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Strength and physical fitness predict the perception of looming sounds

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Abstract

Listeners consistently perceive approaching sounds to be closer than they actually are and perceptually underestimate the time to arrival of looming sound sources. In a natural environment, this underestimation results in more time than expected to evade or engage the source and affords a "margin of safety" that may provide a selective advantage. However, a key component in the proposed evolutionary origins of the perceptual bias is the appropriate timing of anticipatory motor behaviors. Here we show that listeners with poorer physical fitness respond sooner to looming sounds and with a larger margin of safety than listeners with better physical fitness. The anticipatory perceptual bias for looming sounds is negatively correlated with physical strength and positively correlated with recovery heart rate (a measure of aerobic fitness). The results suggest that the auditory perception of looming sounds may be modulated by the response capacity of the motor system.

Keywords: Auditory perception; Looming; Strength; Physical fitness

1. Introduction

Objects that approach an observer have perceptual priority over those that recede, and the ability to respond early in activating the motor system in the face of a rapidly approaching sound source can sometimes mean the difference between life and death. Numerous studies have shown that when listeners are asked to predict the arrival time of looming sound sources they consistently respond early, perceiving them as closer than they actually are (Gordon & Rosenblum, 2005; Neuhoff, 2001; Neuhoff, Planisek & Seifritz, 2009; Rosenblum, Carello & Pastore, 1987; Rosenblum, Gordon & Wuestefeld, 2000; Schiff & Oldak, 1990). Neuroimaging work has shown that looming sounds preferentially activate motor planning areas (Seifritz et al., 2002), thus suggesting a link between auditory perception and the motor behaviors that would be required to evade or engage an approaching object.

Converging evidence has been used to argue that the systematic early response to looming sounds has been shaped by natural selection. In the face of a dangerous looming sound source, perceiving the object as closer than actual would cause a perceptual underestimation of the object's arrival time. This anticipatory error would have little cost and actually give the organism slightly more time than expected to prepare to evade or engage the source. Thus, in this case, a slight systematic perceptual error might be more advantageous than veridical perception (Haselton & Nettle, 2006).

In support of this hypothesis, a growing body of physiological, behavioral and comparative work has highlighted the environmental salience of looming sounds and the priority with which organisms perceptually process these stimuli. For example, looming sounds activate a distributed neural network responsible for auditory space and motion perception, attention, and motor planning that is not similarly activated by receding sounds (Bach et al., 2008; Seifritz et al., 2002). This neural priority for looming sounds is also reflected in behavior. Developmental work shows that infants can discriminate looming sounds better than receding sounds and will exhibit avoidance behaviors in response to looming sounds but not to equivalent receding sounds (Morrongiello, Hewitt & Gotowiec, 1991; Freiberg, Tually & Crassini, 2001). When asked to judge the arrival time of looming sound sources, adult listeners consistently judge the source to have arrived when it is still some distance away (Gordon & Rosenblum, 2005; Neuhoff, 2001; Neuhoff et al., 2009; Rosenblum et al., 1987, 2000; Schiff & Oldak, 1990). Listeners also perceive sounds that approach and stop before

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reaching them as closer than sounds that recede from them and stop at the same point (Neuhoff, 2001; Neuhoff et al., 2009). Similarly, comparative studies show that nonhuman primates have behavioral and neural response patterns that are dependent upon the direction of a moving sound source and are consistent with a bias for looming auditory motion (Ghazanfar, Neuhoff & Logothetis, 2002; Lu, Liang & Wang, 2001; Maier & Ghazanfar, 2007; Neuhoff, 1998).

