

10

INTERACTING PERCEPTUAL DIMENSIONS

JOHN G. NEUHOFF

In many psychoacoustic experiments, the objective is to investigate some aspect of a particular perceptual dimension. Some of the most commonly examined perceptual dimensions include pitch, loudness, perceived spatial location, timing, and timbre. Often, the experimental design dictates that the acoustic characteristics of all but the dimension of interest be held constant and changes in the dimension under investigation occur only from trial to trial. For example, in an experiment on loudness scaling, listeners might assign a particular constant-intensity tone a number that denotes its loudness. On subsequent trials the listener is presented with different intensity tones and is asked to assign a number to the loudness that represents the relationship to the first tone heard. Aside from intensity, all other characteristics of the stimuli (e.g., frequency and spectrum) are held constant. Even in experiments that use dynamic stimuli it is typical to only vary one parameter of the sound at a time. The advantages of this paradigm are clear. It allows greater experimental control and increases the internal validity of the experiment by ruling out the confounding influences of parametric changes in other acoustic dimensions.

However, in the real world things are seldom so tidy. In natural listening environments, sounds continuously undergo simultaneous dynamic changes in multiple perceptual dimensions. It is all too common for sound sources to produce sounds that vary in frequency, intensity, and spectral characteristics all at once. Furthermore, in the rare cases in which sounds *are* produced with constant frequency, intensity, and spectral content, they are rarely perceived as such. Relative motion between the source and the listener or disturbances in the medium can create dynamic change in the acoustic characteristics of the signal. A car horn, for example, produces a signal that is relatively stable in frequency, intensity, and

spectrum. However, as the source draws closer to the listener, the observed intensity grows in accordance with the inverse square law, the fundamental frequency shifts due to the Doppler effect, and the spectrum changes because the damping effect of the atmosphere on high-frequency components is diminished at closer range. Even if there is no relative motion between a static sound source and the listener, a breeze can cause dynamic changes in intensity and spectrum, and other sounds in the environment can create intermittent masking effects. Moreover, the attention and physiological state of the listener can influence any number of perceptual characteristics. Finally, other perceptual modalities (particularly vision) can influence how we hear the world. Sensory systems have evolved together. As such, they provide complementary advantages to organisms in that the weaknesses of one system are often compensated by strengths in another.

In this chapter, we examine both the perceptual interaction of auditory dimensions (such as the effect of change in pitch on loudness) and the interaction of perceptual modalities (namely vision and hearing). Both of these areas have real-world significance in that they constantly occur in natural settings. Both have also been studied very little compared with more traditional areas of psychoacoustic research, such as pitch and loudness.

THE INTERACTION OF AUDITORY DIMENSIONS

The interaction of perceptual dimensions has been of great interest to cognitive psychologists. At issue is whether an object (either auditory or visual) is perceived analytically or holistically. Analytical perception implies that the components or “parts” that make up an object are separately analyzed and then perceptually “glued together” to form the whole. Holistic perception implies that objects are not broken into their component parts but simply perceived as wholes. This debate stems from early perspectives in experimental psychology. The structuralist (analytic) perspective suggests that objects are assembled from their parts. In contrast, the Gestalt approach suggests that objects are perceived holistically and that the relationships between components can be as important as the components themselves. The most recent evidence suggests that the nature of object perception, whether analytic or holistic, depends on the type of object or stimulus characteristics being perceived as well as the conditions that can increase or decrease the salience of dimensional structures (Potts, Melara, & Marks, 1998).

DIMENSIONAL INTERACTION

Garner (1974) proposed a set of converging operations (speeded sorting, restricted classification, and dissimilarity scaling) that have been used to determine whether a set of perceptual dimensions (e.g., pitch and loudness) interact. Typically, only two perceptual dimensions are examined at a time, and observers

are instructed to attend to one and ignore the other. Generally speaking, if static orthogonal trial-to-trial variation of an unattended dimension influences performance in the dimension of interest, the two dimensions are said to be “integral.” If performance on the dimension of interest is unaffected, the dimensions are said to be “separable.” According to this traditional view, stimuli consisting of integral dimensions are initially perceived as dimensionless, unanalyzable, holistic “blobs” (Garner, 1974; Lockhead, 1972, 1979). The psychological distance between stimuli can best be described by a Euclidean metric, and stimuli themselves are processed in a holistic, “unitary” manner (Shepard, 1964). In other words, the perceiver does not have primary access to the dimensions in question and cannot selectively attend to one dimension.

Alternatively, Melara and his colleagues (Melara & Marks, 1990a, 1990b; Melara, Marks, & Potts, 1993a, 1993b) have advanced a model of dimensional interaction that proposes a mandatory and immediate access to interacting dimensions. This access to primary dimensional axes is called attribute-level processing because participants extract individual attributes from the dimensions of interest. With interacting dimensions, the extraction of a dimensional attribute creates a context in which attributes of the other dimension are perceived. This influence of context is called stimulus-level processing. In the case of interacting dimensions, then, the perception of an attribute on one dimension is influenced by the context created by an attribute in the other dimension. For example, a loud tone is perceived differently in the context created by high pitch than in the context created by low pitch (it should be noted that this work employs strict controls to ensure equal loudness of stimuli as a function of frequency).

However, both the traditional and the more recent theories of multidimensional perception have employed only static stimuli methodologies in studying multidimensional perception, thus limiting the generalizability of the findings to stimuli that seldom occur in a natural environment.

Experiments using static stimuli have shown that that trial-to-trial variation in pitch influences loudness judgments and that loudness variation similarly influences pitch (e.g., Melara & Marks, 1990a). It should be noted that this influence is different from the “equal loudness contours” and “equal pitch contours” discovered by Stevens because all of the stimuli are equated for these contours depending on whether pitch or loudness is being judged. Rather, the phenomenon here appears to be a cognitive influence of the trial-to-trial variation in the unattended dimension. For example, if the listener is asked to judge on successive trials whether a pitch is “high” or “low,” trial-to-trial variation in the loudness (“loud” or “soft”) will affect reaction time to judge the pitch. However, the specific nature of this influence has been an issue of considerable dispute. The debate centers on exactly what characteristics or attributes of a multidimensional stimulus are available or can be accessed by a perceiver. Melara, Marks, and their colleagues have argued that the perception of pitch and loudness is an analytic process (Marks, 1989; Melara & Marks, 1990a, 1990b; Melara *et al.*, 1993a, 1993b). Listeners are said to have “primary” access to each of the respective

dimensions. In their view, the interaction of pitch and loudness occurs because the context created by the unattended dimension (e.g., pitch) influences judgments about the attended dimension (e.g., loudness). A high-pitched tone is perceived differently in the context of high loudness than it is in the context of low loudness.

Alternatively, the traditional model of multidimensional interaction suggests that interacting dimensions are perceived holistically (Garner, 1974; Kemler, 1983; Kemler Nelson, 1993; Smith & Kemler, 1978). The stimulus dimensions themselves are not directly perceived without great effort. Instead, integral stimulus dimensions are perceived initially as dimensionless, unitary "blobs" (Lockhead, 1972, 1979; Shepard, 1964). Because perceivers do not have primary access to the stimulus dimensions, they cannot selectively attend to one stimulus dimension. The perceptual experience of such a multidimensional stimulus then is the vector sum of the weighted values on each dimension.

