Rhesus Monkeys (*Macaca mulatta*) Hear Rising Frequency Sounds as Looming

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Rising sound intensity provides an important cue for the detection of looming objects. Studies with humans indirectly suggest that rising pitch can also signal a looming object. This link between rising intensity and rising frequency is puzzling because no physical rise in frequency occurs when a sound source approaches. Putative explanations include (a) the idea that the loudness of sound depends on its frequency, (b) the frequent co-occurrence of rising intensity with rising frequency in vocalizations generates an association between the 2 features, and (c) auditory neurons process amplitude- and frequency-modulated sounds similarly. If these hypotheses are valid, then rhesus monkeys (*Macaca mulatta*)—which share some homologies in the vocal production apparatus and auditory system—should also associate rising frequency with rising intensity, and thus should perceive rising frequency as a looming sound source. A head-turning assay and a preferential-looking paradigm revealed that monkeys show an attentional bias toward rising versus falling frequency sounds and link the former to visual looming signals. This suggests that monkeys hear a rising frequency sound as a looming sound source even though, in the real world, no such link exists.

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Looming signals are signals that indicate the rapid approach of objects and provide highly salient warning cues to animals. Accordingly, behavioral studies in primates (including humans) have shown strong attentional biases for detecting and responding to auditory (Ghazanfar, Neuhoff, & Logothetis, 2002; Neuhoff, 1998) and visual (Ball & Tronick, 1971; Schiff, Caviness, & Gibson, 1962) looming as compared with receding signals. Moreover, rhesus monkeys spontaneously match auditory and visual looming, but not receding signals (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004), and humans show similar biases toward looming in the multisensory domain (Cappe, Thut, Romei, & Murray, 2009) and can use the looming signal in one modality to compensate for disturbances in the other modality (Gordon & Rosenblum, 2005). These biases are thought to reflect the greater behavioral relevance of detecting rapidly approaching as compared with receding objects (Ghazanfar et al., 2002; Maier et al., 2004; Neuhoff, 1998; Neuhoff, Planisek, & Seifritz, 2009). Behavioral biases toward unimodal looming signals are closely paralleled at the neural level in the auditory cortex (Bach et al., 2007; Maier, Chandrasekaran, & Ghazanfar, 2008; Maier & Ghazanfar, 2007; Seifritz et al., 2002), the amygdala (Bach et al., 2007), and the superior temporal sulcus (Hietanen & Perrett, 1996; Maier et al., 2008; Seifritz et al., 2002). In the auditory domain, most of these studies (both behavioral and neural) used rising intensity sounds (with frequency modulation, FM, held constant) to induce a strong looming percept. Rising intensity is the most salient cue for detecting the location of a moving sound source (Rosenblum, Carello, & Pastore, 1987). However, it is not the only cue.

Although not as robust, changing *frequency* can also be used as a cue to detect approaching sound sources (Rosenblum et al., 1987). Listeners presented with rising or falling frequency sweeps with a *constant intensity* will perceive an illusory increase or decrease in loudness, respectively (Neuhoff, McBeath, & Wanzie, 1999). It is important to note that rising frequency change affects illusory loudness judgments greater than falling frequency change; that is, human subjects show a bias toward rising versus falling frequency, possibly because the former is perceived as an increase in loudness and thus a looming sound source (Neuhoff & McBeath, 1996). It is not known why there is a link between rising frequency and rising intensity with sound source motion. Indeed, the link is puzzling: The pitch of a sound source moving at a constant velocity past an observer is generally reported to rise; however, the physical (measured) frequency is constant as it approaches the listener and drops as it departs (Neuhoff & McBeath, 1996). That is, no rise in frequency actually occurs and the rise in pitch that observers consistently report is an illusion—the *doppler illusion*.

Rhesus monkeys and humans share a homologous set of auditory cortical areas (Hackett, Preuss, & Kaas, 2001) and homologous mechanisms for vocal production (Ghazanfar & Rendall, 2008). Their peripheral nervous systems are almost identical (Heffner, 2004). Thus, we hypothesized that a loudness–pitch association with looming sound sources may arise in a mechanistically similar manner in these two species whether rhesus monkeys