However, perceiving and acting in response to looming sounds depend not only on perceptual abilities, but also on the motor capabilities of the listener. Thus, the appropriate timing of motor behaviors is a critical component in the proposed evolutionary contribution to the perceptual bias. Recent work demonstrating a sex difference in the perception of looming (but not receding) sounds suggests that females may perceive looming sounds as closer than males do because of sex differences in the ability to evade or engage looming objects (Neuhoff et al., 2009). Thus, one prediction of the "margin of safety theory" is that individuals who are weaker and less physically fit might require a larger margin of safety than those who are stronger and more physically fit. In other words, the magnitude of the anticipatory perceptual bias in perceiving looming sounds should be scaled to one's physical ability to effectively deal with a looming object. Although the bias for looming sounds is well established, we know of no work showing that estimates of auditory arrival time are tied to the capacity of the motor system to respond. However, visuospatial perception has been shown to be related to physical fitness (Bhalla & Proffitt, 1999; Proffitt, 2006; Raudsepp & Djupsjobacka, 2005), and work in "embodied cognition" has demonstrated some fitness-based perception-action links between the auditory and motor systems (Cristell, Hutchinson & Alessio, 1998; Hutchinson et al., 2000; Seifritz et al., 2002). Similarly, "dynamic" or "state-dependent" models of animal behavior typically account for the physical state of the organism as a contributing factor in determining behavior (e.g., Houston, Clark, McNamara & Mangel, 1988; Schuck-Paim, Pompilio & Kacelnik, 2004).

Here we examined the hypothesis that perceiving the arrival time of a looming sound source would be related to the physical ability of the listener to deal with an approaching auditory object. We presented listeners with a virtual looming sound source and asked them to respond by pressing a key when they perceived that the source had reached them. We then measured each participant's strength and cardiovascular fitness. We predicted that listeners with lower levels of strength and cardiovascular fitness would have a larger anticipatory bias in their perceived auditory arrival time and thus a larger margin of safety in response to looming sounds.

2. Method

2.1. Participants

All 25 male and 25 female participants were between 18 and 43 years of age, reported normal hearing and had no significant health problems. The procedures were approved by the local human subjects review committee, and all participants gave informed consent.

2.2. Stimuli and apparatus

Participants filled out a demographic questionnaire and then heard a 3-D virtual sound source approach along a path parallel to the interaural axis at 15 m/s from distances of 84, 87, 90, 93 and 96 m. Sounds were presented via Sennheiser HD Precision headphones. The virtual listening point was 2 m from the straight-line trajectory of the source (see Fig. 1). The sound was a square wave with a fundamental frequency of 400 Hz and a source intensity of 88 dB SPL. The simulation modeled the physical characteristics that would occur in a natural environment including Doppler shift, atmospheric filtering, gain attenuation due to atmospheric spreading, ground reflection attenuation, and head-related transfer function from the MIT KEMAR data set (Gardner & Martin, 1995). [See Neuhoff et al. (2009) for additional simulation details.] Grip strength was measured with a Smedley Digital Hand Dynamometer Model 12-0286.

2.3. Procedure

We told listeners that a sound would approach from the left or the right and pass in front of them. Listeners were told to press a key when they perceived that the source was directly in front of them. Each starting distance was presented 12 times in random order. Half of the sounds approached from the left and half from the right. Listeners received 10 practice trials with feedback followed by 60 experimental trials without feedback. Feedback consisted of

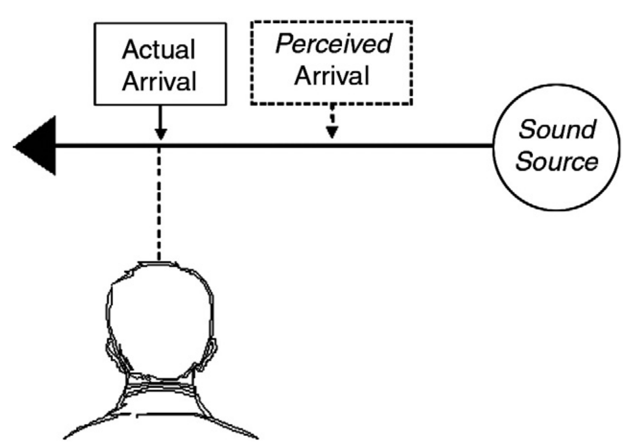

Fig. 1. Participants heard a 3-D virtual sound source approach and pressed a key when the source was perceived to be directly in front of them. Participants tend to respond too soon allowing a perceptual margin of safety.

