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Chapter 12

Adaptive Biases in Visual and Auditory Looming Perception

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In the scientific community, it is almost universally accepted that the remarkable features of our auditory and visual systems have evolved over millions of years. Adaptive perceptual mechanisms that aid survival and reproduction are passed on to subsequent generations. Yet many in the scientific community also hold the belief that our perceptual systems have evolved to give us an "accurate" representation of our environment. Any observed inaccuracies in our perceptual abilities are often considered imperfections in the evolutionary process. However, from an evolutionary perspective, perceptual accuracy is far less important than *utility* in terms of survival and reproduction. While it is true that our perception of the world must be accurate enough for us to perform all of the remarkable feats that we do, it is also true that evolution will always favor perceptual distortions and cognitive biases over veridical representation of the environment when the former provide a greater selective advantage. Perceptual systems have not evolved because they provide an accurate representation of the environment. They have evolved because they bestow specific advantages in survival and reproduction (Popper & Fay, 1997). If a perceptual bias provides a greater evolutionary advantage than an accurate representation, it will be passed on to subsequent generations at a higher rate than veridical perceptual abilities. The biases that occur when perceiving looming objects are examples of this phenomenon.

However, providing evidence to support this assertion presents a unique challenge. Although few doubt that perceptual abilities in some nebulous sense are a product of evolution, the burden of evidence crystalizes considerably when one begins to make a case for the evolution of a specific perceptual trait. Ethical considerations and the time course of human evolution dictate that the traditional experimental method used to test behavioral hypotheses must be modified when our hypotheses regard the evolution of a specific perceptual trait. We can't simply apply an independent variable to a sample and evaluate how it affects human evolution. As such, making a convincing case that a perceptual bias (or any other behavioral trait) has been shaped by evolution requires converging empirical evidence from a wide array of disciplines and methods including physiological, comparative, behavioral, theoretical, cross-cultural, anthropological, medical, and even genetic areas of investigation (Schmitt & Pilcher, 2004). Not every perceptual bias is an adaptation. The dim visual afterimage that occurs after a bright camera flash is a perceptual bias. However, this bias provides no ostensible selective advantage. It is simply a by-product of how the visual system functions. Thus, the degree to which we can be confident that a given bias is an evolutionary adaptation is dependent on the quality and quantity of converging evidence that can be gathered from these diverse areas.

In this chapter, I examine auditory and visual perception of looming objects – objects in motion that approach an observer. Looming objects are a very special class of stimuli that are treated with priority by both the auditory and visual systems because of their importance in ecological and evolutionary terms. However, the auditory and visual systems have evolved to deal with looming objects in different ways and have different strengths and weaknesses. The visual system provides estimates of arrival time that are relatively accurate and precise under good viewing conditions. The auditory system is less accurate and less precise but can be characterized as an "advanced warning" system that provides input into a categorical decision about whether there is time to direct the eyes toward the looming object, or whether evasive actions need to be initiated immediately (Guski, 1992; Seifritz et al., 2002). Unlike vision, the auditory system functions well when visibility is poor and when objects are occluded or are out of the line of sight. Together the two systems provide a perceptual representation that, while not always accurate, enables highly successful interaction with looming objects. We begin this chapter with a review of the literature on unimodal looming perception in both audition and vision. We then examine the smaller body of research that has examined multisensory integration of looming perception.