perceive rising frequency sounds (with intensity held constant) as looming. Because we cannot interrogate our monkeys verbally, and because training them to report by another means would obscure their every day sensory associations, we used two "spontaneous" methods for testing our monkey subjects. We capitalized on our knowledge that monkeys show a strong attentional bias toward rising intensity (looming) sounds over falling intensity ones (Ghazanfar et al., 2002), and that they intermodally link looming sounds to looming visual stimuli (Maier et al., 2004). The logic of our study is as follows: If monkeys perceive rising frequency as rising intensity, then minimally they should show an attentional bias toward rising versus falling frequency sounds. In Experiment 1, we used a head-turning assay to assess whether rhesus monkeys show an attentional bias toward upward versus downward frequency sweeps while the amplitude envelope was held constant (see Figure 1A). In Experiment 2, we used the preferential-looking paradigm to test whether monkeys link rising frequency sounds to looming visual stimuli—stimuli that are highly salient to primates (Franconeri & Simons, 2003; Maier et al., 2004; Schiff et al., 1962; see Figure 1B). Given that humans perceive changes in pitch as indicative of a moving sound source (Rosenblum et al., 1987), if monkeys show attentional biases toward rising frequency (vs. falling frequency) sounds under these two conditions, then this would provide evidence that rising frequency sounds are heard as looming sounds.

Method

We tested male rhesus macaques (*Macaca mulatta*; age range: 4–12 years) who are part of a large colony housed at the Max Planck Institute for Biological Cybernetics. All animals are socially housed and provided with enrichment (toys, hammocks, ropes, etc.). All experimental procedures were in accordance with the local authorities (Regierungspraesidium) and the European Community (EUVD 86/609/EEC) for the care and use of laboratory animals. Details of the experiment procedures are published elsewhere (Ghazanfar et al., 2002; Maier et al., 2004), so we are pithy in our descriptions here.

Experiment 1: One-Shot Playbacks

Sixteen male rhesus monkeys were tested in this experiment to determine whether they had a perceptual bias for rising versus falling frequency sounds. For each test session, an individual was seated in a primate chair and brought to a small semianechoic room for testing. The subject sat with his back toward a black curtain that concealed a hidden speaker. The speaker was positioned at head level, 75 cm away from the subject and to the right.

Eight subjects were presented with a 1000-Hz complex tone composed of a triangle waveform, rising in pitch (see Figure 1A, left panels), while another 8 subjects were presented with a complex tone falling in pitch (see Figure 1A, right panels). Both stimuli were 1 s in duration and either rose or fell 2 semitones; this corresponds to 1000–1122 Hz for rising frequency and 1000–890 Hz for falling frequency sounds. They were sampled at 44.1 kHz and had 10-ms onset and offset to exclude edge effects. Sounds were presented at an intensity of 70 dB SPL (A-weighted) as measured from the monkeys' listening point. The slope of the pitch change was quadratic. A quadratic change corresponds to the time
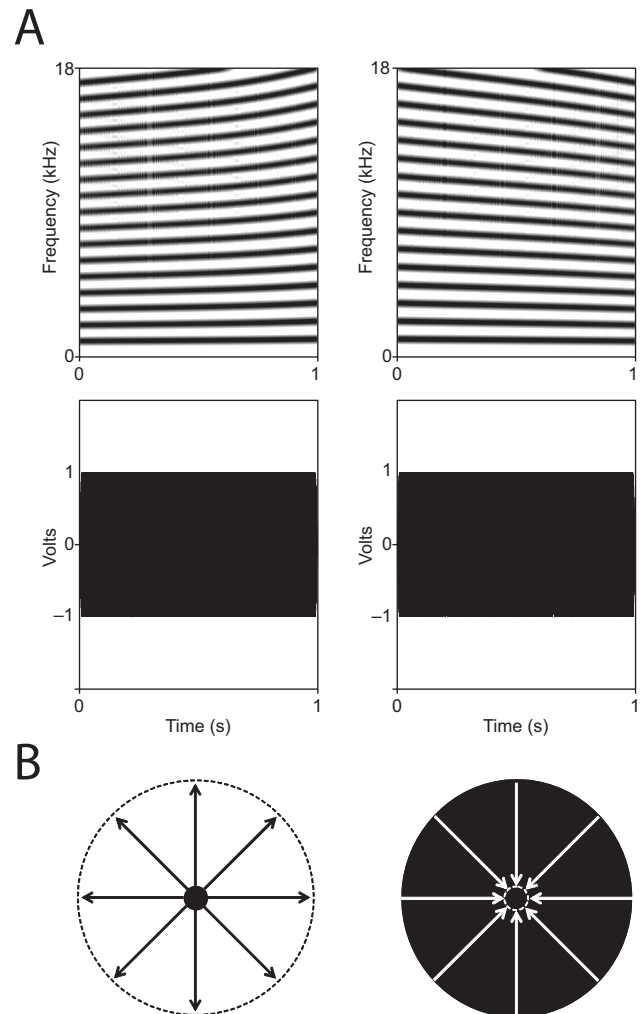