a message on a computer screen that said either “Too soon!” or “Too late!” for responses that were greater than 250 ms prior to or 250 ms after the arrival of the source, respectively. To measure cardiovascular fitness, we then had participants perform a heart rate recovery “step test” in which they stepped up and down on a platform 12 in. high for 3 min, in time to a metronome set at 96 bpm. After 3 min, we measured their resting recovery heart rate for 1 min. Measured this way, lower recovery heart rate indicates a higher level of cardiovascular fitness. Improvements in recovery heart rate have been shown to be caused by improvements in physical fitness due to exercise (MacMillan, Davis, Durham & Matteson, 2006). Finally, we measured grip strength with a hand dynamometer. Grip strength has been shown to be strongly correlated with total muscle strength (Bohannon, 1998, Wind, Takken, Helders & Engelbert, 2010). We asked participants to squeeze a hand dynamometer as tightly as possible two times, once with their right and once with their left hand. We averaged the two to obtain a single score for strength.

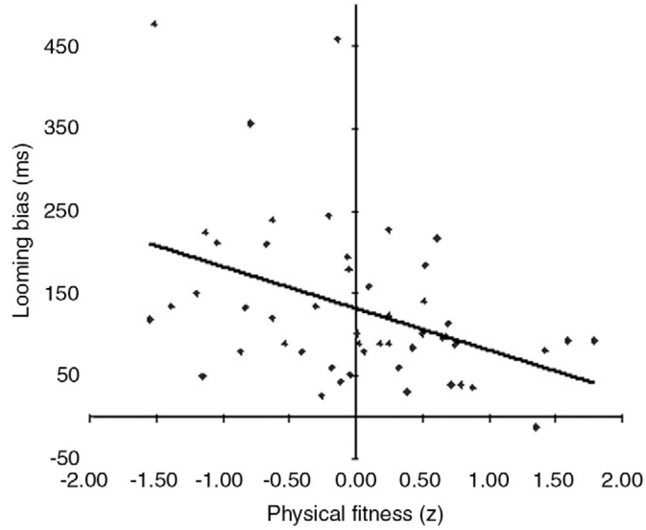

Fig. 2. Composite physical fitness scores based on muscular strength and cardiovascular efficiency significantly predict the perception of arrival time, accounting for 16.8% of the variance.

3. Results and discussion

We found a significant anticipatory looming bias (mean=132.3 ms, S.D.=98.8), indicating that listeners judged the source to have arrived when it was still an average of 1.98 m away ($t_{(49)}$=9.7, p<.001). The anticipatory bias occurred in 49 of 50 participants and was not significantly correlated with self-reported age, height or weight. However, heart rate recovery was positively correlated with the anticipatory looming bias ($r_{(48)}$=.31, p<.05) and accounted for 9.4% of the variance in perceived arrival time. This indicates that participants with poorer cardiovascular fitness perceived looming sounds with a larger margin of safety. We also found that strength was negatively correlated with the anticipatory looming bias ($r_{(48)}$=−.34, p<.01) and accounted for 11.8% of the variance in perceived arrival time. This indicates that stronger participants perceived looming sounds with a smaller margin of safety. To obtain a composite measure of fitness, we converted strength and heart rate data to z-scores. Because higher heart rate indicates poorer fitness, heart rate z-scores were then multiplied by −1. The two transformed fitness scores were then averaged to create a single composite fitness measure for each participant, with higher scores representing better fitness. Composite fitness was negatively correlated with the anticipatory looming bias ($r_{(48)}$=−.41, p<.01) and accounted for 16.8% of the variance in perceived arrival time (see Fig. 2). Within-sex analyses indicated that these results do not appear to be the result of differences between men and women per se. With hypothesis-driven one-tailed tests, we found significant correlations between composite fitness and looming bias of men and women separately. For men only, the correlation was $r_{(23)}$=−.43 (p=.02). For women only, the correlation was $r_{(23)}$=−.27 (p=.07). We also conducted a multiple regression analysis with heart rate, grip strength and sex as predictor variables and perceived arrival time as the dependent variable. Using the enter method, we found a significant model ($F_{(3,46)}$=3.09, p=.036). Adjusted R^2=.113 with a standard error of 92.99. Standardized beta coefficients were as follows: heart rate β=.232 (p=.11), grip strength β=−.259 (p=.21) and sex β=−.151 (p=.88).