Auditory Looming

The Auditory Looming Bias

The auditory looming bias is the strong tendency for listeners to underestimate the arrival time of an approaching sound source. Essentially listeners perceive that the source has arrived when it is still some distance away (Neuhoff, 2001). A looming sound source creates several important sources of dynamic acoustic information that listeners can use to make judgments about the arrival time. Perhaps the most studied is the change in intensity that occurs as a source approaches. Simple changes in intensity are sufficient for activating motion-sensitive areas of the brain (Seifritz et al., 2002), and the pattern of rising intensity that occurs as a source approaches can physically specify the arrival time, a variable termed *acoustic tau* (Guski, 1992; Shaw, McGowan, & Turvey, 1991). For a sound source approaching a listener on a close bypass trajectory, the Doppler shift specifies that the frequency observed at the listening point is slightly higher than that emitted by the source and drops gradually as the source draws near. It then drops dramatically as the source passes the listener and continues to drop gradually as the source recedes. Despite this continual drop in frequency, listeners report a rise in pitch as the source approaches, a phenomenon referred to as the Doppler Illusion (Neuhoff & McBeath, 1996). The illusion is likely due to the rising intensity that occurs as the source approaches and the integral processing of pitch and loudness (McBeath & Neuhoff, 2002; Neuhoff & McBeath, 1996; Neuhoff, McBeath, & Wanzie, 1999).

Rosenblum, Carello, and Pastore (1987) examined the relative effectiveness of Doppler shift, interaural time differences, and overall intensity change in cuing listeners to the arrival time of a looming sound.[1] Intensity change was found to be the dominant cue to the point of closest approach for a passing sound source, followed by interaural temporal differences, then the Doppler effect. Performance was best under full cue conditions. However, even under full cue conditions, listeners still exhibited a systematic bias to hear the sound arrive before it actually did. Subsequent work showed that providing explicit

[1] The term "looming sound" is used in this chapter to refer to the approach of a sounding object and should not be confused with the acoustic pressure wave that approaches at the speed of sound.

feedback on the accuracy of the judgments after each trial diminished but did not eliminate the anticipatory bias (Rosenblum, Gordon, & Wuestefeld, 2000).

There are other potential sources of acoustic information that listeners may use in judging the arrival time of a looming sound, which have yet to be systematically investigated. For example, the ratio of direct to reverberant sound increases as the source draws closer to the listener. The spectral profile of the sound at the listening point also changes due to the decrease in atmospheric damping of high frequencies as the source approaches. Some work has shown greater physiological effects of looming sounds when multiple cues are employed over conditions in which just amplitude changes (Bach, Neuhoff, Perrig, & Seifritz, 2009). This implies that listeners are sensitive to these additional cues and may in fact use them in judging arrival time. Other work has shown that the perceived urgency of the sound source can influence judged arrival time, with more urgent sounds being perceived to arrive sooner (Gordon, Russo, & MacDonald, 2013; Neuhoff, Hamilton, Gittleson, & Mejia, 2014).

The auditory looming bias is closely linked to the bias to hear rising intensity as changing in loudness more than equivalent falling intensity. If listeners overestimate the approach of a looming sound and loudness change is the dominant cue to approach, then the overestimation of rising loudness may be at the heart of the auditory looming bias. However, if we are to argue that this perceptual bias is an adaptation shaped by evolution, then it should be specific to the conditions under which it would provide the greatest advantage in the natural listening environment over our evolutionary history. To test this prediction, Neuhoff (1998) presented listeners with rising and falling intensity tones and asked them to use a slider to indicate the amount of loudness change they heard in each sound. Rising intensity was consistently heard to change more than equivalent falling intensity, and the louder the range of intensity change presented, the greater the disparity between rising and falling loudness change. In a natural listening environment where closer sounds are louder than equivalent distant sounds, these findings suggest a perceptual priority for looming sounds that are close over those that are more distant. Although the effect occurred with harmonic tones, it did not occur when listeners were presented with broadband noise, a finding that is also consistent with the priorities of localizing moving sound sources in a natural environment. Periodic sounds that have a tonal quality are produced by a wide variety of biological organisms and can act as a reliable marker for the identity of a single source. Although broadband noise can be produced by biological organisms, it can also be produced by widely dispersed nonbiological sources (e.g., wind and rain) for which localization may be less important. Thus, the looming bias is most robust under conditions in which it would be most advantageous to survival (see also McCarthy & Olsen, 2017). Recent magnetoencephalography work supports this hypothesis by showing that strength of sustained magnetic fields over bilateral temporal sensors linearly tracks intensity change in a looming harmonic tone but not in looming broadband noise (Bach, Furl, Barnes, & Dolan, 2015)