Figure 1. **A.** Auditory stimuli. Spectrograms and time–amplitude waveforms of the rising-frequency (apparent looming) and falling-frequency complex tones (based on a 1-s 1-kHz triangular waveform). **B.** Visual stimuli. A black disk symmetrically expanding (looming stimulus) or contracting (receding stimulus) on a white background. Stimuli expanded or contracted over the stimulus duration of 1 s.

course of amplitude change of an approaching sound source at constant velocity. Two semitones correspond approximately to an intensity change of 20 dB (McBeath & Neuhoff, 2002), the amount of intensity change used previously in an identical experimental setup (Ghazanfar et al., 2002). The intensity or amplitude envelope was identical and constant between the two sounds.

We used a between-subjects design, and each session consisted of one playback, either a rising frequency complex tone or a falling frequency complex tone. Trials were initiated when the subject looked centrally. Following playback of either trial type, subjects almost always oriented immediately toward the hidden speaker. All orienting responses to playbacks were videotaped using a digital video camera and stored digitally for offline analysis. We measured response durations from the onset of the sound until the time when the subject first began to turn his head back away from the speaker location. This response was unambiguous. Only the

initial orienting response was measured, that is, subsequent head turns were not included in the response measurement. All responses were scored blind to the trial type.

Experiment 2: Preferential Looking

Eighteen monkey subjects were used in this set of experiments to test whether they associated rising frequency sounds with looming visual stimuli.

The visual looming stimulus consisted of a black disk symmetrically expanding (ranging from 0.68 degrees [fully contracted] to 9.94 degrees [fully expanded] eccentricity) on a white background. The receding stimulus was a black disk symmetrically contracting (same dimensions as the looming stimulus) on a white background. Visual stimuli expanded or contracted smoothly over the entire stimulus duration of 1 s. Auditory stimuli were identical to the ones used in the first experiment.

The looming and the receding visual stimuli were played simultaneously on side-by-side 15-in. LCD monitors. Audio tracks were synchronized with both videos and played through a hidden speaker placed directly between and slightly behind the monitors. The videos were played in synchrony. Sounds were presented at an intensity of 70 dB, as in the one-shot playbacks.

For testing, a subject was seated in a primate chair and placed in front of the two monitors at a distance of 72 cm. The monitors were 65 cm apart (center-to-center distance) and at eye level with the subject. All trials were videotaped using a digital video camera placed above and between the monitors, and all equipment was concealed by a black curtain except for the monitor screens and the lens of the camera. The experimenter monitored subject activity from outside the room. During this time, the subject's attention was directed to the center by flashing a 1.2-W light placed centrally between the two monitors. A test session began when the subject looked centrally. A trial consisted of the two videos played in a continuous loop for 30 s with one of the two sounds also played in a loop through the speaker. The left–right position of the two dynamic visual stimuli was counterbalanced. Each subject was tested only once and no reward or training was provided.

We collected high-quality, close-up digital videos of the subjects' behavior with the digital video camera. Clips for analysis were edited to 30 s by identifying the onset of the auditory track and adding 900 frames (30 frames/s × 30 s) from that onset point. Two observers scored each trial; one observer was blind to the experimental condition. For each trial, video scorers judged, frame-by-frame, whether the subject was looking toward the right screen, the left screen, or away from both. The total duration of a subject's looking toward each video (left or right) or away from both was recorded and expressed as the proportion of total looking time.

Scoring which of the screens the monkey subjects were looking toward was unambiguous. The screens were far apart in the horizontal dimension, fairly close to the monkey's face and at eye level. Thus, the monkey had to make large eye or head movements to look to one screen or the other, and it was similarly clear when he was not looking at either screen. To validate this, we measured interobserver reliability on random subset of trials. Observer agreement was .98 ($p < .0001$) as measured by a Pearson r test. Scores from the blind observer are presented in the Results section.

For both the one-shot playbacks and the preferential looking experiment, data are presented as mean and standard errors. One-tailed statistical tests were used as the direction of the effect was predicted a priori on the basis of previous experiments using the same techniques with intensity-based auditory and visual looming stimuli (Ghazanfar et al., 2002; Maier et al., 2004).