Interacting dimensions have typically been defined by performance on speeded sorting, dissimilarity scaling, and categorization tasks using static stimuli. Some more recent work shows that using more ecologically valid dynamic stimuli, the principles of dimensional interaction still hold (Neuhoff & McBeath, 1996; Neuhoff, McBeath, & Wanzie, 1999; Neuhoff, Wayand, & Kramer, 2002; Walker & Ehrenstein, 2000). However, both Garner's and Melara and Marks' models of perceptual interaction would predict such results. If, according to the traditional model, pitch and loudness are processed holistically, listeners would not be able to attend selectively to changes in only one dimension. So when tracking dynamic intensity change, a listener will be influenced not only by changes in intensity but also by changes in frequency. Depending on the degree to which the participant can selectively access frequency and the relative amount of change in each dimension, the holistic analysis may give way to an experience of changing loudness that is quite at odds with the change in acoustic intensity. On the other hand, applying the case of dynamic stimuli to the more recent model of Melara and Marks, we need only assume that a greater degree of dimensional change creates a more influential context in which the dimension of interest is perceived. Then perceivers who extract the stimulus attribute constant loudness in the context of the attribute rising pitch may be so influenced by the context of this rising pitch that they report rising loudness.

To provide a test of these two models under more ecological conditions of dynamic pitch and loudness change, Neuhoff, McBeath, & Wanzie (1999) used a dichotic listening task in which changes in the intensity of broadband noise were presented to one ear and changes in frequency of a complex tone were presented to the other ear. The task of the listener was to judge the amount of loudness change that occurred in the noise while ignoring the pitch change of the tone in the opposite ear. The results showed that when frequency and intensity in opposite ears changed in the same direction, the perceived change in loudness of the noise was greater than when the stimulus attributes changed in opposite directions. Because frequency change in one ear influenced loudness change

in the contralateral ear, the findings suggest that the dynamic interaction of pitch and loudness occurs centrally in the auditory system and is an analytic rather than holistic process. Moreover, the authors suggested that the interaction of pitch and loudness perception has evolved to take advantage of a ubiquitous covariation of frequency and intensity change in natural environments (McBeath & Neuhoff, 2002). At the very least, the findings reflect a shortcoming of traditional static models of loudness perception in a more dynamic setting. The findings also provide support for Melara *et al.*'s analytic and contextually dependent model of the processing of pitch and loudness. It is unlikely that participants perceived the dichotic sounds as one dimensionless blob (Lockhead, 1972, 1979). Thus, it seems reasonable to conclude that the context created by changing frequency in one ear influenced loudness change in the other. The interaction of pitch and loudness under dynamic conditions has also been implicated in the "Doppler illusion" (McBeath & Neuhoff, 2002; Neuhoff & McBeath, 1996; Ryffert, Czajkowska, Jorasz, & Markarewicz, 1979), a finding demonstrating that listeners tend to hear a rise in pitch as a sound source approaches despite the drop in frequency that occurs because of the Doppler shift. The rise in pitch is thought to occur because of the influence of the dramatically rising intensity that occurs as the sound source draws closer to the listener.

The perceptual interaction of pitch and loudness has been proposed as an efficient processing strategy because in nature, there is a reliable correlation between changes in intensity and frequency. When sound sources increase in intensity, they tend to increase in frequency and vice versa. This effect is perhaps most apparent in one of the most commonly occurring sources that humans are exposed to, human speech (Alain, 1993; Brenner, Doherty, & Shipp, 1994; Cutler & Butterfield, 1991; Fisher & Tokura, 1995). Other organisms also produce and attend more closely to calls in which frequency and intensity are positively correlated (Gaioni & Evans, 1986, 1989). Finally, music perception research has shown that there is an expectation that melody lines that rise in frequency will also rise in intensity (Repp, 1995). Scharine (2002) showed that listeners exhibit a lower threshold for tones presented in noise when their change in frequency is positively correlated with their change in intensity, supporting the hypothesis that perceptual interaction is an element that may aid listeners in segregating sound objects.

Walker and Ehrenstein (2000) showed that similar perceptual interaction effects can occur between the dimensions of "relative pitch" (high versus low) and the direction of dynamic pitch change (up versus down), essentially "pitch" and "pitch change." They presented listeners with 250-ms pitch glides that either rose in frequency or fell in frequency and were either initially "high" or "low" in pitch. "Congruent" stimuli were either high-frequency stimuli that became higher or low-frequency stimuli that became lower. "Incongruent" stimuli were those that started at a high pitch and became lower or those that started at a low pitch and became higher. They found that reaction time to identify either relative pitch or direction of pitch change was faster when the stimuli were congruent

than when the stimuli were incongruent. Their results demonstrate that auditory perceptual dimensions do not necessarily map neatly onto acoustic dimensions because in both cases in their experiment the relevant physical dimension of frequency creates the perceptual dimensions of both relative pitch and pitch change.

The auditory dimensions of pitch and timbre have also been shown to interact (Demany & Semal, 1993; Krumhansl & Iverson, 1992; Warrier & Zatorre, 2002). For example, Krumhansl and Iverson (1992) manipulated pitch and timbre in a speeded classification task and showed interference from uncorrelated variation in the unattended dimension and facilitation from correlated variation. However, they also showed that when the variations of pitch and timbre are embedded in longer, more meaningful musical passages, the effect is reduced considerably. Similarly, Warrier and Zatorre (2002) found that providing an increasingly meaningful tonal context in the form of either tone sequences or short melodies reduced the perceptual interaction of pitch and timbre.

Pitt (1994) examined the interaction of pitch and timbre in subjects who were either musicians or nonmusicians. This work confirmed that variation in timber can influence judgments about pitch and vice versa. Interestingly, however, musicians showed less influence than nonmusicians. In addition, nonmusicians showed an asymmetry in their responses such that variation in timbre influenced pitch judgments more than variation in pitch influenced timbre. The musicians showed an influence of one dimension upon the other but no such asymmetry. Other work has shown that the perceptual interaction of pitch and timbre in musicians can influence both perception and performance (Greer, 1969; Worthy, 2000). When wind instrumentalists are asked to play a note that matches a presented stimulus, they play slightly higher in pitch (sharp) when matching bright timbre tones and slightly lower in pitch when matching dark timbre tones (Worthy, 2000). These findings should also be viewed in light of some work that draws a distinction between "perceptual interaction" and "decisional interaction" (Ashby & Townsend, 1986; Maddox, 2001; Maddox & Bogdanov, 2000).

Finally, other dimensions beside pitch, loudness, and timbre have been shown to interact perceptually, including spatial location, tempo, and rhythmic structure (Boltz, 1998; Patel & Balaban, 2000; Phillips & Hall, 2001). For example, the duration of tones can interact with intensity and pitch, particularly in sequences of tones (Tekman, 1997; Thompson & Sinclair, 1993). Higher order dimensions such as the perception of musical accents also interact with intensity (Tekman, 1998). Moreover, if listeners are asked to detect either timing or intensity variations in a sequence of tones, variation in the unattended dimension can influence judgments in the dimension of interest (Tekman, 2002). When the timing and intensity are uncorrelated, variation in the unattended dimension interferes with the detection of variation in the relevant dimension. When variation in the two dimensions is positively correlated, the detection of variation in the dimension of interest is better than it is with the absence of variation in the irrelevant dimension only for listeners who attended to timing. In the case of a negative correlation, the effect is the opposite.

