in Figure 7 are grouped in a similar manner to those in Figure 6. Human behavioral trends displayed in the top two rows show that when the lag-only segment is held constant (value given by the bottom number on the x-axes), and the lead-only segment is varied (value given by the top number on the x-axes) there is no observable relationship for the probability of hearing two sounds (Fig. 7). Notice that the ability to detect two sounds is more dependent on the constant lag-only segment duration, producing a step-like function. This is consistent with the findings of Nelson and Takahashi (in prep.). Again, inter-subject variability among the human responses is very apparent and even more extreme when the lag-only segment is held constant (Fig. 7).

Although this behavioral relationship largely mirrors that seen in the barn owls, there is an interesting deviation. Notice the inverted shapes seen in human subject data, especially noticeable when the lag-only segment is held constant at 3 and 6 ms (plots of the average responses make relationship especially apparent), while the proportion of responses of the barn owls to constant lag-only segments produce fairly flat lines (Fig. 7). Interestingly, the average subject was more likely to perceive a single source with a lead-only duration of 3 and 24ms, while more likely to perceive the lag with a lead-only duration of 6 or 12ms, showing an unclear relationship between the lead-only duration and the perception of the lag (Fig. 7).

Influence of Lag-Only Segment Duration on Localization of the Lead

In addition to the initial question, an interesting relationship was observed between the duration of the lag-only segment and the perception of the *leading* sound. When the lag-only segment was lengthened, regardless of the duration of lead-only segment, all subjects were less likely to accurately localize the lead.

Recall that subjects were asked to record the locations at which they perceived the lead and lag sounds on separate arcs in their response interface (Fig. 3). Figure 8 plots the subjects' responses on the lead arc (left column) and lag arc (right column). The x-axes indicate where the lead or lag (if perceived) was localized, anywhere from the left side (-90) to the right side (90). The black and red speakers represent the locations of the lead and lag sound sounds, respectively. The y-axes indicate the number of localization observations at a specific position, with the results from each subject stacked on top of each other. Thus, a frequency histogram is displayed that shows where subjects localized the lead and/or the lag for different lead/lag pairs, so that groups of vertical bars show an area commonly localized (Fig. 8). In this figure, all lead sounds were presented from the right side, and all lag sounds were presented from the left side, as shown by the corresponding speaker icons. Thus, for example, if subjects tended to perceive and localize only the lead source a peak in the distribution would be observed in the left column (i.e., on the lead arc) underneath the black speaker icon. Similarly, if subjects tended to perceive and localize only the lag source, a peak in the distribution would be observed in the right column (i.e., on the lag arc) underneath the red speaker icon.

When the lag-alone segment was 3ms, subjects often localized the lead with precision, and tended not to report or localize the lag source. However, when they did report the lag source, they localized it either to the left or the right side with more or less equal probability. As the lag-alone segment increased, the number of responses to the lag grew, and lag localization became increasingly bimodal, indicating that subjects could not tell whether the lag sound came from the left or right. Interestingly, the localization of the lead also became increasingly bimodal, and when the lag-only segment was lengthened to 24ms, the subjects were no better at localizing the lead than the lag.

DISCUSSION

Perception of the Lag Is Dependent on the Lag-Only Segment

I hypothesized that echo threshold could be dependent on the lead/lag delay, (i.e. the duration of the lead-alone segment) or alternatively, the duration of lag-alone segment. Consistent with the hypothesis, as well as with the previous findings of Nelson and Takahashi (in prep.) in the owl, the findings from this study suggest that the duration of the lag-only segment is the primary factor in the ability to detect two sources (Fig.6). This supports the new paradigm of the effect of echo delay on the precedence effect presented by Nelson and Takahashi (in prep.); the significance of the echo-delay for the perception of the lagging sound is only that it determines the length of the lag-alone segment. As in owls, human echo threshold is thus determined by the echo-delay large enough to produce a sufficiently long lag-alone segment.

No Clear Relationship Between Lead-Only Segment and Lag Detection

In the traditional and typical precedence effect paradigm, short clicks (typically less than 5ms) are used for leading and lagging sounds, with no temporal overlap between them (Wallach et. al 1949, Yost and Soderquist, 1984, Yang and Grantham, 1997; Keller and Takahashi, 1996, Yin, 1994). The dominance of the leading sound in the perception of the event has traditionally been explained by a putative inhibition-like process, where, at short delays, there is inhibitory activity across the IC to limit activity evoked by the lag. Applying this traditional paradigm to that of this study, where longer noises are superposed temporally, recovery from this inhibition-like process would hypothetically occur when the delay between the onset of the lead and the onset of the lag is substantially lengthened (i.e., a long lead-alone segment). However, this study shows that in humans there is no clear relationship between length of the lead-alone segment and the ability to perceive the lag source. If there were such a relationship consistent with the traditional "click" paradigm, lengthening the duration of the lead-alone segment would release the lag-response from its inhibition-like process, thereby enabling perception of the lag. Consequently, lengthening the lead-alone segment should have accordingly increased the probability of perceiving the lag. My data, however, do not suggest that this relationship exists in the human auditory system (Fig. 7).