Results

In Experiment 1, we tested whether rhesus monkeys showed an attentional bias toward rising frequency sounds versus falling ones. We predicted that if monkeys link intensity with frequency like humans, then they would find the rising frequency more salient because it would simulate a rising intensity sound (Ghazanfar et al., 2002). Figure 2 shows that monkeys who heard a rising frequency complex tone oriented toward the sound source for a longer duration (mean $\pm$ *SEM* = 5.13 $\pm$ 1.06 s; $n = 8$) than monkeys who heard a falling frequency complex tone with an identical (flat) amplitude envelope (2.50 $\pm$ 0.75 s; $n = 8$). This difference was statistically significant, $t(14) = 2.4$, $p = .022$.

To make explicit the link between rising frequency and looming sources, Experiment 2 tested the monkeys on a preferential-looking paradigm in which monkeys could spontaneously choose between looking at a looming or receding visual stimulus while listening to either a synchronized rising or falling frequency complex tone (see Figures 1A and 1B). If the monkeys associate rising frequency with rising intensity (looming), then they should look longer at the screen displaying the looming visual stimulus (Maier et al., 2004). Figures 3A and 3B reveal that monkeys prefer to look at the looming visual stimulus over the receding one when listening to rising frequency sounds (63% of total looking time; $n = 9$), one sample t test, $t(8) = 4.41$, $p = .001$, but no visual preference when listening to falling frequency sounds (47% of total looking time; $n = 9$), $t(8) = -0.42$, $p = .344$. These differences are also apparent when comparing the mean duration of looks to the
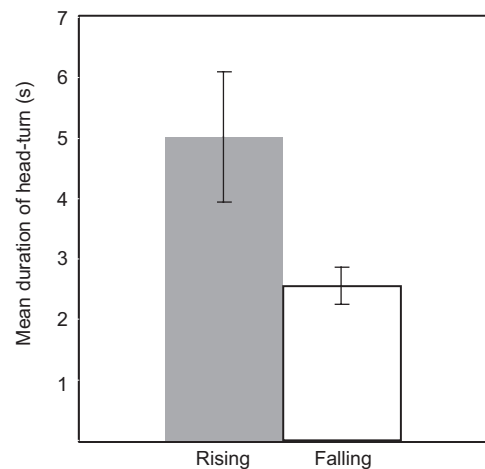

Figure 2. Duration of head-orienting responses to rising and falling frequency complex tones. Gray bar represents mean response to rising frequency sounds ($n = 8$); the white bar represents the mean response to falling frequency sounds ($n = 8$). Y-axis represents duration (in s) of first head turn as measured from the onset of the sound. Error bars represent $\pm$ 1 *SEM*.
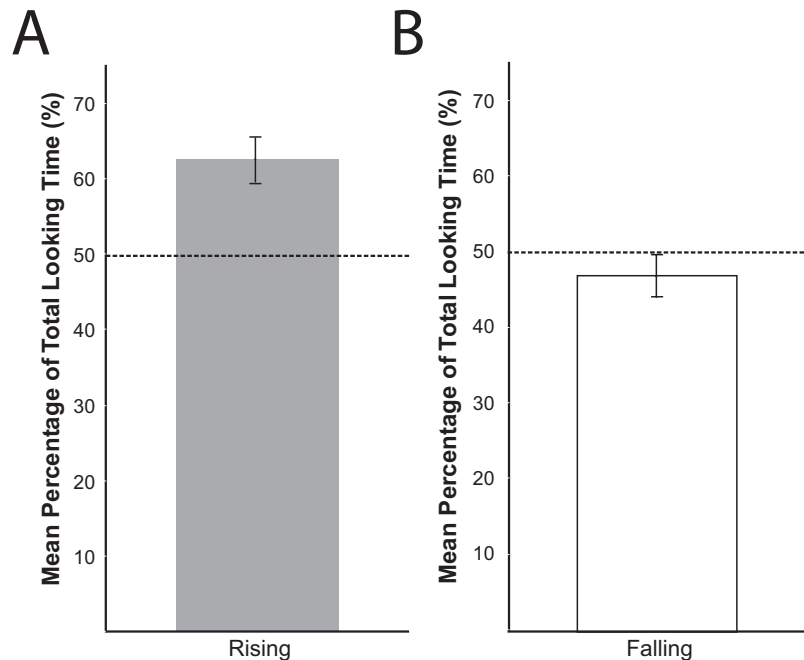
Figure 3. Percentage of looking time at the matching stimulus presented with rising- and falling-frequency complex tone stimuli. Mean percentage of total looking time at the (**A**) looming visual stimuli when listening to the rising frequency complex tone (*n* = 9), and (**B**) at the receding stimulus when listening to the falling frequency tone (*n* = 9). Error bars represent ± 1 *SEM*.