The argument for the looming bias as an adaptation was initially challenged because of the limited number of conditions under which the effect was first demonstrated (Canevet, Scharf, Schlauch, Teghtsoonian, & Teghtsoonian, 1999; Neuhoff, 1999). However, it has now been replicated under a wide variety of experimental conditions and settings (DiGiovanni & Schlauch, 2007; Grassi, 2010; Grassi & Darwin, 2006; Olsen & Stevens, 2010; Olsen, Stevens, & Tardieu, 2010; Ponsot, Meunier, Kacem, Chatron, & Susini, 2015; Ponsot, Susini, & Meunier, 2015; Teghtsoonian, Teghtsoonian, & Canevet, 2005). One of

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the first studies to replicate the effect used a moving loudspeaker in an outdoor environment (Neuhoff, 2001). Blindfolded listeners made terminal egocentric distance estimates of a moving loudspeaker that either approached or receded. The sounding loudspeaker approached from a distance of 12.2 m and came to rest 6.1 m from the listener. The receding loudspeaker began directly in front of the listener and stopped at the same distance, 6.1 m from the listener. Analogous to the rising and falling loudness sounds presented over headphones, the results showed that approaching sounds were perceived to stop closer to the listener than receding sounds, and tones were perceived as stopping closer than noise despite an equal stopping distance from the observation point in all conditions.

The Logic Behind the Adaptation: Error Management Theory

Error Management Theory (EMT) predicts that a wide range of social, cognitive, and perceptual biases have evolved because they increase the likelihood of survival and reproduction. EMT proposes that biases will evolve when judgments are made under conditions of uncertainty, when the decisions have historically had an impact on evolutionary fitness, and when there is an asymmetric cost of making false-positive and false-negative errors (Haselton & Buss, 2000; Haselton & Nettle, 2006; Haselton et al., 2009). All of these conditions are met when a sound source approaches a listener. All perceptual judgments are made under a degree of uncertainty (Mathys et al., 2014), and predicting the arrival time of a looming sound source may have more uncertainty than many other perceptual judgments. Such decisions could also have life or death consequences and thus undoubtedly have had an impact on evolutionary fitness. Finally, the cost of a false positive (responding too early to a looming sound source by escape or avoidance behaviors) pales in comparison to the potentially deadly cost of a false negative (responding too late). Thus, an organism whose neural architecture represented looming sounds as closer than they actually were would have a selective advantage.

In the context of this discussion, the question is often posed: *Wouldn't it be more advantageous to have veridical perception of a looming sound source and let the listener cognitively decide what appropriate actions should be taken?* There are several critical reasons why the answer to this question is "no." First, let us contrast a hypothetical listener with veridical perception to a listener with a bias to hear looming sounds as closer than they are. Each is tasked with predicting the arrival time of a dangerous looming source. On average, the listener with veridical perception predicts perfectly the arrival time of the source, a point we will call 0 seconds to contact. The listener with the looming bias responds consistently early, for example at an average of 500 msec before contact. However, each listener also has a degree of variability associated with their arrival time judgments, each sometimes responding slightly earlier or later than their respective means. Early judgments are not problematic for either listener, as they provide slightly more time than expected to prepare for the arrival of the source. However, a listener with veridical perception who responds just a half-second late is responding after the source has already arrived. Even if the listener with veridical perception makes the cognitive decision to initiate motor behaviors sooner rather than later in order to prepare for the arrival of the source, their responses are still based on a "veridical" judgment of arrival time that in this instance is a half-second too late and pushes the motor response back by a potentially perilous half-second as well. A late response by the listener with the looming bias still leaves enough time to respond safely.