DIMENSIONAL INTERACTION SUMMARY

The notion that distinct changes in acoustic characteristics of a stimulus such as frequency, intensity, and spectrum are perceptually distinct events is intuitively appealing. However, there is growing evidence that suggests that changes in a specific dimension affect not only the overall percept of the stimulus but also specific perceptual characteristics of other perceptual dimensions. In other words, changes in one dimension can affect perceived changes in the others. Some emerging paradigms and methodologies are beginning to elucidate specific neural mechanisms that may be involved in processing these perceptual effects (Dyson & Quinlan, 2002; Melara, Rao, & Tong, 2002; Patching & Quinlan, 2002; Zatorre, Mondor, & Evans, 1999). Given that the auditory system has evolved in an environment where stimuli constantly undergo simultaneous dynamic change of multiple acoustic parameters, perhaps this should come as no surprise.

MULTISENSORY INTERACTION

The perception of space is crucial to behaviors as diverse as traversing terrain, landing aircraft, or catching prey. These navigational abilities are informed by both vision and audition. The relatively distinct channels of modality specific research that are conducted suggest two independent sensory systems. Yet, perceptual modalities clearly interact. Thus, an organism must have some means of combining these distinct sources of information to form a unified representation of external space. If one accepts the position that perceptual abilities evolve because they provide an organism with selective advantages, it should come as no surprise that vision and audition provide complementary capabilities. The localization strengths of one modality compensate for weaknesses in the other. For example, the accuracy of visual spatial localization surpasses that of audition in part because of the depictive representation of the environment that falls on the retinae. The obvious disadvantage of such an arrangement in vision is that no spatial information can be obtained for hidden objects that fail to project a retinal image. There is no similar depictive representation of space in the auditory system. Spatial localization is accomplished in part by computing differences between the characteristics of the acoustic stimulus at each ear. The advantage is that the auditory system can provide spatial information about sound sources that are occluded, out of the line of sight, or present in conditions such as darkness or fog that make viewing impossible.

Humans rely primarily on vision to guide navigation and to a lesser extent audition. It is not surprising, then, that considerably more perceptual research has been conducted on visually guided navigation than on navigation guided by audition. In addition, the overwhelming majority of research, whether visual or auditory, has focused on the navigational implications of a single modality studied in isolation. Yet, in a natural environment distinct sources of auditory and visual

information are integrated seamlessly to form a unified representation of external space that guides navigation (Auerbach & Sperling, 1974; Welch & Warren, 1980). Evidence for this unified spatial representation comes from both behavioral and neurophysiological studies.

The history in perceptual research of greater research efforts toward vision and a concentration on a single modality has been mirrored to a certain extent in neuroscience. We have relatively detailed accounts of the function of structures in the visual pathways compared with those in audition. We know even less about the physiological interaction of the two systems. However, there are some clear examples of auditory and visual interaction at both the neurological and behavioral levels. This chapter first examines some of the perceptual and behavioral evidence of the interaction of visual and auditory information as it pertains to localization and navigation. Next, some physiological findings that begin to provide a neural basis for this interaction are presented.

A UNIFIED SPATIAL REPRESENTATION

It is generally accepted that one function of the auditory system is to orient visual attention and that this ability appears to be present at birth (Heffner & Heffner, 1992; Robinson & Kertzman, 1995; Spence & Driver, 1997). Clearly, though, the interaction of perceptual modalities in navigation is much more complex than simple orienting responses. In many cases, the interaction of vision and audition produces performance that exceeds what would be predicted by the performance of either modality alone (Perrott, Sadralodabai, Saberi, & Strybel, 1991; Stein, Meredith, Huneycutt, & McDade, 1989). In some instances, the combination of visual and auditory stimuli produces inhibitory effects that suppress inappropriate responses given the characteristics of the stimuli (Stein *et al.*, 1989).

When we move through an environment we use different sensory modalities to perceive the characteristics of the terrain, identify potential obstacles, and plan the appropriate motor functions that allow us to reach our destination. Thus, we have different sources of information that guide navigation. The visual system provides information about the layout of the environment and any visible obstacles. The auditory system provides information about both visible and hidden sound sources. The vestibular and kinesthetic senses provide us with information about body position relative to the environment. In some cases, these different sensory channels provide unique information. An obstacle in one's path that is silent can be detected by the visual system but not the auditory system. The locations of predators, machinery, or friends that are hidden from sight are determined through audition. However, in other cases more than one sensory system contributes information about the location of a single object. An ambulance that passes on the street is both seen and heard, so both vision and audition aid in its localization.

Despite the contribution of both unique and redundant information from distinct sensory systems, organisms have a unified representation of external space

that typically transcends perceptual modality (Auerbach & Sperling, 1974). For example, within the localization limits of audition and vision, an object that is both seen and heard can be located in space and spatially referenced with an object that is only seen and another object that is only heard. Together with the characteristics of the terrain, other auditory and visual objects, and the body position of the organism relative to the environment, this array of objects is integrated into a unitary representation of external space.

On the rare occasions that optical and acoustic information are discrepant and the observer recognizes that the visual and auditory modalities are providing conflicting information about the location of an object, distinct modality-specific spatial percepts may become apparent. For example, an airplane flying overhead can give discrepant auditory and visual cues about its location because the speed of sound is much slower than the speed of light. The sound waves emitted by the airplane take more time to reach the observer than the reflected light and so specify a spatial position that is somewhat behind the spatial position specified by vision. When looking skyward to see the plane, observers often orient to the spatial position specified by the sound that the plane emitted seconds earlier, so the gaze is directed to a position behind the plane. When the plane is finally located visually, a strange discontinuity between visual and auditory space is sometimes perceived. More often, however, the unified representation of external space is preserved, and the perceptual system resolves the discrepancy by the "visual capture" of auditory information.

Visual capture of audition is a distortion of perceived auditory location when visual and auditory information specify discrepant spatial positions (Howard & Templeton, 1966; Mateeff, Hohnsbein, & Noack, 1985; Thurlow & Jack, 1973; Warren, Welch, & McCarthy, 1981). In a movie theater, for example, the actors on the screen move their lips, but the vocal sound is projected from a speaker at some distance from the image of the actor. Yet, moviegoers typically do not perceive the discrepancy. The correlation between the visual stimulus (the moving lips) and the auditory stimulus (the voice) is so strong that the perceptual system resolves the spatial discrepancy by shifting the perceived auditory location to match the position of the visual stimulus. The voices sound as though they come from the actors' mouths, and the unified spatial representation is preserved.

BEHAVIORAL EVIDENCE OF MULTI-SENSORY INTERACTION

Perhaps the most well known interaction of vision and audition occurs in the perception of speech (see Rosenblum, this volume, for an extended discussion of this topic). Discrepant auditory and visual speech cues can create auditory percepts that are modified by the visual stimuli. Observers who are presented with the acoustic stimulus /ba/ and simultaneously view a speaker producing /ga/ report hearing /da/ (McGurk & MacDonald, 1976). The "McGurk effect" clearly demonstrates an interaction of the two perceptual modalities when speech cues are

discrepant and has even been shown to occur in prelinguistic infants (Rosenblum, Schmuckler, & Johnson, 1997). Speech has also been shown to be more intelligible if the listener can see the speaker (Massaro & Cohen, 1995; Rosenblum & Saldana, 1996; Sanders & Goodrich, 1971; Sumby & Pollack, 1954). The redundancy of consistent auditory and visual speech information typically affords better performance than information in either modality presented alone.