Differences Between Humans and Owls

Although for both human and owl subjects no relationship was observed between the lead-only segment and perception of the lag, humans and owls responded slightly differently when the lag-only segment was held constant. As previously noted, the barn owls were not more likely to perceive the lagging source at any particular lead-alone segment duration, yet when the lag alone segments were held at 3 or 6ms, several of the human subjects were more likely to perceive a single source at lead-alone durations of 3 and 24ms (Fig. 7). The increased perception of two sources when the lead-alone segment was increased from 3 to 6ms could potentially be due to higher level processing that is not known to be existent in barn owls, or it may reflect the high inter-subject variability apparent throughout the sessions.

Inter-subject variation is known to be an important factor in human behavioral studies, especially when either the stimuli or task is complex. For example, a study using clicks by Freyman et. al (1991) showed that some subjects perceive two sources at relatively short delays (2-4ms) while others perceive one source at delays greater than

10ms. This inter-subject variability is made more prominent by the learning effect (Litovsky et. al, 1999, Freyman et. al, 1991). Human subjects are prone to adopt their own strategies in completing the tasks presented in behavioral studies, and it became immediately obvious that subjects in the current study were training themselves and adopting such idiosyncratic strategies to perform the localization task. In the first session, all subjects seemed to respond very differently to different sounds. For example, certain subjects would be either very likely or unlikely to indicate the perception of two sounds, as well as be very likely or unlikely to indicate wide bar-widths. The subjects also required nearly twice as long to complete the first session compared to later sessions, showing that subjects trained themselves to complete the task with greater efficiency. When interviewed following the completion of the second session, all subjects acknowledged that they had established a more clear idea of what, as they noted, "they were listening for," and all subjects noted that their responses as a whole changed after their experience in the first session.

In the current study, at lag-alone durations of 3ms, only 2 subjects responded to the lead-alone difference between 3 and 6ms, as well as between 12 and 24ms. Likewise, 3 subjects responded in a similar manner when the lag-alone segment was held constant at 6ms (Fig. 7). The behavioral trends from subjects who did not respond in this way closely mirror the trends shown by barn owls. To address this issue in future studies, more subjects would need to participate to minimize inter-subject variability thereby getting a more accurate view of the behavioral trends of humans in general. More combinations of stimuli would also need to be presented, especially within the range of those stimuli eliciting responses to different lead-alone durations, in order to pinpoint a more clear relationship.

The increased perception of a single source when the lead-alone segment was 24ms and the lag-alone segment was either 3 or 6ms could be explained by the relative length of the lead-alone segment versus lagging stimulus. In this case, the subject is listening to 24ms of a single source for a relatively long period of time, while the lag is present only briefly. It could be that with a long lead-alone segment and a comparatively short lag-alone segment, the subjects listen to a single source long enough to discount the lag when it finally arrives. Hypothetically, this phenomenon could be minimized if the entire stimulus duration was lengthened, while the absolute lead-only and lag-only durations remain constant, so that the relative lengths of the lead-alone versus the lag-alone were not so extreme.

Lag-Only Segment Influences Perception of the Leading Sound

An unexpected finding was that the duration of the lag-alone segment make the localization of both the lead and the lag ambiguous (Fig. 8). This apparent error in localization could be due to degraded spatial information for lead in the presence of a more salient lag, but since the localization performance for the lagging sound also became increasingly bimodal, the error is most likely due to an inability of the subjects to determine the temporal order of the two sounds. In the procedural paradigm of this study, leading sounds and lagging sounds were always presented from opposing directions (e.g. lead on the left side, followed by lag on the right side) and never presented from the same side. When interviewed following the completion of a session, subjects acknowledged that at times it "was almost impossible to tell which sound was coming first," leading to localizations of the lead and lag which were both on the opposite sides of the respective sources, which would account for the bimodal localization of the lead/lag pair (Fig. 8). This result may have been an artifact of the lead/lag delays used, as well as the total durations of all stimuli presented. When the lag-alone segment was sufficiently lengthened to allow perception of the lag, the inter-stimulus interval in all cases was still too short to determine the temporal order of the lead and lag. The maximum delay used was 24ms, and the established perceptual threshold for humans to determine temporal order of auditory stimuli is a delay of around 30ms, depending on the subject (Hirsch 1959, Pastore and Farrington, 1996, Lewandowska et. al 2008). Furthermore, observations of temporal order confusion have been documented in studies using click stimuli with similar delays (16-64ms), evoking similar effects on lead and lag perception (Stellmack et. al 1999).