It is also the case that cognitive resources are limited. If the decision to engage the motor system in the face of a looming sound source were entirely under conscious control, then anyone engaged with a high cognitive load at the time would be disadvantaged in that there would be fewer cognitive resources to devote to the approaching danger. However, a recent study that manipulated cognitive load while participants judged the arrival of a looming sound found just the opposite. McGuire, Gillath, and Vitevitch (2015) asked listeners to judge when a looming sound would reach them while under high cognitive load (memorizing a seven-digit number) or low cognitive load (memorizing a two digit number). They found that the looming bias was significantly larger under high cognitive load. That listeners respond sooner rather than later under high cognitive load suggests that the bias to hear sounds as closer than actual is an automatic process that requires little effortful cognitive processing. Rather than (or at least in addition to) a "decision to respond early," the looming bias appears to be a perceptual phenomenon that has evolved to keep organisms safe. This finding is consistent with work in representational momentum and boundary extension that also shows an increase in the magnitude of perceptual bias under high cognitive load (Hayes & Freyd, 2002; Hubbard, Hutchison, & Courtney, 2010; Intraub, Daniels, Horowitz, & Wolfe, 2008).

Converging Evidence for the Looming Bias Adaptation

Behavioral evidence. A wide range of behavioral research has now demonstrated that looming sounds are treated with priority by the auditory system and that listeners demonstrate a consistent underestimation of distance and arrival time when faced with a looming sound (Neuhoff, 1998, 2001, 2016; Neuhoff et al., 2014; Neuhoff, Long, & Worthington, 2012; Riskind, Kleiman, Seifritz, & Neuhoff, 2014; Rosenblum, Wuestefeld, & Saldana, 1993; Rosenblum et al., 1987; Rosenblum et al., 2000). The prioritization of looming sounds is present in infancy. Infants as young as four months old show significant differential responding to looming versus receding sounds by exhibiting defensive avoidance responses to looming sounds that do not occur with equivalent receding sounds (Freiberg, Tually, & Crassini, 2001). By six months, infants have better discrimination abilities for looming versus receding sounds (Morrongiello, Hewitt, & Gotowiec, 1991).

Sex differences have also been demonstrated in the looming bias, with women tending to perceive auditory arrival time as occurring sooner than do men (Neuhoff, Planisek, & Seifritz, 2009; Schiff & Oldak, 1990). In the study of the evolution of behavior, sex differences can be a key piece of evidence for behavioral adaptations. To the extent that men and women have faced different challenges to survival and reproduction over our evolutionary history, we should expect slightly different behavioral adaptations to have evolved to deal with these challenges (Buss, 1995; Byrd-Craven & Geary, 2007).

Although judging the arrival time of a looming sound is essentially a spatial transformation task, the sex difference in the perception of looming sounds is likely not the product of the well-known male advantage in spatial transformation (Kimura, 1999; Silverman, Choi, & Peters, 2007; Voyer, Voyer, & Bryden, 1995). If it were, we would expect sex differences for the perception of sounds that move both toward and away from the listener. However, Neuhoff et al. (2009) presented male and female listeners with both approaching and receding sounds that stopped equidistant from the listening point. Women perceived the looming sounds to be significantly closer than did men. However, there was no difference between the male and female judgments for the receding sounds. If sex differences in the perception of looming sounds were simply the result of more accurate spatial transformation abilities by men, then we should expect those same differences to occur for receding sounds.

That there were no sex differences in the perceived distance of receding sounds may highlight a particular differential environmental challenge that men and women have faced over our evolutionary history – dealing with an approaching threat. Some of the most reliable differences between males and females are in physical strength, running speed (Nicolay & Walker, 2005; Whipp & Ward, 1992). Both of these characteristics could be crucial in dealing with a dangerous looming sound source. Thus, women would stand to benefit from a larger margin of safety in anticipating the arrival of a looming source. Essentially, those least well prepared to engage a dangerous looming sound source should have the greatest auditory looming bias.