In a similar vein, the auditory and visual systems have been shown to work together in localization tasks. Some research has examined the relative contributions of vision and audition in localization. Although there are exceptions (e.g., Schiff & Oldak, 1990), the general findings that come from such experiments are that vision affords superior performance compared with audition and that if one can use both the eyes and ears, localization performance is better than with either modality alone. Bimodal spatial detection of a stimulus, for example, is better than detection by either the auditory or visual system alone (Auerbach & Sperling, 1974; Lakatos, 1995; Perrott *et al.*, 1991). Superior performance in auditory localization tasks under favorable versus unfavorable visual conditions provides further evidence for a bimodal advantage in the perception of external space (Mastroianni, 1982; Platt & Warren, 1972; Warren, 1970). Some work has even shown that sighted listeners who are blindfolded can localize auditory stimuli better than blind listeners (Fisher, 1964). This finding suggests that not only do auditory and visual localization skills interact on a sensory level but also a mental (or neural) representation of external space that is based on both auditory and visual experience provides localization advantages even when only one modality is stimulated (but see Loomis, Klatzky, Golledge, Cicinelli, *et al.*, 1993; Roeder *et al.*, 1999). This finding is consistent with physiological studies showing the development of a neural map of auditory space is highly dependent upon visual experience (King, Hutchings, Moore, & Blakemore, 1988; Knudsen, 1983, 2002; Knudsen & Brainard, 1991; Knudsen & Knudsen, 1985).

In many instances, vision dominates other modalities when the information from the respective modalities is discrepant. Thus, the phrase “seeing is believing” may stem from actual experience, as vision can dominate even proprioceptive judgments. In a classic example of visual dominance, observers who moved their hands along a straight edge nevertheless reported the edge to be curved when they performed the task wearing prism glasses that made the edge appear curved (Gibson, 1933). Visual dominance is common, and there are various theories that attempt to explain it (Lee & Aronson, 1974; Posner, Nissen, & Klein, 1976; Rock, 1966). However, the robustness of this dominance has occasionally been brought into question (Wolters & Schiano, 1989), and under some conditions auditory stimuli can also influence vision (Radeau & Bertelson, 1976; Spence & Driver, 1997). For example, presenting a spatially coincident auditory cue can enhance orientation and attention to a visual stimulus. If the visual and auditory cues are spatially discrepant, performance falls below baseline (visual stimulus only). The increase in performance with spatially coincident stimuli is multiplicative and exceeds the bimodal performance predicted by performance in either modality

alone, suggesting a true interaction of vision and audition in locomotor activities (Stein *et al.*, 1989). In addition, an auditory stimulus can increase both the detection of and the perceived brightness of a light regardless of whether the light and sound are spatially coincident or discrepant (Stein, London, Wilkinson, & Price, 1996; Watkins & Freeher, 1965). Auditory stimuli have also been shown to influence the perception of visual apparent motion (Gilbert, 1939; Hall, Earle, & Crookes, 1952; Staal & Donderi, 1983).

Invariant Environmental Cues

A crucial task in navigation is determining time to contact with another object. This information is important not only if an organism wishes to avoid obstacles, catch prey, or avoid capture but also in fundamental aspects of controlled navigation such as appropriate steering and braking (Lee, 1976; Lee, Simmons, & Saillant, 1995). There are environmental invariants in both vision and audition that can provide information that is potentially useful to an organism in navigating an environment. In vision, the rate of optical expansion (τ) can provide reliable information about time to contact with an approaching object (Lee, 1976; Lee & Reddish, 1981). Although there is some debate about whether the use of τ best describes how organisms anticipate the arrival of an approaching object (Guski, 1992; Neuhoff, 2001; Wann, 1996), it is generally accepted that the information is available in the stimulus. In theory, the visual system does not need to estimate the distance or velocity of an approaching object in order to specify time to contact. It need only register the relative rate of optical expansion produced by the approaching object.

In audition, a similar phenomenon has been identified regarding the rate of change in intensity (Lee, van der Weel, Hitchcock, Matejowsky, & Pettigrew, 1992; Rosenblum, 1986; Shaw, McGowan, & Turvey, 1991). A steady-state approaching sound source produces an observed pattern of intensity change specified by the inverse square law. For example, halving the distance between source and observer increases the observed intensity fourfold. Auditory attention to changing intensity then could plausibly specify time to contact. Studies of auditory looming suggest that listeners can indeed specify time to contact based on the intensity change that occurs as a sound source approaches (Lee *et al.*, 1992; Rosenblum, Carello, & Pastore, 1987; Rosenblum, Wuestefeld, & Saldana, 1993; Schiff & Oldak, 1990).

Thus, a visible approaching sound source provides invariant information about time to contact in both the visual and auditory domains. As a visible sound source approaches an observer, the image of the object grows larger optically in the visual field and its observed acoustic intensity increases. In both modalities the rate of change is dependent upon the velocity of the source and the distance between the source and the observer. Auditory or visual information alone could presumably provide information about time to contact. If the ability to detect time to contact is enhanced by the use of bimodal information in the same manner as detecting spatial position, the use of both optical and acoustic information might

provide more accurate estimates. However, the problem has not been researched in sufficient detail with environmentally rich stimuli. One study that used film of approaching objects failed to find an advantage of audiovisual information over only visual information (Schiff & Oldak, 1990). Clearly, a bimodal advantage would exist if either the auditory or visual information provided by an approaching source were intermittent. In a natural environment, such intermittency surely occurs. Approaching objects may be temporarily occluded or only occasionally make noise. In this case the redundancy of the information carried by the unobstructed modality would presumably provide a performance advantage.

Yet, for there to be a bimodal advantage in specifying time to contact, an organism must first be able to unify the information from the auditory and visual inputs and make judgments of equivalence across perceptual modalities. Humans are relatively good at such cross-modal associations (Marks, 1978; Welch & Warren, 1986). An observer must also detect the correlation between the optical expansion and increasing observed intensity that occur as an object approaches. In humans the ability to make use of this information appears to be present at a very early age. Infants as young as 5 months can detect the correlated relationship between the rising intensity specified by an approaching sound source and its rate of optical expansion (Morrongiello, Hewitt, & Gotowiec, 1991; Pickens, 1994; Walker-Andrews & Lennon, 1985).

The behavioral characteristics of multisensory interactions are apparent and continue to be explored by perceptual researchers. Multisensory perception provides a redundancy of stimulus information that increases the likelihood of stimulus detection, discrimination, and localization. The findings of behavioral investigations of multisensory interaction often prompt neuroscientists to search for the physiological underpinnings of multisensory perceptual experience.

PHYSIOLOGICAL EVIDENCE OF MULTISENSORY INTERACTION

There is a growing cross-fertilization between perception researchers interested in the perceptual experience and behavioral characteristics of an organism and neuroscientists interested in the cellular behavior during perceptual processing. Behavioral research can be used to corroborate neurophysiological findings, examine phenomena that cannot yet be studied at the cellular level, and suggest new areas of inquiry for neuroscientists. Cellular recording can provide information about the structure and function that underlie perceptual experience and behavior. In many instances the response patterns of individual neurons are strikingly parallel to important sensory and perceptual activities that precede environmentally important behavioral responses. For example, cells have been identified that respond to a stimulus moving toward an organism regardless of the direction of approach. The cells respond to any stimulus motion provided that the trajectory of the stimulus is toward the organism's face (Colby, Duhamel, & Goldberg, 1993). Thus, identifying the function of individual neurons

can clearly have significant implications for understanding perception and behavior.

Similarly, studies of perception that illustrate the behavioral interaction of the auditory and visual modalities suggest that there are analogous interactions at the cellular level in the central nervous system. Although multisensory interaction takes place at many sites including the hippocampus (Tamura, Ono, Fukuda, & Nakamura, 1990, 1992) and various cortical areas (Wilkinson, Meredith, & Stein, 1996), the area of the brain that mediates multisensory interaction that is best understood is the superior colliculus (or optic tectum in nonmammalian species).