Though more investigation is necessary to determine a clearer role of the lead-alone segment on the perception of the lagging source, the results of this study show that indeed the phenomenon observed in Nelson and Takahashi (in prep.) largely generalizes to the human auditory system. Since the 1940s, echo threshold has been assumed to be dependent on lead/lag delay, but the findings from this study show that the lead/lag delay is not responsible for this phenomenon. Also, the duration of the lag-alone segment has been shown not only to influence the perception of the lag, but also the lead. A long lag-alone segment appears to hinder the ability of the human auditory system to determine the temporal order of the lead and the lag.

Figures

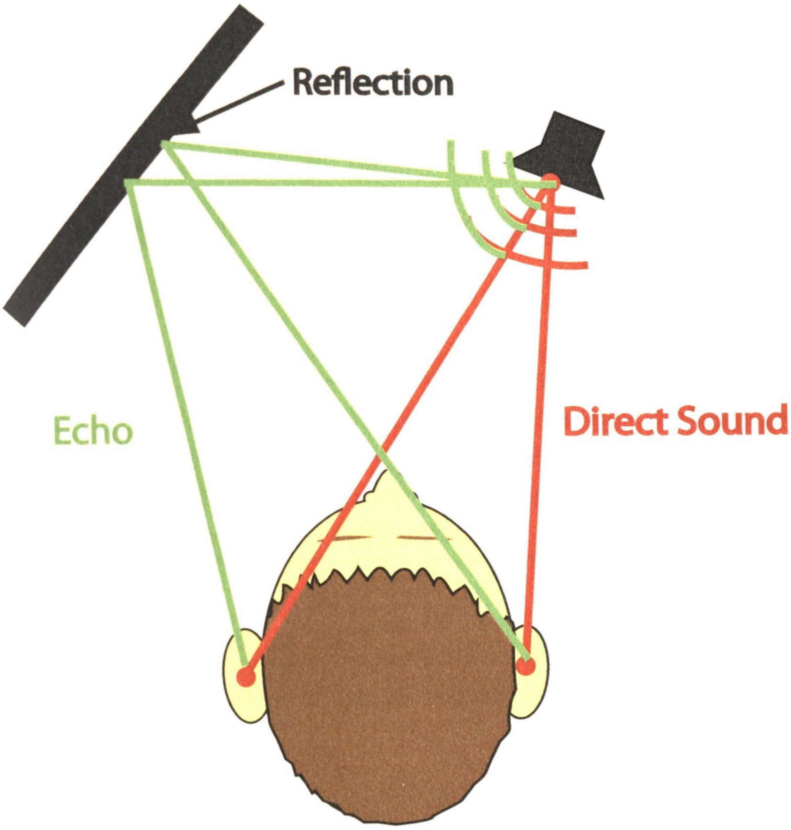

Fig. 1 – Illustration of a complex acoustic environment. Direct sounds (called "leads") travel directly to the listener and arrive at the ear before the reflected sound (also known as the "echo," or "lag"). The human auditory system effortlessly sorts the direct sounds from echoes.