Evidence to support this hypothesis comes from work showing that the magnitude of the looming bias is negatively correlated with strength and physical fitness (Neuhoff et al., 2012). Individual within-sex correlations were also significant, suggesting that the sex differences in the looming bias may be largely due to differences in strength and fitness rather than biological sex per se. The magnitude of the looming bias is also modulated by factors such as affect, anxiety, depression, and even schizophrenia (Bach, Buxtorf, Strik, Neuhoff, & Seifritz, 2011; Ferri, Tajadura-Jimenez, Valjamae, Vastano, & Costantini, 2015; Neuhoff et al., 2014; Tajadura-Jimenez, Valjamae, Asutay, & Vastfjall, 2010)

Comparative Evidence. The argument that a given human behavior is an evolutionary adaptation can be made stronger if the behavior is also found in a closely related species. Thus, if the human bias to perceive looming sounds as closer than actual is an adaptation, then we might expect to observe the bias in related species that have faced similar evolutionary challenges. Ghazanfar, Neuhoff, and Logothetis (2002) presented rhesus monkeys with the same simulated looming and receding sounds that were presented to human listeners in the work by Neuhoff (1998). They found a preferential orienting response to looming sounds over receding sounds that matched the pattern of results found in humans. As with humans, the bias occurred for harmonic tones but not for broadband noise. The concomitant neural activity that underlies the perceptual priority for looming sounds shows the same directional asymmetry (Hall & Moore, 2003). Activity in the lateral belt auditory cortex of monkeys is stronger with looming than with receding sounds, and the processing of looming stimuli appears to involve an interaction between the auditory cortex and the superior temporal sulcus that is not apparent with equivalent receding stimuli (Maier, Chandrasekaran, & Ghazanfar, 2008; Maier & Ghazanfar, 2007).

Physiological. Support for the hypothesis that any perceptual trait is an evolutionary adaptation can be strengthened by identifying specific physiological mechanisms that support the trait. Seifritz et al. (2002) used neuroimaging to examine the neural processing of looming sounds in comparison with receding sounds. They found that looming sounds preferentially activate a distributed neural network that is known to subserve auditory motion perception, attention, and motor planning. These findings support an earlier hypothesis by Guski (1992) that suggested that the function of the auditory system in the face of a looming sound is to provide input into a decision about the appropriate motor behaviors in which to engage. Faced with a looming sound, the auditory system provides advanced warning as evidenced by enhanced autonomic responses. Looming sounds when compared with equivalent receding sounds produce stronger amygdala activation, greater skin conductance, more robust pupil dilation, enhanced phasic alertness, and greater emotional arousal (Bach et al., 2008; Bach et al., 2009; Ferri et al., 2015; Fletcher et al., 2015; Tajadura-Jimenez et al., 2010).

Visual Looming

If the auditory looming bias provides advanced warning of looming objects, the visual system provides a more accurate means of dealing with the source on approach. The anticipatory looming bias that occurs in audition is significantly diminished in vision, and observers are significantly more accurate in making visual time-to-arrival judgments than they are when making equivalent auditory judgments (DeLucia, Preddy, & Oberfeld, 2015; Schiff & Oldak, 1990). However, the evolutionary implications of impending collision are still present in vision. It should also be noted that many of the studies that show an underestimation of visual arrival time introduce uncertainty by occluding the final approach of the object. In these experiments, the object first approaches then disappears before reaching the observer, and observers are asked to judge when the object would have reached them had it not disappeared. Performance increases significantly when viewers can see the entire approach of the object as is evidenced by our ability to interact with objects in the real world successfully (e.g., catching a ball; McBeath, Shaffer, & Kaiser, 1995; Shaffer & McBeath, 2002; Wang, McBeath, & Sugar, 2015b). In audition, the anticipatory looming bias remains even when listeners can hear the full approach of the sound source (Neuhoff et al., 2009; Neuhoff et al., 2012; Neuhoff et al., 2014).