The superior colliculi are symmetrical structures at the top of the brainstem. The structures are composed of seven layers that are functionally divided into two sections. The superficial layers (1–3) are not thought to be involved in sensory integration. The deep layers (4–7) integrate sensory information and send efferent projections to motor areas in the brainstem and spinal cord (Stein & Meredith, 1994).

Traditionally, the superior colliculus has been identified as part of the visual system. However, certain cells in the deep layers respond best to multisensory (auditory, visual, and somatosensory) stimulation (Meredith & Stein, 1983, 1986). Of these cells, those that respond most weakly to a single modality, for example, a noise burst, respond most vigorously when a spot of light and somatosensory stimulation accompanies the noise burst. For spatial information from different modalities to be coordinated, the modality-specific information must converge at some point. The existence of cells that respond best to multimodal input is crucial, therefore, to the perception of a unified external space.

In addition to integrating input from the sense organs, the superior colliculus receives input from various cortex areas. Auditory, visual, and somatosensory cortices have all been shown to converge on multisensory neurons in the superior colliculus. The same multisensory neurons have also been shown to mediate motor behaviors (Meredith & Stein, 1986; Wallace, Meredith, & Stein, 1993). This organization demonstrates cortical control over attentive and orienting behaviors.

In addition to multisensory neurons in the superior colliculus, multisensory neurons have been identified in various cortex areas, typically at the boundaries or transition areas of the modality-specific cortical regions (Stein & Meredith, 1994; Wallace, Meredith, & Stein, 1992). Surprisingly, these multisensory cortical neurons do not synapse with the multisensory neurons in the superior colliculus. Cortical input to the multisensory neurons in the superior colliculus comes from unimodal cortical cells (Wallace *et al.*, 1993). This suggests that distinct processes of sensory integration take place independently in the cortex and superior colliculus. However, input to multisensory neurons in the superior colliculus from the various modality-specific cortical cells is not sufficient for multisensory integration in the superior colliculus. The process is also dependent upon input from the association cortex. Deactivation of input to the superior colliculus from the association cortex eliminates multisensory integration in the superior colliculus, but the multisensory neurons still respond to unimodal

cortical input (Wallace & Stein, 1994). Thus, multisensory integration in the superior colliculus is dependent upon input from the association cortex.

Multisensory neurons in the superior colliculus do not appear to be present at birth. Wallace and Stein (1997) tested developing kittens and found no evidence of multisensory neurons until the kittens were 12 days old. Furthermore, although these early multisensory neurons responded to multimodal input, their response characteristics were weak and erratic. In addition, they did not integrate sensory information in the multiplicative manner found in of adult cats. The response pattern was much like that of fully developed multisensory neurons that had been cut off from input from the association cortex. Thus, it may be that projections from the association cortex to the superior colliculus are not fully developed at birth, thus preventing sensory integration in the superior colliculus (Wallace & Stein, 1997).

Auditory and Visual Spatial Maps

There is an emerging body of research that begins to demonstrate a coordinated neural representation of visual and auditory space. Neurons in the superior colliculus tuned to specific auditory localization cues provide a basis for a map of auditory space. Thus, auditory space is represented by the topographic organization of spatially tuned auditory neurons. Retinotopic organization is also preserved in the superior colliculus, with visual receptive fields providing a neuronal map of visual space. The auditory and visual maps are closely aligned, with visual receptive fields in close proximity to corresponding spatially tuned auditory neurons (Knudsen & Brainard, 1995). In addition, the deep layers of the superior colliculus contain neurons that respond to best to auditory and visual input from a specific spatial location, providing a unified bimodal map of external space (Knudsen & Brainard, 1991; Meredith & Stein, 1986, 1996; Stein & Meredith, 1994).

The neural maps of auditory and visual space in the superior colliculus develop with perceptual experience, and the map of auditory space appears to align itself with the visual map (King *et al.*, 1988). There is considerable plasticity in the development of the auditory map with visual experience playing a critical role. For example, barn owls raised with prism glasses that optically displace the visual field show a corresponding shift in auditory receptive fields that matches the amount of displacement produced by the prisms (Knudsen & Brainard, 1991). The auditory cueing of spatial position is highly dependent upon differences in the characteristics of the acoustic stimuli that arrive at the two ears. Nevertheless, visual experience is so crucial to the development of auditory spatial maps that animals raised with monaural occlusion still have properly aligned auditory maps provided they have normal visual experience (Knudsen, 1983; Knudsen & Knudsen, 1985). Monocularly occluded animals that are raised blind have disorganized auditory maps by comparison (Knudsen & Mogdans, 1992). There is also evidence of neural plasticity in the cortex. For example, if cortical development occurs in the absence of particular modality-specific stimulation, input from other

modalities can overtake these cortical areas. Areas of visual cortex in cats that are raised blind can be taken over by auditory inputs. The result is sharper auditory spatial tuning and improved auditory localization performance (Palleroni & Hauser, 2003; Rauschecker, 1995a, 1995b; Weeks *et al.*, 2000).

For audition to orient visual attention accurately, the auditory and visual maps must be aligned. The correspondence between the spatial maps of the visual and auditory systems is probably a result of the naturally occurring correlation between perceived auditory, visual spatial locations of objects in the environment. Perception research shows that organisms use a unified spatial representation to navigate their environment. The dependence of the development of accurately aligned auditory spatial maps on visual experience suggests that the unified representation of external space may be rooted in the visual map (Welch, DuttonHurt, & Warren, 1986).

CONCLUSION

This discussion has focused primarily on the sensory and perceptual interaction of vision and audition, which clearly provides cues to localization and navigation beyond those of the individual modalities themselves. Distinct modality-specific information is integrated to form a unified representation of external space that is used to guide navigation. The various neural structures responsible for integrating multisensory input provide a substrate on which this unified perceptual experience is formed.

By no means, however, does the audiovisual interaction provide all of the information that organisms use to get around. In humans, vestibular and haptic cues have been shown to interact with both visual and auditory information (Clark & Graybiel, 1966; Clark & Graybiel, 1949; Demer, 1994; Graybiel & Hupp, 1946; Graybiel & Niven, 1951; Lackner, 1974a, 1974b; Paige & Tomko, 1991; Probst & Wist, 1990; Rosenblum & Saldana, 1996; Wade & Day, 1968). Male gypsy moths use the interaction of both visual information and the perception of pheromone concentration to guide flight in locating females (Willis & Carde, 1990; Willis, David, Murlis, & Carde, 1994). Some species use the interaction of olfaction with vision and audition to locate prey (Wells & Lehner, 1978). Echolocating horseshoe bats use both the acoustic characteristics of the reflected sound and the motoric characteristics of the vocalization to guide flight in catching prey (Metzner, 1993).

There are large bodies of work in both perception and neuroscience that have examined unimodal spatial perception. In some cases the complexity of the issues explored necessitates this unimodal approach. Yet, it is apparent that the integration of multisensory information can yield perception and performance that are not predicted by the functioning of any modality in isolation. Some researchers have already begun to examine the interaction of vision, audition, and other modalities in the formation of a unified spatial representation. As technology

emerges to enable further the study of the form and function of the individual modalities, the next research frontier will be understanding more completely their interaction.