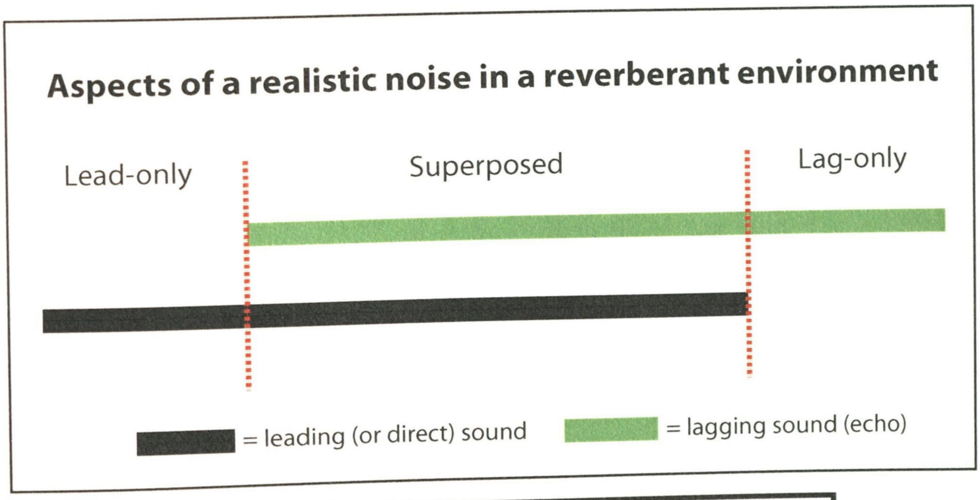

Fig. 2 – Illustration of the three different segments of a realistic noise stimulus in a reverberant environment. Long noises such as the ones displayed, overlap temporally, leaving a superposed segment flanked by a lead-only and lag-only segment, respectively. By contrast, click stimuli do not overlap in time.

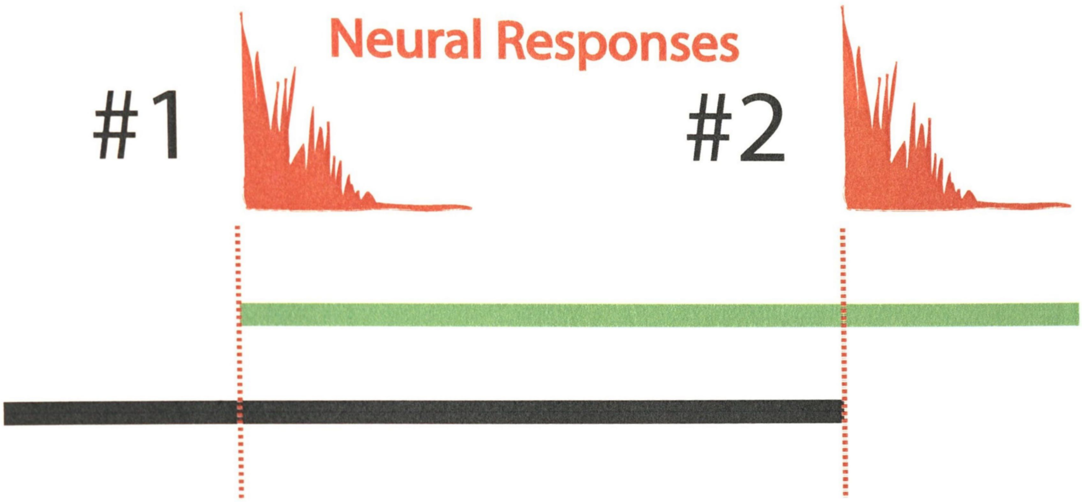

Fig. 3 – Two possible mechanisms for the recovery of the neural response to the lagging source are shown over a plot of the lead (black line) and lag (green line) over time. Either the response to the onset of the lag (#1), or the offset of the lead (#2), is responsible for the neural recovery to the lagging source, and thus responsible for echo threshold.