Under some conditions, there are also sex differences in judgments of visual arrival time that mirror those in audition. Females tend to show greater underestimation of arrival time than males (Hancock & Manser, 1997; Manser & Hancock, 1996; McLeod & Ross, 1983; Montgomery, Kusano, & Gabler, 2014; Schiff & Oldak, 1990). Moreover, an incredibly wide variety of species ranging from insects to humans exhibit defensive responses when presented with visually looming objects (W. Ball & Tronick, 1971; Bower, Broughto, & Moore, 1971; King, Dykeman, Redgrave, & Dean, 1992; Lima, Blackwell, DeVault, & Fernandez-Juricic, 2015; Sato & Yamawaki, 2014; Schiff, 1965; Schiff, Caviness, & Gibson, 1962; Yilmaz & Meister, 2013; Zurek, Perkins, & Gilbert, 2014). Like looming sounds, visually looming objects also prime the human motor system for action and activate the autonomic nervous system (Low, Lang, Smith, & Bradley, 2008; Skarratt, Cole, & Gellatly, 2009; Skarratt, Gellatly, Cole, Pilling, & Hulleman, 2014). All of these factors, including the more accurate judgments of visual time-to-arrival, provide evidence for an evolutionary role in shaping our responses to looming visual stimuli.

Cues to Visual Looming

As an object approaches an observer,. the image cast on the retina dilates. This optical dilation was one of the first investigated sources of information in judging the arrival time of a looming visual object. The inverse of the rate of dilation (called optical tau) can specify time-to-arrival under some conditions, and observers have been shown to be sensitive to this information (Kaiser & Mowafy, 1993; Lee, 1976; Lee & Reddish, 1981; Regan & Hamstra, 1993; Todd, 1981). Tau was initially proposed as a candidate for completely explaining how observers judge visual time-to-arrival (Lee, 1976; Savelsbergh, Whiting, & Bootsma, 1991; Turvey & Carello, 1986). However, this version of tau is limited in that it breaks down when looming objects do not have a constant acceleration, are not symmetrical, and are not on a collision course with the observer (Tresilian, 1999). Optical tau alone also fails to account for how observers can predict the arrival of very small objects or objects that undergo short falls from gravity (Gray & Regan, 1998; Tresilian, 1993). Subsequent work showed that optical tau is just one of a number of available cues. Several other dynamic tau variables, heuristics, and even pictorial cues such as image size can be used to estimate arrival time (DeLucia, 1991; , 2004; Kaiser & Mowafy, 1993; Tresilian, 1993, 1994). For a review, see Tresilian (1999).

Bias for Looming Visual Motion

Despite the relatively accurate perception of visual arrival time under full viewing conditions, there are nonetheless well-documented asymmetries in the perceptual processing of looming versus receding motion. For example, it has been known more than 100 years ago that the motion aftereffect for looming motion persists significantly longer than that for equivalent receding motion (Scott, Lavender, McWhirt, & Powell, 1966; Wohlgemuth, 1911). More recent work has shown that the perceptual asymmetry in perceiving looming and receding develops within the first few months of life (Shirai et al., 2009; Shirai, Kanazawa, & Yamaguchi, 2004, 2006). Observers also perceive looming motion as faster than receding motion, detect the onset of looming motion sooner, and show better detection of changes in looming stimuli than in receding ones (K. Ball & Sekuler, 1980; Bex & Makous, 1997; Geesaman & Qian, 1996; Petersik & Thiel, 2010). Under conditions of uncertainty, viewers show a predisposition to perceive objects as looming rather than receding. For example, C. F. Lewis and McBeath (2004) presented viewers with a 3D bistable apparent motion display that could be perceived as either looming or receding. They found that viewers showed a significant bias to perceive the display as looming.

The emotional characteristics of a looming visual stimulus can influence perceived arrival time. Looming threatening stimuli (spiders and snakes) are perceived to arrive more quickly than nonthreatening stimuli (bunnies and butterflies), and the ratings of fear of the stimulus are correlated with perceived arrival time (Vagnoni, Lourenco, & Longo, 2012, 2015). The more fearful the viewer, the sooner the object is perceived to have arrived. Other threatening stimuli (e.g., threatening faces) show similar effects (Brendel, DeLucia, Hecht, Stacy, & Larsen, 2012). However, the notion that "threat" alone is the critical factor at work here is likely an oversimplification. More recent work has also implicated the role of arousal and stimulus complexity. For example, highly arousing positive stimuli (erotica and money) are perceived to arrive as soon as fearful stimuli, and pictorial stimuli, in general, are perceived to arrive sooner that simple colored rectangles (Brendel, Hecht, DeLucia, & Gamer, 2014).