REFERENCES

- Alain, C. (1993). The relation among fundamental frequency, intensity, and duration varies with accentuation. *Journal of the Acoustical Society of America*, *94*, 2434–2436.
- Ashby, F. G., & Townsend, J. T. (1986). Varieties of perceptual independence. *Psychological Review*, *93*, 154–179.
- Auerbach, C., & Sperling, P. (1974). A common auditory-visual space: Evidence for its reality. *Perception and Psychophysics*, *16*, 129–135.
- Boltz, M. G. (1998). Tempo discrimination of musical patterns: Effects due to pitch and rhythmic structure. *Perception and Psychophysics*, *60*, 1357–1373.
- Brenner, M., Doherty, E. T., & Shipp, T. (1994). Speech measures indicating workload demand. *Aviation, Space, and Environmental Medicine*, *65*, 21–26.
- Clark, B., & Graybiel, A. (1966). Contributing factors in the oculo-gravic illusion. *American Journal of Psychology*, *79*, 377–388.
- Clark, B., & Graybiel, A. (1949). The effect of angular acceleration on sound localization: The audiogyril illusion. *Journal of Psychology*, *28*, 235–244.
- Colby, C. L., Duhamel, J.-R., & Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: Anatomic location and visual response properties. *Journal of Neurophysiology*, *69*, 902–914.
- Cutler, A., & Butterfield, S. (1991). Word boundary cues in clear speech: A supplementary report. *Speech Communication*, *10*, 335–353.
- Demany, L., & Semal, C. (1993). Pitch versus brightness of timbre—Detecting combined shifts in fundamental and formant frequency. *Music Perception*, *11*, 1–14.
- Demer, J. L. (1994). Effect of aging on vertical visual tracking and visual-vestibular interaction. Special issue: David A. Robinson: Four decades of seminal eye movement research. *Journal of Vestibular Research Equilibrium and Orientation*, *4*, 355–370.
- Dyson, B. J., & Quinlan, P. T. (2002). Within- and between-dimensional processing in the auditory modality. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 1483–1498.
- Fisher, C., & Tokura, H. (1995). The given-new contract in speech to infants. *Journal of Memory and Language*, *34*, 287–310.
- Fisher, G. H. (1964). Spatial localization by the blind. *American Journal of Psychology*, *77*, 2–14.
- Gaioni, S. J., & Evans, C. S. (1986). Perception of distress calls in mallard ducklings (*Anas platyrhynchos*). *Behaviour*, *99*, 250–274.
- Gaioni, S. J., & Evans, C. S. (1989). Perception of the frequency characteristics of distress calls by mallard ducklings (*Anas platyrhynchos*). *Behaviour*, *111*, 13–33.
- Garner, W. R. (1974). *The processing of information and structure*. New York: Wiley.
- Gibson, J. J. (1933). Adaptation, after-effect and contrast in the perception of curved lines. *Journal of Experimental Psychology*, *16*, 1–31.
- Gilbert, G. M. (1939). Dynamic psychophysics and the phi phenomenon. *Archives of Psychology (Columbia University)* (237), 43.
- Graybiel, A., & Hupp, D. I. (1946). The oculo-gryal illusion, a form of apparent motion which may be observed following stimulation of the semi-circular canals. *Journal of Aviation Medicine*, *17*, 3–27.
- Graybiel, A., & Niven, J. I. (1951). The effect of a change in direction of resultant force on sound localization. *Journal of Experimental Psychology* (42), 227–230.

- Greer, R. (1969). *The effect of timbre on brass-wind intonation*. Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor.
- Guski, R. (1992). Acoustic tau: An easy analogue to visual tau? *Ecological Psychology*, 4, 189–197.
- Hall, K. R. L., Earle, A. E., & Crookes, T. G. (1952). A pendulum phenomenon in the visual perception of apparent movement. *Quarterly Journal of Experimental Psychology*, 4, 109–120.
- Heffner, R. S., & Heffner, H. E. (1992). Hearing in large mammals: Sound-localization acuity in cattle (*Bos taurus*) and goats (*Capra hircus*). *Journal of Comparative Psychology*, 106, 107–113.
- Howard, I. P., & Templeton, W. B. (1966). *Human Spatial orientation*. London: Wiley.
- Kemler, D. G. (1983). Exploring and reexploring issues of integrality, perceptual sensitivity, and dimensional salience. *Journal of Experimental Child Psychology*, 36, 365–379.
- Kemler Nelson, D. G. (1993). Processing integral dimensions: The whole view. *Journal of Experimental Psychology: Human Perception and Performance*, 19, 1105–1113.
- King, A. J., Hutchings, M. E., Moore, D. R., & Blakemore, C. (1988). Developmental plasticity in the visual and auditory representations in the mammalian superior colliculus. *Nature*, 332, 73–76.
- Knudsen, E. I. (1983). Early auditory experience aligns the auditory map of space in the optic tectum of the barn owl. *Science*, 222, 939–942.
- Knudsen, E. I. (2002). Instructed learning in the auditory localization pathway of the barn owl. *Nature*, 417, 322–328.
- Knudsen, E. I., & Brainard, M. S. (1991). Visual instruction of the neural map of auditory space in the developing optic tectum. *Science*, 253, 85–87.
- Knudsen, E. I., & Brainard, M. S. (1995). Creating a unified representation of visual and auditory space in the brain. *Annual Review of Neuroscience*, 18, 19–43.
- Knudsen, E. I., & Knudsen, P. F. (1985). Vision guides the adjustment of auditory localization in young barn owls. *Science*, 230, 545–548.
- Knudsen, E. I., & Mogdans, J. (1992). Vision-independent adjustment of unit tuning to sound localization cues in response to monaural occlusion in developing owl optic tectum. *Journal of Neuroscience*, 12, 3485–3493.
- Krumhansl, C. L., & Iverson, P. (1992). Perceptual interactions between musical pitch and timbre. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 739–751.
- Lackner, J. R. (1974a). Changes in auditory localization during body tilt. *Acta Oto Laryngologica*, 77, 19–28.
- Lackner, J. R. (1974b). The role of posture in sound localization. *Quarterly Journal of Experimental Psychology*, 26, 235–251.
- Lakatos, S. (1995). The influence of visual cues on the localisation of circular auditory motion. *Perception*, 24, 457–465.
- Lee, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. *Perception*, 5, 437–459.
- Lee, D. N., & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. *Perception and Psychophysics*, 15, 529–532.
- Lee, D. N., & Reddish, P. E. (1981). Plummeting gannets: A paradigm of ecological optics. *Nature*, 293, 293–294.
- Lee, D. N., Simmons, J. A., & Saillant, P. A. (1995). Steering by echolocation: A paradigm of ecological acoustics. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, 176, 246–254.
- Lee, D. N., van der Weel, F. R., Hitchcock, T., Matejowsky, E., & Pettigrew, J. D. (1992). Common principle of guidance by echolocation and vision. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, 171, 563–571.
- Lockhead, G. R. (1972). Processing dimensional stimuli: A note. *Psychological Review*, 79, 410–419.
- Lockhead, G. R. (1979). Holistic versus analytic process models: A reply. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 746–755.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., et al. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, 122, 73–91.