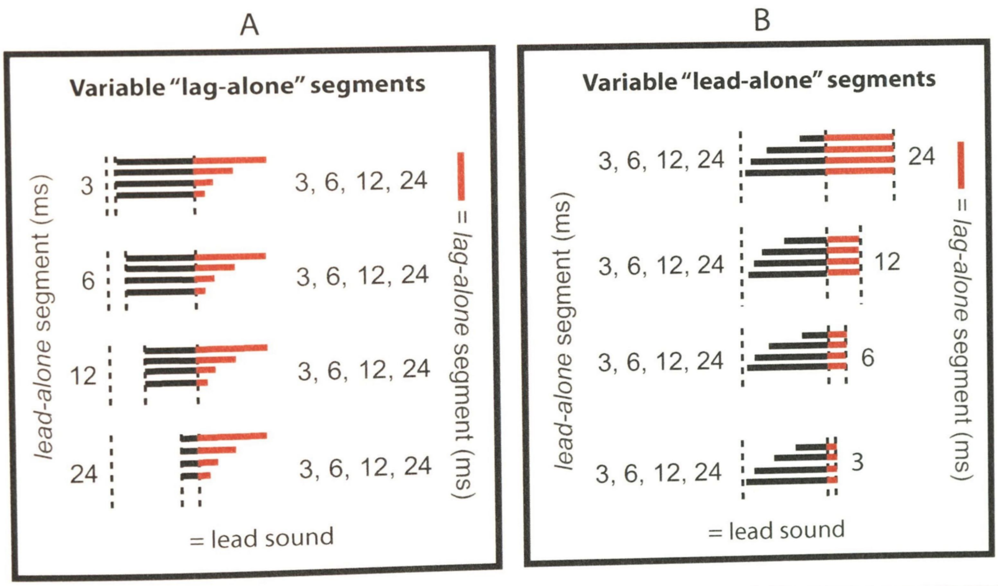

Fig. 4 – All lead/lag pairs are represented in this figure, but organized in two different ways. Each grey line represents the leading sound, while each dark line above it represents its lag/pair, so each lead/lag pair is represented by the grey lead with one of the black/red lags. The red lines represent the lag-only segment of the lagging sound. Part A (left side) displays groups of lead/lag pairs with constant lead-only segments (shown by the values on the left side of the panel) and for each delay displays variable lag-alone segments. Part B (right side) displays groups of lead/lag pairs with constant lag-alone segments, and displays variation in the lead-only segment according to each lag-only segment duration.

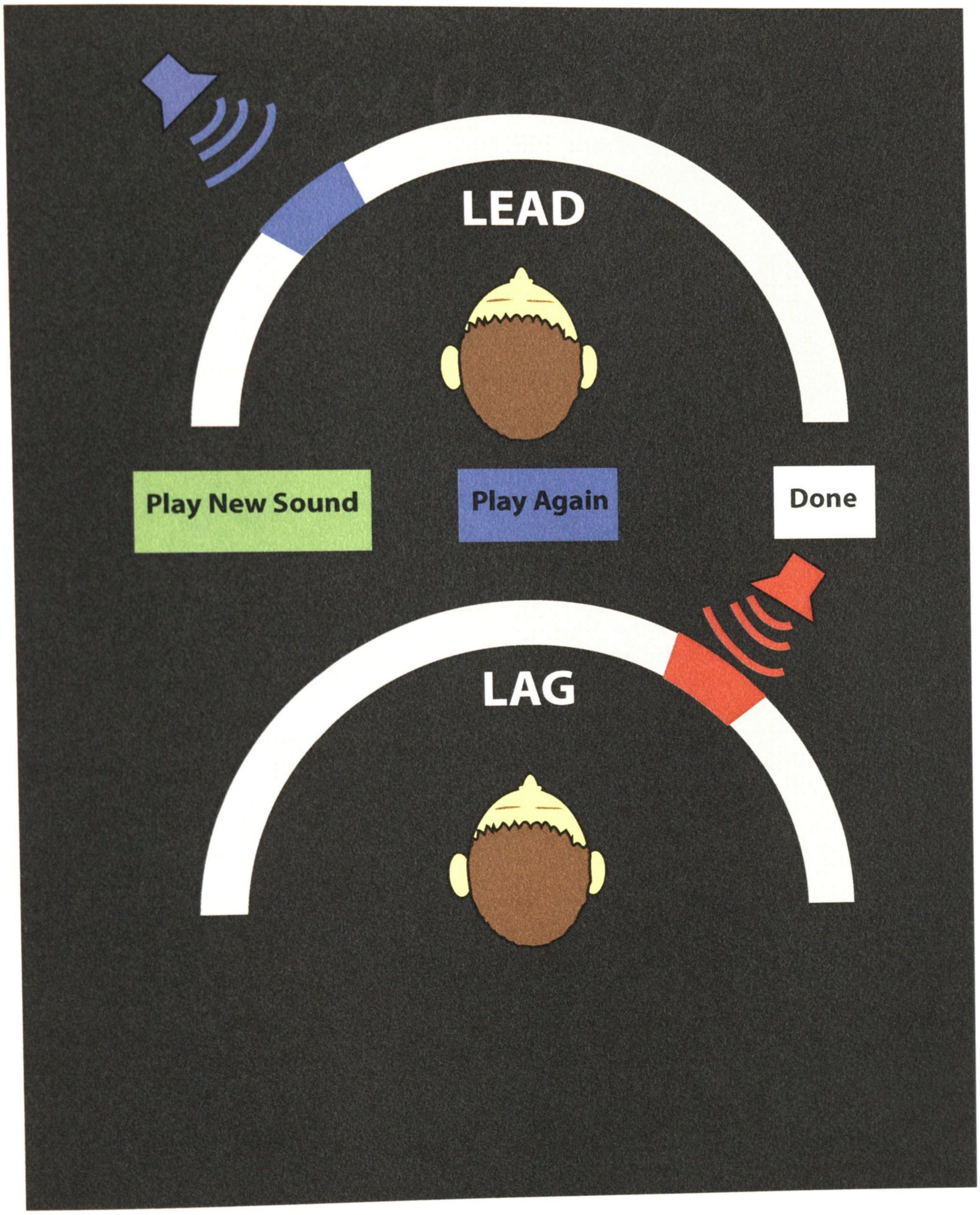

Fig. 5– Illustration of experimental paradigm; Subjects judged the laterality of a lead/lag pair against a reference sound, indicating the position where they localized the lead and lag (if perceived) on the corresponding arcs. Subjects were instructed to adjust the width of the colored bar plotted in order to indicate how certain they were that the sound came from the plotted location (narrow bar = more certain, wide bar = less certain)