Our results are consistent with previous work in embodied cognition which demonstrates that perception can be strongly influenced by potential environmental costs associated with attaining a goal (Proffitt, 2006). For example, Bhalla and Proffitt (1999) showed that physical fitness is related to the visually perceived slant of hills. Those who are less physically fit perceive hills as steeper than those who are more fit. Similarly, Raudsepp and Djupsjobacka (2005) showed that the tendency to overestimate vertical distances relative to horizontal distances is related to maximum handgrip force. Both of these studies suggest that the perceived amount of effort required to interact with an environment is a factor that influences the perception of visual space. Our results suggest that similar processes may be at work in audition. Indeed, previous studies clearly demonstrate fitness-based perception-action links between the auditory and motor systems (Cristell, Hutchinson & Alessio, 1998; Hutchinson et al., 2000; Seifritz et al., 2002).

Previous work has also shown sex differences in the perception of looming auditory stimuli. Females tend to have a greater anticipatory bias in judging the arrival time of looming sound sources than males (Neuhoff et al., 2009; Schiff & Oldak, 1990). The current work suggests that these perceptual differences may be related to more general sex differences on characteristics that might be important in dealing with an approaching threat (e.g., strength).

Our results link auditory perception with the capacity for motor behavior in the face of a looming sound. However, they do not readily identify the mechanisms that contribute to this link. Multiple psychological mechanisms could produce this behavioral result (McKay & Efferson, 2010). For example, listeners may accurately perceive arrival time of approaching sounds and consciously adjust their decisions about the appropriate time to initiate motor behaviors based on their physical state. Alternatively, listeners might genuinely demonstrate a true perceptual bias. In this case, listeners would perceive that the approaching sound has arrived, even when it is still some distance away and believe that they are making a veridical decision about arrival time. We note that these two alternatives are not mutually exclusive and both may contribute to the behavioral bias. However, the results of previous work suggest that the true perceptual bias is at the very least quite likely. Neuroimaging studies have shown preferential neural activation by looming sounds (vs. receding and static control sounds) in a distributed neural network that subserves space recognition, auditory motion perception, and attention (Seifritz et al., 2002). Moreover, when listeners are asked to make stationary egocentric distance estimates of looming and receding sounds that have come to a stop at some distance from the listener (thus reducing the need for a decision about timing an avoidance response), sounds that stop on approach are perceived as closer than sounds that stop on recession (Neuhoff, 2001; Neuhoff et al., 2009). It should also be noted that listeners in the current study listened to virtual sounds over headphone while seated in a laboratory, ostensibly aware that no avoidance behaviors would be required.

Although perceptual processes help organisms survive and interact with the environment, they need not be veridical to be advantageous. As the potential dire consequences of responding late to looming sounds far outweigh the relatively low cost of responding early, a slight anticipatory perceptual error that is scaled to the capabilities of the motor system would likely be more advantageous for survival than veridical perception (Haselton & Nettle, 2006). Here we found that listeners who are the least prepared physically to interact with a looming sound source showed a greater perceptual margin of safety in perceiving auditory arrival time. The anticipatory bias for looming sound sources may allow more time for preparatory behaviors. If so, then a flexible evolved mechanism allowing a greater looming bias in those whose preparatory behaviors take longer to execute or are less effective when initiated could be selected for. Of course, there are potential drawbacks in inferring intra-individual mechanisms from interindividual data (as we have done here); future studies might examine the capacity of changes in fitness levels within an individual to affect changes in the looming bias. The current work suggests that such a longitudinal study could show that increasing one's level of physical fitness over time might lead to a decrease in the auditory looming bias.

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