- Maddox, W. T. (2001). Separating perceptual processes from decisional processes in identification and categorization. *Perception and Psychophysics*, *63*, 1183–1200.
- Maddox, W. T., & Bogdanov, S. V. (2000). On the relation between decision rules and perceptual representation in multidimensional perceptual categorization. *Perception and Psychophysics*, *62*, 984–997.
- Marks, L. E. (1978). *The unity of the senses: Interrelations among modalities*. New York: Academic Press.
- Marks, L. E. (1989). On cross-modal similarity: The perceptual structure of pitch, loudness, and brightness. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 586–602.
- Massaro, D. W., & Cohen, M. M. (1995). Perceiving talking faces. *Current Directions in Psychological Science*, *4*, 104–109.
- Mastroianni, G. R. (1982). The influence of eye movements and illumination on auditory localization. *Perception and Psychophysics*, *31*, 581–584.
- Mateeff, S., Hohnsbein, J., & Noack, T. (1985). Dynamic visual capture: Apparent auditory motion induced by a moving visual target. *Perception*, *14*, 721–727.
- McBeath, M. K., & Neuhoff, J. G. (2002). The Doppler effect is not what you think it is: Dramatic pitch change due to dynamic intensity change. *Psychonomic Bulletin and Review*, *9*, 306–313.
- McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, *264*, 746–748.
- Melara, R. D., & Marks, L. E. (1990a). Interaction among auditory dimensions: Timbre, pitch, and loudness. *Perception and Psychophysics*, *48*, 169–178.
- Melara, R. D., & Marks, L. E. (1990b). Perceptual primacy of dimensions: Support for a model of dimensional interaction. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 398–414.
- Melara, R. D., Marks, L. E., & Potts, B. C. (1993a). Early-holistic processing or dimensional similarity? *Journal of Experimental Psychology: Human Perception and Performance*, *19*, 1114–1120.
- Melara, R. D., Marks, L. E., & Potts, B. C. (1993b). Primacy of dimensions in color perception. *Journal of Experimental Psychology: Human Perception and Performance*, *19*, 1082–1104.
- Melara, R. D., Rao, A., & Tong, Y. X. (2002). The duality of selection: Excitatory and inhibitory processes in auditory selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 279–306.
- Meredith, M. A., & Stein, B. E. (1983). Interactions among converging sensory inputs in the superior colliculus. *Science*, *221*, 389–391.
- Meredith, M. A., & Stein, B. E. (1986). Spatial factors determine the activity of multisensory neurons in cat superior colliculus. *Brain Research*, *365*, 350–354.
- Meredith, M. A., & Stein, B. E. (1996). Spatial determinants of multisensory integration in cat superior colliculus neurons. *Journal of Neurophysiology*, *75*, 1843–1857.
- Metzner, W. (1993). An audio-vocal interface in echolocating horseshoe bats. *Journal of Neuroscience Letters*, *13*, 1899–1915.
- Morrongiello, B. A., Hewitt, K. L., & Gotowiec, A. (1991). Infants' discrimination of relative distance in the auditory modality: Approaching versus receding sound sources. *Infant Behavior and Development*, *14*, 187–208.
- Neuhoff, J. G. (2001). An adaptive bias in the perception of looming auditory motion. *Ecological Psychology*, *13*, 87–110.
- Neuhoff, J. G., & McBeath, M. K. (1996). The Doppler illusion: The influence of dynamic intensity change on perceived pitch. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 970–985.
- Neuhoff, J. G., McBeath, M. K., & Wanzie, W. C. (1999). Dynamic frequency change influences loudness perception: A central, analytic process. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1050–1059.
- Neuhoff, J. G., Wayand, J., & Kramer, G. (2002). Pitch and loudness interact in auditory displays: Can the data get lost in the map? *Journal of Experimental Psychology: Applied*, *8*, 17–25.

- Paige, G. D., & Tomko, D. L. (1991). Eye movement responses to linear head motion in the squirrel monkey: II. Visual-vestibular interactions and kinematic considerations. *Journal of Neurophysiology*, *65*, 1183–1196.
- Palleroni, A., & Hauser, M. (2003). Experience-dependent plasticity for auditory processing in a raptor. *Science*, *299*, 1195.
- Patching, G. R., & Quinlan, P. T. (2002). Garner and congruence effects in the speeded classification of bimodal signals. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 755–775.
- Patel, A. D., & Balaban, E. (2000). Temporal patterns of human cortical activity reflect tone sequence structure. *Nature*, *404*, 80–84.
- Perrott, D. R., Sadralodabai, T., Saberi, K., & Strybel, T. Z. (1991). Aurally aided visual search in the central visual field: Effects of visual load and visual enhancement of the target. *Human Factors*, *33*, 389–400.
- Phillips, D. P., & Hall, S. E. (2001). Spatial and temporal factors in auditory saltation. *Journal of the Acoustical Society of America*, *110*, 1539–1547.
- Pickens, J. (1994). Perception of auditory-visual distance relations by 5-month-old infants. *Developmental Psychology*, *30*, 537–544.
- Pitt, M. A. (1994). Perception of pitch and timbre by musically trained and untrained listeners. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 976–986.
- Platt, B. B., & Warren, D. H. (1972). Auditory localization: The importance of eye movements and a textured visual environment. *Perception and Psychophysics*, *12*, 241–244.
- Posner, M. I., Nissen, M. J., & Klein, R. M. (1976). Visual dominance: An information-processing account of its origins and significance. *Psychological Review*, *83*, 157–171.
- Potts, B. C., Melara, R. D., & Marks, L. E. (1998). Circle size and diameter tilt: A new look at integrality and separability. *Perception and Psychophysics*, *60*, 101–112.
- Probst, T., & Wist, E. R. (1990). Impairment of auditory processing by simultaneous vestibular stimulation: Psychophysical and electrophysiological data. *Behavioural Brain Research*, *41*, 1–9.
- Radeau, M., & Bertelson, P. (1976). The effect of a textured visual field on modality dominance in a ventriloquism situation. *Perception and Psychophysics*, *20*, 227–235.
- Rauschecker, J. P. (1995a). Compensatory plasticity and sensory substitution in the cerebral cortex. *Trends in Neurosciences*, *18*, 36–43.
- Rauschecker, J. P. (1995b). Developmental plasticity and memory. *Behavioural Brain Research*, *66*, 7–12.
- Repp, B. H. (1995). Detectability of duration and intensity increments in melody tones: A partial connection between music perception and performance. *Perception and Psychophysics*, *57*, 1217–1232.
- Robinson, D. L., & Kertzman, C. (1995). Covert orienting of attention in macaques: III. Contributions of the superior colliculus. *Journal of Neurophysiology*, *74*, 713–721.
- Rock, I. (1966). *The nature of perceptual adaptation*. Oxford, England: Basic Books.
- Roeder, B., Teder-Saelejaervi, W., Sterr, A., Roesler, F., Hillyard, S. A., & Neville, H. J. (1999). Improved auditory spatial tuning in blind humans. *Nature*, *400*, 162–166.
- Rosenblum, L. D., Carello, C., & Pastore, R. E. (1987). Relative effectiveness of three stimulus variables for locating a moving sound source. *Perception*, *162*, 175–186.
- Rosenblum, L. D., & Saldana, H. M. (1996). An audiovisual test of kinematic primitives for visual speech perception. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 318–331.
- Rosenblum, L. D., Schmuckler, M. A., & Johnson, J. A. (1997). The McGurk effect in infants. *Perception and Psychophysics*, *59*, 347–357.
- Rosenblum, L. D., Wuestefeld, A. P., & Saldana, H. M. (1993). Auditory looming perception: Influences on anticipatory judgments. *Perception*, *22*, 1467–1482.
- Rosenblum, L. D. (1986). Acoustical information for controlled conditions. In A. Shick, H. Höge, & G. Lazarus-Mainka (Eds.), *Contributions to psychological acoustics: Results of the Fourth Old-*