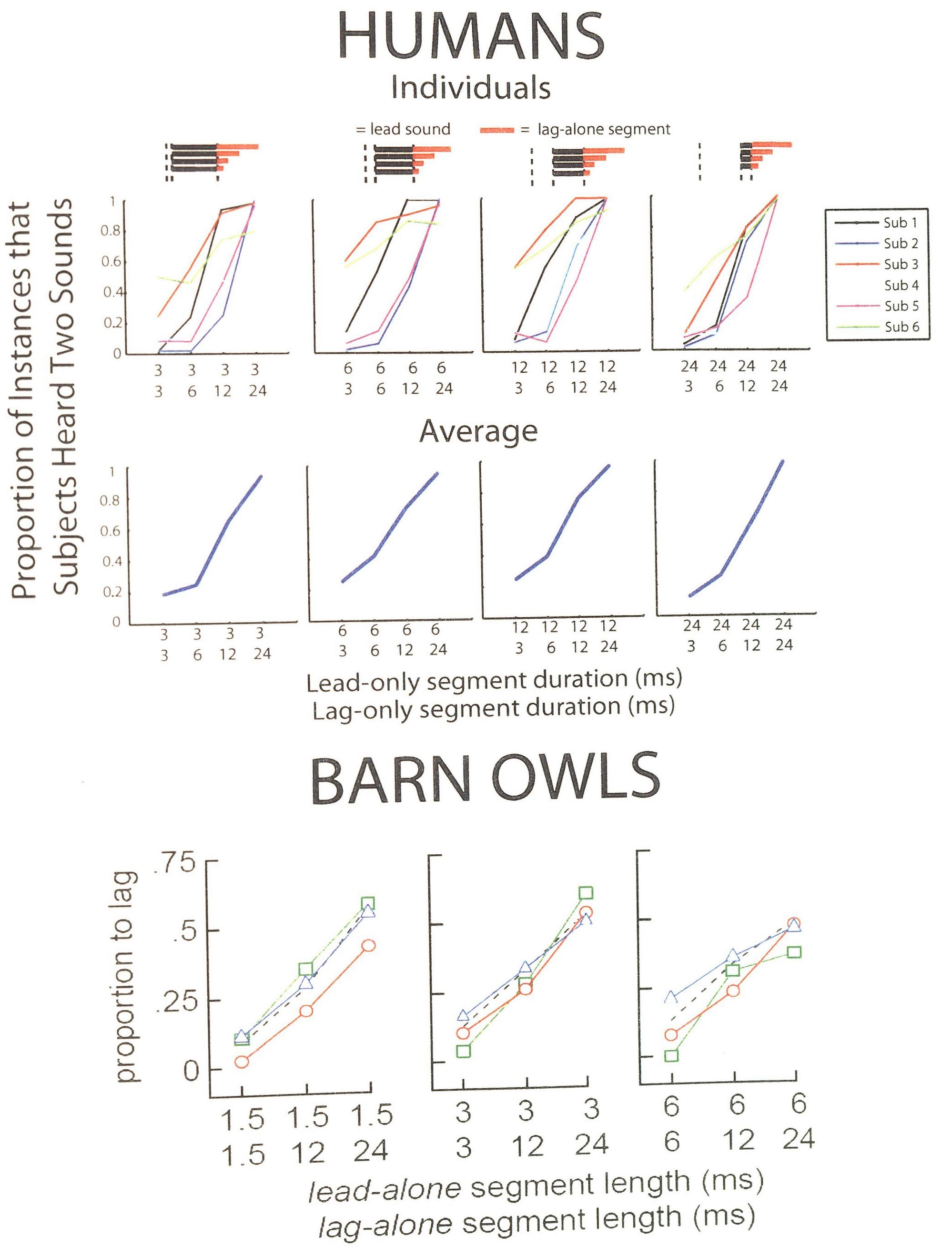

Fig. 6 – Proportion of instances that subjects heard two sounds as a function of lag-only duration for human subjects, and the proportion of responses to the lag for owl subjects. The uppermost plot shows the proportion of instances that human subjects heard two sounds at varying lag-only durations, with the average across subjects plotted directly below. The similarity in the relationship with that observed in the behavioral data of Nelson and Takahashi (in prep.) can be seen by comparing the human data to the barn owl data, displayed at the bottom of the figure.