matching versus nonmatching screens in the looming condition (3.67 ± 0.6 vs. 2.44 ± 0.5 s), paired *t*(8) = 4.40, *p* = .001, but not in the falling frequency sounds/receding visual stimulus condition (3.33 ± 0.6 vs. 4.22 ± 0.8 s), paired *t*(8) = −1.02, *p* = .169. Finally, in the rising frequency condition, all 9 monkeys looked longer at the matching, visual looming screen (sign test, *p* = .002), whereas in the falling frequency condition, only 3 of 9 subjects looked at the matching visual receding stimulus (sign test, *p* = .254).

It is not the case that a simple bias toward visual looming stimuli can explain these patterns of results. On every trial, the monkey was presented with two screens, one with a looming visual stimulus and the other with a receding visual stimulus. Depending on the trial type, the monkeys heard either a rising frequency sound or a falling frequency sound. If the monkeys preferred to look at the visual looming stimulus in general, then they would have done so during the trials with the falling frequency sound. This was *not* the case. The fact that the monkeys did not match receding visual stimuli with falling frequency sounds is consistent with the idea that rising frequency sounds are more salient, more behaviorally relevant. This pattern of results is in line with our previous work, using the same paradigm, where we found that monkeys match rising *intensity* sounds with looming visual stimuli, but do not match falling intensity sounds with receding visual stimuli (Maier et al., 2004). These results are also in agreement with a recent human study (using nearly identical stimuli as in Maier et al., 2004) showing that there is *selective* integration of audiovisual looming stimuli relative to receding stimuli (Cappe et al., 2009).

Of some concern are the short durations of looking times in both the head-turning and preferential-looking assays. In our original studies, the duration of head turns toward looming sounds on the basis of rising intensity was 10 s on average (Ghazanfar et al., 2002), and the duration of looking to the match screen for bimodal looming stimuli was 8.7 s on average (Maier et al., 2004). These values are approximately double for those reported in the current study. This suggests two possibilities: The subjects may be habituating to the behavioral paradigms or the stimuli in the current study are not as salient as the rising intensity-based looming signals. Two lines of evidence suggest that the latter possibility is driving the reduced looking times. First, in humans, intensity is the most salient cue for detection of sound source approach (Rosenblum et al., 1987); thus, one would not expect other acoustic cues to drive behavior to the same degree. Second, we conducted preferential-looking experiments with faces and voices both before and after collecting the results reported here, and these data show no decrement in looking times—they are all around 10 s in duration of looks to the matching screen (Ghazanfar et al., 2007; Jordan, Brannon, Logothetis, & Ghazanfar, 2005).

Discussion

Taken together, our results demonstrate that monkeys have a perceptual bias toward rising frequency sounds and link such sounds to visual looming events. This behavior is exactly parallel to our previous results using rising and falling intensity cues in both the auditory and multisensory domains (Ghazanfar et al., 2002; Maier et al., 2004), suggesting that rising frequency is perceived as a looming sound source. This possibility was suggested indirectly in a human psychophysical study reporting that rising frequency is perceived as an increase in loudness (Neuhoff

et al., 1999). There are at least three, nonmutually exclusive mechanisms that may explain why rising frequency is linked with the perception of looming and they include equal-loudness contours, the intensity–frequency association in conspecific vocalizations, and the similar processing of amplitude- and frequency-modulated sounds in the primate auditory cortex.

The loudness of sounds is influenced by many factors in addition to intensity. One important factor is the frequency of the sound. The loudness of a sound (its perceived intensity) is dependent on its frequency. For example, to be perceived at the same loudness as a 1-kHz tone, a 1.2-kHz (higher frequency) tone must be presented with a greater intensity. This is true for both humans (Moore, 1989) and monkeys (Stebbens, 1966). This systematic relationship between frequency and intensity can be plotted as an "equal loudness contour" and is largely thought to be mediated by factors in the peripheral auditory system (Moore, 1989). Thus, there is an inextricable link between frequency and intensity when it comes to the perception of loudness. Under this mechanism, a sound gradually rising in frequency, but constant in amplitude, could activate the peripheral auditory system to a greater degree as the frequency of the sound increases much in the same manner as it would if frequency was held constant but the intensity rose in level. This would putatively lead to a perception of loudness change.