Looming and receding visual stimuli also have asymmetrical effects on attention. Objects that approach an observer attract attention and are treated with priority. For example, in a visual search task, increasing the number of distractors in a search for a receding target significantly increases search time. However, the same increase in the number of distractors has no effect on search time for looming targets (Takeuchi, 1997). This suggests that detecting looming stimuli occurs automatically. Subsequent work has shown that looming, but not receding, objects capture attention even when they are not relevant to the task at hand (Franconeri & Simons, 2003). The attentional capture effects of looming stimuli appear to be subserved by covert attentional mechanisms that do not require effortful cognitive processing (Kahan, Colligan, & Wiedman, 2011; J. E. Lewis & Neider, 2015). The evolutionary implications of the priority for looming objects are underscored by the finding that the effects of looming stimuli are magnified when the stimuli are on a collision path with the observer and are not dependent on the sudden onset of motion (Lin, Franconeri, & Enns, 2008; von Muhlenen & Lleras, 2007).

Bias for Receding Visual Motion?

Despite the wealth of data demonstrating a perceptual bias for looming visual motion, there are a number of apparently conflicting studies that find a bias for receding motion. For example, observers show better sensitivity as measured by a discrimination task for contracting pattern of dots than an expanding pattern of dots (Edwards & Badcock, 1993; Edwards & Ibbotson, 2007). Viewers have also demonstrated better sensitivity to acceleration when viewing receding versus looming dot patterns (Mueller & Timney, 2014). Some researchers have suggested that the better discrimination for these receding optic flow fields is related to postural stability, where falling backward (which creates receding optic flow) is a greater danger than falling forward (Edwards & Ibbotson, 2007; Mueller & Timney, 2014; but see Holten, Donker, Stuit, Verstraten, & van der Smagt, 2015). Other work suggests that the direction of asymmetry is also dependent on the speed of the optic flow pattern, which varies across studies (Naito, Sato, & Osaka, 2010).

Variability in the nature of the tasks employed may also in part be responsible for the conflicting results. The majority of the studies that find an advantage in the perception of receding stimuli use optic flow fields that are composed of dots. The analogous real-world looming condition would be moving through the world without any indication that a collision is imminent. On the other hand, many of the studies that show a perceptual advantage for looming present a target stimulus that appears to approach the observer on a collision course. Given these differences, both the "postural stability" and the "looming threat" hypotheses may have merit depending on the specific circumstances. Another consideration is that the discrimination tasks typically used in studies that find an advantage for receding stimuli may require more effortful cognitive processing than, for example, visual search or time-to-arrival where attention is captured automatically or where a defensive motor response is appropriate (e.g., Franconeri & Simons, 2003; King et al., 1992; J. E. Lewis & Neider, 2015; Lin et al., 2008). Because the visual features of a looming object are thought to be processed without depleting effortful cognitive resources (Kahan et al., 2011; J. E. Lewis & Neider, 2015), looming objects may impact discrimination and visual search differentially. Looming stimuli activate motor defense mechanisms and responses of the autonomic nervous system (King et al., 1992; Low et al., 2008; Skarratt et al., 2009; Skarratt et al., 2014). This may *facilitate* the automatic responses to looming objects that do not require effortful processing but *interfere* with effortful cognitive judgments such as discrimination. Essentially, the different tasks may differentially invoke either visuo-motor or visuo-cognitive systems and account for the conflicting findings (Goodale & Milner, 1992; Tresilian, 1995).

Multisensory Integration of Looming Stimuli

Despite the fact that most of the research conducted on the perception of looming objects has been unimodal in nature, many looming objects simultaneously produce both visual and auditory cues as they approach. Some work has examined how the presence of both visual and auditory information influences the perception of looming objects and how this multimodal information is integrated. Other work has hypothesized that the information contained in a looming object is "modality-neutral." In other words, regardless of modality, the tau variable information for an approaching source can specify time-to-arrival. If the system is sensitive to this underlying change in information over time, then in theory, the modality with which the approach is perceived should have little effect on the perceived time-to-arrival (Gordon & Rosenblum, 2005).