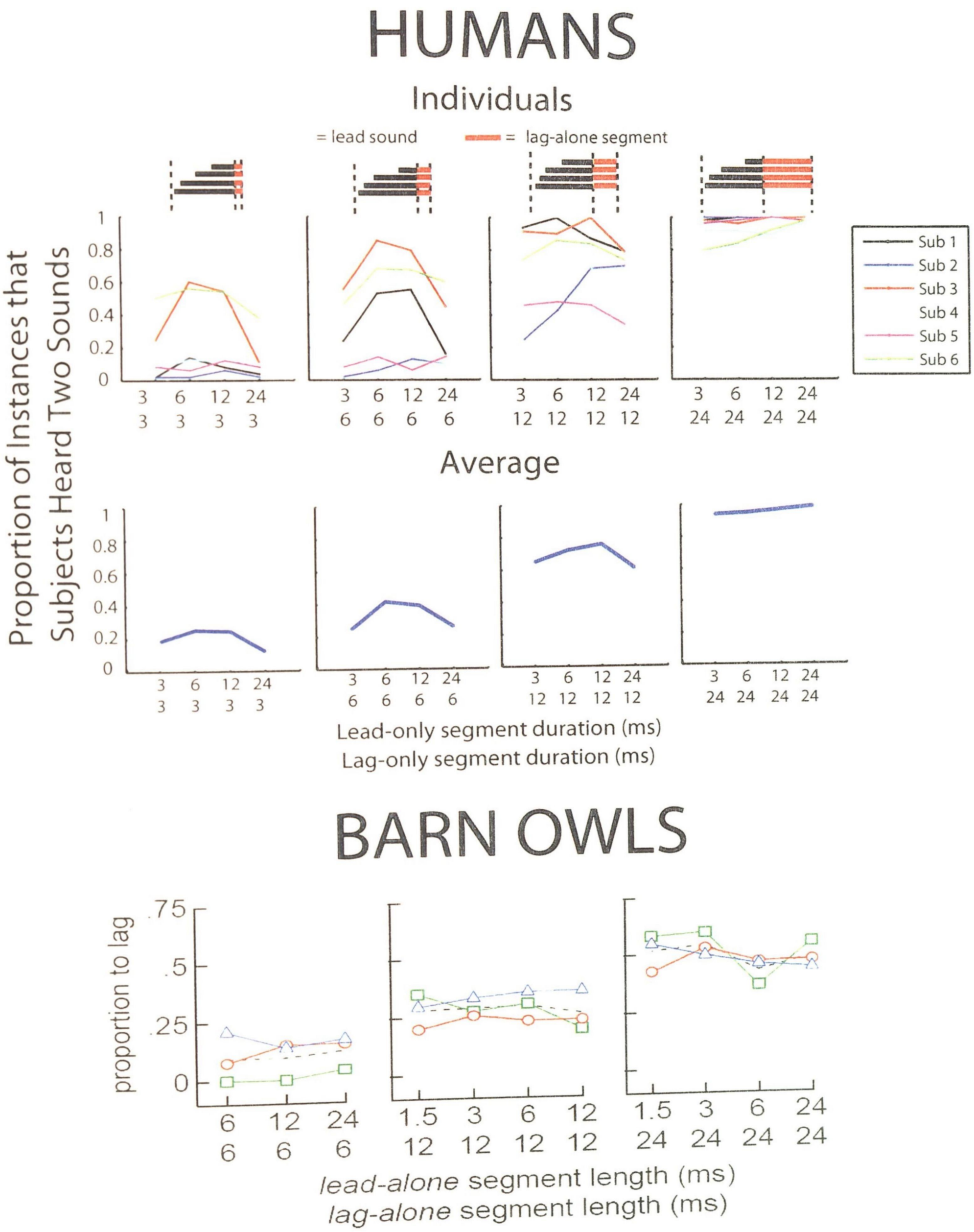

Fig. 7 - Proportion of instances that subjects heard two sounds as a function of lead-only duration for human subjects. Displayed below is the proportion of responses towards the lagging sound for owl subjects. The top plot shows the proportion of instances that human subjects heard two sounds at varying lead-only durations, with the average across subjects plotted directly below. The similarity in the relationship with that observed in the behavioral data of Nelson and Takahashi (in prep.) can be seen by comparing the human data to the barn owl data, displayed at the bottom of the figure. Notice the high human inter-subject variability, as well as the deviation in the relationship between humans and owls. Owl responses produce a fairly linear curve in all instances while the human subjects were more likely to perceive a single source at 3 and 24ms durations.