- enburg Symposium on Psychological Acoustics (p. 455). Oldenburg: Bibliotheks- und Informationssystem der Universität Oldenburg.
- Ryffert, H., Czajkowska, A., Jorasz, U., & Markarewicz, R. (1979). Dynamic approach to sound pitch. *Archives of Acoustics*, 4, 3–10.
- Sanders, D. A., & Goodrich, S. J. (1971). The relative contribution of visual and auditory components of speech to speech intelligibility as a function of three conditions of frequency distortion. *Journal of Speech and Hearing Research*, 14, 154–159.
- Scharine, A. A. (2002). *Auditory scene analysis: The role of positive correlation of dynamic changes in intensity and frequency*. Ann Arbor, MI: University Microfilms International.
- Schiff, W., & Oldak, R. (1990). Accuracy of judging time to arrival: Effects of modality, trajectory, and gender. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 303–316.
- Shaw, B. K., McGowan, R. S., & Turvey, M. T. (1991). An acoustic variable specifying time-to-contact. *Ecological Psychology*, 3, 253–261.
- Shepard, R. N. (1964). Attention and the metric structure of the stimulus space. *Journal of Mathematical Psychology*, 1, 54–87.
- Smith, L. B., & Kemler, D. G. (1978). Levels of experienced dimensionality in children and adults. *Cognitive Psychology*, 10, 502–532.
- Spence, C., & Driver, J. (1997). Audiovisual links in exogenous covert spatial orienting. *Perception and Psychophysics*, 59, 1–22.
- Staal, H. E., & Donderi, D. C. (1983). The effect of sound on visual apparent movement. *American Journal of Psychology*, 96, 95–105.
- Stein, B. E., London, N., Wilkinson, L. K., & Price, D. D. (1996). Enhancement of perceived visual intensity by auditory stimuli: A psychophysical analysis. *Journal of Cognitive Neuroscience*, 8, 497–506.
- Stein, B. E., & Meredith, M. A. (1994). *The merging of the senses*. Cambridge, MA: MIT Press.
- Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multi-sensory integration: Orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience*, 1, 12–24.
- Sumby, W. H., & Pollack, I. (1954). Visual contribution to speech intelligibility in noise. *Journal of the Acoustical Society of America*, 26, 212–215.
- Tamura, R., Ono, T., Fukuda, M., & Nakamura, K. (1990). Recognition of egocentric and allocentric visual and auditory space by neurons in the hippocampus of monkeys. *Neuroscience Letters*, 109, 293–298.
- Tamura, R., Ono, T., Fukuda, M., & Nakamura, K. (1992). Spatial responsiveness of monkey hippocampal neurons to various visual and auditory stimuli. *Hippocampus*, 2, 307–322.
- Tekman, H. G. (1997). Interactions of perceived intensity, duration, and pitch in pure tone sequences. *Music Perception*, 14, 281–294.
- Tekman, H. G. (1998). Effects of melodic accents on perception of intensity. *Music Perception*, 15, 391–401.
- Tekman, H. G. (2002). Perceptual integration of timing and intensity variations in the perception of musical accents. *Journal of General Psychology*, 129, 181–191.
- Thompson, W. F., & Sinclair, D. (1993). Pitch pattern, durational pattern, and timbre: A study of the perceptual integration of auditory qualities. *Psychomusicology*, 12, 3–21.
- Thurlow, W. R., & Jack, C. E. (1973). Certain determinants of the “ventriloquism effect.” *Perceptual and Motor Skills*, 36(3, Pt. 2), 1171–1184.
- Wade, N. J., & Day, R. H. (1968). Apparent head position as a basis for visual aftereffect of prolonged head tilt. *Perception and Psychophysics*, 3, 324–326.
- Walker, B. N., & Ehrenstein, A. (2000). Pitch and pitch change interact in auditory displays. *Journal of Experimental Psychology: Applied*, 6, 15–30.
- Walker-Andrews, A. S., & Lennon, E. M. (1985). Auditory-visual perception of changing distance by human infants. *Child Development*, 56, 544–548.

- Wallace, M. T., Meredith, M. A., & Stein, B. E. (1992). Integration of multiple sensory modalities in cat cortex. *Experimental Brain Research*, *91*, 484–488.
- Wallace, M. T., Meredith, M. A., & Stein, B. E. (1993). Converging influences from visual, auditory, and somatosensory cortices onto output neurons of the superior colliculus. *Journal of Neurophysiology*, *69*, 1797–1809.
- Wallace, M. T., & Stein, B. E. (1994). Cross modal synthesis in the midbrain depends on input from the cortex. *Journal of Neurophysiology*, *71*, 429–432.
- Wallace, M. T., & Stein, B. E. (1997). Development of multisensory neurons and multisensory integration in cat superior colliculus. *Journal of Neuroscience*, *17*, 2429–2444.
- Wann, J. P. (1996). Anticipating arrival: Is the tau margin a specious theory? *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 1031–1048.
- Warren, D. H. (1970). Intermodality interactions in spatial localization. *Cognitive Psychology*, *1*, 114–133.
- Warren, D. H., Welch, R. B., & McCarthy, T. J. (1981). The role of visual-auditory “compellingness” in the ventriloquism effect: Implications for transitivity among the spatial senses. *Perception and Psychophysics*, *30*, 557–564.
- Warrier, C. M., & Zatorre, R. J. (2002). Influence of tonal context and timbral variation on perception of pitch. *Perception and Psychophysics*, *64*, 198–207.
- Watkins, W. H., & Freeher, C. E. (1965). Acoustic facilitation of visual detection. *Journal of Experimental Psychology*, *70*, 332–333.
- Weeks, R., Horwitz, B., Aziz-Sultan, A., Tian, B., Wessinger, C. M., Cohen, L. G., Hallett, M., & Rauschecker, J. P. (2000). A positron emission tomographic study of auditory localization in the congenitally blind. *Journal of Neuroscience*, *20*, 2664–2672.
- Welch, R. B., DuttonHurt, L. D., & Warren, D. H. (1986). Contributions of audition and vision to temporal rate perception. *Perception and Psychophysics*, *39*, 294–300.
- Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, *88*, 638–667.
- Welch, R. B., & Warren, D. H. (1986). Intersensory interactions. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (pp. 25:21–25:36) New York: Wiley.
- Wells, M. C., & Lehner, P. N. (1978). The relative importance of the distance senses in coyote predatory behaviour. *Animal Behaviour*, *26*, 251–258.
- Wilkinson, L. K., Meredith, M. A., & Stein, B. E. (1996). The role of anterior ectosylvian cortex in cross-modality orientation and approach behavior. *Experimental Brain Research*, *112*, 1–10.
- Willis, M. A., & Carde, R. T. (1990). Pheromone-modulated optomotor response in male gypsy moths, *Lymantria dispar* L.: Upwind flight in a pheromone plume in different wind velocities. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, *167*, 699.
- Willis, M. A., David, C. T., Murlis, J., & Carde, R. (1994). Effects of pheromone plume structure and visual stimuli on the pheromone-modulated upwind flight of male gypsy moths (*Lymantria dispar*) in a forest (Lepidoptera: Lymantriidae). *Journal of Insect Behavior*, *7*, 385–410.
- Wolters, N. C., & Schiano, D. J. (1989). On listening where we look: The fragility of a phenomenon. *Perception and Psychophysics*, *45*, 184–186.
- Worthy, M. D. (2000). Effects of tone-quality conditions on perception and performance of pitch among selected wind instrumentalists. *Journal of Research in Music Education*, *48*, 222–236.
- Zatorre, R. J., Mondor, T. A., & Evans, A. C. (1999). Auditory attention to space and frequency activates similar cerebral systems. *Neuroimage*, *10*, 544–554.