The association between rising intensity and frequency could be due to sensory experience with the near-invariant relationship between changes in intensity with changes in frequency in other, nonlooming acoustic events, particularly vocalizations. During speech production, for example, there is a reliable positive correlation between these acoustic features—increases in intensity co-occur with increases in frequency with a high probability (Alain, 1993; Lienard & Di Benedetto, 1999). That is, as you raise your voice, the frequency of your voice (fundamental frequency) also gets higher. Because the vocal production mechanism is largely the same between humans and other primates (certainly at the level of the vocal folds) (Ghazanfar & Rendall, 2008), there is a similar positive correlation between intensity and the fundamental frequency in nonhuman primate vocalizations as well. When macaque monkeys are far from other group members, they produce louder contact calls with higher frequencies than when they are near conspecifics (Sugiura, 2007). Similarly, in baboons, the higher fundamental frequency of dominant male barks relative to subordinate ones is due to the dominant males calling at higher amplitudes than lower ranking males (Fischer, Kitchen, Seyfarth, & Cheney, 2004). Given that humans, baboons, and macaques are likely to implicitly learn the association between higher frequencies with higher intensities in their respective vocalizations, this link allows them to respond adaptively to other classes of sounds when only one of the features is heard—in the present case, rising frequency tones. Because higher frequencies are more salient than lower frequencies in primate communication, this also raises the (albeit, unlikely) possibility that the monkeys simply associate rising pitch with looming visual signals because they are both very salient and not necessarily because rising pitch indicates a moving sound source.

A third mechanism that links frequency with intensity is the response properties of auditory cortical neurons. Primary auditory cortical neurons are sensitive to temporal modulations regardless of whether that modulation was in the amplitude or frequency domain (Liang, Lu, & Wang, 2002). This suggests that there is a common mechanism in auditory cortical neurons for extracting temporal profiles from a variety of complex sounds. Thus, it is possible that rising frequency and rising intensity sounds are treated identically by this population of neurons. However, these neurons process temporal modulations regardless of the spectral content (Wang, Lu, & Liang, 2003), and it is not clear whether such neurons are common in other auditory cortical areas. Furthermore, it is here that the findings with looming signals and generic temporally modulated signals diverge. Auditory cortical responses to looming signals based on rising intensity are very sensitive to spectral content (Maier & Ghazanfar, 2007). Both gamma band activity and spike rate revealed a bias in response magnitude toward looming versus receding sound based on intensity-changing complex tones. White noise stimuli with identical amplitude envelopes did not elicit the same pattern of responses. This difference between responses to rising intensity complex tones versus white noise is exactly paralleled at the perceptual level (Ghazanfar et al., 2002; Maier et al., 2004; Neuhoff, 1998). Thus, it appears that the characteristics of looming sounds—their time course, envelopes, and behavioral saliency—engage the auditory cortex in a different manner than other temporally modulated sounds. The current results then beg the question of how rising frequency sounds (upward frequency modulated, or FM, sweeps) are represented in auditory cortex: Is there a bias toward upsweeps versus downsweeps? Neurons in the lateral belt areas are very selective for FM sweeps relative to pure tone stimuli (Tian & Rauschecker, 2004), but it is not clear whether there is a bias toward up versus down FM sweeps for sounds with the characteristics that typically elicit a looming percept. The results of our study suggest a perceptual consequence for the similarity between responses to AM and FM sounds in auditory cortex and predict that there should be a bias toward rising frequency sounds as there is for rising intensity ones.

Given that the overall intensity of the sounds was held constant, our study provides indirect evidence that monkeys perceive the doppler illusion; that is, because they respond to rising frequency sounds as they do with rising intensity by matching it to a visual looming source (Experiment 2), they thus seem to perceive rising frequency alone as a looming event, *even though looming sound sources are constant in frequency as they approach the observer*. This finding is parallel to those in humans, who are similarly susceptible to perceiving rising frequency as indicating an approaching source even though physical measurements of approaching sound sources moving at a constant velocity reveal that they actually *fall* in frequency (McBeath & Neuhoff, 2002). Indeed, human subjects will rate rising frequency sounds as louder than falling frequency sounds even when the absolute intensity is constant (Neuhoff et al., 1999), a context exactly parallel to our Experiment 1. Thus, even though approaching sound sources drop in frequency, an a priori strong association between rising intensity and rising frequency or the nature of auditory system causes monkeys and, presumably, humans to perceive rising frequency sounds as looming.

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