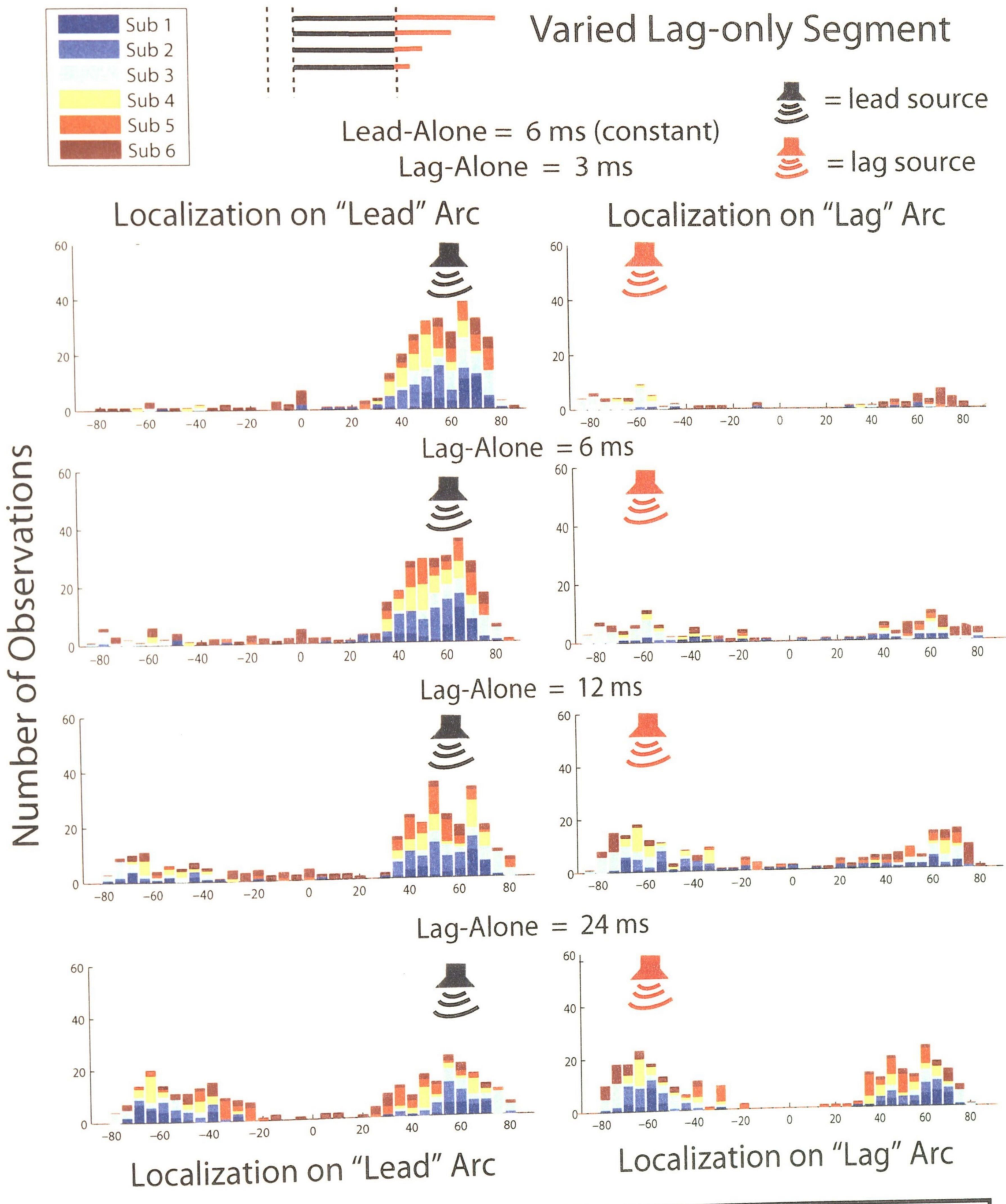

Fig. 8 – Localization of both lead and lag sources for all subjects as a function of lag-only segment duration. The lead-only segment is held at 6ms while placement responses are shown for lag-only durations of 3, 6, 12, and 24ms. The x-axes for all plots refer to location on the arcs (-90=left, 0=midline, 90=right). The source of both the lead (black speaker) and lag (red speaker) are shown at their corresponding locations. Notice how the localization of both the lead and the lag is increasingly bimodal as the lag-only segment is lengthened. This is a typical representation of all lead/lag pairs.

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