However, despite the potential equivalence of information in the two modalities, observers show stark differences in how they use auditory versus visual information in judging arrival time (DeLucia et al., 2015; Schiff & Oldak, 1990). The visual and auditory systems have evolved to solve quite different evolutionary problems in dealing with looming objects. Guski (1992) suggested a kind of "handshaking" that occurs between the two systems, in which audition acts as an advanced warning system that provides information for a categorical decision about engaging appropriate motor behaviors (e.g., either evasive or engaging in visual tracking). The visual system can then provide the more accurate estimates of arrival time that can be used to deal appropriately with the looming object. The "warning system" hypothesis for audition is supported by work that examines time-to-arrival judgments under auditory only, visual only, and audiovisual conditions. A number of these studies have shown that performance in predicting the arrival time of a looming object with both visual and auditory information does not significantly differ from performance when only visual information is available (DeLucia et al., 2015; Hofbauer et al., 2004; Schiff & Oldak, 1990; Zhou, Yan, Liu, Li, & Xie, 2007).

The integration of auditory and visual information is present in infants as early as five months. When presented with matched and mismatched auditory and visual looming and receding signals, infants show greater attention to the stimuli that are matched in direction of travel (Walker-Andrews & Lennon, 1985). As might be expected, they also show greater attention to looming versus receding stimuli. Work with rhesus monkeys shows a similar strong orienting preference for coincident visual and auditory looming stimuli but no analogous response for coincident stimuli that were receding. Consistent with previous work in auditory looming, the orienting preference effect occurred only with tonal auditory stimuli and not with broadband noise (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Maier et al., 2008). Preferential processing and integration of looming versus receding multisensory stimuli also occurs in adult humans and is supported by recent behavioral, EEG, and fMRI experiments (Cappe, Thelen, Romei, Thut, & Murray, 2012; Cappe, Thut, Romei, & Murraya, 2009; Maier et al., 2008; Ogawa & Macaluso, 2013; Tyll et al., 2013).

The processing advantage and environmental importance of looming stimuli are further evidenced when the perception of multimodal looming and receding stimuli are examined under congruent and incongruent conditions. Under congruent conditions, both the auditory and visual stimuli move in the same direction, either toward or away from the observer. Under incongruent conditions, the auditory and visual stimuli move in opposite directions. If listeners are asked to judge the direction of the moving sound and ignore the visual stimulus, performance is better in the presence of receding stimuli. In essence, observers can more easily ignore the incongruent receding visual stimulus. This indicates that looming visual stimuli show stronger visual capture effects than receding visual stimuli (Harrison, 2012). Similar work has shown that varying the congruency of a visual stimulus has little effect on detection rates for looming sounds (where accuracy is generally high). However, a congruent versus an incongruent visual stimulus does increase the detection of receding auditory stimuli (Liu, Mercado, & Church, 2011).

Looming auditory and visual objects have also been shown to influence tactile perception. For example, a looming visual object that approaches the face increases tactile sensitivity at the predicted time and location that the object would contact the face (Clery, Guipponi, Odouard, Wardak, & Ben Hamed, 2015). Similar tactile effects are obtained with looming sounds (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Canzoneri, Magosso, and Serino (2012) found that a sound moving toward an observer's hand speeded up the processing of a tactile stimulus at the hand when the sound was within the boundaries of peripersonal space representation. The effect was significantly stronger for looming sounds than for receding ones (but see Finisguerra, Canzoneri, Serino, Pozzo, & Bassolino, 2015).

Conclusions

Looming objects are salient and behaviorally relevant stimuli that are perceptually and neurally processed with priority when compared with equivalent receding objects. Looming stimuli also preferentially activate the autonomic nervous system and the motor system. They bring about differential emotional, cognitive, and defensive responses. Although this perceptual anisotropy can sometimes create distortions in perceived egocentric spatial relations, they are distortions that over time have enhanced the probability of survival and reproduction. Thus, these perceptual biases have been favored by evolution.